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Body mass and condition of a fynbos bird community: investigating impacts of time, weather and raptor abundance from long-term citizen-science datasets

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Variation in body size, especially mass, is a function of local environmental conditions for any given species. Recent recorded decreases in body size of endotherms have been attributed to climate change in some cases. This prediction is based on the trend of smaller body size of endotherms in warmer climates (Bergmann's rule) and it implies genetic responses rather than phenotypic flexibility. Alternatively, selection for smaller body size or lower mass could be explained by the starvation-predation hypothesis, where lighter individuals have a higher probability of escaping pursuing predators, such as raptors. Evidence that climate warming is driving patterns of size selection in birds in recent times has been mixed. We inspected data on 40 bird species contributed by bird ringers to the South African Ringing Scheme (SAFRING) for changes in body mass and condition as a function of time (year), minimum temperature of the day of capture, maximum temperature of the previous day, and rainfall data in the south-western Cape Floristic Region (fynbos) around Cape Town, South Africa, for the period 1988–2015. The region shows a warming trend over the study period (0.035 °C yr^{-1}). Interannual body mass and condition change were poorly explained by year or temperature. High daily minimum temperature explained loss of body condition for four species, whereas evidence from recaptured birds indicated negative effects of increasing maximum daily temperature, as well as rain. For the alternative hypothesis, because raptor abundance is stable or only weakly declining, there is little evidence to suggest these as a driver influencing mass trends. Any decrease in body mass over the study period that we observed for birds appear more likely to be plastic responses to stress associated with temperature or rainfall at this time, rather than systematic selection for smaller body size, as predicted by Bergmann's Rule.

Masse corporelle et état d'une communauté d'oiseaux fynbos: étude de l'impact du temps, du climat et de l'abondance des rapaces à partir d'ensembles de données de sciences participative de long terme

La variation de la taille du corps, en particulier de la masse, est fonction des conditions environnementales locales pour une espèce donnée. Les diminutions récemment enregistrées de la taille corporelle des endothermes ont été attribuées au changement climatique dans certains cas. Cette prédiction est basée sur la tendance à la réduction de la taille corporelle des endothermes dans les climats chauds (règle de Bergmann) et implique des réponses génétiques plutôt que la flexibilité phénotypique. L'hypothèse de la faim-prédation, selon laquelle les individus plus légers ont une probabilité plus grande de fuir les prédateurs à la poursuite tels que les rapaces, pourrait également expliquer le choix de corps plus petit ou de masse plus faible. Les preuves selon lesquelles le réchauffement climatique entraîne des modèles de sélection de la taille chez les oiseaux ces derniers temps ont été mitigées. Nous avons examiné les données relatives à 40 espèces d'oiseaux fournies par les bagueurs d'oiseaux dans le programme de baguage sud-africain (SAFRING) afin de détecter des modifications de la masse et de l'état du corps en fonction du temps (année), de la température minimale du jour de capture et de la température maximale du jour précédent, et des données pluviométriques dans la région du sud-ouest du Cap Floristic (fynbos) autour du Cap Town, en Afrique du Sud, pour la période 1988–2015. La région présente une tendance au réchauffement au cours de la période d'étude (0.035 °C an^{-1}). La masse interannuelle et le changement d'état étaient mal expliqués par l'année ou la température. Les températures minimales quotidiennes élevées expliquent la perte de condition physique de quatre espèces, tandis que les observations d'oiseaux recapturés indiquent des effets négatifs de l'augmentation de la température maximale quotidienne, ainsi que de la pluie. Pour l'hypothèse alternative, l'abondance des rapaces étant stable ou ne diminuant que faiblement, il y a peu de preuves pour suggérer que ces facteurs influencent les tendances de masse. Toute diminution de la masse

corporelle observée au cours de la période d'étude chez les oiseaux semble plus susceptible d'être une réaction plastique au stress associé aux températures ou aux précipitations, plutôt qu'une sélection systématique pour une taille corporelle plus petite, comme prédit par la règle de Bergmann.

Keywords: banding, Bergmann's Rule, body size change, citizen science, climate change, fynbos

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Introduction

Body mass is commonly recorded while ringing birds for most ornithological studies worldwide. Body mass for any species is usually a function of a range of factors, some intrinsic, like sex, others extrinsic, e.g. food availability or parasite load. Change in mass is related to predictors of starvation risk, such as decreasing temperature, decreasing day length, geographical location and social dominance status (Cresswell 1999; Gosler 1996). Mass is therefore generally a measure with high variability, which should be scaled against a less variable measure, e.g. skeletal measures, to be used as an index of body condition (Green 2001). Long-term datasets that include mass and other body measures, e.g. wing or tarsus, are becoming important, because they can be used to examine effects of climate change on morphology (Parmesan 2006).

The expectation that climate will affect morphology is based largely on observed geographical and long-term variations in morphology (Barnosky et al. 2003; Salewski et al. 2014). Variation in size of homeothermic endotherms are expected to follow Bergmann's rule (Bergmann 1848); i.e. within a genus the smaller species should live in a warmer climate and the larger species in a colder climate, with selection resulting from optimal heat flux from body surface: volume ratios. Rensch (1938) reformulated Bergmann's rule to populations within a species, and this is generally understood as the basis for the biogeographical rule discussed here (see Salewski et al. 2010). In summary, we expect decreased size with warmer temperatures.

Meiri and Dayan (2003) found that 72% of bird species ($n = 94$) showed a spatial pattern following the predictions of Bergmann's rule. Although this pattern has generally not been examined across southern Africa, for at least one species where this trend has been examined (Sombre Greenbul, see Table 1 and Appendix 1 for scientific names), this rule holds (Bonnievie 2014). Temporal changes in body size have also been attributed to Bergmann's rule in some studies (Gardner et al. 2009; Yom-Tov et al. 2006), but there is little evidence that these constitute evolutionary responses and changes may simply be the result of phenotypic plasticity (defined as reversible changes in traits, modulated by the environment) (Teplitsky et al. 2008). However, in the case of a study of Mountain Wagtail in South Africa, using mass as a proxy for body size, selection for a decrease in body size was attributed to changes in temperature (Prokosch et al. 2019). An examination of 120 years of body size and climate data from southern Germany for 11 species did not link bird body-size change to anthropogenic climate change (Salewski et al. 2014). A recent review of 952 species

found a lack of consistent effects in the general relationship between mass and temperature in homeothermic species (Riemer et al. 2018). In summary, there are a multitude of complexities at play that make interpretation of mass change challenging (see details in Millien et al. 2006; Teplitsky and Millien 2014).

Gienapp et al. (2008) suggested that morphological responses to anthropogenic climate change will more likely be the result of phenotypic plasticity and not changes in the genetic composition of populations. If this is true, then we would expect interannual variation in the body size of grown birds to be linked to average annual temperatures rather than time, but time rather than temperature if there is genetic change. In addition, explanatory variables evident over multiple years might suggest potential selective power on genetic components of size. It is also more likely that selective pressure for certain traits will be manifested in populations under decline, as result of those pressures (Hoffmann and Hercus 2000). Population pressure can be examined for species where population trends are known, which is made possible by the long-running Southern African Bird Atlas Project (SABAP).

Changes in body size and condition have been attributed to factors other than climate. Body mass and energy reserves of small birds decrease in response to increased predation risk, as predicted if predation risk is mass-dependent (Gosler et al. 1995; MacLeod et al. 2005); i.e. lighter birds have a higher probability of escaping pursuing predators than heavier birds. Predator pressure, therefore, should be considered when examining mass changes in birds, because increased predator pressure is a selective pressure for lighter birds.

Our study area is situated in the south-western Cape, South Africa, part of the Cape Floristic Region (CFR), and recognised as a biodiversity hotspot (Cowling and Richardson 1995; Myers et al. 2000). Threats from land conversion to agriculture, forestry and urban expansion, and disruption of habitat integrity through alien-plant species invasion to this Mediterranean-type ecosystem have been well documented (Hilton-Taylor and Le Roux 1989; Rouget et al. 2003). Global circulation models suggest that the CFR is subject to rapidly rising temperatures (Klausmeyer and Shaw 2009; Engelbrecht and Engelbrecht 2016), with a corresponding trend of increasing aridity over most of the region (Engelbrecht et al. 2009). Long-term data from Table Mountain National Park, situated in our study area, indicate an increase in mean annual temperature of some 1.5 °C since 1960 (van Wilgen et al. 2015). The fynbos biome

Table 1: Fixed effects from the summary of the model explaining body condition change for recaptured birds as a function of maximum temperature of day prior to capture (maxT), rainfall of the day of capture, rainfall of the previous day, and year. For this model, ring number was nested in species as random effects.

