1	Climatic change and extinction risk of two globally threatened Ethiopian endemic bird				
2	species				
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4	Andrew J. Bladon ^{1*} , Paul F. Donald ^{1,2,3} , Nigel J. Collar ² , Jarso Denge ⁴ , Galgalo Dadacha ⁴ ,				
5	Mengistu Wondafrash ⁵ and Rhys E. Green ^{1,3} .				
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7	¹ Conservation Science Group, Department of Zoology, The David Attenborough Building,				
8	University of Cambridge, Pembroke Street, Cambridge, UK.				
9	² BirdLife International, The David Attenborough Building, Pembroke Street, Cambridge, UK.				
10	³ RSPB Centre for Conservation Science, RSPB, The Lodge, Sandy, Bedfordshire, UK.				
11	⁴ Borana National Park Authority, PO Box 34, Yabello, Borana Zone, Oromiya, Ethiopia.				
12	⁵ Ethiopian Wildlife and Natural History Society, PO Box 13303, Bole Sub City, Addis Ababa,				
13	Ethiopia.				
14					
15	* Corresponding author				
16	Email: <u>andrew.j.bladon@gmail.com</u> (AJB)				

17 Abstract

18 Climate change is having profound effects on the distributions of species globally. Trait-based 19 assessments predict that specialist and range-restricted species are among those most likely to 20 be at risk of extinction from such changes. Understanding individual species' responses to 21 climate change is therefore critical for informing conservation planning. We use an established 22 Species Distribution Modelling (SDM) protocol to describe the curious range-restriction of the 23 globally threatened White-tailed Swallow (Hirundo megaensis) to a small area in southern 24 Ethiopia. We find that, across a range of modelling approaches, the distribution of this species is well described by two climatic variables, maximum temperature and dry season 25 26 precipitation. These same two variables have been previously found to limit the distribution of 27 the unrelated but closely sympatric Ethiopian Bush-crow (Zavattariornis stresemanni). We project the future climatic suitability for both species under a range of climate scenarios and 28 29 modelling approaches. Both species are at severe risk of extinction within the next half century, 30 as the climate in 68-84% (for the swallow) and 90-100% (for the bush-crow) of their current 31 ranges is predicted to become unsuitable. Intensive conservation measures, such as assisted 32 migration and captive-breeding, may be the only options available to safeguard these two 33 species. Their projected disappearance in the wild offers an opportunity to test the reliability of SDMs for predicting the fate of wild species. Monitoring future changes in the distribution 34

and abundance of the bush-crow is particularly tractable because its nests are conspicuous and
 visible over large distances.

37 Keywords: climate change, ecology; endemic birds, ornithology; precipitation, species

38 conservation; Species Distribution Models, temperature, threatened species

39

40 Introduction

41 The effects of climate change on the distribution and abundance of animal and plant species 42 are well documented. They include range shifts and changes in local density, phenology, morphology, behaviour and gene frequencies [1–5]. Because of long-term monitoring of bird 43 44 distributions and population densities in north temperate regions, the best studied of these effects are range shifts and population changes of European and North American birds [4–6]. 45 Range shifts in response to climate warming are characterised by two processes, "cold-edge" 46 47 expansion and "warm-edge" contraction, which begin with increases and decreases in local density at the two edges respectively [7]. At the warm-edge of species' ranges, limitations 48 49 imposed on foraging behaviour, breeding success or survival by rising temperatures and/or 50 associated drought can lead to local population declines [8–13]. Meanwhile, at the cold-edge,

the removal of the lower thermal limit on these processes enables local populations to thrive[6,14,15].

53 However, focus on poleward shifts alone may underestimate the impacts and 54 complexity of climate change, especially in the tropics, where responses of birds are less well 55 known. One meta-analysis suggests that climatic effects on population processes of birds are more likely to involve temperature in temperate regions, and precipitation or aridity in the 56 57 tropics [3]. In Africa, species distribution modelling has predicted multidirectional range 58 contraction, with distributions of southern bird species projected to become more restricted in 59 the Cape Region, and inhabitants of other regions, including the Horn of Africa, projected to 60 decrease their range size, particularly as arid areas expand [16]. In South Africa, two Fynbos 61 endemics, Cape Rockjumper (Chaetops frenatus) and Protea Canary (Serinus leucopterus), whose distributions are limited by temperature, have suffered reductions of over 30% in both 62 63 range extent and reporting rates since the late 1980s, consistent with a loss of potential range predicted by recent climate change and climate envelope models [17]. 64

