

# A trait-based assessment of southern African arid-zone birds' vulnerability to climate change

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## ABSTRACT

Trait-based assessments allow rapid evaluation of species' vulnerability to climate change, but often overlook subtle yet consequential interspecific variation in behavioural and physiological traits. We assessed 241 southern African arid-zone bird species' vulnerability to increasing air temperature associated with climate change. Species' sensitivity was scored using organismal traits (three morphological, 25 ecological, four behavioural, three physiological). We assessed sensitivity under different trait weightings and data availability scenarios to account for data gaps and uncertainty in traits' relative importance. Relative vulnerability was assigned by combining sensitivity and exposure scores. Between 7 % and 17 % of species assessed are highly vulnerable. Passeriformes emerged as the most vulnerable order, relative to other orders assessed, on account of modest heat tolerance limits and reliance on panting, a relatively inefficient avenue of evaporative heat dissipation. Bucerotiformes, Charadriiformes, Accipitriformes and Falconiformes are also highly vulnerable. Caprimulgiformes, Columbiformes, and Strigiformes are least vulnerable, on account of pronounced evaporative cooling capacities and high heat tolerance limits. Vulnerability of Galliformes, Apodiformes and Otidiformes was inconsistent, varying substantially with trait weightings and scenarios, making them priority taxa for research and conservation. Whereas the method tends to inflate sensitivity scores for species with little available data and despite weighting uncertainty, we were able to identify taxa that consistently scored as highly vulnerable and require close attention, based on current knowledge of determinants of climate change sensitivity. Similar trait-based assessments may prove critical for ensuring population declines in unexpectedly vulnerable, or typically overlooked, species do not go unnoticed and appropriate conservation efforts are initiated.

## 1. Introduction

Climate change vulnerability assessments are an increasingly important tool for conservation management, allowing rapid identification of at-risk species to inform research, planning, and resource allocation (Foden and Young, 2016; Thurman et al., 2020; Triviño et al., 2013). There are three main approaches to climate change vulnerability assessments: correlative, mechanistic, and trait-based, each with its own merits and limitations (Foden et al., 2019; Foden and Young, 2016; Pacifici et al., 2015). The correlative approach assesses correlations between a species' distribution and historical climate to identify areas

with potentially suitable future climate (Foden and Young, 2016). Mechanistic models incorporate a broad range of climate change variables, along with biological processes to predict the likely response of species to climate change based on their fundamental niches (Foden and Young, 2016). The trait-based approach considers the association between organismal traits of a species and climate change impacts (Foden et al., 2013). For trait-based assessments, traits thought to determine sensitivity (the degree to which the species is affected) and adaptive capacity (the potential of the species to adjust) are combined with estimates of exposure (the nature and magnitude of climatic environmental changes experienced by the species) to assign species to

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categories of vulnerability (Foden et al., 2013, 2019; Foden and Young, 2016; IPCC, 2007; Pacifici et al., 2015; Williams et al., 2008).

The trait-based approach is often favoured by policymakers and conservation managers when predicting species' vulnerability to climate change as a) it does not require extensive modelling (Pacifici et al., 2015), b) it allows for rapid assessment of multiple species simultaneously and c) the methods and outcomes of the assessments are easily understood and applied (Foden and Young, 2016). However, a limitation of this approach is that vulnerability thresholds (specific trait values above which physiological performance and fitness may rapidly decline, as suggested by previous research, e.g., Czenze et al., 2020; du Plessis et al., 2012; van de Ven et al., 2019) are often unknown, and distinctions between vulnerability categories are arbitrary and relative among only species/taxa assessed in the specific study (Foden et al., 2019; Foden and Young, 2016; Garcia et al., 2014; Pacifici et al., 2015). There is also no consensus approach to scoring and weighting individual traits; most authors weight traits equally, which may not be biologically realistic, nor is there a standard method for combining trait scores into a single vulnerability score (Foden and Young, 2016; Pacifici et al., 2015). Furthermore, there is often uncertainty in the outcomes of assessments because of gaps in available species-level data (Foden and Young, 2016).

Despite these limitations, trait-based assessments have yielded important insights into the vulnerability of animal and plant taxa at global (e.g., Böhm et al., 2016; Foden et al., 2013; Kopf et al., 2017; Zhang et al., 2019), continental (Cabrelli et al., 2014; Nyboer et al., 2019), regional (Case et al., 2015; Chin et al., 2010; Gardali et al., 2012; Moyle et al., 2013; Sousa et al., 2021), and local scales (Harper et al., 2022; Pant et al., 2020). Typically, these assessments involve examination of multiple biological traits likely to determine species' sensitivity to climate change, allocated to broad sensitivity or adaptive capacity 'trait sets' (Foden et al., 2013). Sensitivity trait sets commonly assessed include habitat/microhabitat specialisation, environmental/physiological tolerances, dependence on environmental triggers, dependence on interspecific interactions, rarity, life history, and exposure to other pressures (Foden et al., 2013, 2019). Adaptive capacity trait sets include phenotypic plasticity, dispersal ability and evolutionary potential (sometimes referred to as 'evolvability'; Foden et al., 2013, 2019). However, sensitivity and adaptive capacity may, in reality, both be components of intrinsic sensitivity and could be combined (Foden et al., 2019; Foden and Young, 2016; IPCC, 2014; Thurman et al., 2020). The majority of studies have included multiple, broad-scale traits that fall into these two sets but have generally overlooked finer-scale traits. For example, avian traits considered under the evolutionary potential trait set within adaptive capacity usually include only generation length and mean clutch/brood size (e.g., Böhm et al., 2016; Cabrelli et al., 2014; Foden et al., 2013; Triviño et al., 2013; Zhang et al., 2019), but fine-scale traits that could influence evolutionary potential, such as age at first breeding, parental investment, length of incubation and rearing periods, ability to replace failed clutches and potential for multiple broods per season are rarely incorporated.

There is a growing need to incorporate fine-scale behavioural and physiological traits into climate change vulnerability assessments (Beissinger and Riddell, 2021; Cunningham et al., 2021), since the traits predominantly used to predict range shifts (e.g., dispersal ability, habitat breadth, generation length, thermal ranges) and responses to climate change do not take into account responses of individual species and/or populations in different environments (Beissinger and Riddell, 2021). For example, physiological tolerance limits that determine species vulnerability to heat-related mortality events during extreme heatwaves (e.g., Holt and Boersma, 2022; McKechnie et al., 2021b;

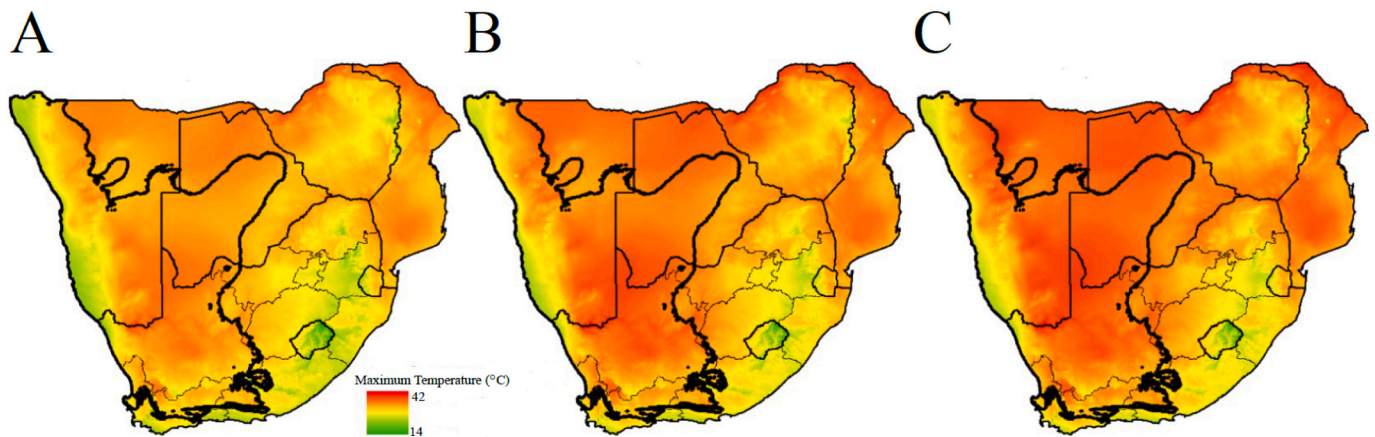
Quintana et al., 2022) vary with body size and the primary avenue of evaporative heat dissipation (McKechnie et al., 2021a). Similarly, vulnerability to sub-lethal fitness costs of chronic exposure to sustained hot weather arise from behavioural trade-offs between thermoregulation and foraging (Cunningham et al., 2021), in turn determined by multiple aspects of foraging behaviour and microsite availability (Cunningham et al., 2015; van de Ven et al., 2019). Although birds are the most frequently assessed taxon (Pacifici et al., 2015) at both global and regional scales, assessments have focused either on broad-scale traits (e.g., Foden et al., 2013), or only a small selection of traits without considering behaviour and physiology ( $\leq 13$  traits; e.g., Amano and Yamaura, 2007; Borges et al., 2019; Gardali et al., 2012; Pocock, 2011; Triviño et al., 2013). Furthermore, there have been no trait-based assessments focusing specifically on the vulnerability of birds inhabiting arid zones, many of which are already experiencing rapid increases in temperature (Shi et al., 2021; van Wilgen et al., 2016).