	Estimate	SE	df	<i>t</i>	<i>p</i>
Intercept	37.658	6.296	20	5.981	0.000
MaxT	-0.272	0.052	15 698	-5.234	0.000
Year	0.104	0.061	10 416	1.695	0.090
Rain	-0.124	0.048	15 427	-2.551	0.011
Lag Rain	0.017	0.050	15 407	0.342	0.733

is the most extensive and biodiverse component of the CFR (Cowling and Richardson 1995). Climate change has been recognised as a specific threat to the fynbos-endemic avifauna (Lee and Barnard 2016) with declines in population size of some species potentially attributed to high costs of thermoregulation at warm temperatures (Milne et al. 2015; Oswald et al. 2018). Body mass and condition have been shown to change in response to environmental stress for one fynbos-endemic species (Cape Sugarbird, Mackay et al. 2017)

In this study, we examine the hypothesis that the body size of birds decreases over time, because of warming patterns, as predicted by Bergmann's rule. We do this by examining change in wing length and body mass in relation to temperature in a set of 40 of the most commonly captured bird species in the south-western Cape, including three of the seven fynbos endemic species: Cape Sugarbird, Orange-breasted Sunbird and Cape Siskin. We furthermore predict that if temperature is a selective pressure on bird populations, then this would be evident over time and that there should be a relationship between population change (as evidence of a population under pressure) and body-size response to temperature, and that these effects may be observed between years. Alternatively, if body condition changes in mass between years are the consequence of phenotypic plasticity rather than directional, genetically mediated change, we will see finer temporal scale changes in mass and condition that are linked to temperature, which we examine at the intra-day scale. Finally, we examine population trends for seven raptor species known to prey upon birds to determine if there has been any population change that might account for overall patterns of mass change in their prey.

Methods

Body metric data

We extracted biometric data on selected species caught for ringing in the CFR from SAFRING datasets managed by the University of Cape Town, South Africa. The source data ($n = 214\ 884$ captures of 61 land-bird species) was contributed mostly by citizen scientist ringers, together with some formal research projects. We used data only from 1988 to 2015, because this period accounts for >95% of all captures, as well as having the best available weather data. We selected those birds caught south of 30° S and west of 21° E, corresponding to greater Cape Town and

the surrounding area (Figure 1). This contained the most consistent ringing records over time: data from ringing sites outside this area were available for only a few years at a time. In addition, capture records from this region indicate movement between these sites (Fraser et al. 1989), indicating this set of birds can be treated as a single population (Calder et al. 2015). This is supported by genetic evidence for some species for which this information is available; because this is a fire driven ecosystem there is a lot of resulting movement at the population level (Chan et al. 2011).

We applied a range of data-cleaning and data-selection criteria to obtain our final dataset of 40 species ($n = 129\ 577$ total captures and recoveries), as this dataset was historically poorly vetted. Selection criteria included removing individuals outside the 99% quantile of each biometric measure calculated by species, which through inspection were likely to represent errors in the database. We used only adult bird measurements (SAFRING age code 4). To provide reasonable annual sample sizes of biometric data we consider only those species with >200 captures across the study period (so each year is represented by 10 or more captures per year). Body mass (g) was the most consistent measurement associated with bird captures over time. An example initial dataset together with R code used to implement the above filtering procedures are provided as Supplementary information (example_datav and SAFRING data prep)

One of the objectives was to calculate a mass index (mass corrected by body size), as a proxy for body condition. Skeletal measures like keel would be preferred measures of body size, but are not recorded by SAFRING contributors. Alternatively, tarsus measurements were reported too erratically for modelling purposes, included in the database only since 2002. Wing measurements, however, do appear consistently in the database from 1998. We examined change in wing length as a function of year using a generalised linear mixed model (glmm) with ringer as random effect using the lme4 package (Bates et al. 2015) in R 3.1.3 (R Core Team 2017), and for all species found this measure to be independent of year (see Figure 2 for an example for Cape Sugarbird, and full results in Supplementary Table 1). Accordingly, from 1998 we were able to calculate a standardised mass index, hereafter referred to as condition, following Peig and Green (2009) (Equation 2) for 40 species:

$$\hat{M} = Mi \left[\frac{Lo}{Li} \right]^{bSMA}$$

where Mi and Lo are, respectively, the body mass and wing length as the linear body measurement of individual i ; $bSMA$ is the scaling exponent estimated by the standard major axis regression of M on L ; Lo is the arithmetic mean value for the study population; and \hat{M} is the predicted body mass for individual i when the linear body measure is standardised to Lo . The scaled mass index has been found to be consistently better correlated with other standardised components of body reserves (e.g. lean dry mass, water, protein) than ordinary least squares regression residuals (Peig and Green 2009).

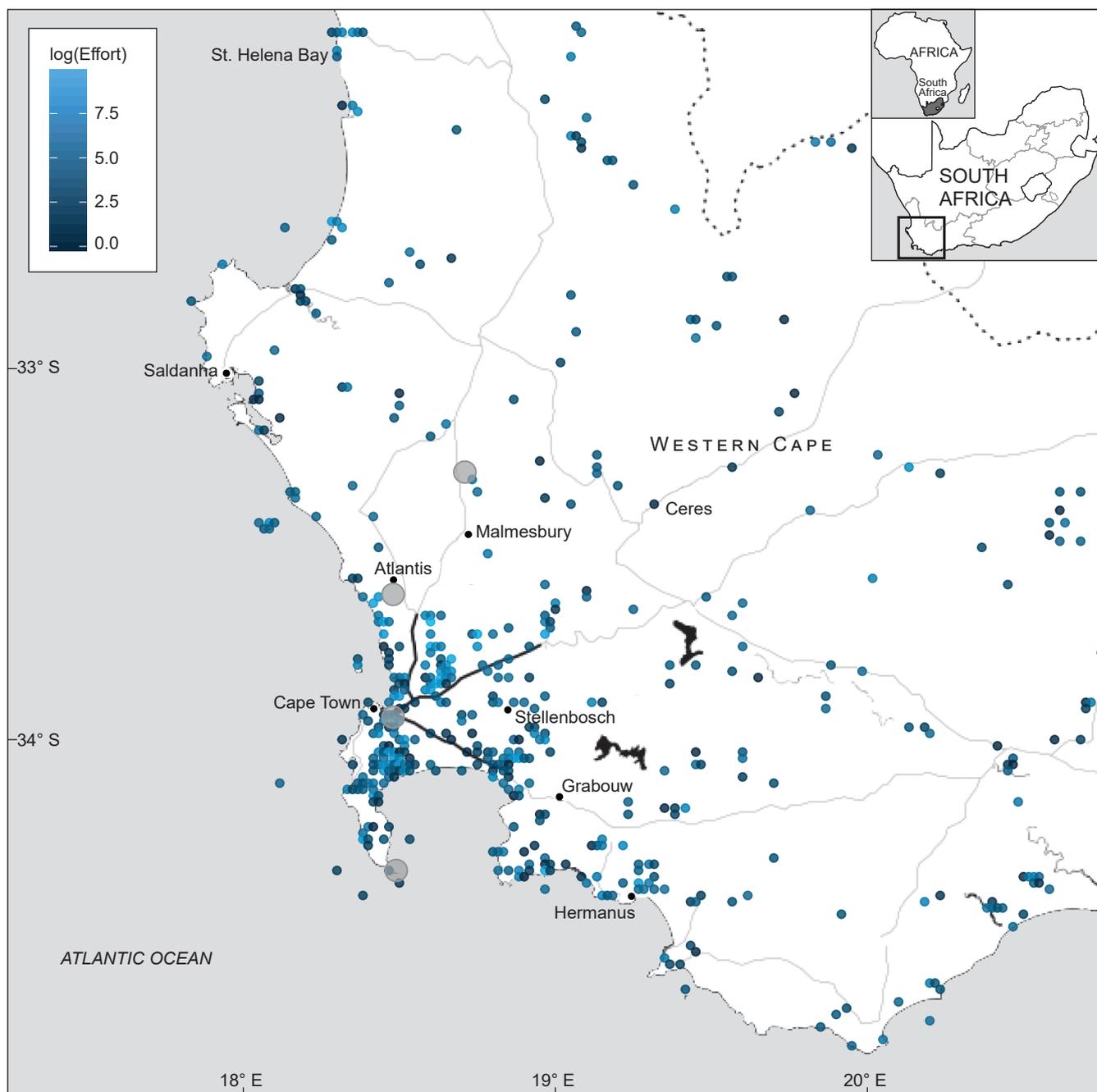


Figure 1: Study site location in the greater Cape Town area, South Africa. The locations of the four weather stations for which climate variables were obtained are from south to north, Cape Point, the Royal Cape Astronomical Observatory, Atlantis and Langgewens, as indicated by the grey circles. Ringing locations are indicated (smaller circles), with lighter colours, indicating more ringing records (Effort). Sparse ringing locations between 30° S and 32° S are not shown.