65 Without remedial conservation action, persistent "warm-edge" declines which 66 outpace any "cold-edge" expansion will eventually lead to population extinctions. A meta-67 analysis of model-based predictions of extinction rates from climate change varied greatly 68 among studies [18–21], ranging from 0% to 54% of species, with a mean of 7.9% [22]. Much

69 variation in these predictions is associated with baseline data of different types and quality and 70 with variation in the climate change scenarios and global circulation models (GCMs) used [23– 71 25], but the overall pattern across studies is for predicted population declines and range 72 contractions to predominate over increases and expansions at a global level [5]. In the face of 73 ongoing climatic change, and the lagged effects which may accrue, many species could already 74 be committed to extinction by 2050 [18]. For species that exhibit direct physiological 75 intolerance of high temperatures [12,13], climate change also threatens to increase the 76 frequency and severity of episodes of high mortality caused by heatwave events [26], even in 77 areas where average climatic conditions remain suitable [27].

The likely severity of climate change impacts on species' populations has been 78 79 assessed by using postulated effects of the ecological and life-history traits of a species on its 80 sensitivity, exposure and capacity to adapt to climate change [20]. Using this approach, Foden 81 et al. [20] assessed the family to which the one of the focal species of our study, the White-82 tailed Swallow (*Hirundo megaensis*) belongs (Hirundinidae; swallows and martins) as being 83 the least vulnerable to climate change of all bird families [20]. However, individual species 84 with restricted ranges and narrow environmental tolerance are likely to be particularly susceptible to climate change [12,16,28]. Assessing the projected impacts of local climate 85

86 change on individual species is, therefore, important for assessing their long-term conservation87 prospects.

88 Species Distribution Models (SDMs) have demonstrated that the peculiarly restricted 89 distribution of the Ethiopian Bush-crow (Zavattariornis stresemanni) is well described by a 90 climate envelope model, encompassing a zone of cooler, drier conditions than surrounding 91 areas [12,29]. The apparent range limitation by maximum temperature may be linked to the 92 effects of ambient temperature on thermoregulatory and foraging behaviour [12]. The small, 93 non-migratory White-tailed Swallow has a global distribution very similar to that of the bush-94 crow [30,31]. Several authors have noted its peculiarly restricted distribution [32–34], which 95 Collar and Stuart [35] suggested might be linked to the 1,500 m altitudinal contour [35]. Since 96 2006, there have been records from outside the previously known breeding range, 100 km to 97 the east on the Liben Plain [36], but there are still no nest records from this region, and it is 98 unclear whether individuals move between the two areas [37]. It seems possible, therefore, that 99 the range of the White-tailed Swallow might be restricted by similar attributes of the local 100 climate, albeit probably by a different mechanism given its very different ecology, phylogeny 101 and phenotype.

Models that successfully predict the current distribution of a species using a small
 number of bioclimatic variables can be used to predict the potential future range under different

104 projected climate scenarios [3,16]. These predictions can be used to target areas for habitat 105 protection and restoration which offer the best hope as thermal refugia for temperature-106 sensitive globally-threatened species [38]. Both the Ethiopian Bush-crow (Endangered) and the 107 White-tailed Swallow (Vulnerable) are categorised as globally threatened in the IUCN Red 108 List [31,39]. Understanding the potential impact of climate change on the range boundaries of 109 the bush-crow and swallow is necessary to develop conservation management plans for them 110 in the newly formed Yabello National Park. In this paper, we fit SDMs to the small global 111 range of the White-tailed Swallow, using the same techniques as for the bush-crow [12]. We 112 then combine the SDMs for both species with projected future climate scenarios for the region, 113 to predict how their potential climatic range is likely to be affected by changes in temperature 114 and precipitation in the future.

