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ORIGINAL ARTICLE

# Urbanization, climate and ecological stress indicators in an endemic nectarivore, the Cape Sugarbird

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**Abstract** Stress, as a temporary defense mechanism against specific stimuli, can place a bird in a state in which growth rates and resistance to diseases are diminished. The Cape Sugarbird *Promerops cafer* is an endemic specialist of the Cape Floristic Region (CFR) of South Africa that may be threatened by urbanization and climate change. Ecological stress due to urbanization and climate may result in disease and morphological abnormalities. We investigated the correlation between urbanization and climate and four ecological stress indicators (tarsal disease, fluctuating asymmetry, body condition and feather fault bars) in 1375 Cape Sugarbirds from 14 sites across the CFR. Sugarbirds at sites with warmer climates had a higher incidence of tarsal disease and fault bars. Birds closer to urban settlements had higher levels of fluctuating asymmetry and fault bars in feathers. There were no clear correlations among stress indicators. Cape Sugarbirds are subject to multiple stressors, and adequate monitoring of population health will require assessment of multiple rather than single stress responses.

**Keywords** Cape Floristic Region · Fynbos · Climate change · Endemic birds · Fault bars · Fluctuating asymmetry · Tarsal disease · Urbanization

## Zusammenfassung

### Verstädterung, Klima und ökologische Stressanzeiger bei einem endemischen Nektarfresser, dem Kaphonigfresser

Stress, als vorübergehender Verteidigungsmechanismus gegen spezifische Reize, kann einen Vogel in einen Zustand versetzen, in dem Wachstumsraten und Resistenz gegen Krankheiten vermindert sind. Der Kaphonigfresser *Promerops cafer* ist ein endemischer Spezialist der Region Cape Floral (CFR) in Südafrika, der von Verstädterung und Klimaveränderung bedroht sein dürfte. Ökologischer Stress aufgrund von Verstädterung und Klima kann zu Krankheiten und morphologischen Anomalien führen. Wir haben den Zusammenhang zwischen Verstädterung und Klima und vier ökologischen Stressanzeigern (Tarsuskrankheit, fluktuierende Asymmetrie, Körperkondition und Hungerstreifen in den Federn) bei 1375 Kaphonigfressern an 14 Standorten quer durch die CFR untersucht. Kaphonigfresser an Standorten mit wärmerem Klima wiesen häufiger Tarsuskrankheiten und Hungerstreifen auf, Vögel aus der Nähe urbaner Siedlungen häufiger fluktuierende Asymmetrie und

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Hungerstreifen. Es gab keine deutlichen Korrelationen zwischen den Stressanzeigern. Kaphonigfresser sind vielfachen Stressfaktoren ausgesetzt, und um die Gesundheit von Populationen adäquat zu überwachen, ist es notwendig, vielfache und nicht nur einzelne Stressantworten zu bewerten.

## Introduction

The world's human population is growing rapidly. Accompanying this is a nearly exponential increase in urbanization, with concomitant pressures on biodiversity. African countries are experiencing unprecedented urbanization, with Cape Town showing the highest per capita population growth in South Africa (Holmes et al. 2012). Cape Town lies at the center of the renowned global biodiversity hotspot, the Cape Floristic Region (CFR), which is severely threatened by land transformation. Approximately 30% of this biome had been transformed by the turn of the century (Rouget et al. 2003), 26% by agriculture and 1.6% (ca. 1440 km$^2$) by urbanization. In addition to land conversion, climate change is a significant environmental driver of biodiversity change in the CFR (Hannah et al. 2002), with significantly increased temperatures and decreased rainfall expected over the next century (Midgley et al. 2003; IPCC 2013).

Urban habitats may pose a risk to birds and induce stress because of scarcity of natural habitat, increases in parasites, diseases or competitors, nutritional deficiency, presence of non-native predators, and intolerance of human activity (Gil and Brumm 2013). Additionally, urbanization reduces the functional diversity of the Cape Floristic Region's nectarivore guild (Pauw and Louw 2012), and can provoke immune responses to urban stress (Steyn and Maina 2015). However, some studies have noted that urbanization did not negatively affect the body condition and disease incidence of certain bird species (Evans et al. 2009a, b).

Fynbos endemic birds are ideal models for studying how some of these fine-scale mechanisms can reveal interacting impacts of urbanization and climate change on biodiversity of the Cape Floristic Region due to their biogeographic setting. The nectar-feeding fynbos endemic Cape Sugarbird *Promerops cafer* is predicted to be vulnerable to both climate change and urbanization, as it is a dietary specialist with a highly restricted range (Broekhuysen 1959; Lee and Barnard 2016). Climate change is predicted to reduce sugarbird survival due to reduction in resource availability, both through range contractions of species of Proteaceae (Hannah et al. 2002), on which sugarbirds depend for nectar, and an increase in frequency of fires (Wilson et al. 2010).

As part of a long-term study of endemic birds of the CFR, Cape Sugarbirds were noted in 2008 to have low and variable frequencies of potential indicators of population stress, including at that time an undiagnosed disease of legs and feet (P. Barnard, unpublished data). Although ornithologists had observed the disease on the Cape Peninsula in the 1980s (M. Fraser and A.G. Rebelo pers. comm.), its prevalence and virulence were not recorded. It has now been clinically confirmed to be an invasive alien *Knemidocoptes* mite responsible for tarsal disease (Latta 2003; Dabert et al. 2011, 2013).

