

Thermal physiology of a range-restricted desert lark

Ryno Kemp^{1,2} & Andrew E. McKechnie^{1,2,*}

Affiliations

¹DST-NRF Centre of Excellence at the FitzPatrick Institute, Department of Zoology and Entomology, University of Pretoria, Hatfield, Private Bag X20, Pretoria, 0028, South Africa

²South African Research Chair in Conservation Physiology, National Zoological Garden, South African National Biodiversity Institute, P.O. Box 754, Pretoria, 0001, South Africa

*Correspondence to Andrew E. McKechnie.email: aemckechnie@zoology.up.ac.za

Abbreviations

EWL: Evaporative water loss

BMR: Basal metabolic rate

RMR: Resting metabolic rate

EHL: Evaporative heat loss

MHP: Metabolic heat production

M_b : Body mass

T_a : Air temperature

T_b : Body temperature

T_{lc} : Lower critical limit of thermoneutrality

T_{uc} : Upper critical limit of thermoneutrality

Abstract

Much recent work on avian physiological adaptation to desert environments has focused on larks (Passeriformes: Alaudidae). We tested the prediction that the threatened red lark (*Calendulauda burra*), a species restricted to very arid parts of South Africa and which is not known to drink, exhibits highly efficient evaporative cooling and makes pronounced use of facultative hyperthermia when exposed to high air temperatures (T_a). We also predicted that *C. burra* possesses similarly low basal metabolic rate (BMR) and total evaporative water loss (EWL) at moderate T_a as reported for species from the deserts of the Middle East. Rest-phase thermoregulation in *C. burra* was characterized by an unusually low lower critical limit of thermoneutrality at $T_a = \sim 21$ °C and a BMR of 0.317 ± 0.047 W, the lowest BMR relative to allometrically-expected values yet reported in any lark. During the diurnal active phase, red larks were able to tolerate T_a up to 50 °C, with the onset of panting occurring at $T_a = 38$ °C. Maximum EWL was 1.475 ± 0.107 g h⁻¹ at $T_a = 50$ °C, equivalent to 620% of minimum EWL at thermoneutrality. The maximum ratio of evaporative heat dissipation to metabolic heat production was 1.58, a value towards the lower end of the range reported for passerines. Our data support the prediction that *C. burra* shows metabolic traits similar to those of other larks inhabiting extremely arid climates, but not the notion that evaporative cooling at high T_a in this species is more efficient than in most passerines.

Keywords: Alaudidae; Basal metabolic rate; Body temperature; *Calendulauda burra*; · Evaporative water loss; Heat tolerance

Introduction

Deserts are characterised by scarce and unpredictable water and food resources combined with temperature extremes and intense solar radiation, conditions likely to exert strong selection on the physiology of arid-zone organisms (Noy-Meir 1973; Tieleman and Williams 2000). Physiological adaptation to aridity may, a priori, be expected to be most apparent in diurnal taxa with comparatively high energy and water requirements and which make limited use of thermally buffered microsites such as burrows; for this reason, the physiological and behavioural mechanisms that allow birds to survive and reproduce in even the harshest, most arid habitats on the planet have proved a long-standing source of interest to ornithologists and ecological physiologists (Dawson 1954; Dawson and Bartholomew 1968; Serventy 1971).

Research on avian physiological adaptations to arid habitats has largely focused on the hypotheses that desert species have evolved reduced basal metabolic rate (BMR) and evaporative water loss (EWL) (Bartholomew and Cade 1963; Dawson and Schmidt-Nielsen 1964; Williams 1996; Tieleman and Williams 2000). Several workers have reported variation in these traits correlated with habitat aridity; for instance, BMR, EWL and daily energy expenditure were found to be consistently lower in birds inhabiting arid habitats compared to those from mesic environments (Tieleman and Williams 2000). However, the extent to which habitat-related variation in these physiological traits arises from phenotypic plasticity versus genetic adaptation remains largely unclear (Tieleman et al. 2002, 2003b).

Larks (Alaudidae: Passeriformes) comprise a speciose avian family that occurs in habitats ranging from mesic grasslands to hyper-arid deserts (de Juana et al. 2018). The species richness of larks is greatest in arid habitats (Alström et al. 2013), making this taxon ideal for testing hypotheses about avian adaptation to arid environments. The Alaudidae has been the subject of extensive study by Tieleman, Williams and colleagues, whose work has revealed *inter alia* that: (1) BMR and evaporative water loss (EWL) are lower in larks inhabiting arid habitats (Tieleman et al. 2003a), but see also (Williams 1999), (2) larks inhabiting desert environments generally do not show a greater extent of phenotypic flexibility in physiological traits compared to mesic species (Williams and Tieleman 2000; Tieleman et al. 2003b) and (3) clutch size, growth rates and energy and water requirements are reduced in arid-zone larks (Tieleman et al. 2004).

Several studies of lark thermal physiology have included measurements of heat and water fluxes at air temperature (T_a) above thermoneutrality (Trost 1972; Tieleman and Williams 2002; Tieleman et al. 2002), but there is still less known about thermoregulation at very high T_a in this group compared to at thermoneutral and lower T_a values. In particular, it remains unclear how the maximum heat tolerance and evaporative cooling capacity of larks compare to those of other taxa. Recent studies using standardised methods that involve high flow rates and consequently very low chamber humidities confirm that large differences exist among and within avian orders in terms of thermoregulation in the heat (Whitfield et al. 2015; McKechnie et al. 2016a; O'Connor et al. 2017; Smith et al. 2017; Smit et al. 2018). Much of this variation appears to reflect the major avenue of evaporative heat dissipation, with passerines and other taxa that predominantly use panting having lower heat tolerance limits and less efficient evaporative cooling than taxa that use cutaneous evaporation or gular flutter (Whitfield et al. 2015; McKechnie et al. 2016a; O'Connor et al. 2017; Smith et al. 2017; Smit et al. 2018). Maximum ratios of evaporative heat loss (EHL) to metabolic heat

production (MHP) reach ~ 2.2 among passerines (Whitfield et al. 2015; McKechnie et al. 2017; Smith et al. 2017), whereas those of columbids and caprimulgids are substantially higher, in some cases reaching ~ 5.0 (McKechnie et al. 2016b; O'Connor et al. 2017; Talbot et al. 2017; Smith et al. 2015).

To further explore avian physiological adaptation to aridity, we characterised the thermal physiology of the red lark (*Calendulauda burra*). The species is endemic to sand dune and gravel plain habitats in South Africa's Northern Cape province (Dean and Ryan 2005) and is red-listed within South Africa as *Vulnerable* (Taylor et al. 2015). The estimated population is ~ 9400 birds (Dean et al. 1991), with just 2% occurring in state-owned reserves (Siegfried 1992). The species diverged ~ 4 MYA from the congeneric dune lark (*C. erythrochlamys*) and Barlow's lark (*C. barlowi*) (Alström et al. 2013). In addition to potentially yielding insights into physiological arid-zone adaptation among birds in general, as a threatened range-restricted species exposed to harsh environmental conditions and not known to drink (Dean and Ryan 2005), the red lark also represents a flagship species for exploring the impacts of climate change on arid-zone birds (e.g., Kearney et al. 2016).

On account of the very arid nature of its habitat (mean annual precipitation of ~ 100 mm year⁻¹ and T_a maxima regularly exceeding 40 °C; ESM Photo 1) we predicted that the red lark has low BMR and EWL at moderate T_a similar to that of species inhabiting the Middle Eastern deserts, such as hoopoe lark (*Alaemon alaudipes*) and Dunn's lark (*Eremalauda dunnii*; Tieleman et al. 2002). We also predicted that thermoregulation at high T_a in *C. burra* is more efficient than is the case for most passerines, and specifically that (a) the onset of panting occurs at higher T_a than in other passerines, (b) facultative hyperthermia is an important mechanism of water saving, and (c) maximum EHL/MHP is higher in *C. burra* than in most passerines. To test these predictions we quantified the relationships between body temperature (T_b), resting metabolic rate (RMR) and EWL during the species' diurnal active phase and nocturnal rest phase.

Materials and methods

Study site and species

We conducted our study at Black Mountain Mine Conservation Area (29°18'S, 18°51'E) in the Koa Valley just south of the town of Aggeneys in South Africa's Northern Cape province. The study site is an arid area dominated by grasses including various species of *Stipagrostis* and scattered shrubs (*Rhigozum trichotomum*) with a mean annual rainfall of ~ 100 mm year⁻¹. During the 3 years preceding our study, however, the site received an average of just 34 mm year⁻¹. We collected data during the austral summer between 11 January 2018 and 10 February 2018, with daily maximum T_a ranging from 30 to 41.3 °C during the study period. A total of 57 red larks were caught using spring traps baited with mealworms during early mornings, with mean \pm s.d. body mass (M_b) for females and males of 31.16 ± 1.31 g ($n = 5$) and 38.34 ± 2.12 g ($n = 52$), respectively. Following capture, each bird was held in an indoor cage (0.8 m³) constructed from shade cloth attached to a plastic frame and provided with ad libitum supply of water and food (mealworms and superworms). The larks were never observed to drink water in captivity.