Climate data

Daily rainfall and maximum and minimum temperatures were obtained for four weather stations with the most consistent data over the study period across the study area from records provided by the South African Weather Service (Figure 1). Some 85% of ringing records fell within 50 km of these stations (south of 33° S and west of 19° E), with the distance between the furthest stations

being 140 km, i.e. spaced 35 km apart on average. We calculated daily and annual means of rainfall and temperature across these stations to account for any single station error, because each station had varying amounts of missing target weather data; and creating a mean value across the region helped account for site-specific missing values. We explored temperature and rainfall change as a function of time through a linear regression by year, as

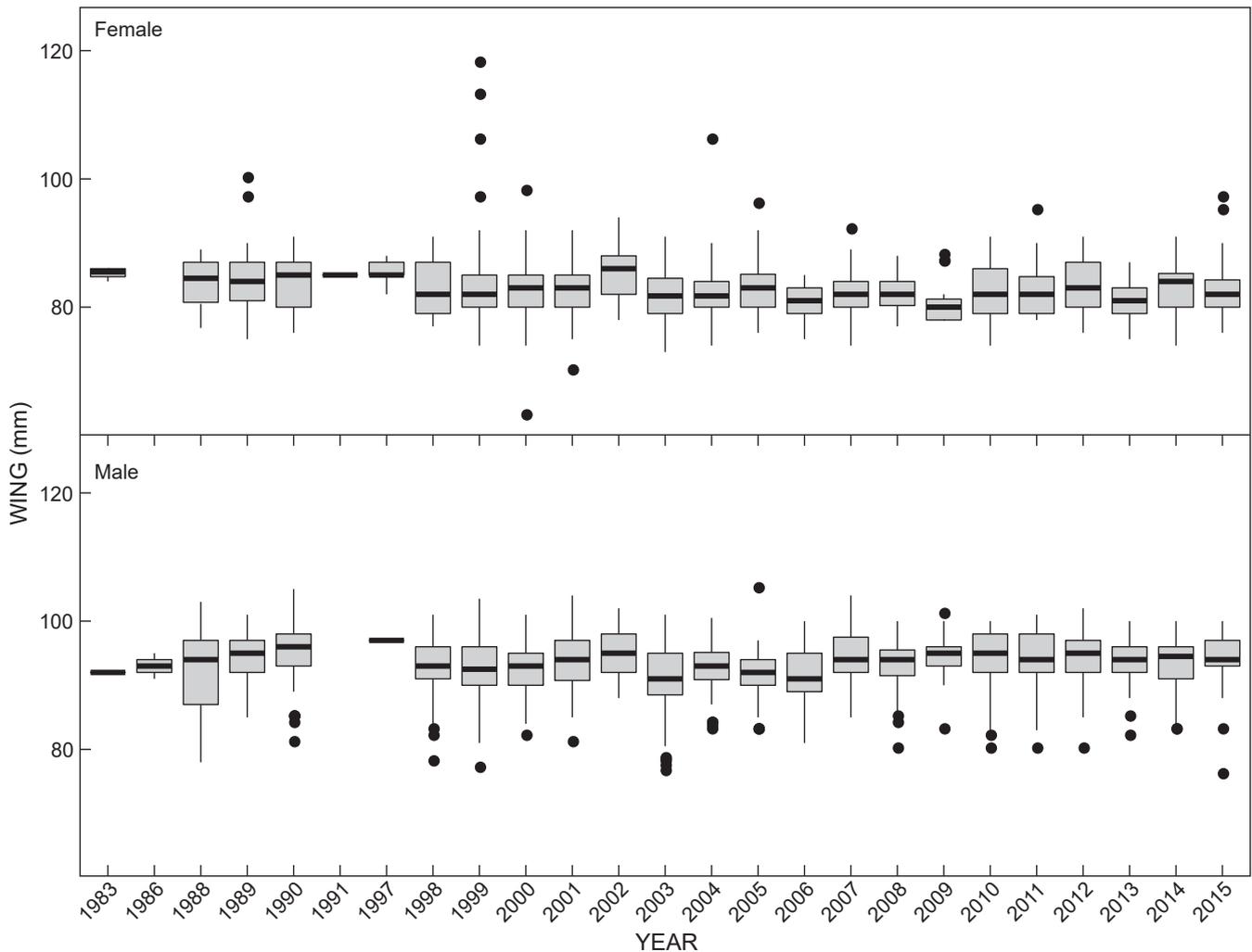


Figure 2: Wing length measurements over time for Cape Sugarbird, split by sex. For no species did wing length change with time when accounting for ringer.

well as the loess non-parametric regression (Cleveland and Devlin 1988). These results are consistent with alternative data sources and predictions for climate change trends (e.g. van Wilgen et al. 2015).

Modelling avian wing-length, mass and condition as a function of weather data

Each capture record was assigned weather variables related to date of capture. To examine the influence of temperature and time on avian mass and thereby condition, we conducted our modelling at two scales: firstly, using summarised mean biometric measurements across year by ringer for mass and condition (interannual comparison); and, secondly, at the daily scale for condition.

For the interannual analysis we implement glmms using the lme4 package (Bates et al. 2015) in R 3.5.3 (R Core Team 2017) for each species to explore mean mass as a function of the interaction between maximum temperature, recorded as the mean of maximum temperature across each year, and time (as years), using scaled data implemented through the scale function in R. In doing so,

we were specifically looking for (a) long term trends with time and (b) interaction effects, e.g. if body mass is lower in hot years. For the 21 sexually dimorphic species we include sex (male or female) as an additional variable. We used ringer as random effect to account for ringer specific variation. We use the lmerTest package (Kuznetsova et al. 2017) to determine p -values. Because we are interested in the contribution of year and temperature to mass or condition change over many species ($n = 40$), Bonferroni corrections were applied to $p = 0.05$, so p -values less than 0.00125 were treated as significant. We acknowledge this could result in Type II errors, and so full model results are presented allowing readers to determine their own levels of significance. We tested resulting regression estimate results using intercept only linear models for significant deviation from zero for the community of birds for mass and wing change as a function of time or temperature.

For each species we examined individual condition as the dependent variable as a function of daily maximum temperature of the previous day and minimum temperature of day of capture, year (as a linear variable) and total daily

rainfall, as well as rainfall from the previous day. Ringer and month (as a factor) were used as random effects where possible, dependent on the information available for each species. Month was included as random effect, because there are phenological differences in mass and wing measurements attributable to breeding season and moult. Sex was used as a fixed effect for sexually dimorphic species where sufficient samples of males or females were obtained. We applied backward-selection to find variables that best explained variation. We used the 'step' function in the lmerTest package (Kuznetsova et al. 2017) to perform automatic backward elimination of fixed effects of the full linear mixed effect model, keeping random effects fixed. This analysis excluded recaptures, which aided independence, but was also done, because most ringing data represented newly ringed birds only, confounding ring number as an additional random effect, because of the low resulting variance, especially because recaptures can occur between ringers. Consequently, recapture data were treated separately.

Birds that were recaptured allowed us to explore temperature dependency and, to a degree, year effects on body condition in individual birds. For this analysis we examined body condition as a function of maximum daily temperature of the day prior to capture, rainfall on the day of capture, rainfall of the previous day, year of capture, using ring numbers nested in species, as well as family (as phylogenetic control), as random effects. This mixed model approach assumes that all species share a common effect of climate on body condition and it is used to determine the overall pattern, rather than species effects. We present the full model result. In addition, to make the results meaningful in terms of the main variables identified as important: maximum daily temperature and rainfall, we present total and percentage body mass change as a function of temperature for each species, the results of species-specific glmms, with ringer as a random effect.