115

116 Materials and methods

117 Modelling the current distribution of the White-tailed Swallow

We collated all available geo-referenced records of White-tailed Swallows and their nests, collected by various observers between 2005 and 2011 [30,36,37], including sightings made during fieldwork on the bush-crow [29]. Nests are usually built in the traditional huts occupied

121 by local people and take the form of mud cups typical of the genus *Hirundo*, but in the absence 122 of adult birds can be distinguished from sympatric hut-nesting swallows by their simple grass 123 lining and unmarked white eggs [37]. Between 2012 and 2015, we conducted 255 walked 1-124 km transects at locations across, and outside, the species' core range (see [12] for further 125 details). White-tailed Swallows were recorded on 19 (7.5%) of these transects. Additionally, 126 in 2014, nest records were documented in the north-west of the species' range as part of an 127 intensive breeding study [40]. We also collected GPS locations for all ad-hoc White-tailed 128 Swallow observations throughout this period, including from the Liben Plain. This work was 129 carried out under permit from the Ethiopian Wildlife Conservation Authority.

130 We previously fitted SDMs for the Ethiopian Bush-crow [12]. Models for the White-131 tailed Swallow were built using the same five climatic variables from WorldClim [41]-132 maximum temperature of the warmest month, temperature seasonality, annual temperature 133 range, precipitation of the wettest quarter, and precipitation of the driest quarter—using the 134 same SDM procedures from the R package 'biomod2' [42]. We used all 574 records of the 135 White-tailed Swallow as presence data. For absence data, we took the mid-point of the 236 1-136 km transect legs on which swallows had not been recorded. Unlike the models for the bushcrow, we did not use the lack of observations from stretches of road transects as true absence 137 138 points because, unlike the bush-crow and its highly visible nests, White-tailed Swallows are

139 much more difficult to detect reliably from a moving vehicle [12]. This is because a) there are 140 a number of other swallow species found in the area [43], making positive identification from 141 a moving vehicle unreliable, b) White-tailed Swallows are small and often occur singly or in 142 pairs [37] and c), if they are like other swallow species, they are likely to forage over a large 143 area and may congregate in areas with plentiful food. These things all make it unreliable to 144 assume that the failure to detect them at a particular place from a moving vehicle denotes a true 145 absence of the species from the surrounding area. To increase the range of environmental 146 variables on which the models were built, we took a random sample of 4,764 pseudo-absences 147 from a region stretching from 1.86°-6.87°N and 33.17°-43.67°E. We chose this extent for 148 consistency with previous studies [12,29], and because it represents a pragmatic compromise 149 between choosing an area large enough to ensure a range of environmental variables extending 150 beyond the species' known distribution – which is important for making predictions based on 151 possible future scenarios – but small enough to make the models biologically relevant to a 152 species with such a restricted range [44]. We restricted these points to be at least 10 km from 153 any presence location. When combined with the 236 transect-based absence records, this gave 154 a total of 5,000 points treated as absences in the analysis for consistency with the bush-crow 155 models [12].

156 For model validation purposes, the White-tailed Swallow's range was divided radially 157 into five geographic segments (Fig 1). We fitted SDMs using seven model algorithms-Generalised Linear Models (GLMs), Generalised Additive Models (GAMs), Flexible 158 159 Discriminant Analysis (FDA), Multiple Adaptive Regression Splines (MARS), Boosted 160 Regression Trees (BRT), Random Forests (RF) and Maximum Entropy (MaxEnt)-and 161 assessed the ability of each model to predict the swallow's current distribution using a k-fold leave-one-out cross-validation (LOOCV) method [12,45]. We fitted each model five times, 162 163 leaving out the data from one of the five radial segments in each case. The fitted model was 164 then used, with the bioclimate variable values, to predict probability of occurrence for each 165 presence/absence location within the segment whose data had been omitted. Having used this 166 k-fold LOOCV approach to make predictions for sites in all five segments, we then used the 167 predictions and the observed presence/absence data for all segments to calculate the Area Under the Receiver Operating Characteristic Curve statistic (AUC-ROC) [3,46]. 168



Fig 1. Global range map for the White-tailed Swallow. The co-ordinates of all presence (blue) and transect-based absence (red) locations used for fitting species distribution models are shown. The rectangular box shows the area across which pseudo-absence locations were drawn for modelling, and current and future simulations were projected. The lines radiating from the centre show the five sectors of the map used for leave-one-out cross-validation of the models. International borders are plotted using the '*wrld_simpl*' dataset available in the '*maptools*' package in R [47,48].