Behavioural and/or physiological data are now available for >130 arid-zone bird species across the American southwest, arid Australia and southern Africa (e.g., Czenze et al., 2020; McKechnie et al., 2016, 2021a; Pattinson et al., 2020; Smit et al., 2016, 2018; Whitfield et al., 2015). Furthermore, the consequences of behavioural trade-offs in several southern African and Australian arid-zone bird species have been evaluated (e.g., Bourne et al., 2020; Cunningham et al., 2013, 2015; du Plessis et al., 2012; Edwards et al., 2015; Rat et al., 2020; Sharpe et al., 2021; van de Ven et al., 2019, 2020), allowing for the incorporation of traits affecting the nature and severity of behavioural trade-offs in vulnerability assessments. Considering the increasing availability of behavioural and physiological data for arid-zone birds, and the severe climate change impacts expected this century (Conradie et al., 2019; Shi et al., 2021; van Wilgen et al., 2016), we developed a trait-based assessment of southern African arid-zone birds. We aimed to integrate lessons learned from previous studies to identify specific physiological and behavioural traits that may serve as indices of avian sensitivity to increased air temperatures and climate change. We also used these traits to quantify species' relative vulnerability to climate change and identify those that should be prioritised for conservation and mitigation efforts. These indices were combined with present and future climate models, to locate regions where vulnerable species may be most under threat, as well as to identify potential thermal refugia. Although the analysis was focused on the southern African arid zone, the traits identified should be applicable to desert regions globally.

## 2. Methods

### 2.1. Species selection

The southern African arid zone spans the Northern, Western and Eastern Cape provinces of South Africa, south and central Namibia and south-western Botswana, encompassing the Nama Karoo, Succulent Karoo and Kalahari and Namib Deserts (Fig. 1). We selected 241 terrestrial arid-zone bird species for this study, representing 22 orders and 54 families (Supplementary Table 1). Passeriformes was the largest order represented, with 135 species in 21 families. Species were selected according to their ranges (Hockey et al., 2005) and presence in the arid zone during spring and summer (October – March, the hottest part of the year) for all or part of their life cycle (residents, nomads, non-breeding and breeding migrants). We excluded water birds and coastal sea- and shorebirds (i.e., those species whose distribution fell along the west coast of South Africa and Namibia).



**Fig. 1.** Average spring-summer maximum temperatures ( $^{\circ}\text{C}$ ; October–March) of southern Africa, with the southern African arid zone demarcated by a bold outline, under A) current conditions B) predicted conditions (2050) under Representative Concentration Pathway 4.5 (RCP 4.5), and C) predicted conditions (2050) under RCP 8.5, based on General Circulation Model MRI-CGCM3. Climate data were downloaded from the WorldClim database, and the arid zone was demarcated as areas with mean annual precipitation  $<400\text{ mm y}^{-1}$ . We present vulnerabilities using exposure calculated under RCP 8.5 in the main text; please see Supplementary Table 2 for vulnerabilities with exposure calculated under RCP 4.5.

## 2.2. Sensitivity assessment

### 2.2.1. Trait selection

We identified 35 traits (24 for non-breeding migrants) likely to influence the sensitivity and/or adaptive capacity (Foden et al., 2019; Thurman et al., 2020; Williams et al., 2008) of birds to increasing air temperatures associated with climate change and allocated each to one of four functional trait groups (morphological, ecological, behavioural and physiological). The ecological trait group included 25 traits (14 for non-breeding migrants). The morphological, behavioural, and physiological trait groups consisted of three, four, and three traits respectively (Table 1; Supplementary material).

Selection of appropriate traits and ‘sensitivity’ thresholds within these traits (see scoring system, below) was informed by previous studies of arid-zone birds (e.g., Bourne et al., 2020; Cunningham et al., 2013; Czenze et al., 2020; Smit et al., 2016), other trait-based assessments of birds (Foden et al., 2013; Gardali et al., 2012; Pocock, 2011; Triviño et al., 2013) and expert workshops with colleagues working in arid-zone avian physiology, movement ecology or trait assessments (seven experts in addition to the authors, across three workshops). Novel traits included thermal windows (morphological trait, e.g., bill length, leg length, presence of bare skin) and ecological traits such as aspects of breeding ecology (e.g., incubation and nestling period lengths, replacement clutches, parental investment), dietary flexibility, water dependence, the likely severity of behavioural trade-offs between foraging and heat dissipation, and specific physiological traits for heat tolerance limits (i.e., maximum tolerable environmental temperature during acute exposure) and maximum capacity for evaporative heat dissipation.

Species-specific data for each trait were obtained, when available, from species accounts in Roberts’ Birds of Southern Africa, 7th Ed. (Hockey et al., 2005), primary literature and field guides. Experts on specific taxa or fields of avian study (e.g., heat dissipation behaviour) contributed unpublished datasets. Where physiological trait values such as heat tolerance limits were not available for a particular species, they were estimated using phylogenetically informed scaling relationships (McKechnie et al., 2021a).

### 2.2.2. Scoring system

For each species, we used an ordinal scoring system to assign a score of ‘low’, ‘moderate’ or ‘high’ to each trait according to the species’ expression of that trait with respect sensitivity thresholds identified during expert workshops, following Foden et al. (2013) and Harper et al.

(2022; see Table 1 and our Supplementary Table 2). For example, the ‘nest exposure’ trait was scored ‘low sensitivity’ for species with concealed nests, ‘moderate’ for those shaded by vegetation etc., and ‘high’ for those exposed to full sunlight. For continuous traits where sensitivity thresholds were unknown (e.g., length of incubation periods), Jenks Natural Breaks were calculated to break the data into the three sensitivity thresholds/groups (e.g., ‘short’, ‘medium’, ‘long’; R package ‘GmAMisc’; Alberti, 2021; R Core Team, 2021). Where data were unavailable, traits were classified as ‘unknown’.

We then used an additive approach, where ordinal scores were converted to a numerical value (i.e., low = 1, moderate = 2, high = 3, unknown = 0), to allow trait scores to be summed (Harper et al., 2022). Each species’ sensitivity score for each trait group was calculated as the sum of the individual trait scores, divided by the maximum score possible for the trait group (i.e., excluding unknown traits which scored zero), following Reece and Noss (2014; see also our worked example in Supplementary material). For non-breeding migrants, all breeding ecology traits ( $n = 11$ ) were excluded from sensitivity calculations. Although different factors drive sensitivity and vulnerability for each taxon, and therefore each trait/trait group will influence sensitivity differently, there are no data available on the relative importance of each trait/trait group, especially at order and species levels, nor is there consensus on trait group weighting. Overall sensitivity scores (i.e., all four trait groups combined) were initially calculated by adding equally weighted scores for each trait group, as summing scores allowed us to avoid speculating the relative importance of each trait/trait group. However, since an equal weighting is often not biologically realistic (Foden and Young, 2016; Pacifici et al., 2015), we also calculated overall scores with three additional weightings for each trait group: weighted according to number of traits per group, and two individual expert opinions on weightings (Reece and Noss, 2014). To account for uncertainties arising from unknown values, following Foden et al. (2013), we scored species according to different data availability scenarios by repeating calculations after scoring all unknown traits as low (=1, optimistic scenario), moderate (=2, intermediate scenario), or high (=3, pessimistic scenario), resulting in a total of 16 evaluations, enabling us to quantify a plausible range of sensitivity scores between these extremes (see Table S3 in Supplementary materials for details on each scenario and evaluation). We report results from the default scenario (i.e., using available data only) with trait groups equally weighted, but evaluations from each alternative weighting and data availability scenario are reported in Supplementary Table 1. Based on their total sensitivity score, each species was categorised as highly sensitive (upper

**Table 1**

Descriptions and examples of trait characteristics and/or sensitivity threshold values for traits selected under each of four functional traits groups that influence avian sensitivity (and therefore vulnerability) to increased air temperatures associated with climate change. Where literature was not available, separation of trait characteristics and sensitivity thresholds were informed by expert opinion and consensus during expert workshops, or in consultation with specific experts as required. Key references either provide rationales for including, or thresholds for, each trait. For more detailed rationales and trait characteristics, see Supplementary materials.