Modelling population change as a function of body condition influenced by temperature

The Southern African Bird Atlas Projects are citizen science projects to which birdwatchers systematically submit geospatially explicit checklists of birds to a central database managed by the University of Cape Town. The first of these (SABAP1) was conducted from 1987 to 1992 (Harrison et al. 1997), whereas the second (SABAP2) was initiated in 2007 and is ongoing, as of 2019, although we use data only up to 2015. Following the methods of Lee et al. (2017), we calculated a population change metric between atlas periods, based on reporting rates for each of the 40 species, using the following equation across the range of each species:

Population change = SABAP2 reporting rate / (SABAP1 reporting rate + SABAP2 reporting rate) - 0.5

This calculation returns a value of between -0.5 and 0.5, with values >0, indicating increases, and values <0, indicating declines. For each species we calculated the beta parameters (i.e. slope coefficients) from a linear

regression of body condition as a function of mean annual temperature. We then examined a model of a regression of population change on these estimates, where species is the sampling unit, to identify any relationship between population change and body condition responses to temperature at the community level.

Time series analysis on annual mean mass, body condition and wing length values

To examine patterns of temporal correlation of mass, body condition and wing length, we examined autocorrelation function output resulting from the 'acf' function from the astsa package (Stoffer 2016). We also used the cross-correlation function ('ccf') to explore the effect of temperature on mass, as indicated in Shumway and Stoffer (2016). This function identifies whether lags or leads of the x-variable (in this case temperature) might be useful predictors of yt (in this case mass or body condition the following year). For each species, we used summarised biometric values (e.g. mean mass by year), but were unable to account for ringer effects in this analysis, because contributions were too erratic over time. As such, we use coefficient values of 0.5 or greater to identify significant autocorrelation or cross-correlation effects, rather than the default 0.4.

Raptors

To determine if changes in predation pressure could be influencing mass measurements, we calculated population change (as described above) for seven small- to medium-sized raptors known to include birds in their diet (Table 1) according to species accounts in Hockey et al. (2005). We also examined SABAP2 interannual trends in reporting rate from across the range of each of the species within the study area.

The standard statistic for the equality of two proportions (Z-score; Underhill and Bradfield 1998) can be used as an index to measure confidence in change in relative abundance that accounts for the number of lists submitted for each quarter degree grid cell for each period, as described in Underhill and Brooks (2014):

$$Z = \frac{P_2 - P_1}{\sqrt{P(1-P)\left(\frac{1}{n_1} + \frac{1}{n_2}\right)}}$$

where P1 and P2 are the reporting rates from SABAP1 and SABAP2, respectively, n1 and n2 are the numbers of checklists on which the reporting rates are based and the reporting rate, P, is given by:

$$P = \frac{n_1 P_1 + n_2 P_2}{n_1 + n_2}$$

We calculate the mean of the Z-score for the grid cells in a species' range as an index of confidence in the direction of population change for each species: large negative values indicate evidence for population decline, large positive values indicate evidence for population increase.

Results

Climate and weather

The weather stations recorded an average annual maximum daytime temperature-warming rate of 0.035 °C for the period 1988–2015. This is equivalent to a 1.05 °C increase in temperature over 30 years (regression estimate by year: 0.035 °C ± 0.008, $t = 4.34$, $p = 0.0002$). However, the relationship was not exactly linear (Supplementary Figure 1), allowing scope to include both parameters in modelling to determine the stronger effect. Warming rates are smaller at the Cape Point station, which is heavily modulated by the surrounding ocean, indicating warming rates at the three non-coastal stations would be higher than the average change reported above (Supplementary Figure 2). However, the mean values are weighted by the three stations that show greater change and warmer temperatures. Whereas, unsurprisingly, average minimum temperature was correlated to maximum temperature (0.5 °C ± 0.12, $t = 3.99$, $p = 0.0004$), change in minimum temperatures was not as strongly correlated with time (regression estimate of minimum temperature by year: 0.016 °C ± 0.008, $t = 2.01$, $p = 0.06$). There was no change in total daily rainfall over time (estimate by year: 0.003 °C ± 0.005, $t = 0.65$, $p = 0.52$), and this measure was also not correlated with either temperature measure (max: -0.14 °C ± 0.11, $t = -1.26$, $p = 0.21$; min: -0.11 °C ± 0.15, $t = -0.73$, $p = 0.47$). Otherwise, the higher winter-rainfall-pattern characteristic of the region was clear, as was the seasonality in monthly temperature across the year (Supplementary Figure 3).

Year and temperature as predictors of interannual body condition and mass change

There was no evidence for a directional change in size either from mass values or wing length values attributable to time as measured in years: regression estimate values did not differ from zero in either case (linear regression using each species estimates for the intercept only model: mass: 0.12 ± 0.11, $t = 1.14$, $p = 0.26$, $df = 39$; wing: 0.12 ± 0.11, $t = 1.14$, $p = 0.26$, $df = 39$; Supplementary Table 1, Figure 3). For the interannual model summary values of mass, neither year nor temperature dominated in terms of the directions of their slopes (21 positive vs 19 negative in each case) and for no species was either of these predictors significant. Although 65% of the 40 species indicated negative coefficients for the interaction between time and temperature, indicating less of an influence of temperature over time and accordingly some possible adaptation to increasing heat, at $p < 0.00125$ this effect was also not significant for any species (Supplementary Table 1). Similarly, for no species was temperature nor time significantly associated with decreases in interannual body condition (Supplementary Table 1). In summary, there was no difference in parameter estimates from regressions for any combination of wing, mass, temperature or time across the community of birds i.e. no evidence for directional body size change across this bird community.

Best predictors of individual body condition

To determine the best predictors of daily body condition, we performed model selection as a function of maximum

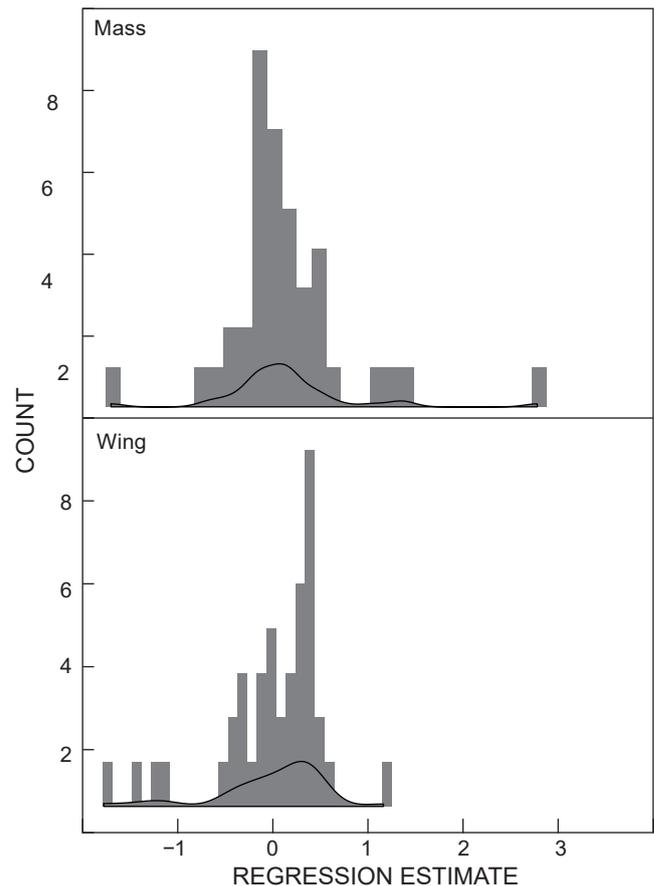


Figure 3: Histograms of the coefficient parameter estimates of models explaining change in wing length and mass, as result of year for 40 bird species from south-western South Africa (interannual change). A density curve (thin black line) is overlain. These plots summarise the individual species models, full results available as Supplementary information.

temperature of previous day, minimum temperature of date of capture, rainfall of day of capture, rainfall of previous day and time (year), accounting for ringer, month, and sex. Daily minimum temperature was the most important of the weather variables, retained for 10 species, and for which the coefficients were significant for four species, in all cases negative (Southern Double-collared Sunbird, Common Waxbill, Cape Weaver and Cape Sparrow; Supplementary Table 2; illustrated in Figure 4). Year was retained as a significant negative predictor of daily body condition in models for just two species (Southern Double-collared Sunbird and Barn Swallow; Supplementary Table 2). Maximum daily temperature was a significant negative predictor of body condition for Southern Masked Weaver and Southern Red Bishop. Daily rainfall was significantly negatively correlated with body condition for Southern Double-collared Sunbird, Malachite Sunbird, and Southern Red Bishop. Higher rainfall of the previous day was associated with increased body condition for Namaqua Dove and Speckled Mousebird.