177 To assess variable importance, we selected results from the model-fitting algorithms 178 with k-fold LOOCV AUC scores greater than 0.6 (MaxEnt, GLM and GAM). Although scores 179 exceeding 0.7 are preferred [49], none of our models obtained this threshold. Since these three 180 models had similar k-fold LOOCV AUC scores (see Results), we assessed variable importance and future climatic suitability based on all three models to avoid biasing our results towards a 181 182 single model algorithm [24,25]. We re-fitted each of these models, using the LOOCV 183 procedure, with each variable left out in turn and calculated the k-fold LOOCV AUC statistic 184 for each of these models. Delta AUC scores were then calculated by subtracting the k-fold 185 LOOCV AUC for the models with the variable missing from the k-fold LOOCV AUC for the 186 model with all bioclimate variables included. In order to compare variable importance between 187 the swallow and the bush-crow, we standardised these scores by dividing the delta AUC score 188 for each variable by the sum of the delta AUC scores from all five variables in the model [12].

189

190 **Projecting future climatic suitability for the Ethiopian Bush-crow**

191 and White-tailed Swallow

In addition to the recent climatic data we used for model building, the WorldClim database[41] contains future projections of the same bioclimatic variables from a range of GCMs and

194 Representative Concentration Pathways (RCPs) [50,51]. We obtained projections of annual 195 values of bioclimate variables from WorldClim for six GCMs (S1 Table) and all four RCPs for 196 which results are available [41]. We calculated projected average values for each bioclimate 197 variable in two years: 2050 (by averaging projections for the period 2041–2060) and 2070 198 (average for 2061–2080) (S2 Table). We combined these projected bioclimate values with our 199 SDMs, built under current conditions, to project the potential range of both species under 200 different scenarios from the expected probability of occurrence for each 30 arc-second grid 201 cell.

202 The four RCPs considered (RCP2.6, RCP4.5, RCP6.0, RCP8.5) cover a range of 203 possible radiative forcing values for 2100, from 2.6 to 8.5 W/m² [51], taking account of multi-204 gas emission scenarios. The lowest emissions scenario, RCP2.6, assumes that atmospheric greenhouse gas concentrations peak before 2050 and decline thereafter, while the other three 205 206 scenarios assume progressively higher and later stabilisation of greenhouse gas concentrations. 207 The best-estimate global mean surface temperature increases are respectively 0.3–1.7°C, 1.1– 208 2.6°C, 1.4–3.1°C and 2.6–4.8°C by 2100, relative to the mean of 1986–2005 [50]. Together 209 the four RCPs represent the range of scenarios considered plausible by the Intergovernmental 210 Panel on Climate Change [52].

The choice of GCM and modelling technique can significantly impact climate change predictions, and the effect increases with distance of future projections, tending to outweigh differences arising from the initial dataset used or climate change scenario (i.e. RCP) selected [24,25]. However, projections of future range changes are more consistent for species with restricted environmental niches like the bush-crow and swallow [24].

We used *k*-fold LOOCV AUC comparison of SDMs built using current climate data for the Ethiopian Bush-crow [12] and White-tailed Swallow to select the model algorithms which produced the highest AUC scores when projected over each species' current distribution (BRT and RF for the bush-crow, and MaxEnt, GLM and GAM for the swallow). We then refitted these models using all available data (i.e. not using the LOOCV procedure), and projected the results under the six GCMs, four RCPs and for two projection years (2050 and 2070) [41] to assess the potential impacts of climate change on the two species.

To determine the projected future range sizes of the two species, we first calculated maximum kappa for the current range simulations according to each model algorithm. We used the probability of occurrence threshold which yielded maximum kappa under current conditions to convert the probability of occurrence for each future scenario into binary presence–absence scores in each cell, and summed the area of the cells where the species' presence was predicted. We took the mean area across all six GCMs and the projected model

algorithms for each species, to produce the mean potential climatically suitable area under each
RCP/time-period scenario. By subtracting the remaining climatically suitable area under each
scenario from the current simulated range size (based on maximum kappa) for the best-fitting
models, we calculated the mean percent loss of climatically suitable range under each scenario
for each species.