Air and body temperature measurements

We inserted a thermistor probe (model TC-100, Sable Systems, Las Vegas, NV, USA) sealed with a rubber grommet through the side of each metabolic chamber (see below) to

measure T_a during the gas exchange measurements. T_b was measured every 10 s with an abdominally injected temperature-sensitive passive integrated transponder (PIT) tag (Biomark, Biose ID, USA). A portable transceiver system (Biomark, HPR Plus, USA) linked to an antenna was placed adjacent to each metabolic chamber. At the start of the fieldwork season, we calibrated a sample of 10 PIT tags in a circulating water bath against a digital thermocouple reader (model RDXL12SD, Omega, Stamford, CT, USA) over temperatures ranging from 25 to 50 °C in 5 °C increments.

Gas exchange measurements

We used an open flow-through respirometry system to measure oxygen consumption ($\dot{V}O_2$), carbon dioxide production ($\dot{V}CO_2$) and EWL during the night measurements and $\dot{V}CO_2$ and EWL during the day measurements over T_a ranges of 5–35 °C and 25–52 °C, respectively. We used 4-L airtight containers with a ~ 1 cm layer of mineral oil (to prevent evaporation from urine and faeces) at the bottom and a plastic mesh platform elevated ~ 10 cm above the oil layer. Atmospheric air scrubbed of water vapour by passing it through a series of columns of silica gel followed by Drierite was supplied to each chamber by an air pump (model DAA-V515-ED, Michigan, USA). The chambers were placed in a modified ice chest (~ 75 liters) in which T_a was regulated via a Peltier device (model AC-162, TE Technology Inc., Traverse City, MI, USA) and a custom-built controller. The dried air was split into three channels (a single baseline and two experimental channels) for night measurements, and two channels (a baseline and one experimental channel) for day measurements. A needle valve (Swagelok, Solon, OH, USA) was used to regulate the flow rate in the baseline channel, and two mass flow controllers (Alicat Scientific Inc., Tuscon AZ, USA) calibrated against a soap bubble flow meter (Baker and Pouchot 1983) regulated the flow rates in the experimental channels. In each chamber, the air inlet was placed close to the top and the air outlet below the mesh platform to maximize air mixing. The mass flow controllers maintained a constant flow rate of 1 L min⁻¹ to the chambers during night measurements. In contrast, flow rates during the daytime measurements were selected to maintain water vapour pressures as low as possible (< 1 kPa) within the chamber but still allow accurately measurable differences in water vapour and CO₂ between incurrent and excurrent air, following Whitfield et al. (2015). These daytime flow rates varied between 1 and 25 L min⁻¹ depending on T_a and the birds' behaviour while in the chamber. Birds tended to remain calmer with higher flow rates and low humidity (< 0.5 kPa) when exposed to very high T_a .

A subsample of excurrent air from each chamber was pulled through a CO₂/H₂O analyser (LI-840A, LI-COR, Lincoln NE, USA) regularly calibrated as described by Whitfield et al. (2015) and an O₂ analyser (FC-10A, Sable Systems, Las Vegas NV, USA) regularly calibrated as described by Cory Toussaint and McKechnie (2012). A personal computer with Expedata software (Sable Systems, Las Vegas NV, USA) was used to acquire voltage outputs from the analysers and convert them to digital signals using an analog–digital converter (model UI-3, Sable Systems, Las Vegas NV, USA) at a 5-s interval.

Experimental protocol

During the night measurements, $\dot{V}CO_2$ and $\dot{V}O_2$ were measured over T_a ranging from 5 to 35 °C in increments of 5 °C. Each run lasted approximately 9 h, with birds experiencing two T_a values per night in random sequence, the first from 20:30 to 00:30 and the second from 00:30 to 05:00. Data collected during the first hour at each T_a were excluded

from analyses. All measurements were conducted during the larks' nocturnal rest phase between sunset and sunrise, with one or two individuals per night. Each bird spent less than 48 h in captivity and, on average, lost ~ 3% of M_b . A total of 37 individuals (34 males and 3 females) was used during the night trials, with each individual experiencing only two T_a values during the course of a single night before being released at its site of capture. Data collection involved a repeating sequence of subsampling from the baseline channel for 10 min, followed by each metabolic chamber for 30 min thereafter.

During the day measurements, VCO_2/VCO_2 and EWL were recorded over a stepped series of progressively higher T_a values (Whitfield et al. 2015). Individuals were either exposed to $T_a = 25\text{ }^\circ\text{C}$ to $T_a = 40\text{ }^\circ\text{C}$ in $5\text{ }^\circ\text{C}$ increments, or to $T_a = 40\text{ }^\circ\text{C}$ to $T_a = 52\text{ }^\circ\text{C}$ in $2\text{ }^\circ\text{C}$ increments. Each individual was exposed to a given T_a value for approximately 30 min, following the approach of Whitfield et al. (2015), and spent less than 4 h in captivity. A total of 20 individuals (18 males and 2 females) were used during day measurements. For measurements at $T_a > 40\text{ }^\circ\text{C}$, each bird was initially placed in the chamber at $T_a = 35\text{ }^\circ\text{C}$ for 15–30 min to habituate before T_a was increased to $40\text{ }^\circ\text{C}$. Each set of measurements typically lasted < 3 h. Each bird's behaviour in the chamber was continuously monitored with a video camera and an infrared light source. Following Whitfield et al. (2015), measurements were terminated when birds displayed prolonged escape behaviour (agitated jumping, pecking and/or wing flapping), any signs of distress (loss of coordination or balance) or a sudden decrease in EWL and RMR or when T_b exceeded $45\text{ }^\circ\text{C}$ (we considered this as the thermal endpoint). When the measurements were terminated each individual was immediately removed and placed in the indoor cage at room temperature with ad libitum supply of water and food (mealworms and superworms) where it was continuously monitored until T_b stabilized at normothermic levels ($40\text{--}42\text{ }^\circ\text{C}$). Birds were later released at the site of capture. We were able to opportunistically monitor many of the birds post-release (immediately after capture and during subsequent weeks), and observed no evidence for any obvious adverse effects of being captured and used for these measurements. In almost all cases individuals lost $< 5\%$ of M_b during measurements.

Data analyses

We corrected for analyser drift and lag using the relevant algorithms in Expedata software (Sable Systems, Las Vegas NV, USA) for both night and day measurements. For night measurements, equations [9.4]–[9.6] from Lighton (2008) were used to calculate VCO_2/VCO_2 and VO_2/VO_2 values, using equation [9.3] for excurrent flow rate estimates in all calculations. The lowest 5-min period of VCO_2/VCO_2 and VO_2/VO_2 at each T_a value was used to calculate RMR or BMR for each individual. Respiratory exchange ratio (RER) was calculated as $VCO_2/VO_2/VCO_2/VO_2$. Thermal equivalence values from Table 4-2 from Withers (1992) were used to convert measurements of gas exchange to metabolic rates (W). The RER was 0.71 ± 0.06 between $T_a = 5\text{ }^\circ\text{C}$ and $35\text{ }^\circ\text{C}$, and in the small number of instances where RER was < 0.71 we assumed RER = 0.71. We calculated total thermal conductance ($\text{mW }^\circ\text{C}^{-1} \text{cm}^{-2}$) from rest-phase data following Noakes et al. (2013), using an allometrically predicted external surface area of 92.3 cm^2 (Walsberg and King 1978).

For day measurements, equations 10.5 and 10.9 from Lighton (2008) were used to calculate VCO_2/VCO_2 and EWL from the lowest stable 5-min periods of CO_2/CO_2 and water vapour at a given T_a , assuming $0.803\text{ mg H}_2\text{O mL vapour}^{-1}$. We calculated RMR from VCO_2/VCO_2 assuming RER = 0.71 (Walsberg and Wolf 1995) and EHL assuming $2.406\text{ J mg H}_2\text{O}^{-1}$ at $40\text{ }^\circ\text{C}$ (Tracy et al. 2010), respectively. The mean T_b was estimated over

the same period. We excluded all data points from active individuals from our analysis and also excluded data from females on account of most birds caught being males.

Piecewise linear regression models (Sizer package; Sonderegger 2012) were fitted to data to identify inflection points in RMR, EWL, T_b and EHL/MHP as a function of T_a in R 2.13.1 (R Core Team). We then fitted linear mixed effect models (*nlme* package; Pinheiro et al. 2009) to RMR, EWL and T_b above and below the respective inflection points, including individual identity as a random effect. Both T_a and M_b were initially included in the models, with the best model for each response variable subsequently selected based on Akaike information criterion (AIC) values (*MuMin* package; Bartoń 2013). Because the inclusion of M_b did not improve model fit, it was excluded from the final models. Values are presented as means \pm s.d.