Increasing maximum temperature on the day prior to capture for birds that were recaptured was strongly

Table 2: Standardised population change in key raptor species relative abundance between atlas periods. Mean Z is the mean of the Z-scores (confidence scores) for the pentads across the range of the species. Similarly for population change (pop change) and standard deviation of population change (SD pop change). Not referenced in the text

	Mean Z	Mean pop change	SD pop change
Black Harrier	-0.41	-0.17	0.39
<i>Circus maurus</i>			
African Goshawk	-0.30	-0.09	0.36
<i>Accipiter tachiro</i>			
Rufous-chested Sparrowhawk	-0.57	-0.17	0.40
<i>Accipiter rufiventris</i>			
Black Sparrowhawk	0.59	0.05	0.42
<i>Accipiter melanoleucus</i>			
Rock Kestrel		-0.20	0.28
<i>Falco rupicolus</i>			
Lanner Falcon	-0.20	-0.12	0.38
<i>Falco biarmicus</i>			
Peregrine Falcon	0.75	0.09	0.45
<i>Falco peregrinus</i>			

negatively associated with change in body condition (see Table 1 for summary of fixed effects) across this set of birds. Rainfall on the day of capture was also negatively associated with body condition, and although the magnitude of the effect was greater, rainfall was associated with more measurement uncertainty (wider confidence intervals). Rainfall of the previous day was not correlated with body condition, and neither was year, although for year the trend was positive, probably related to individual aging effects (older birds are heavier). Across species, in terms of effects of increasing maximum temperature on mass, effect size was generally small, with most change less than 1% of body mass per degree change in temperature (Appendix 1). However, for Malachite Sunbird a 1 °C change potentially equates to a 5% change of body mass.

Time series analysis on annual mean mass, body condition and wing length values

Levels of year-to-year correlation of mean mass values were low for this set of species, with correlation of lag year >0.5 for only five (12.5%, Appendix 2) out of 40 species: Karoo Scrub-robin, Orange-breasted Sunbird, Southern Double-collared Sunbird, Cape Weaver and Yellow Canary.

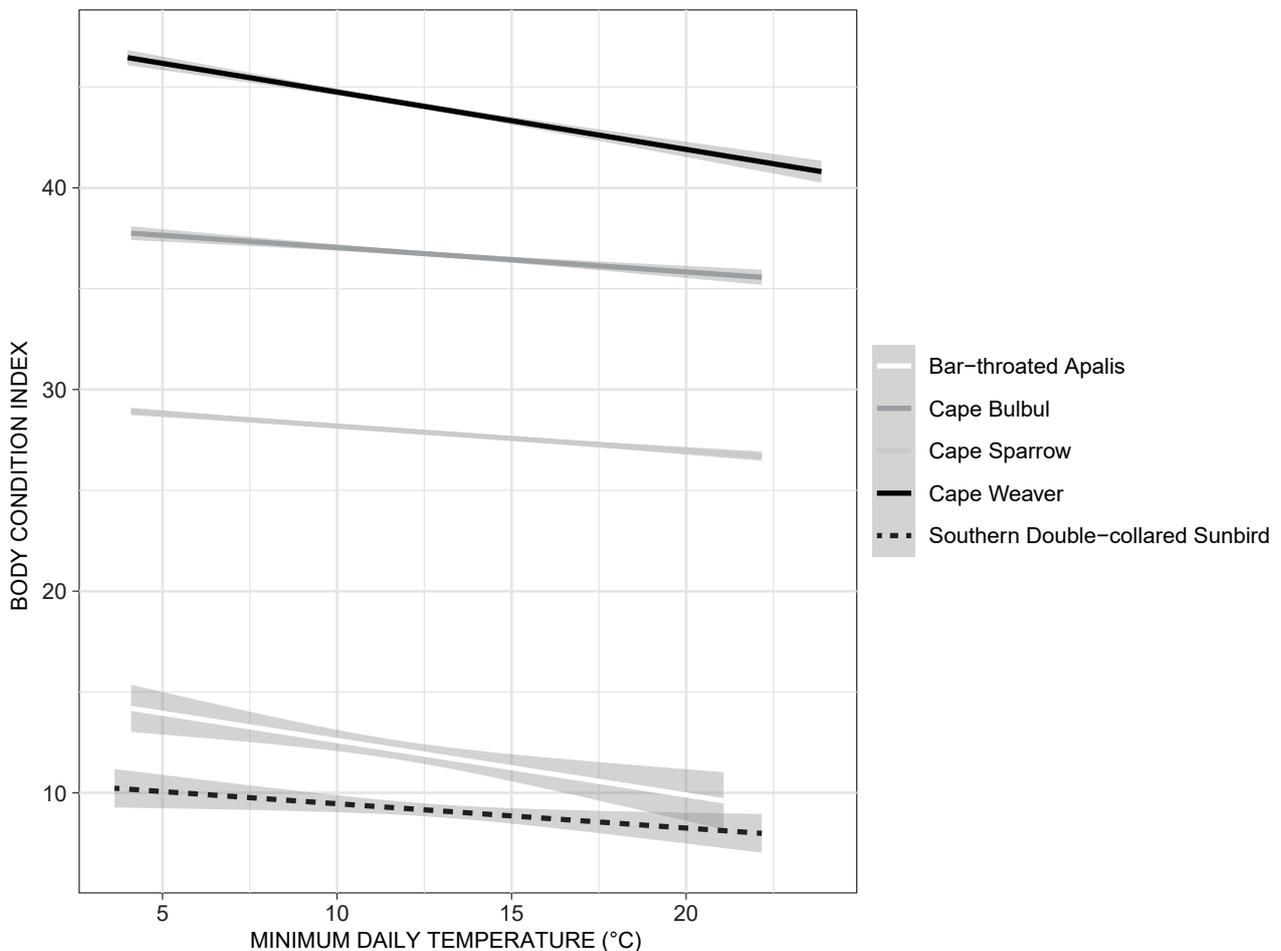


Figure 4: Daily body condition was influenced by minimum daily temperatures for 10 of the 40 study species: in each case a decline in the body condition index was observed. Slopes are linear regressions, with standard error as grey shading.