234

235 **Results**

236 Modelling the current distribution of the White-tailed Swallow

237 SDMs fitted for the White-tailed Swallow found that three model algorithms performed best: 238 Maximum Entropy (MaxEnt, *k*-fold LOOCV AUC score = 0.627), Generalised Linear Models 239 (GLM, *k*-fold LOOCV AUC score = 0.619) and Generalised Additive Models (GAM, *k*-fold 240 LOOCV AUC score = 0.601). These scores were much lower than the best-performing model for the Ethiopian Bush-crow (BRT, *k*-fold LOOCV AUC score = 0.824; [12]). Precipitation in 241 242 the driest quarter produced the highest delta AUC score under each algorithm (MaxEnt = 0.146, 243 GLM = 0.047, GAM = 0.089), followed by maximum temperature of the warmest month 244 (MaxEnt = 0.121, GLM = 0.040) or precipitation in the wettest season (GAM = 0.038; Fig 2, 245 S3 Table). Response plots indicated well-defined dry-season rainfall (50-70 mm) and

maximum temperature (30–35°C) thresholds, above which White-tailed Swallows did not
occur (Fig 3, S1 Fig). The GLM and GAM models predicted White-tailed Swallow occurrence
across a slightly wider range of dry-season rainfall values, and at slightly higher temperatures,
than did the MaxEnt model (Fig 3).



251 Fig 2. Comparison of the relative importance of five bioclimate variables in models describing the geographical range of the Ethiopian Bush-crow (taken from [12]) and 252 253 White-tailed Swallow. For the bush-crow, bars represent standardised delta AUC scores from 254 the model fitted using the algorithm which gave the best fit (boosted regression trees). For the swallow, bars represent the mean standardised delta AUC scores from the three best-255 256 performing models (Maximum Entropy, Generalised Linear Models, Generalised Additive Models), which were indistinguishable based on their k-fold LOOCV AUC scores. Lines 257 258 represent the range of standardised delta AUC scores from the three algorithms for the swallow.



259

Fig 3. The relationship of modelled partial probability of occurrence of White-tailed Swallow to (left) maximum temperature of the warmest month and (right) precipitation of the driest quarter. All other bioclimate variables are held constant. Curves show the predicted responses determined using the three model algorithms (Maximum Entropy, Generalised Linear Model, Generalised Additive Model) that gave the highest AUC values in a *k*-fold leave-one-out cross-validation test. Equivalent plots for all five bioclimate variables and all model algorithms are presented in S1 Fig.

267

268 **Projecting future climatic suitability for the Ethiopian Bush-crow**

269 and White-tailed Swallow

Projections of future bioclimate values within the current range of both the swallow and the bush-crow indicated an increase in maximum temperature beyond the threshold at which the two species currently occur, while there was less projected change in precipitation (Fig 4, S2 Table). There was some variation between GCMs in the location and size of the predicted potential range of each species for a given RCP and time period. However, a severe future decline in projected suitable area was observed across RCPs under each GCM, primarily caused by rising temperature (Figs 5 and 6). Under all scenarios, both species' potential ranges

- are projected to contract markedly, in some cases leading to a total loss of suitable area by
- 278 2070.





280 Fig 4. The relationship of modelled partial probability of occurrence of a+b) White-tailed 281 Swallow and c+d) Ethiopian Bush-crow to a+c) maximum temperature of the warmest month and b+d) precipitation of the driest quarter, compared to current and future 282 283 projected mean values. Black vertical lines indicate the current mean value of each bioclimate 284 variable [41] within a convex hull fitted around each species' distribution. Red vertical lines 285 show the projected mean value in 2070 for each of four Representative Concentration Pathways (RCP) (IPCC 2014). Red shading shows the range of projected mean values across six Global 286 287 Circulation Models for each RCP, and appears darker where these ranges overlap (therefore 288 corresponding to more likely scenarios). See Fig 3 for further details on response curves.



290 Fig 5. Projected current and future potential range for the White-tailed Swallow, based 291 on climate-only SDMs. Predictions for the four IPCC RCPs are presented in two future dates, 292 2050 and 2070. Each panel represents the mean probability of occurrence under each scenario, 293 averaged across six GCMs and the three best-performing model algorithms (MaxEnt, GLM 294 and GAM) under current conditions, according to k-fold LOOCV AUC. Dark green shows 295 areas with a high probability of climatic suitability, fading through brown to grey, which shows 296 areas with a low probability of climatic suitability. The blue polygon shows convex hulls fitted 297 around the White-tailed Swallow's current distributions in the core range and on the Liben 298 Plain, whilst the dashed line shows the complete hull if these two populations are considered 22

- 299 to be continuous. International borders are plotted using the 'wrld_simpl' dataset available in
- 300 the 'maptools' package in R [47,48].