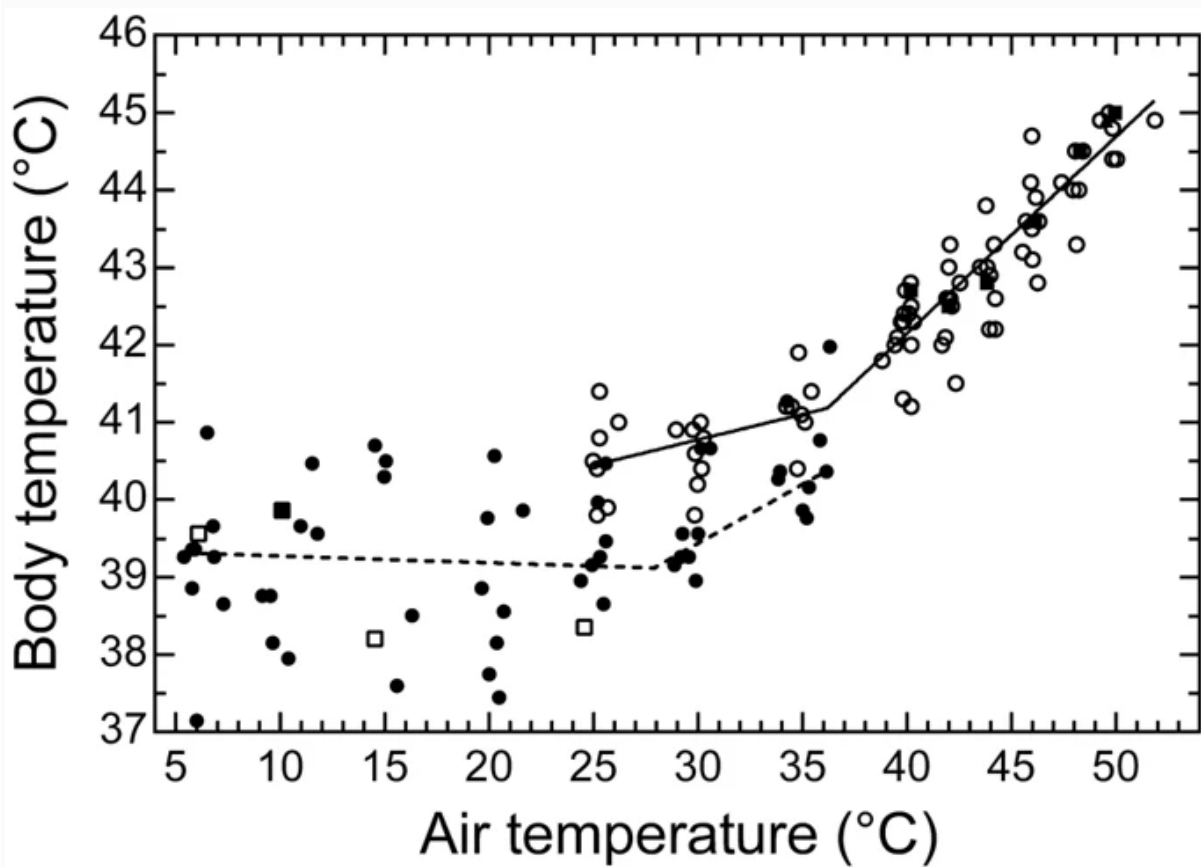


Fig. 1. Body temperature (T_b) of red larks (*Calendulauda burra*) as a function of air temperature (T_a). Rest-phase data for males and females are shown by black circles and open squares, respectively. Active-phase data for males, females and active individuals are shown by open circles, black squares and black triangles, respectively. Segmented linear regression models were used to provide the best fit for rest-phase (dashed line) and active-phase (solid line) with estimated inflection points of $T_a = 27.9$ °C and $T_a = 36.2$ °C, respectively (data points for females and active males were excluded from these analysis). For active-phase T_b , the relationship above the inflection at $T_a = 36.2$ °C was best described as $T_b = 0.254T_a + 31.920$ (slope and intercept from mixed model including individual identity as random predictor)

Results

Body temperature and heat tolerance limits

The normothermic rest-phase T_b ranged between 39.2 ± 1.0 °C ($n = 9$) at $T_a = \sim 5$ °C and 39.4 ± 0.6 °C ($n = 7$) at $T_a = \sim 25$ °C and did not vary with T_a (Fig. 1). However, rest-phase T_b increased significantly ($t = 8.399$, $P < 0.001$) above an inflection at $T_a = 27.9$ °C to a maximum of 40.5 ± 0.7 °C ($n = 9$) at $T_a = \sim 35$ °C. During day measurements, the active-phase T_b increased slightly but significantly ($t = 3.381$, $P < 0.005$) with T_a below an inflection of $T_a = 36.2$ °C, from 40.6 ± 0.5 °C ($n = 8$) at $T_a = \sim 25$ °C to 41.2 ± 0.5 °C ($n = 7$) at $T_a = \sim 35$ °C (Fig. 1). Above this inflection point T_b increased significantly ($t = 17.641$, $P < 0.001$) to a maximum of 44.7 ± 0.3 °C ($n = 5$) at $T_a = \sim 50$ °C, with a single highest T_b value of 45.0 °C recorded at $T_a = 49.7$ °C (Fig. 1). The larks maintained a positive $T_b - T_a$ gradient up to $T_b = 42.9$ °C (95th percentile of T_b for all $T_b > T_a$). The circadian amplitude between the active-phase mean and rest-phase mean T_b varied from 1.2 °C at $T_a = \sim 25$ °C to 0.6 °C at $T_a = \sim 35$ °C. Five birds reached their heat tolerance limit at $T_a = 50$ °C, although a single individual reached $T_a = 52$ °C.

Resting metabolic rate

A segmented linear regression model was fitted to the rest-phase and active-phase RMR and revealed lower and upper inflection points at $T_a = 20.5$ °C and $T_a = 36.6$ °C, respectively. We interpret these values as the lower (T_{lc}) and upper critical limits (T_{uc}) of thermoneutrality, respectively. Visual inspection of RMR above the T_{lc} (Fig. 2) suggests a decline with increasing T_a , but there was no statistically significant change ($t = -1.617$, $P = 0.134$). The minimum mean rest-phase RMR was 0.317 ± 0.047 W at $T_a = \sim 35$ °C, which we consider to represent the BMR for *C. burra* individuals in this study. At $T_a < T_{lc}$, the mean rest-phase RMR increased significantly ($t = -9.655$, $P < 0.001$) with decreasing T_a to a maximum rest-phase RMR of 0.629 ± 0.092 W at $T_a = \sim 5$ °C. The mean active-phase RMR was not significantly related to T_a ($t = 0.526$, $P = 0.615$) within the thermoneutral zone, with a mean active-phase RMR of 0.308 ± 0.057 W ($n = 9$) at $T_a = \sim 30$ °C. However, above the T_{uc} , the mean active-phase RMR increased significantly ($t = 5.000$, $P < 0.001$) to a maximum of 0.527 ± 0.076 W ($n = 5$) at $T_a = \sim 50$ °C, equivalent to 171% of the minimum thermoneutral daytime RMR. The mean active-phase RMR at $T_a = \sim 25$ °C suggests an increase in active-phase RMR at $T_a < 25$ °C; however, we were not able to fit a piecewise linear regression model as a result of insufficient data at lower T_a . During the active-phase measurements, the onset of panting occurred at $T_a = 38.0 \pm 1.7$ °C ($n = 19$).

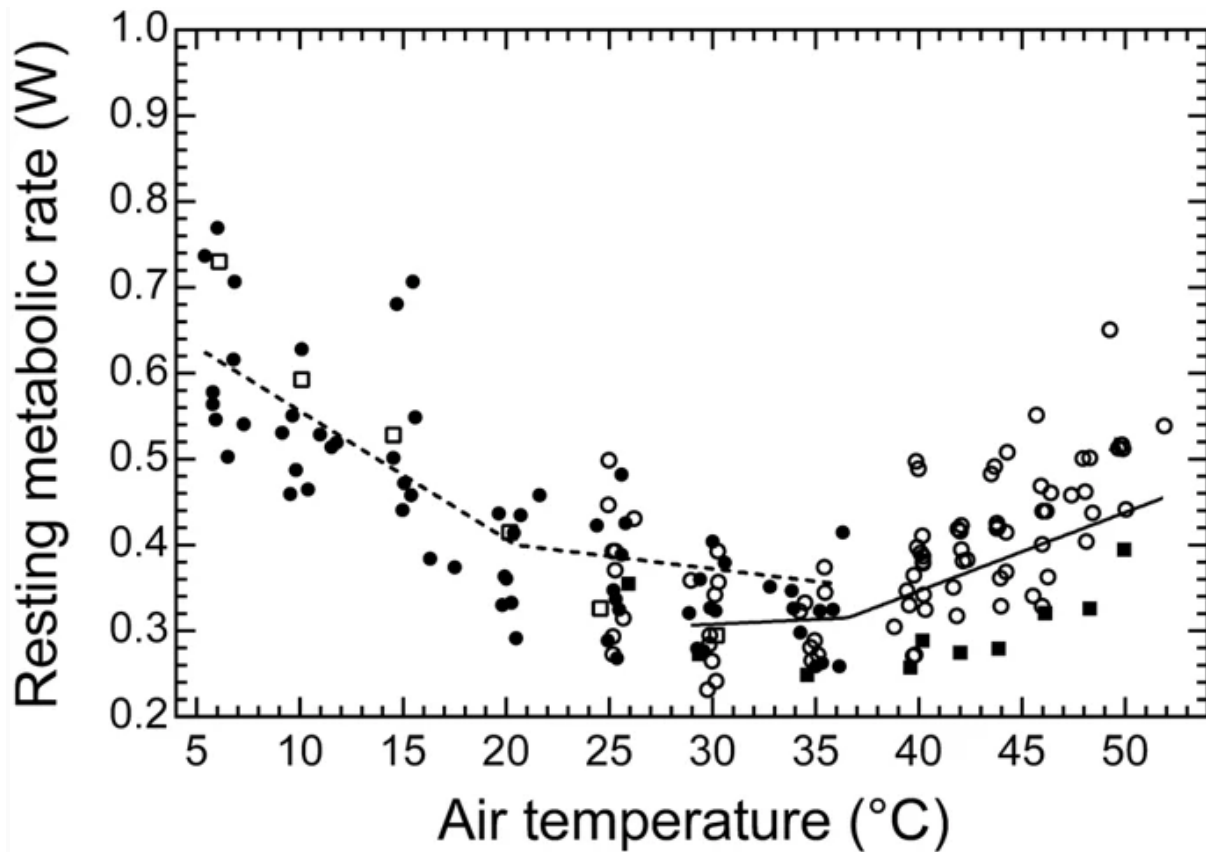


Fig. 2. Resting metabolic rate (RMR) of red larks (*Calendulauda burra*) as a function of air temperature (T_a). Rest-phase data for males and females are shown by black circles and open squares, respectively. Active-phase data for males, females and active individuals are shown by open circle, black squares and black triangles, respectively. Segmented linear regression models were used to provide the best fit for rest-phase (dashed line) and active-phase (solid line) with an estimated inflection points of $T_a = 20.5$ °C and $T_a = 36.6$ °C, respectively (data points for females, active individuals and at $T_a = \sim 25$ °C were excluded from these analysis). For active-phase RMR, the relationship above the inflection at $T_a = 36.6$ °C was best described as $RMR = 0.009T_a - 0.003$ (slope and intercept from mixed model including individual identity as random predictor)