Trait code	Trait	Description of variable	Trait characteristics and sensitivity thresholds	Key reference (s)
<b>Morphological traits</b>				
M1	Thermal window index <sup>a</sup>	Index of potential for heat dissipation via thermal windows, calculated as the sum of a bird's relative leg diameter, leg length, body shape, and beak length (relative to average body mass), as well as the estimated percentage of unfeathered skin	Low = 10.84 < x ≤ 62.92 Moderate = 4.03 < x ≤ 10.84 High = 0.89 ≤ x ≤ 4.03 Unknown = no data	<a href="#">Janse van Vuuren et al., 2020</a> <a href="#">McKechnie and Wolf, 2010</a> <a href="#">Tattersall et al., 2017</a>
M2	Morphological sexual dimorphism	Males and females differ in body mass by ≥25 %	Low = Not dimorphic Moderate = None High = Dimorphic Unknown = No data	<a href="#">Alonso et al., 2016</a>
M3	Behavioural sexual dimorphism	One sex has display behaviour that exposes it to more solar radiation during courtship compared to the other sex	Low = no displays, aerial displays Moderate = Elevated/exposed perch display High = Ground display Unknown = Undescribed	<a href="#">Kemp et al., 2020</a>
<b>Ecological traits</b>				
E1	Foraging microsite	Preferred microsite for foraging	Low = Off-ground, perch-and-wait, aerial Moderate = on-and off-ground High = On-ground Unknown = Undescribed	<a href="#">Cunningham et al., 2015</a>
E2	Foraging exposure	Extent of exposure to solar radiation while foraging	Low = Shade, among vegetation Moderate = Semi-shade, shade and sun only High = Sun only Unknown = Undescribed	<a href="#">Cunningham et al., 2015</a> Expert-informed

**Table 1 (continued)**

Trait code	Trait	Description of variable	Trait characteristics and sensitivity thresholds	Key reference (s)
E3	Primary diet	Predominant diet, particularly during spring or summer	Low = Meat, Generalist Moderate = Insects, fruit, nectar, plant material High = Seeds, Specialist Unknown = Undescribed	<a href="#">Abdu et al., 2018</a> <a href="#">Smit et al., 2019</a>
E4	Dietary flexibility	Diet switches occur depending on season, breeding status or food source availability	Low = Switches based on site, season, breeding Moderate = Can switch if necessary High = Does not switch food types Unknown = Undescribed	Expert informed
E5	Ecological specialism	Relies on other species for roost/nest sites, or other aspects of survival and/or reproduction	Low = No dependence on other species Moderate = Relies on ≥2 other species High = Relies on one other species only Unknown = Undescribed/no observations	<a href="#">Foden et al., 2013</a> Expert informed
E6	Water dependence	Reliance on free-standing water	Low = Regular Drinker Moderate = Hot/Occasional Drinker High = Non-drinker Unknown = Undescribed/no observations	<a href="#">Czenze et al., 2020</a>
E7	Nest type	Shape and structure of the nest	Low = Excavated/natural cavities, burrows Moderate = Closed nests, chambers, crevices High = Ground scrapes, open nests, platforms Unknown = Undescribed, non-breeding migrant	<a href="#">Deeming and Mainwaring, 2015</a> <a href="#">Zann and Rossetto, 1991</a> Expert informed
E8	Nest exposure	Nest exposure to solar radiation	Low = Concealed Moderate = Sheltered (in branches, vegetation) High = Exposed Unknown =	<a href="#">AlRashidi et al., 2011</a>

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Table 1 (continued)

Trait code	Trait	Description of variable	Trait characteristics and sensitivity thresholds	Key reference (s)
E9	Chick type	Altricial, precocial or semi-altricial	Undescribed, non-breeding migrant Low = Precocial Moderate = Semi-precocial High = Altricial Unknown = Undescribed, non-breeding migrant	Cunningham et al., 2013 Wiley and Ridley, 2016
E10	Incubation period <sup>a</sup>	Average duration of the incubation period (days)	Low = $9.75 \leq x \leq 20.5$ Moderate = $20.5 < x \leq 36$ High = $36 < x \leq 57$ Unknown = no data, non-breeding migrant	Pocock, 2011 Sharpe et al., 2019, 2021
E11	Nestling period <sup>a</sup>	Average duration of the nestling period from hatching to fledging (days)	Low = $8.25 \leq x \leq 28$ Moderate = $28 < x \leq 62.5$ High = $62.5 < x \leq 148$ Unknown = No data, non-breeding migrant	Cunningham et al., 2013 van de Ven et al., 2020
E12	Parental care	Extent to which parents or other conspecifics are involved in parental care, i.e. uniparental, biparental, cooperative	Low = Cooperative, facultative-cooperative Moderate = Biparental High = Uniparental Unknown = Undescribed, non-breeding migrant	AlRashidi et al., 2010 Covas et al., 2008
E13	Average clutch size <sup>a</sup>	Average number of eggs laid per clutch	Low = $6.6 < x \leq 12$ Moderate = $2.8 < x \leq 6.6$ High = $1 \leq x \leq 2.8$ Unknown = No data, non-breeding migrant	Foden et al., 2013 Pocock, 2011 Expert informed
E14	Successful broods per season <sup>a</sup>	Average number of successful broods per breeding season	Low = $\geq 2$ broods/year, multi-brooded Moderate = $< 2$ broods/year High = $< 1$ brood/year Unknown = No data, non-breeding migrant	Pocock, 2011 Expert informed
E15	Replacement clutches	Replacement clutches in response to failure or loss of a clutch	Low = Regular replacement Moderate = Occasional replacement High = No	Expert informed

Table 1 (continued)

Trait code	Trait	Description of variable	Trait characteristics and sensitivity thresholds	Key reference (s)
E16	Summer breeder	Main breeding season coincides with the hottest part of the year (October–March)	replacement, brood parasite Unknown = No data, non-breeding migrant Low = False (March–August) Moderate = None High = True (September–February) Unknown = No data, non-breeding migrant	Cunningham et al., 2013 du Plessis et al., 2012 Sharpe et al., 2021
E17	Rainfall dependent breeding	Extent to which breeding is triggered by rainfall	Low = Not rainfall dependent Moderate = Additional/opportunistic broods, extended breeding, earlier laying High = Highly rainfall dependent Unknown = No data, non-breeding migrant	Bourne et al., 2020
E18	Age at first breeding <sup>a</sup>	Average age at commencement of breeding (years)	Low = $1 \leq x \leq 2$ Moderate = $2 < x \leq 5$ High = $5 < x \leq 7$ Unknown = No data	Expert informed
E19	Generation length <sup>a</sup>	Average generation length (years)	Low = $3.5 \leq x \leq 6.4$ Moderate = $6.4 < x \leq 11.6$ High = $11.6 < x \leq 18.3$ Unknown = No data	Foden et al., 2013 Expert informed
E20	Movement ecology	General movement patterns within an arid zone	Low = Nomad, local nomad Moderate = Resident, non-breeding migrant, elevational migrant High = Breeding migrant Unknown = Undescribed	Gardali et al., 2012 Pocock, 2011 Expert informed
E21	Desert habitat specialist	Endemic to desert habitats, does not occur outside arid areas	Low = False ( $> 1$ habitat occupied) Moderate = None High = True (1 habitat occupied, in arid zone)	Foden et al., 2013 Expert informed

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Table 1 (continued)

Trait code	Trait	Description of variable	Trait characteristics and sensitivity thresholds	Key reference (s)
E22	Range size <sup>a</sup>	Area a species occupies within the arid zone (km <sup>2</sup> )	Unknown = Undescribed Low = 950,329.1 < x ≤ 1,337,148.5 Moderate = 498,692.5 < x ≤ 950,329.1 High = 4,123.8 ≤ x ≤ 498,692.5 Unknown = No data	Amano and Yamaura, 2007 Expert informed
E23	Thermal range <sup>a</sup>	Difference between absolute maximum and minimum spring-summer air temperatures (October-March) across a species' range in the arid zone (°C)	Low = 20.8 < x ≤ 23.5 Moderate = 18.4 < x ≤ 20.8 High = 14.3 ≤ x ≤ 18.4 Unknown = No data	Jiguet et al., 2006 Triviño et al., 2013
E24	Behavioural trade-offs between foraging and thermoregulation	Extent to which foraging is curtailed by heat dissipation behaviours such as panting or shade-seeking	Low = No to minimal Trade-off Moderate = Moderate Trade-off High = Severe Trade-off Unknown = Undescribed/ no observation	Cunningham et al., 2015 Edwards et al., 2015 van de Ven et al., 2019
E25	Endemism	Endemic to southern Africa	Low = Not Endemic Moderate = Near Endemic High = Endemic Unknown = Undescribed	Expert informed
B1	Behavioural traits PropAct	Proportion of time a bird is active at air temperatures between 35 and 40 °C (Pattinson et al., 2020; Smit et al., 2016)	Low = <0.33 Moderate = 0.33–0.67 High = >0.67 Unknown = No data	Smit et al., 2016 Pattinson et al., 2020
B2	Sociality	Social structure during spring and summer	Low = Solitary or pairs only Moderate = solitary up to small - medium groups, seasonally social High = Highly social, medium - large groups Unknown = Undescribed	Cunningham et al., 2017 Rat et al., 2020
B3	Active period	Time of the day when most activity occurs	Low = Nocturnal Moderate = Crepuscular High = Diurnal	Expert informed