Fig 6. Projected current and future potential range for the Ethiopian Bush-crow based on climate-only SDMs. Predictions for the four IPCC RCPs are presented for two future dates, 2050 and 2070. Each panel represents the mean probability of occurrence under each scenario, averaged across six GCMs and the two best-performing model algorithms (BRT and RF) under current conditions, according to *k*-fold LOOCV AUC. Dark green shows areas with a high probability of climatic suitability, fading through brown to grey, which shows areas with a low

probability of climatic suitability. The blue polygon shows the convex hull fitted around the
bush-crow's current distribution. International borders are plotted using the '*wrld_simpl*'
dataset available in the '*maptools*' package in R [47,48].

Summarised across models, and depending on which RCP is realised, the species are projected to lose 85–96% (bush-crow) and 56–79% (swallow) of potential range by 2050, and 90–100% (bush-crow) and 68–84% (swallow) by 2070, relative to the current mean climatically suitable area according to the best climate-only models for each species ([12]; Table 1). Such decreases will leave remaining areas which are likely to be too small to support viable populations.

Table 1. The area of mean current and future potential White-tailed Swallow and Ethiopian Bush-crow ranges based upon climate-only SDMs. Current ranges are the mean area of suitable climate according to the best two (bush-crow: [12]) and three (swallow) model algorithms. Future potential ranges are averaged across projections from the same algorithms and six GCMs under each Year/RCP scenario, with the range of values presented in parentheses. Percentages are calculated relative to the mean simulated current range.

	White-tailed Swallow		Ethiopian Bush-crow	
<u>Scenario</u>	<u>Mean potential range</u> / km² (min–max)	<u>Mean percent</u> <u>left (min–max)</u>	<u>Mean potential range</u> / km² (min–max)	<u>Mean percent</u> <u>left (min–max)</u>
Current	8,311 (6,571–9,532)	-	3,495 (3,384–3,606)	-
Year 2050, RCP 2.6	3,642 (0–8,568)	44 (0–103)	522 (0–1,988)	15 (0–57)
Year 2050, RCP 4.5	2,218 (0–6,591)	27 (0–79)	263 (0–1,490)	8 (0–43)
Year 2050, RCP 6.0	1,761 (0–6,753)	21 (0–81)	202 (0–1,959)	6 (0–56)
Year 2050, RCP 8.5	1,713 (0–6,188)	21 (0–74)	136 (0–954)	4 (0–27)
Year 2070, RCP 2.6	2,664 (0–6,380)	32 (0–77)	342 (0–2,160)	10 (0–62)
Year 2070, RCP 4.5	1,583 (0–5,360)	19 (0–64)	173 (0–1,463)	5 (0–42)
Year 2070, RCP 6.0	1,274 (0–4,631)	15 (0–56)	65 (0–373)	2 (0–11)
Year 2070, RCP 8.5	1,367 (0–7,950)	16 (0–96)	5 (0–37)	0 (0–1)

324 **Discussion**

Like the Ethiopian Bush-crow [12,29], the global distribution of the White-tailed Swallow is closely correlated with aspects of the local climate, being drier and cooler within the range edge than outside it. The mechanism by which two such unrelated species, with very different 25 328 behaviour and ecology and with no evidence of an interdependent relationship, have come to 329 have such similar ranges, apparently defined by the same climatic variables, is unknown. The 330 habitats used by the two species are similar, and consist of a mixture of rather degraded savanna 331 scrub and open grassland with well-spaced trees. Habitats in areas adjacent to the species' ranges appear to be remarkably similar to those within it, and the fit of models of bush-crow 332 333 distribution was not markedly improved when habitat variables were included [29,40]. We are 334 not aware of any species in other taxonomic groups that share these two species' patterns of 335 distribution. For the bush-crow, range restriction is explained, at least in part, by the inability 336 of birds to forage efficiently at temperatures above its climatic limit, because of the 337 thermoregulatory need to pant and seek shade [12]. For the swallow, the mechanism 338 constraining it is unknown, but may be mediated by a decline in breeding success at higher 339 ambient temperatures [40].

