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THE ROYAL SOCIETY

Animal behaviour

Cool birds: facultative use by an introduced species of mechanical air conditioning systems during extremely hot outdoor conditions

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Rapid climate change across the globe is having dramatic effects on wildlife. Responses of organisms to shifting thermal conditions often include physiological and behavioural accommodations, but to date these have been largely viewed and studied as naturally evolved phenomena (e.g. heat avoidance, sweating, panting) and not necessarily as strategies where animals exploit other anthropogenic conditions or resources. Moreover, the degree to which native versus introduced species show thermal plasticity has generated much conservation and ecological interest. We previously have observed introduced rosy-faced lovebirds (Agapornis roseicollis) perching in the relief-air vents on building faces in the Phoenix, Arizona, USA, metropolitan area, but doing so only during summer. Here, we show that such vent-perching events are significantly associated with extreme outdoor summer temperatures (when daily local highs routinely exceed 40°C). In fact, the temperature threshold at which we detected lovebirds starting to perch in cool air vents mirrors the upper range of the thermoneutral zone for this species. These results implicate novel, facultative use of an anthropogenic resource-industrial air-conditioning systems—by a recently introduced species (within the last 35 years) to cool down and survive extremely hot conditions in this urban 'heat-island' environment.

1. Introduction

Earth's climate is transforming at an unprecedented pace, and such environmental changes are having diverse and rapid impacts on organisms. Growing seasons, food sources, and species distributions have shifted [1], and extreme climate events have spiked [2], exposing our planet's flora and fauna to novel thermal peaks and ranges.

As selection pressures for heat tolerance intensify worldwide, we have seen a number of behavioural and physiological adjustments by animals to elevated thermal conditions [3,4]; these include decreased activity, increased evaporative cooling mechanisms, and cooler/shaded microsite selections [5]. The extent to which species can plastically or adaptively implement these and related strategies may critically determine their survival and success in warming land-scapes [6], which include both natural populations and areas as well as introduced species and human-altered (e.g. urban, agricultural) environments. Cities and their inhabitants in fact may suffer from greater 'heat-island' effects (i.e. due to impervious-surface coverage; [7]), and introduced species may show superior thermal adaptability [8], thereby posing threats to extinction and proper conservation of native species.

Despite the fact that many organisms use natural mechanisms or resources to buffer their exposure to elevated ambient temperatures [5], we are not





Figure 1. Photographs of rosy-faced lovebirds perched in building relief-air vents in Tempe, Arizona, USA.

aware of any empirical studies showing that free-ranging organisms exploit anthropogenic resources to offset elevated thermal environmental challenges. Recently, we have observed individuals from an introduced species of parrot (rosy-faced lovebirds, Agapornis roseicollis, which are native to southwestern Africa) in the Phoenix, Arizona, USA metropolitan area [9] perching within exterior building vents (figure 1) at certain times of the year. Because early reports of this were common during summer months and because these relief-air (i.e. exhaust) vents (see electronic supplementary material) offer cool air flow to the building's exterior, we hypothesized that these animals were seeking industrial air-conditioning systems to cool off at a time of year when outdoor temperatures are extremely high locally (i.e. exceeding 40°C). We conducted a year-long census of lovebird perching in exterior building vents to test the extent to which outdoor temperature, and other possible environmental predictors, explain variation in the vent-perching frequencies of lovebirds.

2. Methods

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At three times per day (randomly selected morning, afternoon, and evening time points) on three randomly selected days per week across one full year (2 August 2018–2 August 2019), we conducted *ca* 2 min lovebird observation sessions on the Life Sciences A wing north building face, on the campus of Arizona State University in Tempe, AZ, USA (see electronic supplementary material for more details). At the start of each session, we used on-site information from Google Weather to document current ambient outdoor temperature (°C), relative humidity (%), and wind speed (km h⁻¹); we also estimated overhead cloud cover (to the nearest 20%) and human foot traffic near the building (on a 0–5 integer scale, with 0 being no nearby humans and 5 being dozens of people passing by per minute between class periods). Observers blind to the hypotheses being tested then

walked the length (*ca* 40 m) of the north building face, noting visually if and how many lovebirds were present in relief-air vents. We did not observe birds/vents if it was raining. Due to logistical obstacles, exhaust temperatures were not measured during the study and could not be estimated retrospectively. Relative humidity was converted to absolute humidity for statistical analyses (using https://www.calculator.net/dew-point-calculator.html).