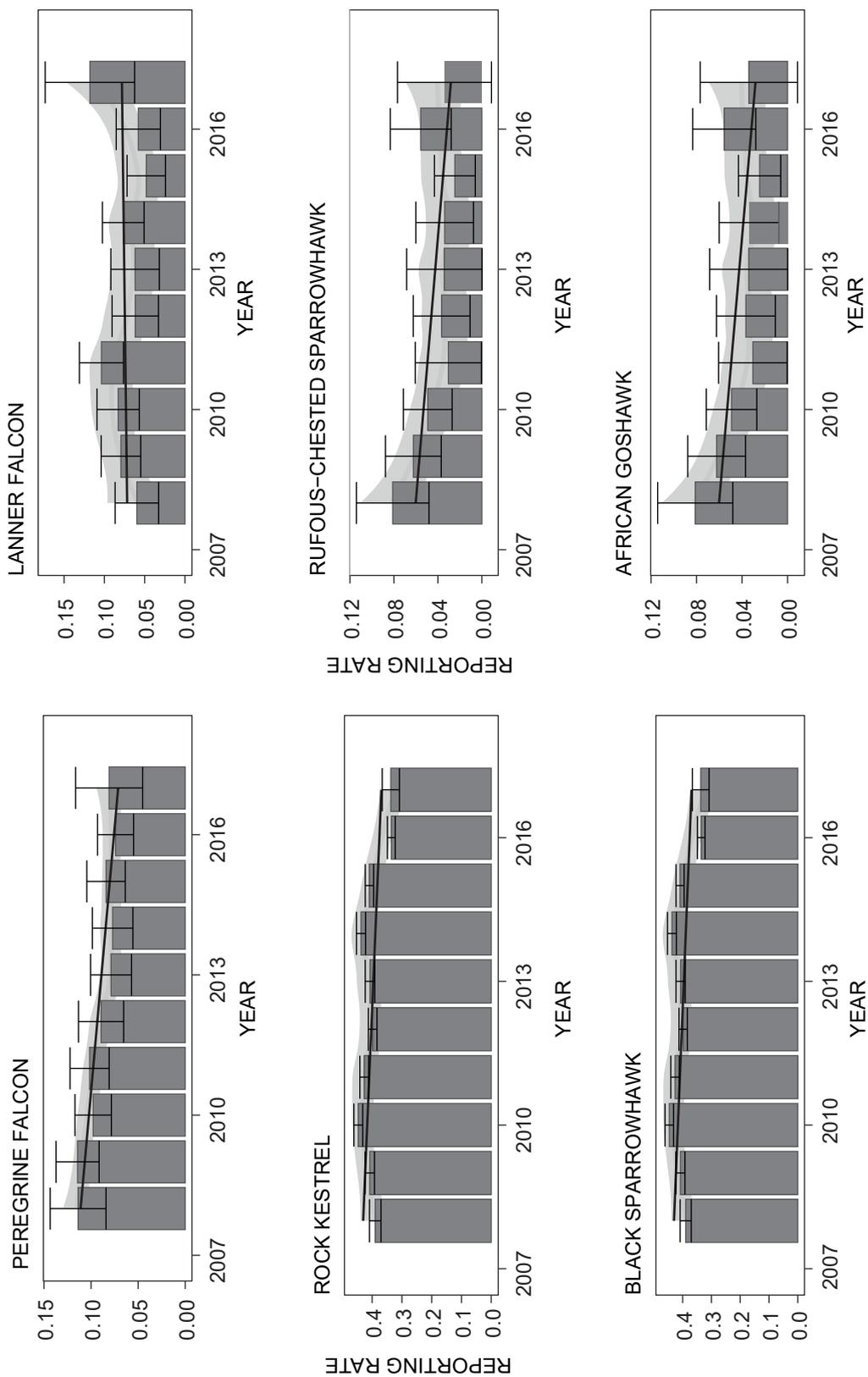


Figure 5: Interannual change in reporting rate for six of the most common raptors in the greater Cape Town area known to include birds in their diet. Bars are mean reporting rate across pentads delimited for this study, with error bars representing standard deviation. The lines indicate linear regression trends across the years, with standard error as grey shading.

The Double-collared Sunbird was the only species of the 40 to show temporal correlation between years for wing measurements, but this was not explained by temperature (cross-correlation coefficient (ccf) of mass with temperature of previous year = 0.35; Appendix 2). For three species, mass was negatively influenced by temperature of the previous year: Orange-breasted Sunbird (ccf = -0.57), House Sparrow (-0.43) and Cape Siskin (-0.53).

Relationship between body condition estimates and population change

There was no relationship between coefficients derived from body condition estimates as a function of maximum temperature, and population change between atlas periods for this set of 40 species (coefficient estimate: 0.005 ± 0.03 , $t = 0.16$, $p = 0.87$, $R^2 = 0$), suggesting little overall change in abundance measures resulting from maximum temperature impacts on body condition for this bird community.

Population metrics of raptors: addressing the starvation-predation hypothesis

Between atlas periods, trends for this set of raptors was weakly negative for five of seven species, with low associated confidence measures (Z-scores) for each (Table 1), i.e. no significant change, and consequently unlikely to be confounding interpretations of mass or body condition change. SABAP2 trends from 2007 to 2017 for all species, except for Lanner Falcon, were negative (Figure 5). These trends are counter to expectations derived for body condition and mass change for birds in the face of increasing predation pressure: for patterns of decreasing mass and body condition, increasing trends in encounters with predators would have been expected. In summary, changes in raptor populations do not seem to be confounding interpretation of body size change in this bird community.

Discussion

This analysis of wing length, mass and body condition (mass as a function of wing length), from measurements of birds submitted to the SAFRING database showed no evidence for a consistent decline in species' size in response to the overall warming observed. Therefore, we found little support for predictions arising from Bergmann's rule when applied to time rather than space. There was also no obvious population change, measured as change in abundance between atlas periods, for this community of birds as measured by each species' annual body condition response to high temperatures. This implies little systematic selective pressure across the 40 bird species within the present time frame as result of temperature. However, our time-series analysis indicated that in certain instances temperature can have a carry-over effect on mass between years for some species.

There are several possible explanations for why trends in these measures over time were non-significant, including: the relatively short time period considered (<30 years), our imposed level of statistical confidence, and the requirement to control for several confounding variables, including data gatherer (ringer), time of year (month) and sex. There may also be other contributing variables not considered,

e.g. McLean et al. (2018) found that different habitat types (wet/dry habitats) can have a strong effect on how temperature impacts body condition.

The species set represents the most commonly captured species and excludes some species from this region shown to be climatically vulnerable and in decline, such as Cape Rockjumper *Chaetops frenatus* (Milne et al. 2015). Overall, the study region is a coastal Mediterranean type climate, i.e. a mild climatic region with few temperature extremes. By contrast, changes in body size attributed to climate change for Australia were sampled across a nearly continental scale (Gardner et al. 2009). Much of Australia experiences extremely hot temperatures, compared with our study site.

Although slightly more species showed decreasing body mass over time than increases for this set of bird species, reasons for this might not be related to temperature. Environmental change independent of climate change can influence body size, e.g. diet (Tornberg et al. 1999), food availability (Little et al. 2017), habitat quality (Garant et al. 2005), stress (Thiel et al. 2008) and predation risk (MacLeod et al. 2005). Secondary effects of climate change on external variables may also occur. For instance, two granivorous species showed a lag in mass effect, as a consequence of temperature of preceding years, which may be a response to food availability, because plant growth and seed set are compromised in, for example, some grass species, as a consequence of heat stress (Prasad et al. 2008). The influence of ringer on mass measurements was pronounced, and any changes in ringer methods over time could not be accounted for here.

There was no strong evidence to indicate that changes in raptor populations were influencing body size patterns. Had more pronounced trends in decreasing body mass or raptor population change been observed, then the starvation-predation hypothesis could also have been invoked (Gosler et al. 1995), because both temperature and predation pressures select for smaller size. However, because the abundance of bird-eating raptors in our study area are stable or weakly decreasing over time, an observation consistent with other raptor studies from South Africa (Amar et al. 2016; Little and Navarro 2019), it is unlikely that raptors are contributing to any body mass or size changes. Should raptor declines continue, it is even possible that body mass may increase as a response in the future.

By contrast to limited observed effects on measurements over time, there was better support that variation is better explained by phenotypic plasticity e.g. changes in body condition was related to temperature, and this was especially evident for our analysis of the set of recaptured birds, which weighed less with increasing temperature. However, the magnitude of these effects on mass was small: for example, adult Cape Weavers lost 0.05 g (0.1% of body mass) for each degree increase in temperature. Interestingly, body-condition effects were observed as a function of daily temperature for several species. For four of the species, minimum daily temperature was negatively correlated with body condition. This means that for days that were consistently warm, body condition was generally lower, regardless of the maximum temperatures reached, suggesting prolonged warm periods may be detrimental to

body condition for several species in this set of birds. Most species can take behavioural measures (e.g. shade seeking; Cunningham et al. 2015) to avoid extreme temperatures that last for a short period: these are likely to translate into energetic costs only if foraging or other behaviours are compromised or if adverse conditions persist over a long period of time, e.g. an entire day in this case.

Year was a negative predictor of condition for the aerial insectivore, the Barn Swallow, also the only migratory species in this dataset. Unlike most other species in this dataset, the Barn Swallow has also been the focus of several studies. The recent trend for earlier arrival of Barn Swallows at their northern-hemisphere breeding areas is well documented worldwide (e.g. Deguchi et al. 2012; Turner 2009), and has been ascribed to global warming. Climate change also appears to be impacting other parameters of the species' phenology and life history, including interclutch interval (Møller 2007) (which influences body mass and may, in turn, have a knock-on effect on juvenile survival rates (Raja-aho et al. 2017)), moult, arrival and departure dates from its wintering grounds (Altwegg et al. 2012; Møller et al. 2011) and the location of these wintering grounds (Ambrosini et al. 2011). There are relatively fewer data on the effect of environmental conditions on Barn Swallow metrics, although Robson and Barriocanal (2008) found that local weather conditions can influence body condition. Significantly, Møller and Szép (2005) found that climate change was increasing male tail length, a secondary sexual character, a phenomenon that has important implications for survival and mate choice in the species. Møller et al. (2018) also suggest that a warming climate reduces the size of all mensural traits from the set of northern hemisphere species they consider, and also decreases developmental instability of wings in birds.