Our models for the swallow failed to achieve the high AUC scores found in our previous study of the bush-crow. This is unsurprising because of the lower quality of data available for the swallow. The range of the bush-crow can be very precisely delineated due to the bird's distinctive appearance and highly conspicuous nests, which are visible for up to a kilometre [12,29,53]. In contrast, the swallow is an unobtrusive, wide-ranging aerial forager, and its nests are usually concealed within huts [37]. For this reason, our training data contained

346 very few 'known' absences for the swallow compared to the bush-crow, and this probably 347 resulted in the differences in estimated model accuracy. Nonetheless, the similarity across 348 different model algorithms in both the area of predicted occurrence and the importance of the 349 dry-season precipitation and maximum temperature variables suggest that the overall result is 350 robust.

351 Our projections of potential range reductions of the two species under a selection of 352 GCMs, whilst varying in severity between models, are consistent across all predictions. The 353 outcomes for both species are of conservation concern, with severe loss of potential range under 354 all GCMs and RCPs, even as soon as 2050. Many scenarios, particularly for the bush-crow, 355 indicate total loss of potential range by 2070. Even under RCP2.6, the most optimistic scenario 356 which requires strong mitigation strategies to be employed urgently [52], the bush-crow is projected to lose 85% of its potential range by 2050 and 90% by 2070, and the swallow 56% 357 358 and 68% in the same periods. For neither species did the models predict that any areas around 359 their current ranges would become suitable, as they already occupy the coolest area in the 360 region. Studies modelling changes in ranges and reporting rates of species (the latter being 361 proxies for local abundance) often predict declines in both, indicating that models of range extent alone are likely to overestimate future population sizes [54]. It is therefore likely that 362 decreases in population density within the remaining climatically suitable areas will also occur. 363

364 Despite the uncertainty inherent in species distribution modelling and the projection of potential ranges under future climate scenarios, numerous studies have found that climate 365 366 envelope models fitted to species' present distributions can reliably predict future changes in 367 range boundaries and population trends [4,55–58]. The greatest uncertainty in projections tends to arise from the choice of modelling technique and baseline climate data used in model fitting, 368 369 and of GCM used for model projections [23-25]. We investigated a suite of modelling techniques, and selected those with the highest predictive capacity under current conditions, 370 371 preferring methods which performed well using k-fold leave-one-out cross-validation. As our 372 results were validated by data independent of, and spatially separate from, those used for model 373 fitting [12], we consider the models reasonably robust.

374 An additional source of uncertainty arises from the accuracy of the present-day distribution data. For the bush-crow, the high AUC scores achieved by the models when 375 376 predicting the species' current distribution [12] reflects the quality of the underlying data, and 377 suggests that future predictions are likely to be robust. Moreover, as part of a study not reported 378 in this paper, we conducted six walked transects, 6–10 km long, at sites selected to be at the 379 edge of the known geographical range of the bush-crow, as established by the data used in this 380 paper. Each transect was placed so that it began within the known range and ended outside it. 381 In all cases no bush-crows were detected in the portion of the transects lying outside the

previously known range, adding further confidence to the accuracy of the present-day distribution data. For the swallow, the lower AUC scores create uncertainty in the present-day models, which is likely to reflect under-recording of the species' presence. When carried through to future projections, this could lead to under-predicting the area which will remain climatically suitable. However, even allowing for some uncertainty in the magnitude of the projected loss of suitable range, the direction of the response was consistent across models, and severe enough to warrant conservation concern.

Projections of species' future ranges made using climate-only models usually have higher apparent precision than those incorporating non-climate variables as well because, for all the uncertainty in climate projections, the uncertainty in predictions of change in land cover and other human impacts is much larger [3]. While climatic factors accurately describe current bush-crow [12] and swallow occurrence, future projections of these models still represent the maximum potential distribution of each species under each climate scenario, with further restrictions imposed by habitat availability and human land-use [3,29].

396 Documented extinctions implicating climate change have been driven by biotic 397 interactions [59], and to date none appears to have been driven solely by temperature 398 intolerance [7]. The Ethiopian Bush-crow may therefore be a rare example of an endothermic 399 species directly limited by heat intolerance, making it particularly sensitive to direct effects of

400 temperature change, compared with other species studied so far [12,29,60]. For the White-401 tailed Swallow, temperature may directly affect breeding success by inhibiting the adults' 402 ability to provide food [40]; it certainly seems improbable that an aerial insectivore, with inter-403 continental migrants as congeners, should occupy such a restricted range because of limited 404 food availability or breeding sites.