Urbanization may increase the spread of disease via increased host contact rates, warmer microclimates (Hamer et al. 2012), and provision of resources at bird feeders and baths (Bradley and Altizer 2006). Therefore, within urban areas of the Cape Floristic Region, where such anthropogenic resources are commonly provided, the Cape Sugarbird may be more at risk of tarsal disease (Munday 2006).

Here we use four ecological stress indicators to estimate the impact of urbanization and climate on the endemic Cape Sugarbird: tail fluctuating asymmetry, fault bars, body condition and tarsal disease. Firstly, fluctuating asymmetry is a deviation from normal development causing a difference in size of characters on the left and the right side of the body (Palmer and Strobeck 2003; Møller and Swaddle 1997). Thus, the degree of asymmetry may be an indirect measure of the fitness of an individual through its potential to buffer genetic or environmental stress related disturbances (Clarke 1995; Møller and Swaddle 1997). A number of environmental stressors can cause fluctuating asymmetry, such as abnormal temperatures, reduced nutrition, lack of suitable food resources, noise pollution and the degradation and fragmentation of natural habitats (Parsons 1992; Swaddle and Witter 1994; Møller and Swaddle 1997; Lens et al. 1999). However, there is disagreement with the use of linking FA to stress and it should not be used as the sole stress predictor (De Coster et al. 2013).

Secondly, fault bars on feathers, which are transparent bands on feathers perpendicular to the shaft, are considered indicators of stress in birds, as they may be induced by the release of glucocorticoid hormones (Doolen 1999; Bortolotti et al. 2002). The reason for fault bars is irregularly developed or missing barbules, and feathers with such bars are weakened and more likely to break (Murphy et al. 1989). Nutritional stresses are viewed as the most common cause of fault bars (Slagsvold 1982; Machmer et al. 1992). However, any form of environmental stress that alters a bird's homeostasis may induce fault bars, including stressors related to urbanization (Ritchie et al. 1994; Doolen 1999).

Thirdly, body condition is an important indicator of ecological stress. The definition of body condition typically concerns the magnitude of energy stores (usually fat mass) relative to a linear measurement of size (Green 2001). Here we used the scaled body mass index as an indicator of condition (Peig and Green 2009). Body condition can change seasonally which may make this a more complex indicator to assess.

Fourthly, parasites constitute a major cause, as well as an indicator, of ecological stress because parasites utilize their hosts for nourishment and shelter. Ectoparasites can profoundly influence the survival and fitness of birds (Atkinson and van Riper 1991) by inducing stress (Merino et al. 1998; Martínez et al. 1999; Rinehart et al. 2002). The mite genus *Knemidocoptes* burrows into and inhabits the unfeathered skin of birds, such as the tarsus (legs) and feet, causing scaly-leg or tarsal disease (Latta and O'Connor 2001). Symptoms of *Knemidocoptes* infection are the formation of nodules creating spongy wart-like protrusions, which cause swelling (Schmidt and Roberts 2000; Procter and Owens 2000). Infection can cause serious abnormalities such as deformed tarsi and feet and loss of digits, negatively affecting walking, perching, and hence, potentially, survival (Pence et al. 1999). We assume that the main cause of observed tarsal abnormalities is due to this mite, as diagnostic opportunities were few, although we acknowledge the possibility of other pathogens.

In this study, we asked whether urbanization and climate variables affect the incidence of tarsal disease, body condition, fault bars and tail fluctuating asymmetry in the Cape Sugarbird. Such analyses of multiple ecological stress indicators are surprisingly rare (Brown 1996). We hypothesized that frequencies of tarsal disease and other stress proxies are positively correlated with proximity to larger and denser human settlements. We also examined the correlation of these variables with altitude, mean annual precipitation and mean annual temperature.

## Materials and methods

### Study sites

We sampled 14 study sites within the Cape Floristic Region (Fig. 1). This study focuses on the fynbos biome within the CFR (Rebelo and Siegfried 1990; Lombard et al. 1997). Mean annual precipitation at the 14 sites ranges from 323 to 1021 mm, mean annual temperature from 13.4 to 17.1 °C (Hijmans et al. 2005), and altitude from 44 to 1164 m (NASA 2000). The sites range from large, high-density urban settlements on the Cape Peninsula near Cape Town through small, low-density urban settlements (e.g. Rooi Els, Hermanus) to rural areas with sparse human settlements (e.g. Baviaanskloof). Statistics South Africa (StatsSA) uses enumeration areas (EAs), defined for human population censuses, to classify regions as urban or rural. EAs are classified on geographic traits, aerial photographs and administrative boundaries (StatsSA (Statistics South Africa) 2011; Laldaparsad 2012). Study sites were classified under the 2011 EA data as formal residential, parks and recreation (both classified in this study as known urban areas) and farms or vacant land (both classified in this study as known rural areas) (Table 2; StatsSA (Statistics South Africa) 2011).