Table 1 (continued)

Trait code	Trait	Description of variable	Trait characteristics and sensitivity thresholds	Key reference (s)
B4	Primary avenue of evaporative heat loss	Primary pathway of evaporative heat dissipation	Unknown = Undescribed Low = Gular Flutter or cutaneous Moderate = panting and gular flutter (diversity) High = panting only Unknown = Undescribed/ no observation	McKechnie et al., 2021a
Physiological traits				
P1	Heat tolerance limits (°C) <sup>b</sup>	Maximum environmental temperature before the onset of compromised locomotor capacity during acute heat exposure	Low = >55 °C Moderate = 50–55 °C High = 45–50 °C (<50 °C) Unknown = No data	Czenze et al., 2020 McKechnie et al., 2021a
P2	Maximum air temperature associated with lethal dehydration risk (°C)	Maximum environmental temperature associated with lethal dehydration risk (cumulative evaporative losses exceed assumed dehydration tolerance limit of 15 % body mass over 5-h period during hottest part of day)	Low = >50 °C Moderate = 45–50 °C High = 40–45 °C (<45 °C) Unknown = No data	Albright et al., 2017 Conradie et al., 2019
P3	Maximum ratio of evaporative heat loss to metabolic heat production	Measure of the efficiency of heat dissipation pathways and a major determinant of maximum environmental temperature tolerance (EHL: MHP)	Low = >4 Moderate = 2–4 High = 1–2 (<2) Unknown = No data	McKechnie et al., 2021a Expert informed

<sup>a</sup> Vulnerability Thresholds for continuous variables where thresholds were not known by experts were calculated using Jenks' Natural Breaks (R Package GmAMisc, Alberti, 2021), and so these values cannot be used for other studies, but are rather specific to this dataset. Future studies incorporating this assessment method and these traits should calculate the thresholds for their dataset using Jenks' Natural breaks, or consider other methods of delineating their data into threshold groups (e.g., Foden et al., 2013; Foden and Young, 2016; Harper et al., 2022).

<sup>b</sup> Where data were not available in literature, heat tolerance limits were calculated using the Heat Tolerance Limit equation for 'all species', in McKechnie et al. (2021a), with the exception of the Columbidae and Caprimulgidae.

third); moderately sensitive (middle third) or not sensitive (low sensitivity, lower third; Harper et al., 2022; Zhang et al., 2019). A robustness score for sensitivity scores and vulnerability categories across the 16 evaluations was calculated as the number of evaluations where a score or category remained consistent, regardless of the weighting of trait

groups or scoring of unknown traits (see Supplementary Table 1).

### 2.3. Exposure estimation and potential thermal refugia

Species' exposure was estimated as a combination of the difference between the current and predicted future midpoint of minimum and maximum temperatures within their individual ranges (in °C), and the difference between current and predicted future summer maximum temperatures (Foden et al., 2013). Climate data were downloaded from the WorldClim database (<https://www.worldclim.org/>). Current temperatures were obtained from historical climate data of maximum and minimum temperatures for each month from 1970 to 2000 (Fick and Hijmans, 2017). Future (2050) temperatures were modelled under business-as-usual Representative Concentration Pathway 8.5 (RCP8.5) as the worst-case scenario, based on General Circulation Model MRI-CGCM3 (Nashwan and Shahid, 2020). For both midpoint temperature difference and maximum temperature difference, each species' exposure was classified as high (upper third of data), moderate (middle third) or low (lower third). A species was ranked as overall highly exposed if it was categorised as high for both midpoint temperature difference and maximum temperature difference (Foden et al., 2013). Species not categorised as high for both exposure measures were ranked according to their lowest category. Exposure and vulnerability calculations under RCP4.5 are presented in Supplementary Table 2, but overall results do not differ between the different pathways. Potential thermal refugia for all arid zone bird species within southern Africa were identified by mapping the difference between current and predicted future average spring-summer (October-March) maximum temperatures in southern Africa, under RCP 8.5.

### 2.4. Identifying vulnerable species

Species vulnerability was classified using a logic matrix, where a species had to be ranked as high for both sensitivity and exposure to be classified as highly vulnerable (Chin et al., 2010; Foden et al., 2013; see our worked example in Supplementary material). Vulnerability of species that ranked other than high for either sensitivity or exposure were

ranked according to their lowest ranking (e.g., a species with moderate exposure and high sensitivity was ranked as moderately vulnerable overall).

## 3. Results

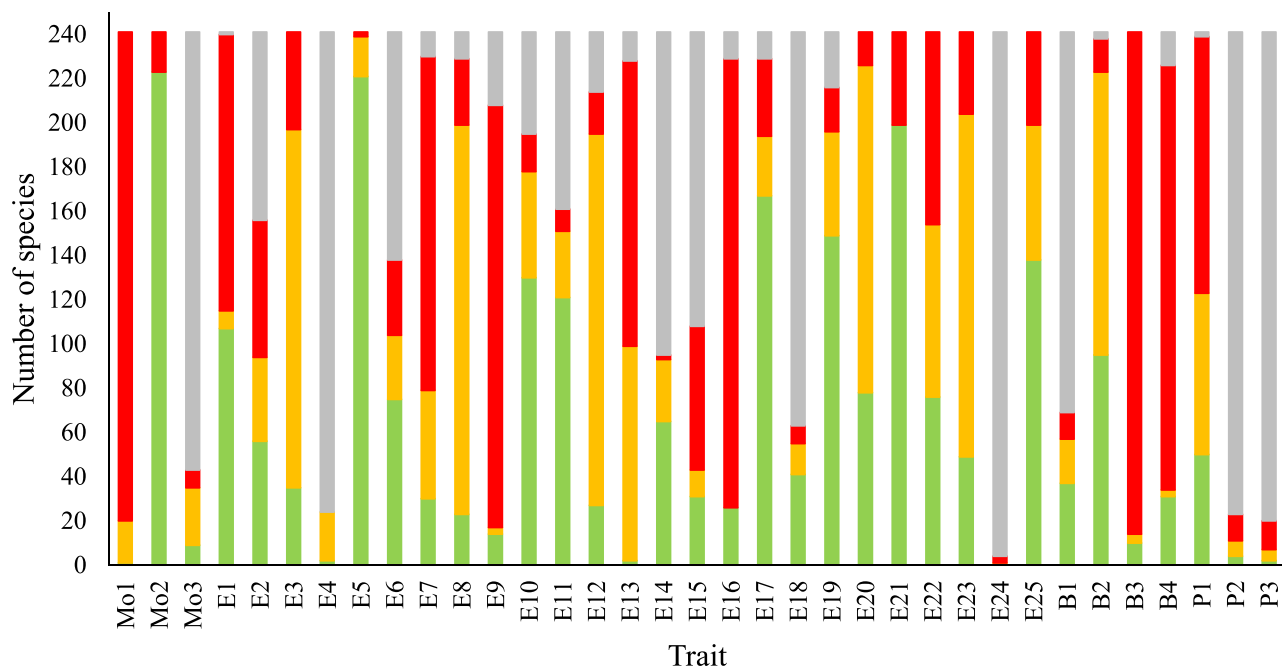
### 3.1. Data availability

Data availability ranged from complete (i.e., available for all species) for some traits (e.g., thermal window index, primary diet, movement ecology, active period, etc.) to incomplete for other traits, particularly behavioural (e.g., behavioural trade-offs between foraging and thermoregulation), and physiological traits (e.g., maximum ratio of evaporative heat loss to metabolic heat production; Fig. 2). Overall, all species were scored as 'highly sensitive' for at least one trait.

### 3.2. Sensitivity scores, weightings and data availability scenarios

Additive sensitivity scores for the default scenario with trait groups weighted equally ranged from 0.447 to 0.850 across all 241 species (Supplementary Table 1). Passeriformes emerged as the most sensitive order, with 76 species across 16 families comprising most species in the upper third for sensitivity. The five most sensitive species were Barlow's lark (*Calendulauda barlowi*, 0.850); grey-backed cisticola (*Cisticola subruficapilla*, 0.842); rock martin (*Ptyonoprogne fuligula*, 0.833); spike-heeled lark (*Chersomanes albofasciata*, 0.831); and African quailfinch (*Ortygospiza atricollis*, 0.820). Caprimulgiformes, Columbiformes and Strigiformes emerged as the least sensitive orders. The five least sensitive species were European nightjar (*Caprimulgus europaeus*, 0.447); Verreaux's eagle-owl (*Bubo lacteus*, 0.447); western barn owl (*Tyto alba*, 0.455); spotted eagle-owl (*Bubo africanus*, 0.478); and Cape eagle-owl (*Bubo capensis*, 0.479).