405 Given the strong responses of the bush-crow to direct impacts of temperature, 406 management interventions to compensate for effects of climate change on its distribution and 407 abundance would need to have a large effect. The same may be true for the swallow. Whether 408 the two species can minimise the impact of rising temperatures within their current range 409 through behavioural change seems improbable, although it is perhaps significant that bush-410 crow nests built on electricity pylons, which are taller than most available natural nest sites and 411 hence may be cooler, were recently recorded for the first time [53]. "Assisted migration" [61] 412 seems equally unfeasible. Our models failed to find any suitable climate within 150-400 km 413 of the current range, indicating that translocations would need to move the species over large 414 distances, into new environments and the ranges of species to which they have no prior 415 exposure. For an aerial insectivore like the swallow, finding large areas with suitable habitat and temperatures projected to persist long into the future is a challenging prospect [62]. 416 417 Possibly the omnivorous bush-crow [60] could be bred in captivity and released experimentally

into candidate sites to increase the chances of success [62]. However, such actions would have
to be carefully managed and monitored to avoid any negative impacts on native fauna from
releasing a non-native, dietary generalist [60,63].

421 Other species exhibiting strong responses to temperature have already suffered a 422 reduction in range, indicating an inability to respond physiologically to rising temperatures 423 [17]. Two African species, Rudd's Lark (Heteromirafra ruddi) and Botha's Lark (Spizocorys 424 fringillaris), are already projected to suffer complete range loss by 2055 under two out of three 425 GCMs considered [54]. The Ethiopian Bush-crow and White-tailed Swallow must be added to 426 this list of species at high risk of extinction due to climate change within their native range. 427 Both species could become model systems for furthering our understanding of species' 428 distributions, testing our models' ability to predict future changes, and assessing whether there 429 is scope for conservation interventions to reduce the negative impacts of climate change. These 430 two species have particular benefits as model species: the range boundaries of the Ethiopian 431 Bush-crow, and changes therein, can be very precisely identified due to its distinctive and 432 highly visible nests, and the White-tailed Swallow appears to nest largely in inhabited huts, 433 making them both relatively easy to find and well known to local people, and raising the 434 possibility that changes in its range and population could be tracked using questionnaire surveys. Both species are already star attractions in a region home to five endemic birds [43,64], 435

and have the potential to become flagship species for the impacts of climate change on aviandiversity in Africa.

438

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629

630 Supporting information

631 S1 Table. Six Global Circulation Models (GCMs) used for the projection of bioclimate

- 632 variables under future climate scenarios.
- 633 S2 Table. Current and projected future values of five bioclimate variables within a convex
- 634 hull fitted around the current distributions of the White-tailed Swallow and the Ethiopian
- 635 Bush-crow. Current values are the minimum, mean and maximum values across all cells within

the species' range. Projected values are the minimum, mean and maximum values of the mean

637 across all cells within the species' current range under six different Global Circulation Models

638 (S1 Table) at each of two years (2050 and 2070) and under each of four Representative

639 Concentration Pathway (RCP) scenarios [52]. Bioclimate variables are abbreviated as follows:

- 640 Precip wet = precipitation of the wettest quarter; Precip dry = precipitation of the driest quarter;
- 641 Temp season = Temperature seasonality; Max temp = Maximum temperature of the warmest

month; Temp range = Annual temperature range [41]. The current range used for the swallow
includes two hulls fitted around the core range and the Liben Plain independently, but does not
include the area in between.

S3 Table. Delta AUC scores for models of White-tailed Swallow distribution, fitted
without each climate variable in turn, under the three best-performing model algorithms
(MaxEnt, GLM, GAM), and compared to values for the best-performing model (a
Boosted Regression Tree, BRT) for the Ethiopian Bush-crow, taken from [12].

649 S1 Fig. The response of partial probability of White-tailed Swallow occurrence to five 650 bioclimatic variables. Lines show the predicted responses to each variable according to each 651 of seven model algorithms fitted using the 'biomod2' package [42] in R [48], with all other 652 variables held constant.