Rest-phase thermal conductance

An inflection point occurred in rest-phase thermal conductance at $T_a = 20.3$ °C, below which conductance was minimal and constant, averaging 0.207 ± 0.028 mW °C⁻¹ cm⁻² (Fig. 3). At $T_a > 20.3$ °C thermal conductance increased approximately threefold to 0.634 ± 0.110 mW °C⁻¹ cm⁻² at $T_a = \sim 35$ °C (Fig. 3). The corresponding values for dry heat transfer coefficient were 0.188 ± 0.026 mW °C⁻¹ cm⁻² and 0.407 ± 0.068 mW °C⁻¹ cm⁻².

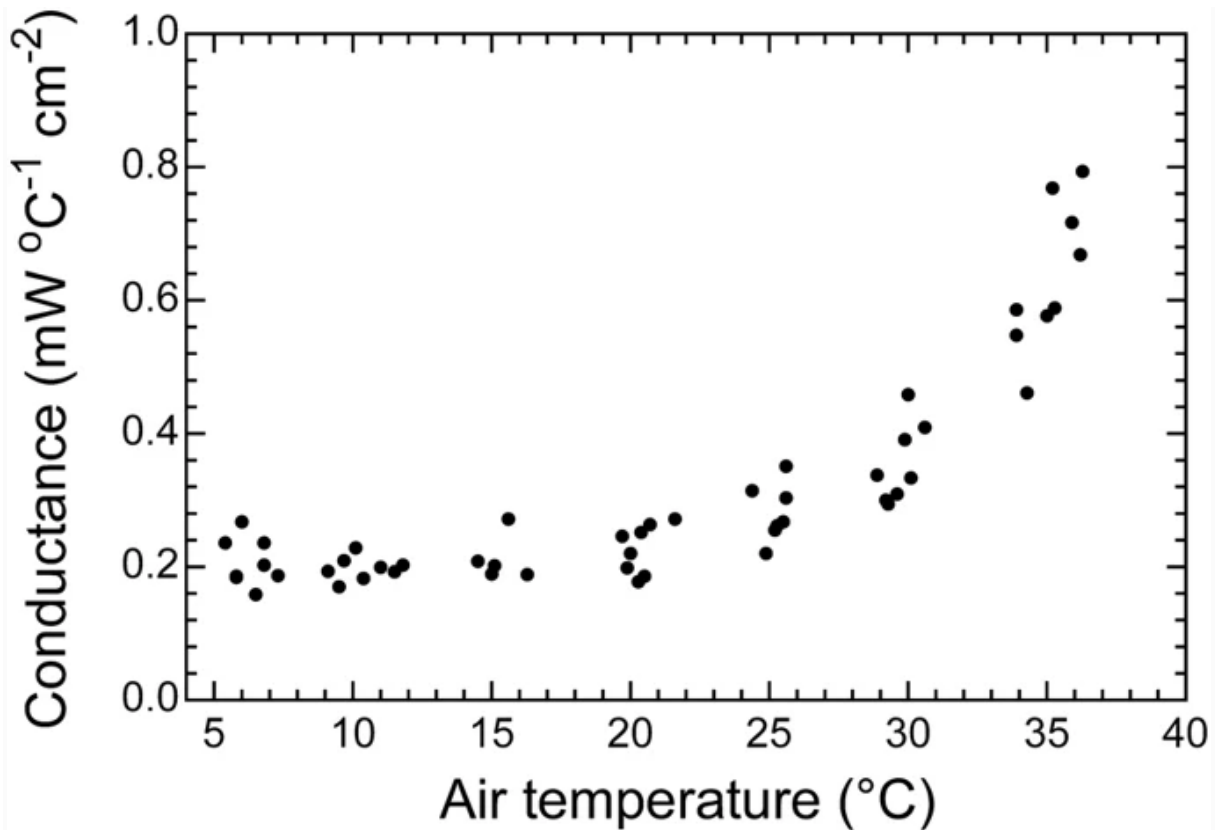


Fig. 3. Rest-phase thermal conductance of red larks (*Calendulauda burra*) as a function of air temperature (T_a)

Evaporative water loss

Segmented linear regression models fitted to the rest-phase and active-phase EWL data identified inflection points at $T_a = 17.7$ °C and $T_a = 36.1$ °C, respectively (Fig. 4). Rates of rest-phase EWL were not significantly related to T_a below the lower inflection point at $T_a = 17.7$ °C ($t = 19.904$, $P = 0.831$). However, above this inflection point the mean rates of rest-phase EWL increased significantly ($t = 5.430$, $P < 0.001$) to a maximum mean value of 0.157 ± 0.046 g h⁻¹ ($n = 10$) at $T_a \sim 35$ °C. Rest-phase EWL at $T_a = 25$ °C was 0.117 ± 0.044 g h⁻¹, equivalent to 49% of the active value at the same T_a . During the active phase, rates of EWL were not significantly different below the inflection point at $T_a = 36.1$ °C ($t = 0.684$, $P = 0.504$), ranging from 0.238 ± 0.108 g h⁻¹ ($n = 9$) to 0.255 ± 0.078 g h⁻¹ ($n = 8$) at $T_a \sim 25$ °C and 35 °C, respectively (Fig. 4). However, above this inflection point the mean rates of EWL increased significantly ($t = 19.904$, $P < 0.001$) to a maximum value of 1.475 ± 0.107 g h⁻¹ ($n = 5$) at $T_a \sim 50$ °C, a 6.2-fold increase compared to the value at $T_a \sim 30$ °C and equivalent to $3.7 \pm 0.3\%$ M_b h⁻¹. A single highest value of 1.879 g h⁻¹ was recorded in an individual at $T_a = 51.9$ °C (Fig. 4). The relationship between T_a and mass-specific EWL (EWL_{MS}; mg g⁻¹ h⁻¹) above the inflection point was best described by the linear model $EWL_{MS} = 2.064T_a - 67.220$ ($r^2 = 0.878$).