Adjusting the weighting of each score according to trait group size or expert opinion resulted in changes in sensitivity scores, with some species shifting between sensitivity categories (see Table 2 for a randomly selected subset of 45 species; Supplementary Table 1). Sensitivity scores decreased (i.e., became less sensitive) for 56 species when at least one



**Fig. 2.** Number of arid-zone bird species scored low (green), moderate (orange), high (red) or unknown/not available (grey) for each sensitivity trait. Mo = Morphological Traits, E = Ecological Traits, B = Behavioural Traits and P = Physiological Traits. See Table 1 for each trait code and description. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

different weighting was applied, with 124 species remaining in the same category (Supplementary Table 1). Sensitivity scores increased (i.e., became more sensitive) for 57 species, while four species' scores either decreased or increased under the different weightings (Supplementary Table 1). However, the maximum change in any species' sensitivity score was 0.2, and this approach allowed us to account for the varying impacts that different trait groups may exert on sensitivity. Pronounced changes in sensitivity occurred when accounting for uncertainty with different data availability scenarios (optimistic, moderate and pessimistic), with only 49 species remaining in the same category as in the default scenario and equal weighting. Twenty-eight species were categorised as either more or less sensitive, depending on the weighting and data availability scenario (Table 2, Supplementary Table 1). Eighty-five species were categorised as less sensitive, while 79 species were

categorised as more sensitive for at least one data availability scenario and/or weighting calculation, when compared to the default scenario with equal weighting (Supplementary Table 1). Five species shifted categories dramatically when applying the pessimistic scenario, with sensitivity categories for all four weightings changing from high/moderate to low, relative to other species. Such dramatic shifts are a result of these five species having less missing data than the other species assessed. The species which shifted to a low sensitivity category were only missing data for  $\leq 6$  traits, and despite high values (i.e., a score of three) being substituted in for the pessimistic scenario evaluations, their scores remained more consistent than those of species which were missing more data. In contrast, species with more missing data experienced a greater increase in their sensitivity scores, resulting in a shift to a more sensitive category, and a greater shift relative to species with more

**Table 2**

Sensitivity scores for a randomly selected subset of 45 arid-zone bird species for the following trait groups: Mo = Morphological E = Ecological, B = Behavioural and P = Physiological. Coloured squares represent species' relative sensitivity rankings for various weighting calculations and data availability scenarios (Evaluations 1–16); red (H) = high sensitivity (upper third), orange (M) = moderate sensitivity (middle third), and green (L) = low sensitivity (lower third). This table graphically illustrates the effect that different weightings of scores exert on the relative sensitivity of each species, with some consistent within in their overall sensitivity ranking (i.e., high, moderate, low) but others varying. For a complete list of all species assessed, see Supplementary Table 1.

Order	Family	Common name	Scientific name	Mo	E	B	P	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Passeriformes	Alaudidae	Barlow's Lark	<i>Calendulauda barlowi</i>	0.667	0.822	0.889	1	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H
Passeriformes	Malacotidae	Black-crowned Tchagra	<i>Tchagra senegalus</i>	0.667	0.667	0.889	1	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H
Passeriformes	Cisticolidae	Rufous-eared Warbler	<i>Malcorus pectoralis</i>	0.667	0.651	0.889	1	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H
Passeriformes	Muscicapidae	Herero Chat	<i>Namibornis herero</i>	0.667	0.698	0.889	1	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H
Passeriformes	Fringillidae	Black-headed Canary	<i>Serinus alario</i>	0.667	0.719	0.889	1	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H
Passeriformes	Hirundinidae	Rock Martin	<i>Ptyonoprogne fuligula</i>	0.667	0.667	1	1	H	H	H	H	M	H	M	H	H	H	H	H	H	H	H	H
Passeriformes	Sturnidae	Burchell's Starling	<i>Lamprolornis australis</i>	0.667	0.596	0.889	1	H	M	H	H	H	H	H	H	H	H	H	H	H	M	H	H
Passeriformes	Estrildidae	Violet-eared Waxbill	<i>Granatina granatina</i>	0.667	0.619	0.917	1	H	H	H	H	H	H	H	H	H	M	H	H	H	M	H	H
Passeriformes	Estrildidae	Red-billed Firefinch	<i>Lagonosticta senegalensis</i>	0.667	0.621	0.889	1	H	H	H	H	H	H	H	H	H	M	H	H	H	M	H	H
Passeriformes	Estrildidae	Black-faced Waxbill	<i>Brahmilia erythronotos</i>	0.667	0.619	0.889	1	H	H	H	H	M	H	H	H	M	H	H	H	M	H	H	H
Passeriformes	Fringillidae	Yellow Canary	<i>Crithagra flaviventris</i>	0.667	0.634	0.917	1	H	H	H	H	H	H	H	H	H	H	H	H	M	M	M	H
Passeriformes	Muscicapidae	Chat Flycatcher	<i>Melaenornis infuscatus</i>	0.667	0.65	0.75	1	H	H	M	H	H	H	H	H	M	M	H	M	M	M	M	M
Passeriformes	Fringillidae	Black-throated Canary	<i>Crithagra atrogularis</i>	0.667	0.587	0.917	1	H	M	H	H	H	H	H	H	M	M	H	H	M	L	M	M
Passeriformes	Sylviidae	Common Reed-Warbler	<i>Acrocephalus baeticatus</i>	0.667	0.604	0.889	1	H	M	H	H	M	L	M	M	H	M	H	H	H	H	H	H
Passeriformes	Alaudidae	Red Lark	<i>Calendulauda burra</i>	0.667	0.741	0.778	0.834	M	H	H	M	H	H	H	H	H	H	H	H	M	H	M	M
Passeriformes	Malacotidae	Crimson-breasted Shrike	<i>Laniarius atrococcineus</i>	0.667	0.619	0.75	1	M	M	M	M	H	H	H	H	H	H	H	M	H	M	M	M
Passeriformes	Viduidae	Shaft-tailed Whydah	<i>Vidua regia</i>	0.667	0.649	0.75	1	M	H	M	H	H	M	H	H	M	M	H	M	M	H	M	H
Passeriformes	Hirundinidae	Pearl-breasted Swallow	<i>Hirundo dimidiata</i>	0.667	0.596	0.778	1	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	H
Accipitriformes	Accipitridae	Black Kite	<i>Milvus migrans</i>	1	0.667	0.889	0.333	M	H	M	L	H	H	H	M	H	H	H	H	H	H	H	M
Accipitriformes	Accipitridae	Jackal Buzzard	<i>Buteo rufifasciatus</i>	1	0.651	0.778	0.333	M	M	M	L	M	H	M	M	H	M	M	M	M	M	M	M
Bucerotiformes	Phoeniculidae	Violet Wood-Hoopoe	<i>Phoeniculus damarensis</i>	0.667	0.611	0.889	0.667	M	M	M	M	M	L	M	L	M	M	M	M	M	M	M	M
Apodiformes	Apodidae	Bradfield's Swift	<i>Apus bradfieldi</i>	0.667	0.689	0.834	0.667	M	H	M	M	L	L	L	M	M	M	M	H	H	H	H	H
Passeriformes	Hirundinidae	Brown-throated Martin	<i>Riparia paludicola</i>	0.667	0.5	0.889	1	M	L	M	M	M	L	L	M	M	L	M	M	M	L	M	H
Passeriformes	Pycnonotidae	African Red-eyed Bulbul	<i>Pycnonotus nigricans</i>	0.667	0.561	0.834	0.778	M	L	M	M	H	M	H	H	M	L	M	M	L	L	L	L
Passeriformes	Alaudidae	Grey-backed Sparrowlark	<i>Eremopterix verticalis</i>	0.556	0.649	0.917	0.889	M	H	M	M	H	H	H	H	H	H	H	H	L	M	L	L
Passeriformes	Ploceidae	Sociable Weaver	<i>Philetairus socius</i>	0.667	0.606	0.917	0.667	M	M	M	M	H	H	H	H	M	H	M	L	L	L	L	L
Passeriformes	Muscicapidae	Anteater Chat	<i>Myrmecocichla formicivora</i>	0.667	0.54	0.75	1	M	L	M	M	H	L	M	M	M	L	M	L	M	L	L	M
Passeriformes	Sturnidae	Wattled Starling	<i>Creatophora cinerea</i>	0.667	0.567	0.834	0.667	M	L	L	L	M	L	M	M	M	L	M	L	M	L	L	L
Coraciiformes	Meropidae	Swallow-tailed Bee-eater	<i>Merops hirundineus</i>	0.667	0.549	0.667	1	M	L	M	M	L	L	L	M	L	L	M	L	M	L	M	M
Galliformes	Phasianidae	Orange River Francolin	<i>Scleroptila gutturalis</i>	0.667	0.698	0.667	0.333	L	M	L	L	L	L	H	L	L	M	L	L	M	L	M	L
Bucerotiformes	Bucerotidae	Monteiro's Hornbill	<i>Tockus monteiri</i>	0.667	0.731	0.889	0.333	L	H	M	L	M	H	M	M	M	H	M	M	M	H	M	M
Accipitriformes	Accipitridae	White-backed Vulture	<i>Gyps africanus</i>	0.5	0.682	1	0.333	L	M	L	L	L	H	M	L	L	M	M	L	H	M	M	L
Otidiformes	Otididae	Karoo Korhaan	<i>Eupodotis vigorsii</i>	0.667	0.667	0.834	0.333	L	M	L	L	L	L	L	L	L	M	L	M	H	M	M	M
Accipitriformes	Accipitridae	Augur Buzzard	<i>Buteo augur</i>	0.667	0.684	0.778	0.333	L	M	L	L	L	M	L	L	L	M	L	L	L	H	M	L
Falconiformes	Falconidae	Pygmy Falcon	<i>Polihierax semitorquatus</i>	0.667	0.617	0.75	0.667	L	M	L	M	M	M	M	M	L	M	M	L	L	L	L	L
Coraciiformes	Coraciidae	Purple Roller	<i>Coracias naevius</i>	0.667	0.569	0.778	0.667	L	L	L	L	L	L	L	L	L	L	L	L	M	M	M	M
Apodiformes	Apodidae	Common Swift	<i>Apus apus</i>	0.667	0.545	0.834	0.667	L	L	L	L	L	L	L	L	L	L	L	M	L	M	M	M
Colliformes	Collidae	Red-faced Mousebird	<i>Urocolius indicus</i>	0.667	0.55	0.667	0.667	L	L	L	L	M	L	L	L	L	L	L	L	L	L	L	L
Falconiformes	Falconidae	Greater Kestrel	<i>Falco rupicoloides</i>	0.667	0.591	0.778	0.667	L	L	L	L	L	M	L	L	L	L	L	L	L	L	L	L
Cuculiformes	Cuculidae	Jacobin Cuckoo	<i>Clamator jacobinus</i>	0.556	0.634	0.583	0.667	L	L	L	L	L	M	L	L	L	L	L	L	L	L	L	L
Piciformes	Picidae	Acacia Pied Barbet	<i>Tricholaema leucomelas</i>	0.667	0.524	0.75	0.667	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L
Cuculiformes	Cuculidae	Great Spotted Cuckoo	<i>Clamator glandarius</i>	0.667	0.617	0.667	0.667	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L
Caprimulgiformes	Caprimulgidae	Freckled Nightjar	<i>Caprimulgus tristigma</i>	0.667	0.579	0.556	0.5	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L
Columbiformes	Columbidae	Speckled Pigeon	<i>Columba guinea</i>	0.667	0.65	0.667	0	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L