### Study species

The Cape Sugarbird is a specialist nectarivore and fynbos endemic feeding mainly on nectar of ~22 species of Proteaceae. It is the most valuable bird pollinator of this fynbos family (Skead 1967; Collins and Rebelo 1987; Cheke et al. 2001). When their territories lack flowering Proteaceae, especially in the dry season, Cape Sugarbirds can travel up to 160 km in search of flowering proteas between breeding seasons, and males can return to the same breeding site annually (Fraser 1997; Calf et al. 2003). The winter breeding season is from July to November (Cheke et al. 2001), though recent records show earlier autumn breeding (April–June; Hockey et al. 2005). The sugarbird's specialized diet and restricted range likely contribute to its vulnerability (Simmons et al. 2004). However, sugarbirds will forage in urban areas in the day and return to mountain fynbos to roost (Cheke et al. 2001). Although sugarbirds exhibit these daily movements, individuals can be readily identified as urban or rural as they differ in the use of these habitats.

### Data collection

The contribution of data from a collective of researchers (see Acknowledgments) was compiled into a dataset of 2012 Cape Sugarbirds captured in mistnets, using standard ringing, sexing and morphometric measurement methods (De Beer et al. 2001). Cape Sugarbirds were examined for four ecological stress indicators, although not all indicators were recorded at all sites (Table 2). Females were identified by the narrow sixth primary feathers, presence of a brood patch, and/or shorter tail feathers (<200 mm) in comparison to males. We did not consider additional samples of birds that could not be confidently sexed ($N = 387$) or were recaptured ($N = 138$). We considered only adult Cape Sugarbirds over 1-year old, distinguished from sub-adults by a distinctly yellow vent (Seiler and Fraser 1985). This reduced the final sample for analysis to 1375 individuals.

### Body condition

We calculated a bird's body condition using the scaled body mass index (Peig and Green 2009), with the scaling

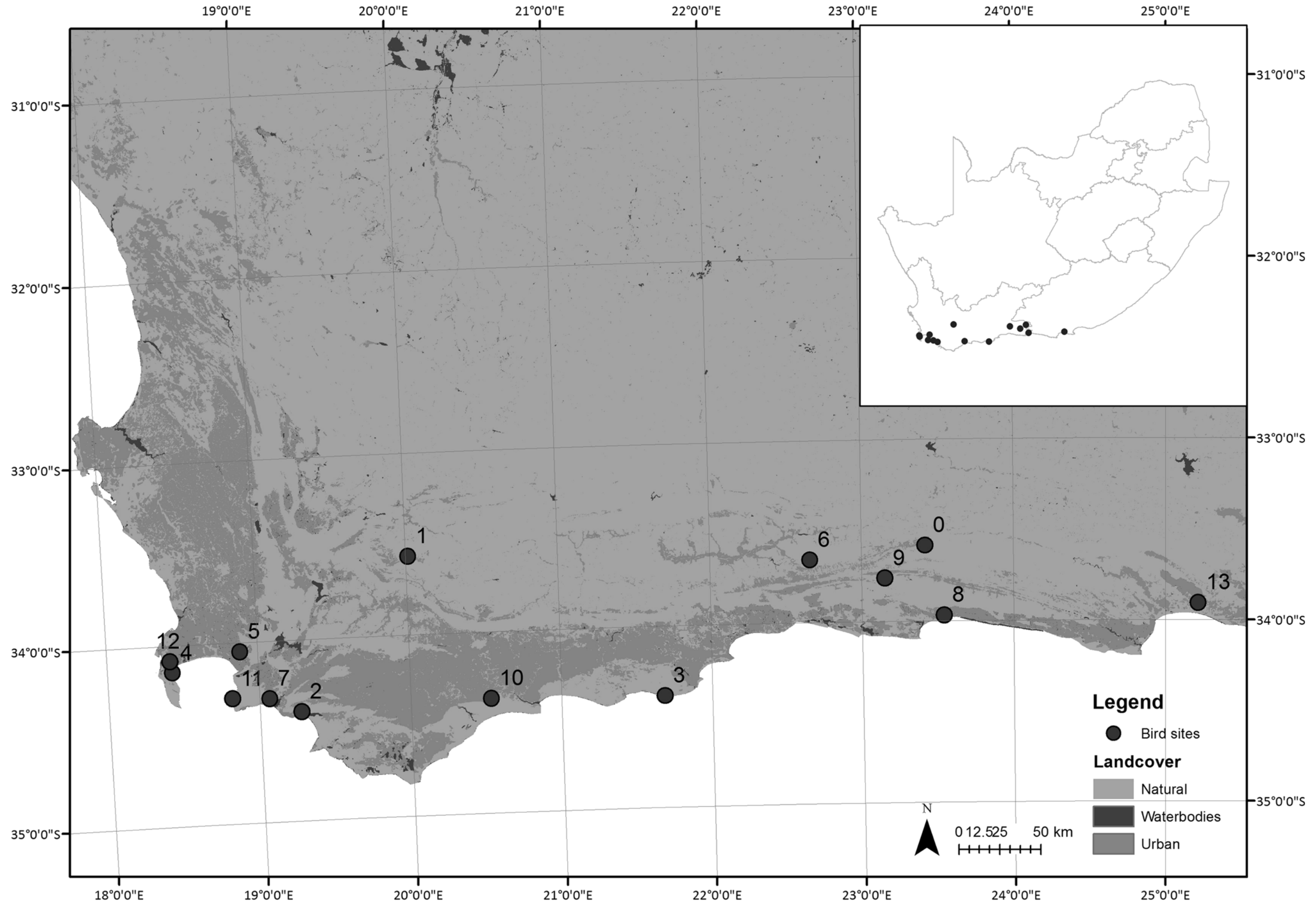

**Fig. 1** An overview of the Western Cape, with locations of the 14 study sites. Numbers represent study sites: *0* Blue Hill Nature Reserve, *1* Drie Kuilen, *2* Fernkloof, *3* Fynbos Strand, *4* Glencairn Elsies Peak, *5* Helderberg Nature Reserve, *6* Kamanasie, *7* Kleinmond, *8* Natures Valley, *9* Outeniqua, *10* Potberg Klippies, *11* Rooi Els, *12* Silvermine, *13* Van Stadens