We analysed data both for all observation sessions (n = 537total) and for only those sessions in which we detected one or more lovebirds in the vents (n = 47 sessions), using JMP 15.2.0 software (SAS Institute Inc., Cary, NC). For all-sessions data, we used logistic regression to assess effects of temperature, absolute humidity, wind speed, time of day, cloud cover and human foot traffic on lovebird presence in vents (coded in this model as Yes/ No, i.e. were there any lovebirds in vents at this time?). For the sessions where lovebirds were present in vents, we used standard least-squares regression to examine effects of these predictors on the number of lovebirds counted in vents. For all analyses, we used the Bayesian information criterion (BIC), due to our large nand few predictor variables [10,11], to identify best-fit models among possible subsets. When multiple predictors were significant in a best-fit model, we used relative weight analysis [12] to compare the importance of each predictor in explaining variation in the lovebird response variable. Because of strong correlations among some statistically significant predictors in our models, we also used variance inflation factors (VIFs) to consider impacts of collinearity on our results (electronic supplementary material).

3. Results

(a) General observations

Lovebirds were observed perched in building vents during 47 out of the total of 537 observation sessions (8.8%). When lovebirds were detected in vents, we observed an average of 7.9 (±1.4 SEM) lovebirds, with a range of 1–43 vent-perching lovebirds per session. Lovebirds perched in vents only between 11 June and 21 October, even though lovebirds are now a resident and locally abundant introduced species within the developed boundaries of Phoenix, AZ, USA (electronic supplementary material).

(b) Predicting lovebird presence in relief-air vents

In the full model, temperature and cloud cover were significant predictors of lovebird presence in vents (table 1). However, the best-fit model contained outdoor temperature as the lone predictor of variation in lovebird presence in exterior building vents (table 1 and figure 2a), such that lovebirds were more likely to perch in vents when the outdoor temperature was high.

(c) Predicting number of lovebirds present in relief-air vents

When considering only the observation sessions (n = 47) in which we detected one or more lovebirds in relief-air vents, we found in our full model that outdoor temperature and absolute humidity were significant predictors of the number of lovebirds perched in vents, and these were the two predictors retained in the best-fit model (table 1). We sighted more lovebirds in relief-air vents at higher outdoor temperatures and higher absolute humidities (table 1). We also noted, upon inspection of the scatterplots, that quadratic curves might provide better fits of temperature and absolute humidity to lovebird quantity than linear fits, and in fact a model of

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Table 1. Outputs from models examining effects of environmental variables—temperature, absolute humidity, cloud cover, wind speed, and human foot traffic—and time of day on (*a*) presence of lovebirds in relief-air vents, (*b*) number of lovebirds perched in vents (in sessions when one or more lovebirds were observed; linear fit) and (*c*) number of lovebirds perched in vents (quadratic fits of both temperature and absolute humidity). SLS = standard least squares. Boldfaced terms indicate statistically significant parameters. Whole model statistics are italicized under the model type. Chi-square values are displayed in (*a*); *t*-values are displayed in (*b*) and (*c*). In (*a*), R² (U) is based on the negative log likelihood or uncertainty (U) of the model parameters. See electronic supplementary material, table S3 for other top models, for comparison to the best-fits presented in (*a*)–(*c*) below.

model	type	predictor	estimate	χ^2 or t	p
(a) logistic	global	temperature	0.28	31.64	<0.0001
$R^2 = 0.33$		absolute humidity	0.06	2.04	0.15
		cloud cover	-0.02	5.76	0.016
		wind speed	0.02	0.36	0.55
		human foot traffic	0.09	0.35	0.56
		time of day	-0.00	1.06	0.30
	best-fit <i>BIC</i> = 236.98	temperature	0.26	40.5	<0.0001
(b) SLS	global	temperature	1.30	3.60	0.0009
$R^2 = 0.34$		absolute humidity	0.82	2.22	0.032
		cloud cover	-0.02	-0.34	0.73
		wind speed	0.30	0.89	0.38
		human foot traffic	— 1.69	—1.48	0.15
		time of day	-0.004	-0.62	0.53
	best-fit	temperature	1.32	3.87	0.0004
	BIC = 345.61	absolute humidity	0.84	2.58	0.013
(c) quadratic	best-fit	temperature ²	0.02	4.26	0.0001
	BIC = 343.67	absolute humidity ²	0.05	2.69	0.010