Evaluations: 1: Default scenario, traits groups equally weighted; 2: Default scenario, trait groups weighted according to group size (M and P = 8.6 %, E = 71.4 %, B = 11.4 %) 3: Default scenario, trait groups weighted according to expert 1's opinion (M and P = 20 %, E = 35 %, B = 25 %); 4: Default scenario, trait groups weighted according to expert 2's opinion (M and B = 15 %, E and P = 35 %); 5: Optimistic scenario, traits groups equally weighted; 6: Optimistic scenario, trait groups weighted according to group size; 7: Optimistic scenario, trait groups weighted according to expert 1's opinion; 8: Optimistic scenario, trait groups weighted according to expert 2's opinion; 9: Intermediate scenario, traits groups equally weighted; 10: Intermediate scenario, trait groups weighted according to group size; 11: Intermediate scenario, trait groups weighted according to expert 1's opinion; 12: Intermediate scenario, trait groups weighted according to expert 2's opinion; 13: Pessimistic scenario, traits groups equally weighted; 14: Pessimistic scenario, trait groups weighted according to group size; 15: Pessimistic scenario, trait groups weighted according to expert 1's opinion; 16: Pessimistic scenario, trait groups weighted according to expert 2's opinion.



data available, suggesting that their actual sensitivity may change significantly once unknown data become available. Robustness scores showed that 54 % of species' sensitivity score categories did not change across >12 of the 16 evaluations (i.e., >75 % of evaluations), while 76 % of species' vulnerability categories were consistent across >12 of the 16 evaluations (Supplementary Table 1).

### 3.3. Exposure and potential thermal refugia

Under an RCP 8.5 scenario, midpoint temperature is projected to increase by an average of  $2.43 \pm 0.02$  °C by 2050 (mean  $\pm$  SE, range = 1.16 °C–3.17 °C) among the 241 species' ranges. Maximum summer temperatures are projected to increase by an average of  $2.66 \pm 0.03$  °C (range 0.69 °C–4.14 °C) by the year 2050. Overall, 78 species were classified as highly exposed, 79 species were moderately exposed and 84 species were assigned a low exposure score. When the difference between current and future (2050; RCP8.5) average spring-summer maximum temperatures (October–March) is mapped, potential thermal refugia are apparent (Fig. 3). Some regions of the arid zone will experience a >3 °C increase in temperature, particularly in central Namibia and Botswana, with the broader arid zone increasing by 2–3 °C. Within the current arid zone itself, the Roggeveld, Komsberg and Nuweveld, as well as the Namibian coast will likely become important thermal refugia in terms of temperature for arid zone species, particularly less nomadic species. There are potential temperature refugia outside of the current arid zone, situated along the eastern regions of southern Africa, and the western coastlines. These regions may include the south and east coasts of South Africa (KwaZulu Natal and Eastern Cape), extending into the Highveld and parts of eastern Zimbabwe and Mozambique. However, migration to these regions is unlikely as they are outside of arid zone birds' current distributions, suitable habitats may not be available, and competition with existing species that are better adapted to these environments is probable. Furthermore, there may be additional thermoregulatory constraints in regions with increased humidity, as it has been proposed that humidity is a major selective pressure in the evolution of avian thermoregulation (Freeman et al., 2022).

### 3.4. Vulnerable and at-risk species

Passeriformes emerged as the most vulnerable order, with 15 species from nine families comprising the most vulnerable species overall

(Table 2; Fig. 4B). Estrildidae and Alaudidae were the most vulnerable passerine families, each with four highly vulnerable species. Under the default scenario, 77 species emerged with moderate vulnerability and 147 species with low vulnerability (Supplementary Table 1). The five most vulnerable species, which had the highest sensitivity scores and scored high for both sensitivity and exposure under all weightings and data availability scenarios were blue waxbill (*Uraeginthus angolensis*), eastern clapper lark (*Mirafra fasciolata*), chestnut weaver (*Ploceus rubiginosus*) and long-tailed paradise whydah (*Vidua paradisaea*), and black-crowned tchagra (*Tchagra senegalus*). Bucerotiformes, Charadriiformes, Accipitriformes, and Falconiformes often had  $\geq 3$  species that were also highly vulnerable (Fig. 4C–F; see Supplementary Fig. 1 for vulnerability rankings for all 22 orders assessed). The five least vulnerable species were also those that were scored as the five least sensitive, namely European nightjar (*Caprimulgiformes*), Verreaux's eagle-owl, western barn owl, spotted eagle-owl and Cape eagle-owl (*Strigiformes*).

Under the default scenario, vulnerability changed for 27 % of species when trait groups were weighted differently, with 36 species becoming more vulnerable than when traits were equally weighted (Supplementary Table 1). Vulnerability remained the same for 174 species and decreased for 28 species. Black kite (*Milvus migrans*) and red-capped lark (*Calandrella cinerea*) were the only species to move from moderate vulnerability to either low or high vulnerability, depending on the trait group weighting.