exponent estimated from the slope of the regression of mass on tarsus length divided by Pearson's correlation coefficient *r*. To investigate the influence of season we undertook a linear regression of the body mass index against month as categorical variable, with site as a random effect, on each sex separately using the lme4 package (Bates et al. 2013).

### Fault bars

A rectrix is the stiff, main feather in a bird's tail which helps control the direction of flight. All rectrices present (10–12) were examined for fault bars. Each bird was visually inspected for the presence of fault bars (a score of 1) or their absence (a score of 0).

### Fluctuating asymmetry

Lengths of the longest paired fully-grown left and right rectrices of each individual were measured in mm using flat metal rulers. These were then standardized to absolute tail length to account for sex-specific effects as an index of fluctuating asymmetry.

### Tarsal disease

Individual birds were examined for the incidence of tarsal disease, recorded as either present or absent.

### Urbanization, climate and altitude

The distance in meters from capture site to the closest urban edge of the nearest settlement was measured using the Measurement tool (line measurement) in ArcMap$^{TM}$ 10 software by ESRI. Co-ordinates of each study site were plotted (Fig. 1) and a shape file of towns added as a layer. The size of the closest settlement was ranked on scale of 1 (village with population of ca. 10,000) to 5 (city with population >500,000). Each capture site was classified as urban or rural based on 2011 census data (StatsSA (Statistics South Africa) 2011). Mean annual precipitation and mean annual temperature were obtained from the

WorldClim database (Hijmans et al. 2005). Altitude (m.a.s.l.) at each site was obtained by using the site point shape file with the SRTM90 DEM from NASA (NASA 2000). However, altitude was strongly negatively correlated with mean annual temperature ($r = -0.95$, $P < 0.001$) and hence was dropped from full models to avoid collinearity (see below).

### Data analysis

We estimated repeatability of measurements, calculated as the intra-class correlation (Falconer and MacKay 1996) for a sample of individual birds captured on two or more occasions in the same or in different years. Repeatability for tarsal disease was 0.859 (SE = 0.027, $F = 14.195$, df = 93, 79, $P < 0.0001$), for fault bars 0.376 (SE = 0.084, $F = 2.426$, df = 90, 65, $P < 0.0001$), for fluctuating asymmetry 0.789 (SE = 0.041, $F = 12.580$, df = 80, 37, $P < 0.0001$), and for body condition 0.336 (SE = 0.085, $F = 2.333$, df = 86, 51, $P = 0.0007$). While repeatabilities were large for tarsal disease and fluctuating asymmetry, they were low but still highly significant for fault bars and body condition. Some of the variation among individuals was most likely due to measurement errors or age related change in morphology. Either way, we have demonstrated significant repeatability.

In exploratory analysis, we conducted correlations between stress indicators and environmental variables using the corr.test function from the psych package Revelle (2014) in R (R Core Team 2015). To illustrate the direction and magnitudes of the stressors we conduct a principal component analysis (PCA) using the prcomp function using information in the set of Cape Sugarbirds for which all stress indicator data was available ($n = 683$), with data automatically scaled and centered.

Generalized linear models were performed on the response variables. The four response variables used were presence or absence of tarsal disease, fault bars, fluctuating asymmetry, and the body condition index. Each response variable was run with the predictor variables sex, distance from capture site to closest urban edge, settlement size, mean annual temperature, mean annual precipitation, and urban vs. rural classification. Site was added as a random term to all models, and month as a random term for the body condition model in order to account for seasonal effects. Initial models were fitted using the lme4 package (Bates et al. 2013). Best-fitting models were selected based on Akaike Information Criterion (AIC) values from a model selection list created using the dredge function from the MuMIn package in R (Barton 2011). Further, we calculated averaged models based on the models within 2 AIC of the top model (if applicable), presenting full-model average coefficients as results.

To test for spatial autocorrelation, we conducted a Mantel test using the ecodist package (Goslee and Urban 2007) in R. Mantel tests are used to determine whether samples taken from a small area are more similar than those taken further apart (Goslee and Urban 2007). We thus tested for a relationship between the locations of capture sites and stress indicators. As sample sizes differed between measures, each indicator was tested separately. As per standard use, the number of randomizations was set to 1000 (Manly 1986; Luo and Fox 1996). If R lies outside the 95th percentile, there is spatial autocorrelation in the data.

## Results

The four condition measures were weakly correlated with each other with the largest Kendall correlation coefficient being −0.13 (body condition and fault bars; Table 1), but with opposing signs (illustrated in Fig. 2). Rainfall and temperature were also weakly positively correlated ($r = 0.33$, Table 1). Condition variables and environmental variables were weakly correlated with the largest $r$ being −0.16 (tarsal disease and altitude; or $r = 0.16$ for tarsal disease and temperature, Table 1). The 14 study sites are briefly described in Table 2, while the condition variables for the sites are described in Table 3. There is no clear distinction between urban and rural caught birds, although urban birds display more variability in the expression of the stress indicators (wider 90% confidence ellipse, Fig. 2). The summary metrics from model output are in Table 4 (see Online Appendix for detailed results of all models).