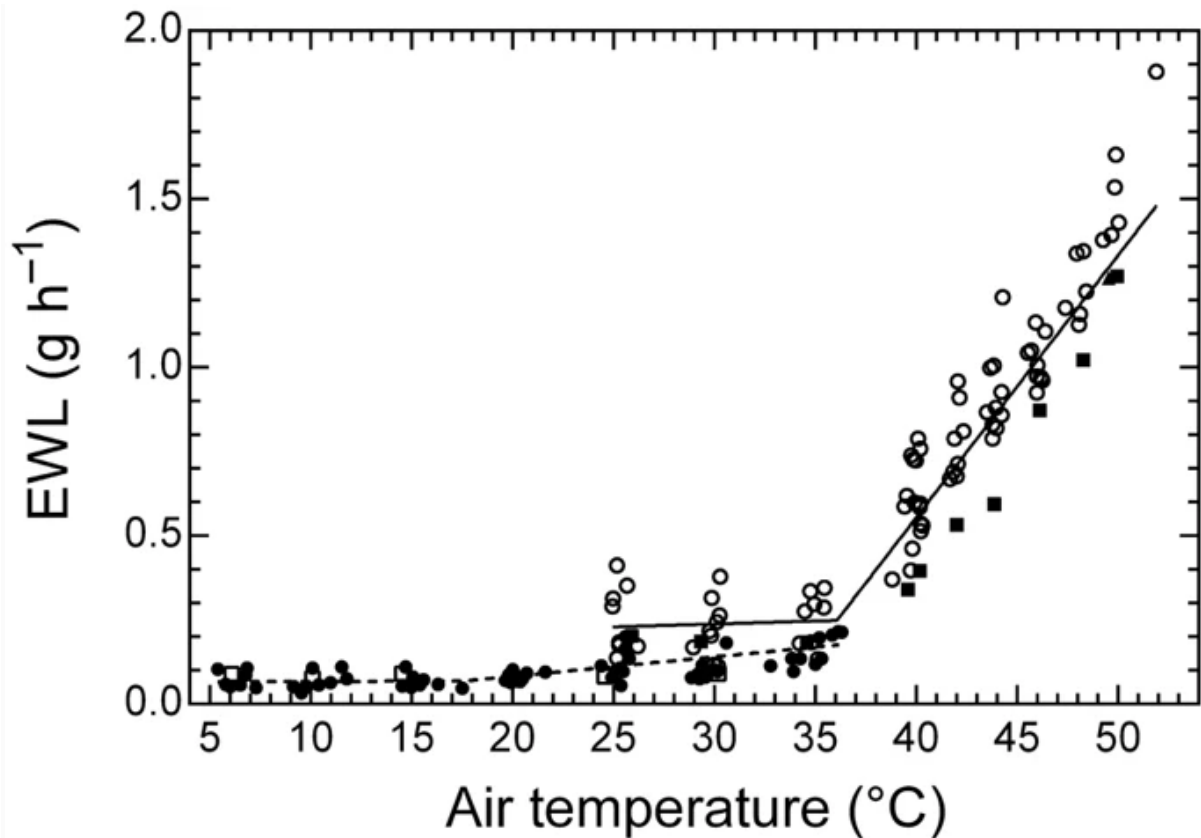


Fig. 4. Evaporative water loss (EWL) of red larks (*Calendulauda burra*) as a function of air temperature (T_a). Rest-phase data for males and females are shown by black circles and open squares, respectively. Active-phase data for males, females and active individuals are shown by open circle, black squares and black triangles, respectively. Piecewise linear regression models were used to provide the best fit for rest-phase (stripped line) and active-phase (solid line) with an estimated inflection points of $T_a = 17.7$ °C and $T_a = 36.1$ °C, respectively (data points for females and active individuals were excluded from these analysis). For active-phase EWL, the relationship above the inflection at $T_a = 36.1$ °C was best described as $EWL = 0.079T_a - 2.526$ (slope and intercept from mixed model including individual identity as random predictor)

The mean ratio of EHL/MHP during the active-phase was less than 0.500 ($n = 7-8$) at T_a ranging from 25 to 35 °C. However, at $T_a \sim 40$ °C the mean ratio was slightly higher (0.884 ± 0.140 ; $n = 15$) and increased significantly ($t = 13.841$, $P < 0.001$) to a maximum of 1.579 ± 0.253 ($n = 5$) at $T_a \sim 50$ °C with a single maximum value of 1.940 at $T_a = 51.9$ °C (Fig. 5). An inflection point was apparent at $T_a - T_b = -7.0$ °C when EHL/MHP was plotted against the $T_a - T_b$ gradient (Fig. 5) and the y-intercept above the inflection point was at $EHL/MHP = 1.11$, i.e., on average 111% of MHP was dissipated evaporatively when $T_b = T_a$.

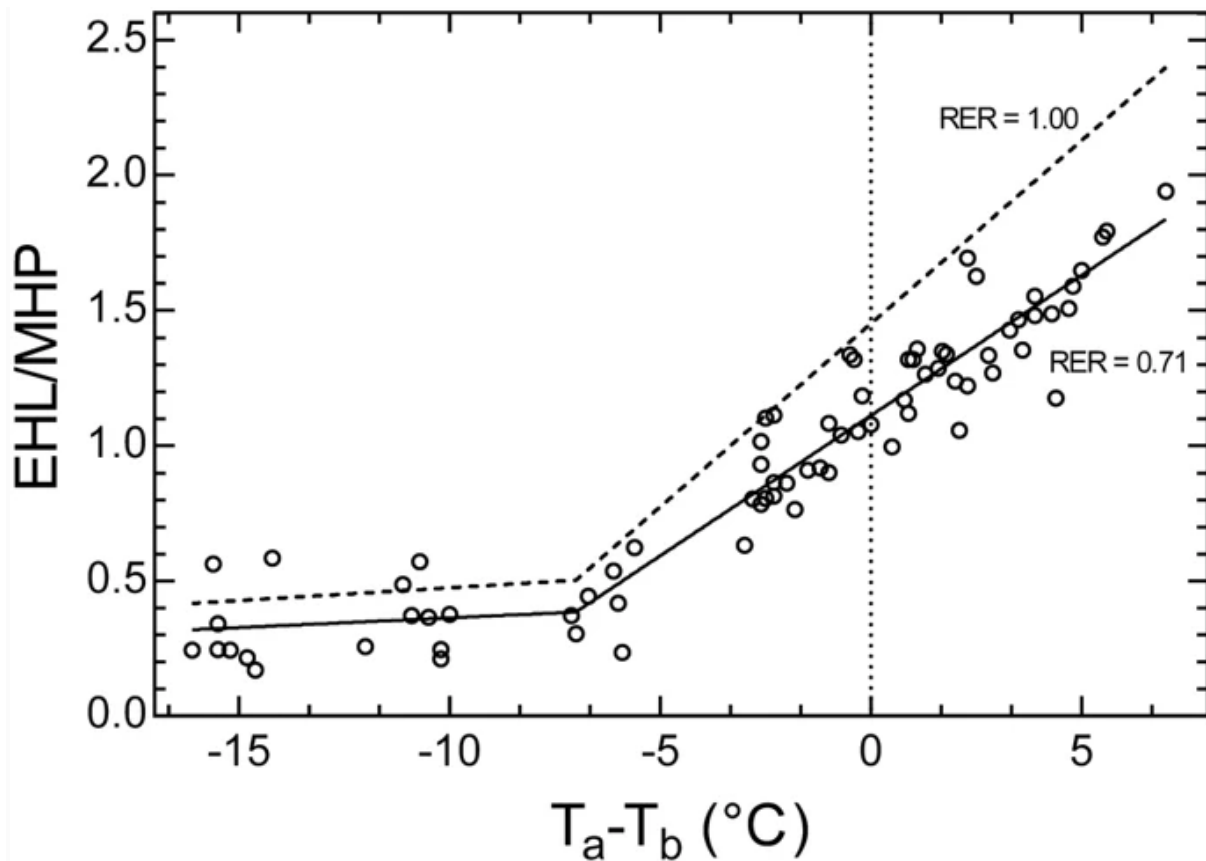


Fig. 5. Relationship between the ratio of evaporative heat loss (EHL) and metabolic heat production (MHP) against the gradient between air temperature (T_a) and body temperature (T_b) in red larks (*Calendulauda burra*). A segmented linear regression model provides the best fit with an inflection point apparent at $T_a - T_b = -7.0$ °C. The solid and dashed lines provided the best fit assuming a respiratory exchange ratio (RER) of 0.71 and 1.00, respectively. Above the inflection point, the relationship between EHL/MHP and $T_a - T_b > -7.0$ °C assuming RER = 0.71 is $\text{EHL/MHP} = 0.104(T_a - T_b) + 1.110$ ($r^2 = 0.864$) and assuming RER = 1.00 is $\text{EHL/MHP} = 0.136(T_a - T_b) + 1.451$

Discussion

Thermoregulation in the red lark, a threatened and range-restricted desert specialist, is characterised by normothermic T_b similar to other passerines, a relatively wide TNZ and low BMR. At T_a exceeding normothermic T_b , relationships between T_b , RMR and EWL are broadly consistent with patterns documented for other passerines, and maximum evaporative cooling capacity and heat tolerance limits are well within the range typically reported for this order.

Body temperature

The mean rest-phase T_b of *C. burra* is ~ 2 °C lower than that reported for two other southern African arid-zones larks, the congeneric dune lark (*C. erythrochlamys*) which is restricted to the sand dunes of the Namib Desert (Williams 1999), and spike-heeled lark (*Chersomanes albofasciata*; Tieleman et al. 2003b) which occurs sympatrically with *C. burra* at our study site. It is also ~ 1.3 °C lower than values reported for two Arabian Desert species (*Alaemon alaudipes* and *Eremalauda dunni*), and ~ 2.4 °C lower than those of two species occupying mesic habitats at temperate latitudes (*Alauda arvensis* and *Lullula arborea*; Tieleman et al. 2002). However, we suspect that this interspecific variation in T_b may at least in part

reflect methodological differences among studies. Williams (1999), Tieleman et al. (2002) and Tieleman et al. (2003b) used thermocouples to measure T_b at the end of metabolic measurements, whereas we monitored T_b continuously using PIT tags. Since our approach did not require handling and involved continuous T_b measurements throughout the night, we were more likely to detect minimum resting levels in undisturbed, resting birds. The mean rest-phase T_b of *C. burra* was similar to the mean T_b reported for 59 passerines (38.9 ± 0.87 °C; Prinzing et al. 1991). During day measurements, the mean normothermic active-phase T_b of *C. burra* was slightly lower than the mean value for 298 passerines of 41.6 ± 1.1 °C (Prinzing et al. 1991). Far less is known about T_b in free-ranging larks, but congeneric fawn-coloured larks (*C. africanoides*) housed in large outdoor aviaries in midsummer in the Kalahari Desert showed active-phase T_b that was typically between 42.0 and 43.5 °C (Cunningham et al. 2017; Thompson et al. 2018).

We observed a linear increase in T_b at T_a above normothermic T_b , a typical avian response to heat exposure (Dawson and Fisher 1969; Marder and Gavrieli-Levin 1986). Because our study species is threatened, we opted to end measurements when individuals reached $T_b = 45$ °C, with only two individuals (one male and one female) reaching their thermal endpoints at $T_b < 45$ °C. However, we consider it unlikely that red larks can tolerate T_b much higher than this value, as recent data suggest that in many birds from phylogenetically diverse taxa physiological function is comprised at $T_b > 45$ °C (Whitfield et al. 2015; McKechnie et al. 2016a; Smith et al. 2017; McWhorter et al. 2018), even though there are a few historical records of birds briefly tolerating $T_b = 46$ °C (Brush 1965) and even $T_b = 48$ °C (Randall 1943). At $T_a = 46$ °C, the highest common T_a at which T_b has been measured in passerines from the arid zones of southern Africa, Australia and North America, the T_b of *C. burra* fell within the range reported for passerines of similar body mass (43.1–43.9 °C; Whitfield et al. 2015; McKechnie et al. 2017; Smith et al. 2017).