Overall, 7–17 % of southern African arid zone birds are highly vulnerable to climate change impacts under this trait-based assessment (Fig. 4A). When accounting for uncertainty with different data availability scenarios, 50 % of species changed vulnerability rankings (Supplementary Table 1). A total of 60 species (20 %) became more vulnerable, while the vulnerability of 51 species (21 %) decreased, compared to the default scenario with traits equally weighted. Nine species' (4 %) vulnerabilities either decreased or increased, depending on the trait group weighting and data availability scenario. Passerines remained the most vulnerable order under all evaluations, with members from eight other orders occasionally classified as highly vulnerable under different trait group weightings and/or data availability scenarios (Supplementary Fig. 1). Under all data availability scenarios, more species were classified as highly vulnerable when sensitivity scores were weighted according to trait group size (Evaluations 2, 6, 10 and 14). This could be due to the greater amount of data available for ecological traits (i.e., an artefact of missing data for other trait groups), or birds may be

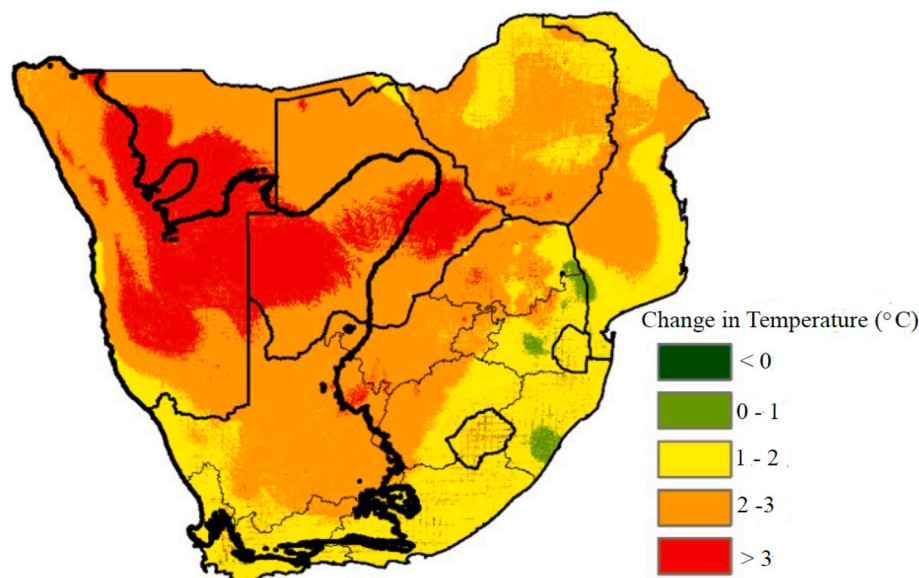


Fig. 3. Difference in current and future (2050) average summer maximum air temperatures (°C; October–March) in southern Africa, under Representative Concentration Pathway 8.5 (RCP8.5), based on General Circulation Model MRI-CGCM3. Climate data were downloaded from the WorldClim database.

more vulnerable on ecological axes, as these traits directly influence their exposure to solar radiation and increased temperatures (e.g., foraging habits, nest structures, water dependence, thermal ranges).



(caption on next page)

**Fig. 4.** Percentage of species ranked with high vulnerability (red), moderate vulnerability (orange) and low vulnerability (green) in A) all species ( $n = 241$  species), B) Order Passeriformes ( $n = 135$  species), C) Order Bucerotiformes ( $n = 7$  species), D) Order Charadriiformes ( $n = 78$  species), E) Order Accipitriformes ( $n = 23$  species) and F) Order Falconiformes ( $n = 7$  species). Evaluations: 1: Default scenario, traits groups equally weighted; 2: Default scenario, trait groups weighted according to group size (Morphological (Mo) and Physiological (P) = 8.6 %, Ecological (E) = 71.4 %, Behavioural (B) = 11.4 %); 3: Default scenario, trait groups weighting according to expert 1's opinion (Mo and P = 20 %, E = 35 %, B = 25 %); 4: Default scenario, trait groups weighted according to expert 2's opinion (Mo and B = 15 %, E and P = 35 %); 5: Optimistic scenario, traits groups equally weighted; 6: Optimistic scenario, trait groups weighted according to group size; 7: Optimistic scenario, trait groups weighted according to expert 1's opinion; 8: Optimistic scenario, trait groups weighted according to expert 2's opinion; 9: Intermediate scenario, traits groups equally weighted; 10: Intermediate scenario, trait groups weighted according to group size; 11: Intermediate scenario, trait groups weighted according to expert 1's opinion; 12: Intermediate scenario, trait groups weighted according to expert 2's opinion; 13: Pessimistic scenario, traits groups equally weighted; 14: Pessimistic scenario, trait groups weighted according to group size; 15: Pessimistic scenario, trait groups weighted according to expert 1's opinion; 16: Pessimistic scenario, trait groups weighted according to expert 2's opinion. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

## 4. Discussion

### 4.1. Overall vulnerability

Overall, more than half of the 241 bird species assessed were classified as having low vulnerability to climate change (59–62 % of species), with 23–32 % of species classified as moderately vulnerable. Between 7 % and 17 % of species were classified as highly vulnerable, with Passeriformes emerging as the most vulnerable order (52–100 % of species in the highest vulnerability category). This is in line with predictions by Conradie et al. (2020) and McKechnie et al. (2021a), and supported by observed patterns during a recent mass mortality event in eastern South Africa in November 2020 (McKechnie et al., 2021b). During this event, 44 out of 47 carcasses found in the search areas were songbirds – of which nearly half were blue waxbills (McKechnie et al., 2021b), a species identified here as one of the five most vulnerable. Additionally, Foden et al. (2013) conducted a global trait-based vulnerability assessment, which included 234 of the 241 bird species assessed here. Although Foden et al. (2013) only assigned species to either a high or low vulnerability, and we include an additional ‘moderate’ category, 52 % of species were assigned to the same vulnerability category in both studies (high or low; species-level results presented by Foden et al. (2013) were comparable to our evaluation 5), with passerines making up 59 % of highly vulnerable species. Of the 112 species whose vulnerabilities differed between the two studies, 60 % of these differences were due to the addition of the moderate vulnerability category in this study.

Because many physiological and behavioural traits vary phylogenetically (e.g., Pattinson et al., 2020), sensitivity, and therefore vulnerability, of some taxa arises primarily from physiological traits, and from behavioural (and/or ecological) traits for others. Passerines consistently scored as highly sensitive on behavioural and ecological traits related to exposure to solar radiation (i.e., active periods, foraging microsite, nest type, and summer breeding), and physiological traits related to heat tolerance and/or dissipation (i.e., heat tolerance limit, primary avenue of evaporative heat loss). Songbirds rely on panting for evaporative heat dissipation, a less efficient avenue of evaporative cooling than the cutaneous evaporation or gular flutter that occur in many non-passerine orders (McKechnie et al., 2021a). Additionally, passerines have modest heat tolerance limits compared to many non-passerines (McKechnie et al., 2021a). These intrinsic factors may render this order more vulnerable to climate change, particularly as temperatures increase. However, the inclusion in this assessment of traits not directly related to acute heat exposure, such as breeding ecology, enforces that passerines are, in general, highly vulnerable, as these traits also expose them to increased environmental temperatures for extended periods of time.

The least vulnerable groups were non-passerine orders, specifically the nightjars (Caprimulgiformes), doves and pigeons (Columbiformes) and owls (Strigiformes). Low vulnerability for nightjars and owls reflects, in part, their nocturnal activity (behavioural trait), insectivorous or carnivorous diets and off-ground (sallying, perch-and-wait, particularly for owls) foraging strategies (ecological traits). These groups also

scored “low” sensitivity scores for heat tolerance limit, and primary avenue of evaporative heat loss, suggesting a physiological component to their low vulnerability. Species from all three orders rely on gular flutter and/or cutaneous evaporation for heat dissipation, which is more efficient than panting (McKechnie et al., 2021a). Caprimulgids, in particular, seem to have evolved highly efficient evaporative cooling in response to nocturnality and their use of often exposed daytime roost sites, compared to diurnal species (O'Connor et al., 2018b). In columbids specifically, cutaneous evaporation allows tolerance of extremely high air temperatures (McKechnie et al., 2016), reducing vulnerability to acute heat exposure. However, increasing temperatures associated with climate change will still negatively impact these less vulnerable orders, as roosting microclimates become less effective at buffering the birds against higher temperatures (O'Connor et al., 2018b), and as the risk of dehydration increases with evaporative water requirements while roosting on warmer, exposed ground during the day (e.g., nightjars, O'Connor et al., 2018a).

Assessing the vulnerability of each order is not straightforward and is also influenced by other variable traits such as diet (foraging guild) and drinking habit, coupled with the availability of natural and artificial water sources. Each foraging guild experiences different constraints and challenges in maintaining water balance and heat tolerance limits which is, in part, related to the amount of pre-formed water obtained from their diets (insectivores, carnivores, nectarivores) or free-standing water (granivores; Czenze et al., 2020; Smit et al., 2019). All foraging guilds are at risk of lethal dehydration and/or hyperthermia as both water and food resources are negatively affected by increasing temperatures (Albright et al., 2017; Riddell et al., 2019).

### 4.2. Environmental and evolutionary considerations

The southern African arid zone has a history as an evolutionary hotspot for larks (Alaudidae; Alström et al., 2013; Ryan et al., 1998; Ryan and Bloomer, 1999) and other taxa, resulting in many species with limited ranges and specific habitat requirements, making each of them sensitive to climate change. Indeed, six of these range-restricted lark species were classified as highly sensitive to increased air temperatures in this study. There is evidence for changes in avian body size (measured as changes in wing size; Gardner et al., 2009, 2014), and increases in appendage size (for heat dissipation; Campbell-Tennant et al., 2015; Symonds and Tattersall, 2010; Tattersall et al., 2017) in response to increasing temperatures. However, these changes are complex and variable, are likely phylogenetically and ecologically constrained and may also be influenced by other factors, such as changes in habitat quality and nutrition, or morphological shifts may only be triggered once a temperature threshold is exceeded (Gardner et al., 2019).