Although the Southern Double-collared Sunbird body condition was also found to be decreasing with time, this was also the only species with significant temporal autocorrelation across biometrics. Encouragingly, for the fynbos endemic, the Cape Sugarbird, neither time nor temperature were considered important predictors of body condition. However, it has previously been noted that for the Cape Sugarbird, urban environment and temperature stress were related to decreases in body condition across its range, with marked differences between males and females (Mackay et al. 2017). In addition, if effects are non-linear (e.g. decreased body condition at both low and high temperature), our modelling approach might not detect such relationships, although quadratic terms of weather variables were used in exploratory analysis and not found to be significant.

It is possible that datasets over greater timescales or in different parts of South Africa with greater climatic variability may produce different results and reach different conclusions regarding body size change. Going forward, we encourage bird ringers in the SAFRING ringing scheme to consistently record body metric data, including mass, head, tarsus and wing lengths, as temperature rises are occurring across South Africa (van Wilgen et al. 2015) and will continue into the future, as a result of climate change. How African birds will change in terms of body size is still unclear and requires additional investigation.

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Appendix 1: Effects of rain and maximum daily temperature on changes in mass for recaptured birds; n is the number of samples, SE = standard error, df = degrees of freedom, Percentage change is the mean percentage body weight change with one degree increase in temperature or 1 mm increase in rainfall, respectively, calculated as the model estimate divided by the bird mass

Name	Mass (g)	n	Covariate	Estimate	SE	df	t -value	p	Percentage change
Cape Robin-Chat	29.6	1 721	Intercept	44.920	5.725	136.377	7.846	0.000	
<i>Cossypha caffra</i>		1 721	maxT	-0.139	0.241	131.751	-0.576	0.565	-0.47%
		1 721	rain	-0.536	0.514	142.729	-1.042	0.299	-1.81%
White-throated Canary	29.2	48	Intercept	12.692	1.925	286.269	6.594	0.000	
<i>Crithagra albogularis</i>		48	maxT	-0.015	0.084	284.463	-0.178	0.859	-0.05%
		48	rain	-0.107	0.127	280.752	-0.837	0.403	-0.36%
Southern (Common) Fiscal	43.3	180	Intercept	19.629	2.779	21.883	7.063	0.000	
<i>Lanius collaris</i>		180	maxT	-0.014	0.096	21.668	-0.147	0.884	-0.03%
		180	rain	-2.523	4.069	14.207	-0.620	0.545	-5.83%
Cape Weaver	44.3	3 999	Intercept	64.097	2.371	50.422	27.037	0.000	
<i>Ploceus capensis</i>		3 999	maxT	-0.050	0.086	28.467	-0.577	0.569	-0.11%
		3 999	rain	0.174	0.123	27.503	1.412	0.169	0.39%
Cape Bulbul	36.9	685	Intercept	28.833	2.170	61.521	13.286	0.000	
<i>Pycnonotus capensis</i>		685	maxT	-0.010	0.087	41.514	-0.112	0.911	-0.03%
		685	rain	-0.323	0.245	36.689	-1.317	0.196	-0.87%
Yellow Canary	16.9	252	Intercept	13.627	2.048	50.000	6.653	0.000	
<i>Crithagra flaviventris</i>		252	maxT	-0.036	0.082	50.000	-0.444	0.659	-0.22%
		252	rain	-0.191	0.245	50.000	-0.780	0.439	-1.13%
Cape Wagtail	22.8	129	Intercept	37.719	0.893	611.836	42.250	0.000	
<i>Motacilla capensis</i>		129	maxT	-0.038	0.038	603.894	-1.021	0.308	-0.17%
		129	rain	0.019	0.081	593.643	0.233	0.816	0.08%
Southern Red Bishop	27.3	1 700	Intercept	20.643	0.805	202.000	25.641	0.000	
<i>Euplectes orix</i>		1700	maxT	-0.012	0.032	202.000	-0.389	0.697	-0.05%
		1 700	rain	0.013	0.079	202.000	0.160	0.873	0.05%
Cape Sparrow	27.8	906	Intercept	20.900	2.640	12.875	7.916	0.000	
<i>Passer melanurus</i>		906	maxT	-0.232	0.111	12.427	-2.087	0.058	-0.83%
		906	rain	0.483	0.569	13.984	0.849	0.410	1.74%
Southern Masked Weaver	32.7	3 434	Intercept	26.155	2.080	21.288	12.575	0.000	
<i>Ploceus velatus</i>		3 434	maxT	0.188	0.084	18.377	2.229	0.039	0.58%
		3 434	rain	0.032	0.122	14.830	0.264	0.795	0.10%
Laughing Dove	100.0	119	Intercept	30.703	1.022	1 673.834	30.034	0.000	
<i>Streptopelia senegalensis</i>		119	maxT	-0.010	0.042	1 672.403	-0.233	0.816	-0.01%
		119	rain	-0.092	0.078	1 641.395	-1.180	0.238	-0.09%
Levaillant's Cisticola	11.4	1 367	Intercept	12.346	1.358	12.940	9.092	0.000	
<i>Cisticola tinniens</i>		1 367	maxT	0.017	0.052	12.803	0.329	0.748	0.15%
		1 367	rain	0.423	0.288	10.609	1.470	0.171	3.72%
Fiscal Flycatcher	29.8	168	Intercept	30.092	0.433	834.387	69.534	0.000	
<i>Sigelus silens</i>		168	maxT	-0.088	0.018	820.320	-4.752	0.000	-0.29%
		168	rain	-0.063	0.047	789.913	-1.337	0.182	-0.21%
Speckled Mousebird	52.3	46	Intercept	33.720	0.548	1 078.366	61.512	0.000	
<i>Colius striatus</i>		46	maxT	0.029	0.021	989.233	1.367	0.172	0.06%
		46	rain	-0.068	0.073	892.421	-0.929	0.353	-0.13%
Southern Double-collared Sunbird	8.4	289	Intercept	143.768	12.655	20.781	11.361	0.000	
<i>Cinnyris chalybeus</i>		289	maxT	-0.052	0.463	16.469	-0.112	0.912	-0.62%
		289	rain	0.732	0.729	16.915	1.004	0.329	8.69%
Bokmakierie	62.7	61	Intercept	19.030	7.523	118.987	2.530	0.013	
<i>Telophorus zeylonus</i>		61	maxT	0.352	0.312	118.994	1.127	0.262	0.56%
		61	rain	-0.809	1.667	117.647	-0.485	0.628	-1.29%
Cape Bunting	20.2	208	Intercept	48.474	0.564	3 430.726	85.943	0.000	
<i>Emberiza capensis</i>		208	maxT	-0.145	0.024	3 363.840	-5.917	0.000	-0.72%
		208	rain	-0.048	0.044	3 366.020	-1.085	0.278	-0.24%
Olive Thrush	80.4	172	Intercept	78.828	12.902	4.298	6.110	0.003	
<i>Turdus olivaceus</i>		172	maxT	-0.220	0.476	3.771	-0.463	0.669	-0.27%
		172	rain	-112.712	13.451	3.352	-8.380	0.002	
Acacia Pied Barbet	38.8	150	Intercept	9.799	0.259	318.166	37.807	0.000	
<i>Tricholaema leucomelas</i>		150	maxT	-0.011	0.011	312.075	-1.052	0.293	-0.03%
		150	rain	0.000	0.019	303.031	0.004	0.997	0.00%
Cape Siskin	13.4	20	Intercept	35.614	4.789	155.638	7.437	0.000	
<i>Crithagra totta</i>		20	maxT	-0.232	0.202	151.975	-1.150	0.252	-1.73%
		20	rain	-0.272	0.652	152.326	-0.417	0.677	-2.03%

Appendix 1: (cont.)