The slope of T_b versus T_a at $T_a > T_{uc}$ in *C. burra* is intermediate between the corresponding values for two similarly sized passerines, the white-browed sparrow-weaver (*Plocepasser mahali*; slope = 0.21; Whitfield et al. 2015) and spiny-cheeked honey-eater (*Acanthagenys rufogularis*; slope = 0.30; McKechnie et al. 2017), and almost identical to that of the northern cardinal (*Cardinalis cardinalis*; slope = 0.27; Smith et al. 2017). Besides these three ~40-g species, the value for *C. burra* is well within the range for the passerines for which comparable data exist (Whitfield et al. 2015; McKechnie et al. 2017; Smith et al. 2017); these comparisons thus do not support our prediction that *C. burra* makes more extensive use of facultative hyperthermia compared to other passerines.

The heat tolerance limit (HTL) of $T_a = 50$ °C for *C. burra* is 4 °C lower than that of the similarly-sized white-browed sparrow-weaver (Whitfield et al. 2015) and just above that of the spiny-cheeked honeyeater (McKechnie et al. 2017). This observation raises the possibility that the consistently higher HTL of three southern African ploecids (Whitfield et al. 2015) compared to those of five Australian species from several families (McKechnie et al. 2017) reflects a phylogenetic difference and members of the Ploceidae generally have higher HTLs than other passerine families examined so far.

Resting metabolic rate

Thermoregulation in *C. burra* generally conforms to the classic Scholander–Irving model of endothermic homeothermy (Scholander et al. 1950), with a distinct zone of thermoneutrality.

An inflection in rest-phase RMR occurred at $T_a = 20.5$ °C. Although visual inspection suggested that at higher T_a rest-phase RMR decreases with increasing T_a (Fig. 2), there was no significant relationship between RMR and $T_a > 20.5$ °C. Therefore, we consider $T_a = 20.5$ °C to be the T_{lc} of *C. burra*, an argument supported by the inflection in thermal conductance at almost exactly the same T_a . This is, to the best of our knowledge, the lowest T_{lc} yet reported for a lark, being slightly lower than the $T_{lc} = 22.2$ °C reported for skylarks and considerably lower than values for other desert larks: 32.7 °C, 31.5 °C and 27.3 °C for hoopoe lark, Dunn’s lark and dune lark, respectively (Trost 1972; Williams 1999; Tieleman et al. 2002). Combined with the active-phase T_{uc} of 36.6 °C (see below), the low T_{lc} results in *C. burra* having an unusually wide TNZ. Moreover, the BMR of *C. burra* is the lowest relative to allometrically expected values yet measured in a lark (Fig. 6), being equivalent to ~ 72% of the value predicted for a 38-g passerine (Londoño et al. 2015) and ~ 26% lower than the BMR of similarly-sized hoopoe larks held in outdoor aviaries (Tieleman et al. 2002; Fig. 6).

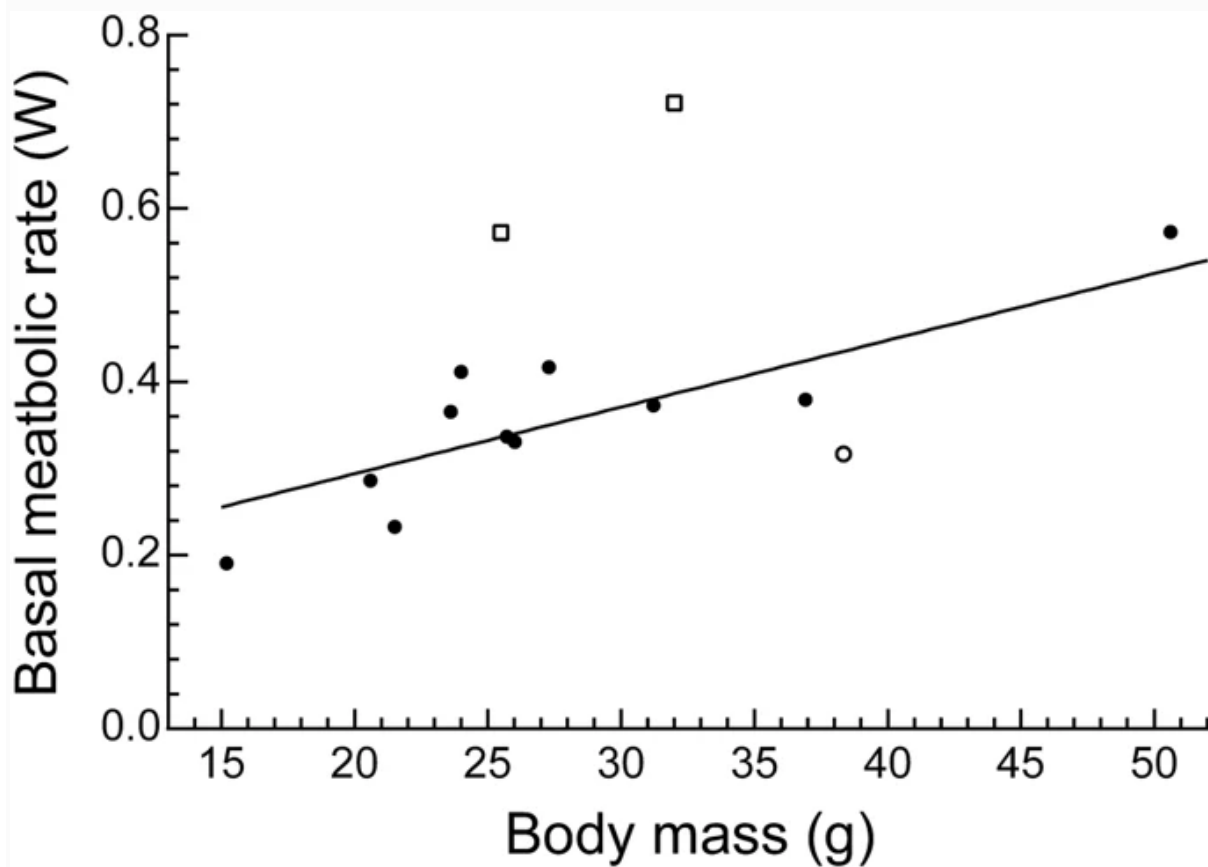


Fig. 6. Relationship between basal metabolic rate (BMR) and body mass (M_b) among 14 lark species. Data for mesic and desert larks (following Tieleman et al. 2003b) are indicated by open squares and black circles, respectively, and the datum for red lark (*Calendulauda burra*) is shown by an open circle. The solid line is the scaling relationship for BMR in passerines identified by Londoño et al. (2015)

The low BMR of the red lark contrasts with the value of 0.417 W measured in the congeneric 27-g dune lark, close to allometrically expected values (Williams 1999). Compared to the BMR predicted in a more recent scaling analysis (Londoño et al. 2015), the dune lark’s BMR of is equivalent to 118% of that expected for a 27-g passerine, supporting Williams’ (1999) arguments concerning the relatively high BMR of the latter species. However, direct

comparisons of the BMRs of these two *Calendulauda* species are complicated for several factors. First, Williams caught dune larks in mid-winter, whereas our study took place in summer. Many birds show substantial seasonal changes in BMR, which in subtropical latitudes may involve either increases or decreases in winter (reviewed by McKechnie et al. 2015). Second, Williams' measurements of BMR took place after individuals trapped in the Namib had been transported to Cape Town and housed in captivity for at least 3 weeks, whereas our measurements took place in the field immediately after capture. Thermal acclimation induces rapid adjustments in avian BMR (reviewed by McKechnie and Swanson 2010), and for this reason we cannot exclude the possibility that the dune larks in Williams' (1999) study increased BMR during their period in captivity.

One unexpected observation to emerge from our data is that the minimal active-phase RMR is indistinguishable from BMR (i.e., minimal rest-phase RMR; Fig. 2). Avian RMR is typically substantially higher during the active-phase; for a 38-g passerine, active-phase RMR at thermoneutrality is predicted to be 32% higher than rest-phase values (Aschoff and Pohl 1970). This virtual absence of circadian variation in RMR in *C. burra* is no doubt functionally linked to the smaller-than-expected difference between active- and rest-phase T_b ; the 1.0–1.5 °C difference at $T_a = 25$ °C and 30 °C is approximately half the circadian amplitude expected for a 38-g passerine (Aschoff 1982). One explanation might be that the larks are reducing metabolic heat production during the hot daylight hours to minimize evaporative cooling requirements on account of their hot, arid environment, but evaluating this possibility requires comparative data from other lark species in a range of habitats.