### Body condition

The body condition index of male sugarbirds was significantly higher than that of females (Fig. 3; Table 4). The best model explaining body condition (AIC = 6889) and the summary model of the three models within 2 AIC of the top model contained sex as the only significant predictor. Non-significant predictor variables in the summary model included urban vs. rural, distance to urban edge and temperature. There was no evidence of spatial autocorrelation for body condition across sites (Mantel $r = 0.1$, $P = 0.2$).

The body condition index was positively correlated with body mass ($r = 0.54$, df = 1555, $P < 0.0001$), mass divided by tarsus raised to the third ($r = 0.80$, df = 1555, $P < 0.001$), and residual body mass from a regression of body mass on tarsus length ($r = 0.84$, df = 1555, $P < 0.001$). Hence we can dismiss the possibility that our

**Table 1** Correlation matrix of the key stress indicators and main environmental predictors used in the analyses

| | Tarsal disease | Fault bars | Fluctuating Asymmetry | Body condition | Altitude | Urban edge | Urban size | Temperature |
|---|---|---|---|---|---|---|---|---|
| Fault bars | −0.01 | | | | | | | |
| Asymmetry | −0.04 | **−0.09** | | | | | | |
| Body_condition | 0.00 | **−0.13** | **0.11** | | | | | |
| Altitude | **−0.16** | **−0.09** | 0.00 | 0.06 | | | | |
| Urban edge | **−0.12** | **−0.15** | 0.02 | 0.02 | **0.73** | | | |
| Urban size | 0.07 | **−0.14** | 0.06 | 0.04 | **0.25** | **0.44** | | |
| Temperature | **0. 16** | **0.1** | −0.01 | **−0.08** | **−0.96** | **−0.69** | **−0.23** | |
| Rainfall | 0. 05 | −0.05 | 0.00 | −0.03 | **−0.37** | **−0.13** | **−0.44** | **0.33** |

Here we present correlations based on untransformed data and only for the set of data for which complete data were available ($n = 683$ individuals). Values are Kendall's rank order correlations $\tau$ with those with $P < 0.05$ indicated in bold

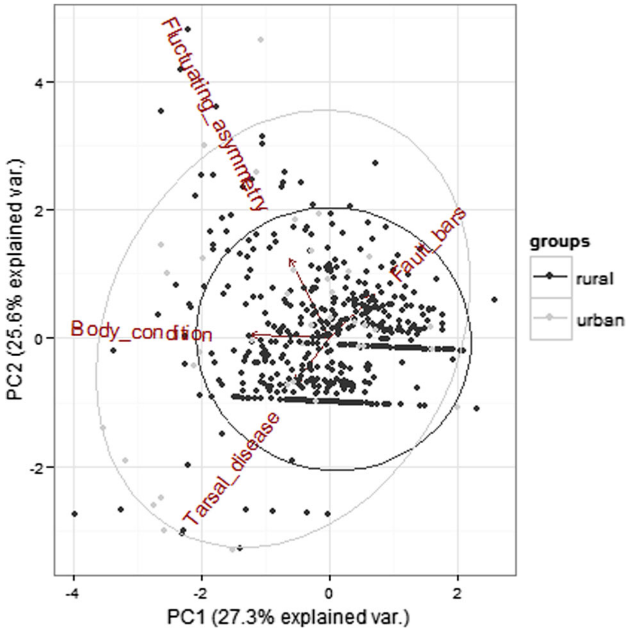

**Fig. 2** A plot of axes 1 and 2 of the PCA on 683 Cape Sugarbirds determined by stress indicators. *Ellipses* represent 90% confidence ellipses for birds classified as urban and rural. Different variables are shown

condition index provided a biased estimate of condition (Green 2001).

### Tarsal disease

Incidence of tarsal disease was low, with 71 (6.6%) of 1006 birds recorded with some level of disease. Tarsal disease increased significantly with increasing temperature, and the model containing only log temperature was the best model (Fig. 4; Table 4; AIC = 416, estimate ±SE = 8.7 ± 1.6, $z = 5.4$, $P < 0.001$). The next best model (AIC = 421) included sex and distance to urban edge as significant predictors. There was no evidence of spatial autocorrelation for tarsal disease across sites (Mantel $r = -0.11$, $P = 0.8$).

### Fault bars

Incidence of fault bars was high (655 or 59% of 1109 individuals), decreasing with increasing rainfall and distance from urban edge (Fig. 5). The urban/rural site classification and human population size of the nearest settlement were not significant predictors in the summary model, consisting of three models within 2 AIC of the top model with AIC = 1131 (Table 4). There was no evidence of spatial autocorrelation for incidence of fault bars across sites (Mantel $r = 0.04$, $P = 0.35$).

### Fluctuating asymmetry

Fluctuating asymmetry was frequently observed: 412 (68%) of 603 individuals. Males had higher incidence of fluctuating asymmetry than females (male: 80.7%, female: 55.1%), and urban more than rural birds (urban: 87.7%, rural: 66.3%; Fig. 6). Distance to urban edge and the interaction between rural and sex classes were not significant predictors in the summary model, consisting of three models within 2 AIC of the top model with AIC = 700 (Table 4). There was no evidence of spatial autocorrelation for incidence of fluctuating asymmetry across sites (Mantel $r = 0.05$, $P = 0.28$).