temperature² and absolute humidity² improved the best-fit model (table 1 and figure 2b). The relative weight for temperature² (78%) was significantly greater than that for absolute humidity² (22%), based on the fact that the confidence-interval test for significance did not overlap with zero. Note also that we tested for an effect of the interaction between temperature and absolute humidity on lovebird presence, but the interaction terms (both temperature × absolute humidity and temperature² × absolute humidity²) in each respective model were not statistically significant (both p > 0.5).

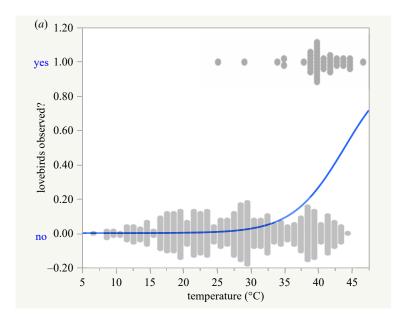
(d) Temperature and lovebird vent perching

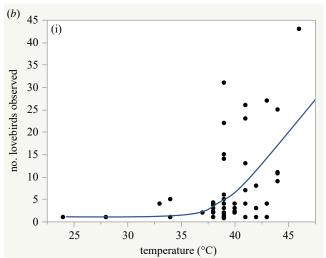
Mean outdoor temperature during sessions in which we observed lovebirds perched in vents was $39.3 \pm 0.57^{\circ}\text{C}$ (range = $24\text{--}46^{\circ}\text{C}$). For 44 of the 47 sessions where lovebirds were seen perching in vents, the outdoor temperature was $\geq 34^{\circ}\text{C}$, and for two of the three sessions where the temperature was less than 34°C , we only saw a single lovebird perched in a vent. Interestingly, both best-fit curves—for our logistic and standard least-squares regression models comparing temperature to lovebird presence and lovebird quantity, respectively (figure 2)—have inflection points around 37°C , and this temperature approximates the upper limit of the thermoneutral zone for this species (35°C) [13].

4. Discussion

Here, through regular tracking of bird abundance and local environmental variables over the course of a year, we demonstrate facultative use of an anthropogenic resource—building relief-air vents—by an introduced parrot species during extreme outdoor thermal conditions. Despite being locally present and abundant throughout the year, rosy-faced lovebirds preferentially perched in these vents during certain months (June–October) and in association with ambient temperature. Specifically, lovebirds were more likely to be present in vents when daily summer/autumn temperatures were high, and as outdoor temperatures climbed progressively above 37°C we detected exponentially greater numbers of lovebirds perching in the vents.

There are numerous examples of natural microsite selections by terrestrial animals to mitigate extreme hot [14,15] and cold [16] outdoor temperatures (e.g. seeking cool tree shade by day, warm cavities overnight), but objectively documented cases where human resources/environments are used by wildlife for such thermal buffering are comparatively scarce. Polecats (Mustela putorius) from Europe, for example, rest and sleep inside buildings during winter [17], and European starlings (Sturnus vulgaris) perch atop chimneys more often at lower winter temperatures, though there were potentially confounding effects of precipitation [18]. Also, there are many anecdotes of effective anthropogenic resource-based heating or cooling methods in pets and domesticated animals (e.g. frozen water bottles to assist with cooling in chickens, outdoor pet cats sleeping on warm engine blocks under automobile hoods to avoid the overnight cold). However, such instances predominantly focus on cold-weather mitigation, and despite the many possible examples, we encourage more direct empirical study of the potential thermal impacts and benefits of human activities on domesticated and wild animals living near us [19]. This should include experimental