The onset of panting occurred at a slightly higher T_a than the estimated $T_{uc} = 36.6$ °C, but this difference may reflect an experimental artefact as birds were not facing the camera at all times and it is possible that some panting was unobserved. Our prediction that *C. burra* commences panting at higher T_a than most passerines is not supported by the available data: five Australian passerines all commenced panting at $T_a = 40$ – 42 °C (McKechnie et al. 2017). A non-passerine southern African arid-zone specialist, Burchell's Sandgrouse, commenced panting and gular flutter only at $T_a = 44$ °C (McKechnie et al. 2016a).

The T_{uc} of *C. burra* falls within the range typical of passerines (Whitfield et al. 2015; McKechnie et al. 2017; Smith et al. 2017) and is similar to values for dune lark (35.1 °C), skylark (35.1 °C) and hoopoe lark (37.5 °C), but 7 °C lower than that of Dunn's lark (43.6 °C) (Tieleman et al. 2002). Above the T_{uc} the RMR of *C. burra* increased to a maximum equivalent to ~ 160% of minimal thermoneutral values, a fractional increase similar to that reported for three southern African ploceid passerines (30–60%; Whitfield et al. 2015) and five Australian passerines (50–100%; McKechnie et al. 2017). These increases in RMR at high T_a are consistent with panting being the predominant avenue of evaporative heat dissipation among larks (Tieleman and Williams 2002) and passerines in general.

Evaporative water loss

Red larks showed the typical avian relationship between active-phase EWL and T_a : low and constant EWL at moderate T_a and rapid, approximately linear increases in EWL at T_a approaching or exceeding normothermic T_b (Fig. 4). Relative to the EWL at $T_a = 25$ °C predicted for a 38-g arid-zone passerine by Williams (1996; data for active- and rest-phase combined), active-phase EWL for *C. burra* was equivalent to 176%, whereas rest-phase EWL was equivalent to just 85% of the predicted value. Rest-phase EWL at $T_a = 25$ °C in *C.*

burra is similar (9.3% higher) to the corresponding value in hoopoe larks (Tieleman et al. 2002).

The inflection T_a above which EWL increased rapidly above thermoneutral levels in *C. burra* ($T_a = 36.1$ °C) was slightly lower than predicted for a 38-g bird (36.8 °C; McKechnie and Wolf 2010), and the slope of mass-specific EWL versus $T_a > T_{lc}$ was equivalent to 88% of the predicted value (McKechnie and Wolf 2010). The mass-specific EWL slopes for five Australian passerines (158–219% of predicted values) and three southern African ploceid passerines (99–175%; Whitfield et al. 2015; McKechnie et al. 2017) were much steeper than that of *C. burra*. The maximum fractional increase in EWL in *C. burra* ($6.2 \times$ minimal levels) is substantially lower than the average observed in three southern African ploceid passerines (15.1 ± 3.9 ; Whitfield et al. 2015) but only slightly lower than those of five Australian passerines (7.3 ± 0.8 ; McKechnie et al. 2017) and seven Sonoran Desert passerines (7.0 ± 2.7 ; Smith et al. 2017). The maximum cooling efficiency (i.e. maximum EHL/MHP) of *C. burra* falls towards the lower end of the range recently reported for passerines (1.2–2.22; Whitfield et al. 2015; McKechnie et al. 2017; Smith et al. 2017), and our prediction that maximum EHL/MHP is higher in *C. burra* than in most passerines was not supported.

The maximum evaporative cooling capacity of *C. burra* (i.e., maximum EHL/MHP) was estimated as 1.579 assuming lipid metabolism (i.e., RER = 0.71), with a y-intercept of 1.11 for EHL/MHP versus $T_a - T_b$ (Fig. 5). The latter value is almost exactly that expected on theoretical grounds, because the maintenance of a stable T_b requires that 100% of metabolic heat production is dissipated evaporatively. This observation suggests that the birds in our study were indeed post-absorptive and metabolising lipids during metabolic measurements. Recalculating EHL/MHP assuming RER = 1.00 (i.e., carbohydrate metabolism) yields a maximum EHL/MHP of 2.062 and a y-intercept of 1.487 (Fig. 5), so we are confident that our assumption of lipid metabolism is correct.

The relatively modest fractional increases in EWL and maximum EHL/MHP values we observed in *C. burra* suggest that, as a species that is thought to never drink (Dean and Ryan 2005), it may not have evolved a high capacity for evaporative cooling. Although a pronounced capacity to dissipate heat evaporatively would doubtless have adaptive value for a species inhabiting a hot environment with sparse shade, large elevations in EWL above baseline levels may be problematic in terms of water conservation. Moreover, as is the case for other passerines, the primary avenue of evaporative heat dissipation in *C. burra* is panting, a less efficient process than cutaneous evaporation or gular flutter and thus imposing constraints on the economy of evaporative cooling. At present, however, too few data exist on thermoregulation at high T_a in larks to rigorously explore how evaporative cooling capacity is correlated with habitat or behavioural variables such as use of drinking water.

Observations of the behaviour of the red larks we made on very hot days during the course of this study also suggest that evaporative cooling is strongly constrained by the need to conserve water. For instance, a lark for which we obtained video footage while it rested in the shade on a very hot day ($T_a = \sim 39$ °C at the time of recording) showed several behaviours suggestive of minimising water losses for evaporative cooling (ESM Video 1). Specifically, the lark's underparts were in contact with the cool sand in the shade, its eyes were closed for most of the time, and panting had the appearance of a carefully regulated process with no forced ventilation of the thoracic cavity evident (ESM Video 1).

Conclusion

Red larks inhabit one of the most arid regions of South Africa. Despite regularly experiencing T_a approaching or exceeding 40 °C together with intense solar radiation and inhabiting an environment with limited shaded microsites, the species is independent of drinking water (Dean and Ryan 2005). Relationships between metabolic rate, T_b and evaporative heat dissipation are broadly consistent with those of passerines in general, with quantitatively similar increases in RMR, T_b and EWL to those documented in other species investigated under comparable conditions. The species does, however, have an unusually wide TNZ, as well as the lowest BMR relative to allometric predictions yet reported for a lark. The low BMR and rest-phase EWL at moderate T_a support our predictions that *C. burra* is convergent with larks from the extremely arid Middle Eastern and North African deserts in terms of baseline energy and water requirements. Our data did not, however, support our predictions that in red larks the onset of panting occurs at higher T_a or that evaporative cooling is more efficient (i.e., higher maximum EHL/MHP) than in other passerines. The magnitude of facultative hyperthermia in red larks is quantitatively similar to that of other passerines investigated to date, and so there is no evidence suggesting that this species makes more extensive use of hyperthermia than most passerines, at least under laboratory conditions. However, T_b data from free-ranging red larks are needed to confirm this conclusion.

Larks have proved an exceptionally interesting avian taxon for testing hypotheses about avian physiological and behavioural adaptation to aridity (Trost 1972; Tieleman and Williams 2002; Tieleman et al. 2002, 2003a, b, 2004). Most work on the family has focused on RMR and EWL at thermoneutral and lower T_a (Tieleman et al. 2002, 2003a, b) and we suspect that future studies of heat tolerance limits and evaporative cooling capacity will prove fruitful for exploring trade-offs between dehydration and hyperthermia avoidance, particularly in species that occupy extremely arid environments and never drink. Moreover, we also think larks will be an extremely useful taxon in which to examine how trade-offs between thermoregulation and foraging constrain body condition and breeding success, and how chronic, sublethal fitness costs during sustained hot weather will affect the persistence of desert larks in the face of anthropogenic climate change (e.g., du Plessis et al. 2012; Cunningham et al. 2013).

Acknowledgements

We thank Black Mountain Mine for allowing us to conduct research on their property in the Koa River Valley and Kobus Smit of Vedanta Resources for his assistance and support. We are grateful to Clarise Kemp and Marc Freeman for assistance in the field, and to an anonymous reviewer whose constructive comments greatly improved the quality of the manuscript. All procedures were approved by the Animal Ethics Committee of the University of Pretoria (protocol EC41-17) and the Research Ethics and Scientific Committee of the South African National Biodiversity Institute (protocol P17-29). Red larks were captured under permit from the Northern Cape Department of Environment and Nature Conservation (FAUNA 1209/2017). This work was made possible by funding from the DST-NRF Centre of Excellence at the FitzPatrick Institute and is also based on research supported in part by the National Research Foundation of South Africa (Grant Number 110506). Any opinions,

findings and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Research Foundation.