Environmental changes, particularly in harsh, arid environments, can cause a species to alter their behaviour in response to these changes, or behavioural plasticity. Birds make behavioural trade-offs during hot conditions to reduce their risk of lethal dehydration and/or hyperthermia. Such trade-offs may include changes in foraging behaviour, which consequently decreases foraging efficiency (Cunningham et al., 2015; du Plessis et al., 2012; van de Ven et al., 2019), modification of incubation

behaviours (e.g., parental cooperation, egg shading, belly soaking; AlRashidi et al., 2010, 2011; Sharpe et al., 2021), and changes in breeding phenology (e.g., start date, duration; Lv et al., 2020; Sharpe et al., 2021). However, these breeding behavioural changes are beneficial only during brief periods of high temperatures, and not during sustained heatwaves when egg mortality is likely (Sharpe et al., 2019, 2021).

Our trait-based assessment involves an implicit assumption that traits are static and fixed within species. However, many physiological traits show phenotypic plasticity, which may involve short-term, reversible (phenotypic plasticity, Piersma and Drent, 2003) or non-reversible ontogenetic effects (developmental plasticity, Piersma and Drent, 2003). Considerable phenotypic flexibility in traits related to heat tolerance has been documented in one of the species assessed here, the white-browed sparrow-weaver (*Plocepasser mahali*, Noakes et al., 2017; Noakes and McKechnie, 2019; Smit et al., 2013). Data for this species suggest phenotypic flexibility is the primary source of intraspecific variation along climatic gradients (Noakes et al., 2017; Noakes and McKechnie, 2019). Such phenotypic flexibility has implications for vulnerability to climate change, particularly during short-term, acute and/or extreme heat events (Boyles et al., 2011; Conradie et al., 2019, 2020; Smit et al., 2013). The role of developmental plasticity is less clear, although recent findings for zebra finches suggest conditions pre-hatching may have significant effects on heat tolerance later in life (Mariette and Buchanan, 2016).

The adaptive value of phenotypic plasticity (morphological, behavioural and/or physiological) in the context of climate change remains questionable, as plasticity may buffer some species from selection and potentially prevent physiological adaptation to hotter environments of the future (e.g., Duputié et al., 2015). A closely related question is whether the limits of individuals' reaction norms for plastic traits extend to climatic conditions beyond those currently experienced (Murren et al., 2015; Oostra et al., 2018). Since physiological thresholds and/or scope for behavioural plasticity may differ between taxa and populations (AlRashidi et al., 2011; Smit et al., 2013), detailed assessments at the population level are needed, rather than across species ranges, especially in the case of species occurring across a wide range of climates.

#### 4.3. Limitations and recommendations

Trait-based assessments of climate change vulnerability have several limitations. Currently, we do not have a clear understanding of how traits and trait groups could interact with each to influence a taxon's sensitivity and vulnerability. This is an active area of research in climate change vulnerability of species, but remains a major challenge (e.g., Beissinger and Riddell, 2021; Cunningham et al., 2021; McKechnie et al., 2021a). While probably not biologically realistic to weight traits equally, this may be the most appropriate option when there is a lack of consensus on how traits interact, and the relative importance of particular traits for species' vulnerability (Foden and Young, 2016; Pacifici et al., 2015). Uncertainty is further exacerbated by data gaps, and we have attempted to alleviate some of the uncertainty by presenting different weightings of each trait group under different data availability scenarios (Foden et al., 2013), and utilising a 'colour-block' coding system (Reece and Noss, 2014). Since our results are relative rather than absolute measures of vulnerability, we cannot directly compare them to other vulnerability assessments of the same species in other regions (e.g., Foden et al., 2013), or to other species, but we were nevertheless able to identify species of concern within the southern African arid zone. Most importantly, we were able to recognise species which consistently emerged as vulnerable, regardless of the trait group weighting and data availability scenario applied (Reece and Noss, 2014), and species of concern, which frequently change vulnerability rankings, sometimes from low vulnerability to high vulnerability, under different trait groups weightings and data availability scenarios, and/or

have a wide range of sensitivity scores (e.g., Rüppell's korhaan *Eupodotis rueppellii*). These species should be of research and conservation priority, as they may prove just as vulnerable as those species that are consistent in their ranking. It is also concerning that of the 15 species identified as most vulnerable, only the African rock pipit (*Anthus crenatus*) is Red-Listed (Near Threatened; BirdLife International, 2023); perhaps future Red-List assessments should consider vulnerability to climate change as a criterion when determining species' Red-List categories.

Whereas the inclusion of novel traits compared to previous climate change vulnerability assessments permits more rigorous assessment of species' sensitivity, uncertainty is intensified by behavioural and physiological traits for which data are limited. The importance of including these traits is increasingly recognised (Beissinger and Riddell, 2021; Cunningham et al., 2021), but such data are available for only a small subset of species. In this assessment, *PropAct* (the proportion of time a bird is active at air temperatures between 35 and 40 °C) was unavailable for 72 % of assessed species, and heat dissipation behaviour data were based on family traits (B. Smit, unpubl. data), rather from observations of individual species. Physiological data are also sparse, with data unavailable for >90 % of species, although traits like heat tolerance limit can be estimated using known taxon-specific scaling relationships. Uncertainty can be reduced by targeted research on traits where data are lacking, combined with species-specific research.

Several gaps remain in our knowledge of the population densities and distributions of birds in the southern African arid zone. Lee et al. (2018, 2019) described methods for estimating population size using data collected from a citizen science database (SABAP2), but the arid-zone regions are remote and under-sampled, and these methods do not yield reliable estimates in such areas. A species' range may be more (or less) restricted than calculated as accurate range sizes of arid zone birds are largely unavailable and we were unable to account for habitat and/or microsite use on a local scale (Beissinger and Riddell, 2021). Detailed population and distribution studies on birds in this region, especially those identified as vulnerable, would allow for population size to be included as a trait in future assessments.

We chose to exclude some traits from this assessment, as they may be beneficial in some instances but disadvantageous in others. Some avian trait-based assessments have included body size as a trait (e.g., Amano and Yamaura, 2007; Pocock, 2011; Triviño et al., 2013). However, the evolutionary and thermoregulatory advantages of different body sizes are unclear, and determinants of vulnerability may vary between small and large birds. For instance, body mass is a major determinant of a bird's evaporative cooling demands, and smaller bird species are more prone to lethal dehydration during extreme heat on account of their larger surface area to volume ratios and greater mass-specific metabolic evaporative cooling requirements (McKechnie and Wolf, 2010). However, smaller birds also have access to a wider range of microsites within a thermal landscape than larger birds and change their behaviour less at high temperatures than larger birds (Pattinson et al., 2020; Smit et al., 2016). We included social structure (solitary, pairs, small/large groups, etc.) as a behavioural trait, but excluded group size, as the effect of group size on sensitivity to increased temperatures is unclear. Birds in larger groups may benefit from increased foraging efficiency and protection against predators (Beauchamp, 2010). However, these same large groups may be more vulnerable during periods of high temperatures and/or extreme heat events as the social networks in these groups break down, and groups become less cohesive and individuals more aggressive towards each other (Rat et al., 2020). Additionally, subordinate birds in groups may be even more vulnerable as their access to resources may be limited during periods of extreme temperatures due to behaviour of more dominant group members (Cunningham et al., 2017), and resource availability for all group members might decrease as a result of intragroup competition when environmental conditions are harsh (Ridley, 2016).



## 5. Conclusion

We were able to rapidly assess species' sensitivity, exposure and vulnerability to the impacts of climate change, while incorporating novel behavioural and physiological traits. Even with data gaps and uncertainty in the relative importance of each trait and/or trait group, we were able to identify those species that are at-risk, regardless of the trait group weighting or data availability scenario, as well as those species that may have an unpredictable response to the impacts of climate change. Most species that are categorised as highly vulnerable in this study include species not often considered of conservation concern (e.g., blue waxbill, chestnut weaver), as opposed to more charismatic, threatened species (e.g., South Africa's national bird, the blue crane *Grus paradisea*). Without assessments such as this one, population declines of these unexpectedly vulnerable species could go unnoticed until it is too late to implement any meaningful conservation efforts. Birds in arid regions may be under more imminent threat than those in more mesic environments, and rapid assessment will allow for targeted research on at-risk species to fill important data gaps, in an attempt to understand, and possibly mitigate, the impacts of climate change on arid zone species.

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## CRedit authorship contribution statement

**Stephanie Payne:** Investigation, Data curation, Methodology, Formal analysis, Visualisation, Writing – Original draft preparation, Writing – Review and editing. **Susan Cunningham:** Conceptualisation, Supervision, Methodology, Writing – Review and editing. **Caroline Howes:** Formal analysis, Visualisation, Writing – Review and editing. **Andrew McKechnie:** Conceptualisation, Supervision, Methodology, Funding acquisition, Writing – Review and editing.

## Declaration of competing interest

The authors declare no competing interests.

## Data availability

Data used in the research are available on request.

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