## Discussion

Stress, as a temporary defense mechanism against specific stimuli, can place a bird in a state of general nonspecific stress, in which growth rates and resistance to many diseases are diminished (Siegel 1980). Therefore, stress and stress indicators are of prime importance for conservation. This study addresses the impact of weather and

**Table 2** Site descriptions of the 14 study sites with associated ecological stress indicators measured at each site [tarsal disease (TD), fluctuating asymmetry (FA), fault bars (FB) and body condition (BC)] and site covariates for each site: urban or rural, distance to urban edge (Urban edge in km), ranked size of nearest settlement (Urban size), altitude (m), mean annual temperature (MAT in °C) and mean annual precipitation (Rainfall in mm)

| Locality | Stress Indicators | Urban vs rural | Altitude | Urban edge | Urban size | MAT | Rainfall |
|---|---|---|---|---|---|---|---|
| Blue Hill Nature Reserve | TD, FA, FB, BC | Rural | 1147 | 17.3 | 1 | 13.6 | 657 |
| Drie Kuilen | BC | Rural | 1000 | 23.4 | 3 | 13.7 | 323 |
| Fernkloof | TD, BC | Urban | 208 | 1 | 3 | 16.2 | 583 |
| Fynbos Strand | BC | Rural | 116 | 22 | 1 | 17.2 | 505 |
| Glencairn/Elsies Peak | TD, FA, FB, BC | Urban | 69 | 0.4 | 2 | 16.3 | 817 |
| Helderberg Nature Reserve | TD, BC | Urban | 207 | 3 | 4 | 16 | 888 |
| Kammanassie | TD, FA, FB, BC | Rural | 1164 | 26 | 2 | 13.4 | 637 |
| Kleinmond | TD, FA, FB, BC | Urban | 123 | 2.2 | 2 | 16 | 666 |
| Nature's Valley | TD, FA, FB, BC | Rural | 224 | 1.7 | 1 | 16.1 | 968 |
| Outeniqua | TD, FA, FB, BC | Rural | 764 | 31.6 | 2 | 14.8 | 822 |
| Potberg Klippies | BC | Rural | 416 | 28 | 1 | 16.4 | 592 |
| Rooi Els | TD, FA, FB, BC | Urban | 44 | 0 | 1 | 16.4 | 611 |
| Silvermine | TD, FA, FB, BC | Urban | 300 | 1.2 | 5 | 16 | 1021 |
| Van Stadens | TD, FA, FB, BC | Rural | 220 | 7.3 | 2 | 16.9 | 543 |

**Table 3** The 14 study sites with their associated sample sizes and proportion of records with tarsal disease (TD), fault bars (FB), fluctuating asymmetry (FA) and mean and standard deviation of body condition (BC mean and BC SD, respectively)

| Locality | *N* | FB | TD | FA | BC mean | BC SD |
|---|---|---|---|---|---|---|
| Blue Hill NR | 335 | 0.552 | 0.018 | 0.645 | 33.5 | 4.1 |
| Drie Kuilen | 16 | | | | 34.9 | 6.1 |
| Fernkloof | 208 | | 0.070 | | 33.7 | 4.7 |
| Fynbos Strand | 45 | | | | 35.0 | 4.6 |
| Glencairn/Elsies Peak | 101 | 0.688 | 0.129 | 0.946 | 36.4 | 5.7 |
| Helderberg Nature Reserve | 97 | | 0.000 | | 33.8 | 5.3 |
| Kammanassie | 233 | 0.443 | 0.021 | 0.695 | 34.4 | 3.8 |
| Kleinmond | 16 | 0.313 | 0.250 | 0.800 | 30.9 | 4.8 |
| Nature's Valley | 70 | 0.449 | 0.129 | 0.667 | 34.1 | 3.4 |
| Outeniqua | 51 | 0.392 | 0.078 | 0.644 | 32.0 | 2.8 |
| Potberg Klippies | 49 | | | | 32.3 | 6.0 |
| Rooi Els | 29 | 0.875 | 0.103 | 0.818 | 36.1 | 4.9 |
| Silvermine | 21 | 1.000 | 0.143 | 0.500 | 35.3 | 4.7 |
| Van Stadens | 104 | 0.657 | 0.091 | 0.639 | 32.6 | 4.0 |

urbanization on stress ecology of a fynbos endemic bird from Africa, the Cape Sugarbird. It is an inherent but often untested assumption that ecological stress indicators reflect aspects of fitness, with individuals with higher index values suffering from reduced fecundity or viability (Brown 1996). Likewise, it is an inherent assumption that different stress indicators are positively correlated. There is published evidence consistent with both these assumptions. For example, in several bird species, individuals with more fault bars have a reduced probability of escape from predators (Møller et al. 2009), and those with higher levels of fluctuating asymmetry suffer reduced fecundity and survival (Møller 1999). We are unaware of any direct evidence showing that tarsal disease is linked to reduced survival prospects, although many studies have linked disease to increased mortality (Atkinson and van Riper 1991). There are few explicit studies showing increased fecundity and survival among individuals with elevated condition index values (see Balbontín et al. 2012 for an exception). Reduced body mass may reflect a strategic reduction in costs of flight, rather than poor phenotypic quality (Norberg 1981). Yet there is significant empirical