Ethics declarations

Ethical approval

All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

References

- Alström P, Barnes KN, Olsson U, Barker FK, Bloomer P, Khan AA, Qureshi MA, Guillaumet A, Crochet P-A, Ryan PG (2013) Multilocus phylogeny of the avian family Alaudidae (larks) reveals complex morphological evolution, non-monophyletic genera and hidden species diversity. *Mol Phylogenetics Evol* 69(3):1043–1056
- Aschoff J (1982) The circadian rhythm of body temperature as a function of body size. In: Taylor CR, Johansen R, Bolis L (eds) *A companion to animal physiology*. Cambridge University Press, Cambridge, pp 173–188
- Aschoff J, Pohl H (1970) Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergröße. *J für Ornithiol* 111:38–47
- Baker WC, Pouchot JF (1983) The measurement of gas flow. Part II. *J Air Pollut Control Assoc* 33(2):156–162
- Bartholomew GA, Cade TJ (1963) The water economy of land birds. *Auk* 80:504–539
- Bartoń K (2013) *MuMIn*: multi-model inference, R package version 1.9.13
- Cory Toussaint D, McKechnie AE (2012) Interspecific variation in thermoregulation among three sympatric bats inhabiting a hot, semi-arid environment. *J Comp Physiol B* 182:1129–1140
- Cunningham SJ, Martin RO, Hojem CL, Hockey PAR (2013) Temperatures in excess of critical thresholds threaten nestling growth and survival in a rapidly-warming arid savanna: a study of common fiscals. *PLoS One* 8(9):e74613
- Cunningham SJ, Thompson ML, McKechnie AE (2017) It's cool to be dominant: social status alters short-term risks of heat stress. *J Exp Biol* 220:1558–1562
- Dawson WR (1954) Temperature regulation and water requirements of the brown and Abert towhees, *Pipilo fuscus* and *Pipilo aberti*. In: Bartholomew GA, Crescitelli F, Bullock TH, Furgason WH, Schechtman AM (eds) *University of California Publications in Zoology*, vol 59. University of California Press, Berkeley, pp 81–123
- Dawson WR, Bartholomew GA (1968) Temperature regulation and water economy of desert birds. In: Brown GW (ed) *Desert biology*. Academic Press, New York, pp 357–394
- Dawson WR, Fisher CD (1969) Responses to temperature by the spotted nightjar (*Eurostopodus guttatus*). *Condor* 71:49–53

- Dawson WR, Schmidt-Nielsen K (1964) Terrestrial animals in dry heat: desert birds. In: Dill DB (ed) Handbook of physiology: adaptation to the environment. American Physiological Society, Washington, D.C., pp 481–492
- de Juana E, Suarez F, Ryan PG (2018) Larks (Alaudidae). In: del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E (eds) Handbook of the Birds of the World Alive. Lynx Edicions, Barcelona. <https://www.hbw.com/node/52302> (**Retrieved from 18 June 2018**)
- Dean WRJ, Ryan PG (2005) Red Lark. In: Hockey PAR, Dean WRJ, Ryan PG (eds) Roberts birds of southern Africa. The Trustees of the John Voelcker Bird Book Fund, Cape Town, pp 871–872
- du Plessis KL, Martin RO, Hockey PAR, Cunningham SJ, Ridley AR (2012) The costs of keeping cool in a warming world: implications of high temperatures for foraging, thermoregulation and body condition of an arid-zone bird. *Glob Change Biol* 18:3063–3070
- Kearney MR, Porter WP, Murphy SA (2016) An estimate of the water budget for the endangered night parrot of Australia under recent and future climates. *Clim Change Responses* 3(1):14
- Lighton JRB (2008) Measuring metabolic rates: a manual for scientists. Oxford University Press, Oxford
- Londoño GA, Chappell MA, del Rosario Castañeda M, Jankowski JE, Robinson SK (2015) Basal metabolism in tropical birds: latitude, altitude, and the “pace of life”. *Funct Ecol* 29:338–346
- Marder J, Gavrieli-Levin I (1986) Body and egg temperature regulation in incubating pigeons exposed to heat stress: the role of skin evaporation. *Physiol Zool* 69:532–538
- McKechnie AE, Swanson DL (2010) Sources and significance of variation in basal, summit and maximal metabolic rates in birds. *Curr Zool* 56(6):741–758
- McKechnie AE, Wolf BO (2010) Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. *Biol Lett* 6:253–256
- McKechnie AE, Noakes MJ, Smit B (2015) Global patterns of seasonal acclimatization in avian resting metabolic rates. *J Orn* 156(1):367–376
- McKechnie AE, Smit B, Whitfield MC, Noakes MJ, Talbot WA, Garcia M, Gerson AR, Wolf BO (2016a) Avian thermoregulation in the heat: evaporative cooling capacity in an archetypal desert specialist, Burchell’s sandgrouse (*Pterocles burchelli*). *J Exp Biol* 219:2137–2144
- McKechnie AE, Whitfield MC, Smit B, Gerson AR, Smith EK, Talbot WA, McWhorter TJ, Wolf BO (2016b) Avian thermoregulation in the heat: efficient evaporative cooling allows for extreme heat tolerance in four southern Hemisphere columbids. *J Exp Biol* 219:2145–2155
- McKechnie AE, Gerson AR, McWhorter TJ, Smith EK, Talbot WA, Wolf BO (2017) Avian thermoregulation in the heat: evaporative cooling in five Australian passerines reveals within-order biogeographic variation in heat tolerance. *J Exp Biol* 220(13):2436–2444
- McWhorter TJ, Gerson AR, Talbot WA, Smith EK, McKechnie AE, Wolf BO (2018) Avian thermoregulation in the heat: evaporative cooling capacity and thermal tolerance in two Australian parrots. *J Exp Biol* 221(6):jeb168930

- Noakes MJ, Smit B, Wolf BO, McKechnie AE (2013) Thermoregulation in African Green Pigeons (*Treron calvus*) and a re-analysis of insular effects on basal metabolic rate and heterothermy in columbid birds. *J Comp Physiol B* 183(7):969–982
- Noy-Meir I (1973) Desert ecosystems: environment and producers. *Annu Rev Ecol Syst* 4:25–51
- O'Connor RS, Wolf BO, Brigham RM, McKechnie AE (2017) Avian thermoregulation in the heat: efficient evaporative cooling in two southern African nightjars. *J Comp Physiol B* 187(3):477–491
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Development Core Team (2009) *nlme*: Linear and nonlinear mixed effects models. R Package version 3.57
- Prinzinger R, Preßmar A, Schleucher E (1991) Body temperature in birds. *Comp Biochem Physiol* 99A(4):499–506
- Scholander PF, Hock R, Walters V, Irving L (1950) Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation and basal metabolic rate. *Biol Bull* 99(2):259–271
- Serventy DL (1971) Biology of desert birds. In: Farner DS, King JR (eds) *Avian biology* vol I. Academic Press, New York, pp 287–339
- Smit B, Whitfield MC, Talbot WA, Gerson AR, McKechnie AE, Wolf BO (2018) Avian thermoregulation in the heat: phylogenetic variation among avian orders in evaporative cooling capacity and heat tolerance. *J Exp Biol* 221(6):jeb174870
- Smith EK, O'Neill J, Gerson AR, Wolf BO (2015) Avian thermoregulation in the heat: resting metabolism, evaporative cooling and heat tolerance in Sonoran Desert doves and quail. *J Exp Biol* 218:3636–3646
- Smith EK, O'Neill JJ, Gerson AR, McKechnie AE, Wolf BO (2017) Avian thermoregulation in the heat: resting metabolism, evaporative cooling and heat tolerance in Sonoran Desert songbirds. *J Exp Biol* 220(18):3290–3300
- Talbot WA, McWhorter TJ, Gerson AR, McKechnie AE, Wolf BO (2017) Avian thermoregulation in the heat: evaporative cooling capacity of arid-zone Caprimulgiformes from two continents. *J Exp Biol* 220(19):3488–3498
- Taylor MR, Peacock F, Wanless RM (2015) *The 2015 Eskom Red Data Book of Birds of South Africa, Lesotho and Swaziland*. BirdLife South Africa, Johannesburg, South Africa
- Thompson ML, Cunningham SJ, McKechnie AE (2018) Interspecific variation in avian thermoregulatory patterns and heat dissipation behaviours in a subtropical desert. *Physiol Behav* 188:311–323
- Tieleman BI, Williams JB (2000) The adjustment of avian metabolic rates and water fluxes to desert environments. *Physiol Biochem Zool* 73(4):461–479
- Tieleman BI, Williams JB (2002) Cutaneous and respiratory water loss in larks from arid and mesic environments. *Physiol Biochem Zool* 75(6):590–599
- Tieleman BI, Williams JB, Buschur ME (2002) Physiological adjustments to arid and mesic environments in larks (Alaudidae). *Physiol Biochem Zool* 75(3):305–313
- Tieleman BI, Williams JB, Bloomer P (2003a) Adaptation of metabolic rate and evaporative water loss along an aridity gradient. *Proc R Soc Lond* 270:207–214

- Tieleman BI, Williams JB, Buschur ME, Brown CR (2003b) Phenotypic variation of larks along an aridity gradient: are desert birds more flexible? *Ecology* 84(7):1800–1815
- Tieleman BI, Williams JB, Visser GH (2004) Energy and water budgets of larks in a life history perspective: parental effort varies with aridity. *Ecology* 85(5):1399–1410
- Tracy CR, Welch WR, Pinshow B, Porter WP (2010) Properties of air: a manual for use in biophysical ecology, 4th edn. The University of Wisconsin Laboratory for Biophysical Ecology: Technical Report, no 4
- Trost CH (1972) Adaptations of horned larks (*Eremophila alpestris*) to hot environments. *Auk* 89:506–527
- Walsberg GE, King JR (1978) The relationship of the external surface area of birds to skin surface area and body mass. *J Exp Biol* 76:185–189
- Whitfield MC, Smit B, McKechnie AE, Wolf BO (2015) Avian thermoregulation in the heat: scaling of heat tolerance and evaporative cooling capacity in three southern African arid-zone passerines. *J Exp Biol* 218:1705–1714
- Williams JB (1996) A phylogenetic perspective of evaporative water loss in birds. *Auk* 113(2):457–472
- Williams JB (1999) Heat production and evaporative water loss of dune larks from the Namib desert. *Condor* 101:432–438
- Williams JB, Tieleman BI (2000) Flexibility in basal metabolic rate and evaporative water loss among hoopoe larks exposed to different environmental temperatures. *J Exp Biol* 203:3153–3159