Name	Mass (g)	n	Covariate	Estimate	SE	df	t-value	p	Percentage change
Cape Turtle Dove <i>Streptopelia capicola</i>	142.2	45	Intercept	8.441	3.326	96.000	2.538	0.013	
		45	maxT	0.126	0.143	96.000	0.878	0.382	0.09%
		45	rain	0.005	0.534	96.000	0.009	0.993	0.00%
Cape Canary <i>Serinus canicollis</i>	15.4	25	Intercept	25.027	0.722	182.482	34.670	0.000	
		25	maxT	-0.008	0.031	179.558	-0.260	0.795	-0.05%
		25	rain	-0.050	0.061	165.478	-0.828	0.409	-0.33%
Grey-backed Cisticola <i>Cisticola subruficapilla</i>	10.6	100	Intercept	22.846	2.793	268.283	8.178	0.000	
		100	maxT	-0.002	0.128	266.272	-0.015	0.988	-0.02%
		100	rain	-0.139	0.167	254.241	-0.832	0.406	-1.31%
Karoo Scrub Robin <i>Cercotrichas coryphoeus</i>	19.9	279	Intercept	104.575	4.925	103.352	21.233	0.000	
		279	maxT	0.021	0.209	95.717	0.102	0.919	0.11%
		279	rain	-0.572	0.601	98.939	-0.952	0.343	-2.87%
Bar-throated Apalis <i>Apalis thoracica</i>	11.7	296	Intercept	12.080	0.252	1 095.723	47.859	0.000	
		296	maxT	-0.021	0.010	1 063.357	-2.051	0.040	-0.18%
		296	rain	-0.026	0.029	912.207	-0.896	0.371	-0.23%
Long-billed Crombec <i>Sylvietta rufescens</i>	12.4	135	Intercept	13.815	2.746	129.000	5.031	0.000	
		135	maxT	-0.034	0.119	129.000	-0.290	0.773	-0.28%
		135	rain	-0.237	0.286	129.000	-0.827	0.410	-1.91%
Common Waxbill <i>Estrilda astrild</i>	9.5	492	Intercept	12.561	2.341	43.737	5.365	0.000	
		492	maxT	0.185	0.104	43.051	1.790	0.081	1.95%
		492	rain	0.043	0.126	26.706	0.340	0.736	0.45%
Cape Grassbird <i>Sphenoeacus afer</i>	28.4	32	Intercept	32.721	1.578	2.000	20.741	0.002	
		32	maxT	0.362	0.002	2.000	164.342	0.000	1.28%
		32	rain	-1.626	0.039	2.000	-41.439	0.001	-5.73%
House Sparrow <i>Passer domesticus</i>	25.0	196	Intercept	74.878	3.053	138.486	24.525	0.000	
		196	maxT	0.243	0.121	107.537	2.014	0.046	0.97%
		196	rain	-0.690	0.407	117.901	-1.694	0.093	-2.76%
Cape Sugarbird <i>Promerops cafer</i>	34.1	1340	Intercept	9.753	0.256	286.193	38.169	0.000	
		1340	maxT	-0.016	0.011	273.233	-1.465	0.144	-0.05%
		1340	rain	-0.023	0.032	213.235	-0.724	0.470	-0.07%
Brimstone Canary <i>Crithagra sulphuratus</i>	27.9	101	Intercept	17.484	0.965	2.995	18.118	0.000	
		101	maxT	-0.101	0.025	1.002	-4.048	0.154	-0.36%
		101	rain	1.260	0.301	1.007	4.182	0.148	4.52%
Malachite Sunbird <i>Nectarinia famosa</i>	16.4	54	Intercept	152.789	5.330	87.768	28.665	0.000	
		54	maxT	-0.830	0.225	83.945	-3.694	0.000	-5.05%
		54	rain	-0.380	0.313	79.158	-1.214	0.228	-2.31%
Cape Batis <i>Batis capensis</i>	12.2	53	Intercept	39.183	2.774	25.909	14.127	0.000	
		53	maxT	-0.131	0.109	25.998	-1.198	0.242	-1.07%
		53	rain	1.566	1.336	25.498	1.172	0.252	12.78%
Common Starling <i>Sturnus vulgaris</i>	74.3	21	Intercept	37.795	2.900	170.987	13.034	0.000	
		21	maxT	0.248	0.125	170.453	1.978	0.050	0.33%
		21	rain	0.098	0.133	170.700	0.737	0.462	0.13%
Pin-tailed Whydah <i>Vidua macroura</i>	15.2	6	Intercept	9.149	2.111	267.999	4.334	0.000	
		6	maxT	0.000	0.093	267.548	0.002	0.999	0.00%
		6	rain	-0.314	0.136	227.770	-2.308	0.022	-2.07%
Namaqua Dove <i>Oena capensis</i>	43.1	5	Intercept	34.729	0.544	2934.601	63.784	0.000	
		5	maxT	-0.065	0.023	2851.233	-2.771	0.006	-0.15%
		5	rain	-0.069	0.049	2788.532	-1.414	0.157	-0.16%
Sombre Greenbul <i>Andropadus importunus</i>	35.9	29	Intercept	29.749	0.723	1397.309	41.144	0.000	
		29	maxT	-0.078	0.030	1364.051	-2.575	0.010	-0.22%
		29	rain	-0.108	0.064	1427.946	-1.692	0.091	-0.30%
Barn Swallow <i>Hirundo rustica</i>	19.4	29	Intercept	52.876	4.920	40.571	10.747	0.000	
		29	maxT	0.070	0.203	42.294	0.346	0.731	0.36%
		29	rain	0.236	0.189	42.999	1.248	0.219	1.22%
Red-winged Starling <i>Onychognathus morio</i>	129.7	109	Intercept	40.863	6.217	42.985	6.573	0.000	
		109	maxT	-0.527	0.272	42.186	-1.939	0.059	-0.41%
		109	rain	-0.391	2.645	43.921	-0.148	0.883	-0.30%
Orange-breasted Sunbird <i>Anthobaphes violacea</i>	9.3	334	Intercept	15.313	2.488	237.000	6.156	0.000	
		334	maxT	0.078	0.104	237.000	0.753	0.452	0.84%
		334	rain	-0.078	0.209	237.000	-0.372	0.710	-0.84%

Appendix 2: Correlation coefficients from temporal autocorrelation analysis of mean measurements between years for mass, body condition (BCI) and wing length for time lag period 1 (year). Cross correlation coefficients are provided for time lead period for the effect of temperature on mean mass of the following year. Values >0.5 are highlighted in bold. Cape Siskin and Orange-breasted Sunbird have lower mass given warmer temperatures of the previous year

Name	Mass	BCI	Wing	Ccf T vs mass
Cape Turtle Dove	-0.184	-0.346	0.133	0.146
Laughing Dove	0.332	0.105	-0.141	-0.031
Namaqua Dove	-0.074	-0.047	0.245	-0.119
Speckled Mousebird	0.057	0.077	0.006	-0.211
Acacia Pied Barbet	0.040	-0.119	0.252	0.198
Barn Swallow	-0.031	-0.097	-0.058	-0.044
Cape Bulbul	0.368	0.388	0.112	-0.205
Sombre Greenbul	-0.161	0.052	-0.007	-0.009
Olive Thrush	0.198	0.110	-0.012	0.093
Cape Robin-Chat	0.116	0.172	-0.382	0.013
Karoo Scrub Robin	0.631	-0.055	0.239	-0.290
Cape Grassbird	0.030	-0.153	0.046	-0.181
Long-billed Crombec	0.408	0.362	0.221	0.333
Bar-throated Apalis	0.150	0.136	0.161	0.072
Grey-backed Cisticola	0.080	0.234	0.078	0.205
Levaillant's Cisticola	0.222	0.240	-0.141	0.209
Fiscal Flycatcher	0.035	-0.045	-0.016	0.250
Cape Batis	-0.008	-0.115	0.258	0.354
Cape Wagtail	0.082	-0.058	0.203	-0.306
Southern (Common) Fiscal	0.053	-0.100	-0.192	0.275
Bokmakierie	0.466	0.275	0.176	-0.216
Common Starling	-0.016	0.051	0.040	-0.036
Red-winged Starling	0.076	0.146	-0.130	0.149
Cape Sugarbird	0.086	0.121	-0.089	-0.057
Malachite Sunbird	-0.045	-0.021	0.479	-0.017
Orange-breasted Sunbird	0.696	0.574	-0.146	-0.570
Southern Double-collared Sunbird	0.601	0.546	0.615	0.353
House Sparrow	0.680	0.475	-0.107	-0.430
Cape Sparrow	0.487	0.494	0.455	-0.140
Cape Weaver	0.556	0.479	0.537	0.078
Southern Masked Weaver	0.259	0.286	0.507	0.189
Southern Red Bishop	-0.078	0.300	0.224	-0.130
Common Waxbill	-0.036	-0.358	0.177	-0.037
Pin-tailed Whydah	-0.224	-0.021	0.104	-0.097
Cape Siskin	0.304	0.215	0.062	-0.526
Cape Canary	-0.166	-0.026	0.126	0.008
Brimstone Canary	0.022	-0.114	0.115	0.105
White-throated Canary	-0.005	0.019	0.215	0.273
Yellow Canary	0.384	0.559	0.302	0.227
Cape Bunting	-0.074	-0.023	-0.305	-0.041