**Table 4** Summary metrics from model output across the four stress indicator variables, with summary model results for body condition, fault bars and fluctuating asymmetry and best model by AIC for tarsal disease

| | Body condition | Fault bars | Fluctuating asymmetry | Tarsal disease |
|---|---|---|---|---|
| No. birds in analysis | 1184 | 825 | 603 | 1006 |
| *N* sites (intercept) | 14 | 9 | 9 | 11 |
| Estimate | 32.9 | 9.687 | 0.033 | −46.433 |
| SE | 2.24 | 3.247 | 0.199 | 8.210 |
| *z* | 14.6 | 2.979 | 0.168 | −5.656 |
| *P* | 0.000 | 0.003 | 0.867 | 0.000 |
| Male | | | | |
| Estimate | **1.44** | | **1.263** | |
| SE | **0.26** | | **0.189** | |
| *z* | **5.6** | | **6.674** | |
| *P* | **0.000** | | **0.000** | |
| Sex male:urban | | | | |
| Estimate | | | −0.055 | |
| SE | | | 0.420 | |
| *z* | | | 0.132 | |
| *P* | | | 0.895 | |
| SizeUrban | | | | |
| Estimate | | −0.011 | | |
| SE | | 0.067 | | |
| *z* | | 0.165 | | |
| *P* | | 0.869 | | |
| Ue | | | | |
| Estimate | −0.014 | **−0.029** | 0.003 | |
| SE | 0.028 | **0.008** | 0.008 | |
| *z* | 0.494 | **3.451** | 0.346 | |
| *P* | 0.621 | **0.001** | 0.729 | |
| Urban | | | | |
| Estimate | 0.271 | 0.038 | **1.473** | |
| SE | 0.62 | 0.177 | **0.465** | |
| *z* | 0.437 | 0.217 | **3.159** | |
| *P* | 0.662 | 0.828 | **0.002** | |
| Log (mean annual rainfall) | | | | |
| Estimate | | **−1.397** | | |
| SE | | **0.493** | | |
| *z* | | **2.831** | | |
| *P* | | **0.005** | | |
| Log (mean annual temperature) | | | | |
| Estimate | 0.002 | | | **8.698** |
| SE | 0.014 | | | **1.626** |
| *z* | 0.157 | | | **5.349** |
| *P* | 0.875 | | | **0.000** |

Estimate is the estimate of the coefficient of the covariate, with *SE* standard error. *z* is the *z* statistic, with $P = \Pr(>|z|)$. Values in bold font are statistically significant

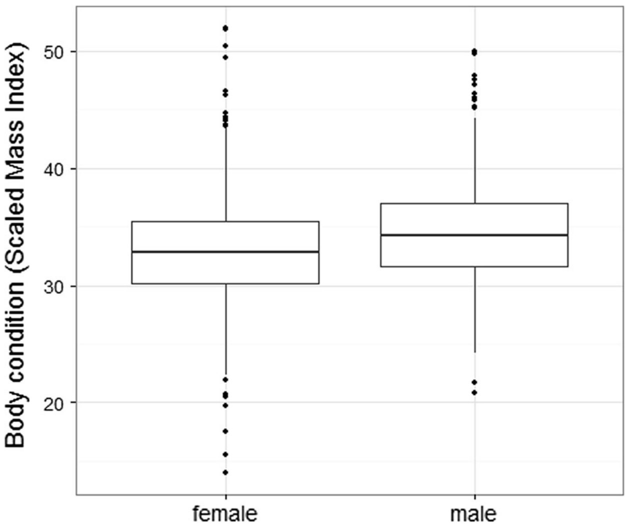

**Fig. 3** Boxplots of body condition of Cape Sugarbirds by sex, indicating median, interquartile range, 5- and 95-percentiles and extreme values. There was a significant difference in mean body condition between the sexes across the study area

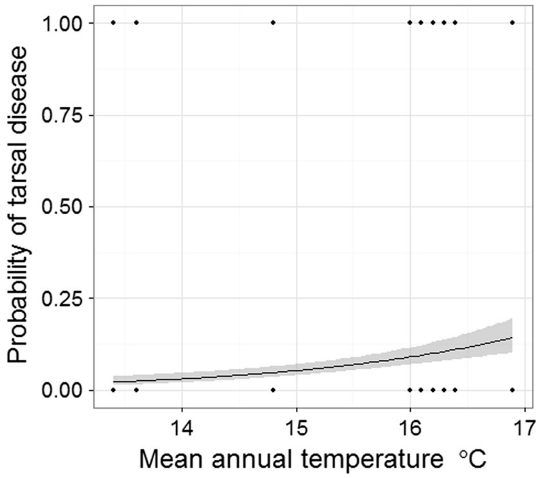

**Fig. 4** Probability of tarsal disease in Cape Sugarbirds as a function of mean annual temperature of capture site. *Grey shading* is 95% CI of the regression

evidence that ecological stress indicators, indeed, reflect inherent condition, and thus potentially correlate with elevated fecundity and survival.