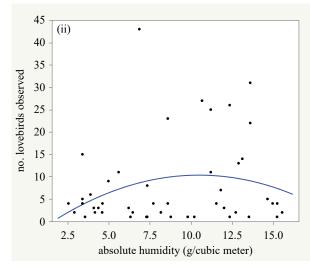


Figure 2. (*a*) Results of logistic regression analyses depicting the significant relationship between outdoor temperature and the presence (1) or absence (0) of lovebirds perched in relief-air vents. Best-fit line is shown in blue, and individual datapoints (in grey) are staggered vertically to reveal overlapping observations. (*b*) Results of standard least-squares regression analyses depicting the significant relationships between the number of lovebirds perched in relief-air vents and outdoor temperature (image at (ii); blue line depicts the exponential fit from table 1*c*) as well as absolute humidity (image at (ii); also with quadratic line depicted), when at least one bird was detected. Points are staggered (along *y*-axis) to show overlapping observations.

approaches, which have essentially been absent in these study systems, such as building vent (opening/closure) manipulations, coupled with vent microclimate measurements (including absolute humidity, which, in addition to temperature, had a small effect on lovebird vent perching), to determine if lovebirds will avoid closed vents and relocate to opened, cool air vents. It will also be valuable to probe heat-transfer mechanisms in these vents, including possible impacts of direct cool air flow as well as active cooling of feet as birds perch on aluminium vent flashing (figure 1).

Our findings centre on a mechanical system that provides cool air flow to the outdoors, in an environment with an extreme climate. Phoenix, Arizona is the hottest city in North America; on average, the city sees 110 days where daily temperatures reach or exceed 38°C, and 20 days per year when temperatures reach or exceed 43°C [20]. Extreme conditions call for extreme survival adaptations or acclimated responses [21,22] and may increasingly do so as climates continue to vary and warm across the globe [23]. Lovebirds inhabit sunny and dry habitats in their native southwestern African environments, and during summer (December—

January) temperatures in some of these xeric regions can exceed 40°C (e.g. Namib Desert) [9], suggesting that lovebirds from their native range must similarly cope with extreme high temperatures. However, they largely do not cohabit with humans in their native range and thus may exploit natural cool/water resources to avoid overheating [9]. Indeed lovebirds from southern Africa nest in rocky crevices, sociable weaver (Philetairus socius) nest compartments, house roofs and other thermally buffered vegetation microsites [24], suggesting that they may be predisposed to locating cooler roosting locations in their introduced range. The fact that this species has thrived in the Phoenix metropolitan area since it first appeared ca 35 years ago [25], and is known for its opportunistic water-seeking behaviour in both its native and introduced range [9] (e.g. man-made water bodies and irrigation canals in Phoenix), is consistent with other data on the success of opportunistic species in colonizing new environments [26], including human-dominated areas [27]. Urban colonizers and invasive species often show superior behavioural flexibility and innovation capabilities [28,29].

In sum, we show behavioural responsiveness to hot outdoor temperatures by a free-living endothermic vertebrate, specifically by exploiting industrial cooling infrastructure in the built environment. The distribution of introduced rosyfaced lovebirds in the Phoenix metropolitan area—such that they have not effectively expanded into natural desert surroundings-suggests that their success in colonizing and continuing to occupy this new environment has been reliant on human-provided resources, perhaps mostly water, but also, as our data suggest, additional means of cooling during harsh summer/autumn days. Fine-scale physiological and behavioural investigations of organisms should continue to yield key insights into how Earth's biota can plastically or adaptively respond to continued human-induced rapid environmental change [22]. Although our findings add to the list of putative benefits that human activities can provide to the survival and/or reproduction of animals living around us [30], they also highlight harmful environmental consequences of wildlife resource use in cities, such as energy waste in buildings with outdated infrastructure as well as how non-native species may better exploit urban conditions and threaten native biodiversity [31]. As cities continue to expand or are redesigned, this cost-benefit balance should factor significantly into urban

planning efforts, with aims of prioritizing the interests and needs of humans and native wildlife, while limiting the success and impacts of invasive taxa.

Ethics. This research was conducted under the approval of the Institutional Animal Care and Use Committee at Arizona State University (protocol no. 18-1659R).

Data accessibility. Data have been made available through Dryad [32]: https://doi.org/10.5061/dryad.r7sqv9s8r.

Authors' contributions. K.J.M. designed the study; R.M. and K.J.M. collected data, analysed data, and wrote manuscript. All authors agree to be held accountable for the content therein and approve the final version of the manuscript.

Competing interests. We declare we have no competing interests.

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