We documented positive, but weak, relationships between some of the four condition indices. This indicates that condition indices may not always be positively correlated, but also that stress indicators may reflect different components of stress. Brown (1996) made a similar conclusion across a large number of bird studies. The large samples in our study show that this lack of positive correlation is not a statistical power issue. We conclude that stress indicators are not simplistically correlated in Cape

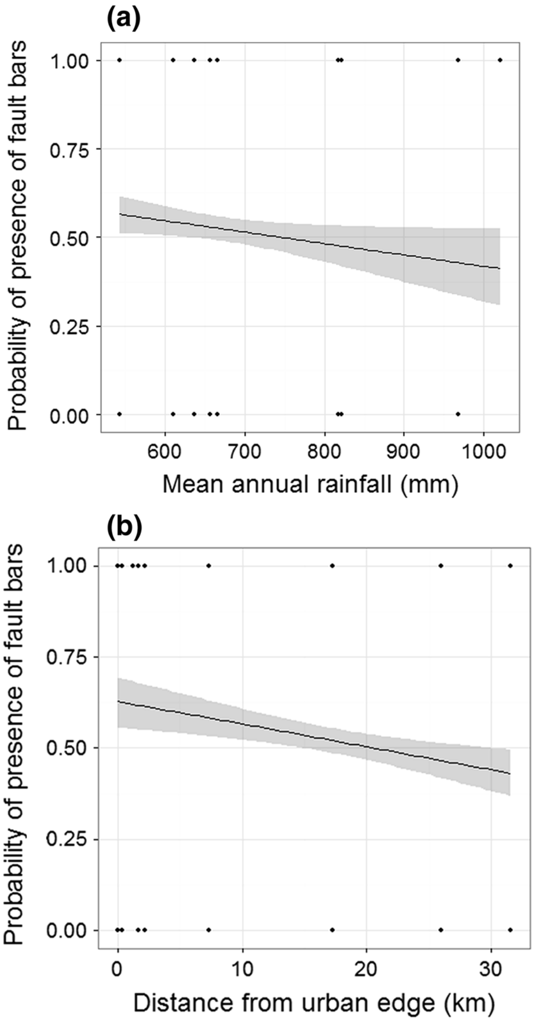

**Fig. 5** **a** Probability of presence of fault bars in rectrices of Cape Sugarbirds as a function of mean annual rainfall (mm) of capture sites. *Grey shading* is 95% CI of the regression. **b** Probability of presence of fault bars in rectrices of Cape Sugarbirds as a function of distance from nearest urban edge to capture site (km). *Grey shading* is 95% CI of the regression

Sugarbirds, and perhaps other species, and that developing a general index of body condition is not straightforward.

We found that tarsal disease was best explained by temperature in modeling. Sugarbirds from our sites with higher mean temperatures had higher prevalence of tarsal disease. Latta (2003) showed that tarsal disease incidence on Cape Sugarbirds was higher in areas with low rainfall. Dry, warm climates can create optimal conditions for survival and reproduction of the *Knemidocoptes jamaicensis* mites that cause tarsal disease (Van Riper 1991; Munday 2006). Warm temperatures may also increase susceptibility of Cape Sugarbirds to tarsal disease if heat stress weakens the bird's immune system (Deerenberg et al. 1997; Saino et al. 1997). Thus, increasing temperatures may facilitate the spread of *Knemidocoptes* throughout populations of endemic Cape Sugarbirds. In our study, the incidence of tarsal disease decreased with altitude, possibly because *K. jamaicensis* cannot survive low temperatures at high altitude (Latta and O'Connor 2001).

We found higher rates of fault bars in drier sites, and those closer to human settlements. Fault bars are associated with starvation, malnourishment, difficult climatic and environmental conditions, dehydration, overheating, illness, cooling, noise pollution and the degradation and fragmentation of natural habitats (Parsons 1992; Ritchie et al. 1994; Swaddle and Witter 1994; Doolen 1999; Lens et al. 1999). Furthermore, fault bars often lead to feather breakage and the associated risk of mortality due to impaired aerodynamics (Møller et al. 2009). We predict that decreased rainfall and drying will thus tend to increase this measure of stress in Cape Sugarbirds.

Sugarbirds at urban sites were more often asymmetric than those at rural sites. Many other studies have shown habitat effects on the incidence and extent of fluctuating asymmetry (Møller and Swaddle 1997). Furthermore, male sugarbirds had higher rates of fluctuating asymmetry than females. This is expected, given significant sexual size dimorphism in tail length, with males having much longer tail feathers than females (Møller and Swaddle 1997). However, the conclusions made from linking FA to environmental stress should be interpreted with caution due to the controversy surrounding its application (see De Coster et al. 2013).

We found no direct evidence of a link between scaled body mass index and proximity to urban areas, or any other urbanization variable. Hence, we found no evidence of a habitat link to body condition. This is contradictory to an extensive array of previous bird studies linking urbanization to low body condition (Richner 1989; Pierotti and Annett 2001; Ruiz et al. 2002; Partecke et al. 2006; Mennechez and Clergeau 2006; Liker et al. 2008; Shochat et al. 2010). Our findings also imply that body mass indices may not consistently reflect the amount of body fat, but rather mirror phenotypically plastic temporary changes in weight linked to the cost of flight (Norberg 1981) or life history events such as breeding. It is also important to note that in our study we controlled statistically for seasonal change in condition.

Our study suggests that climate variables are associated with the expression of tarsal disease and fault bars in the Cape Sugarbird. Additionally, tarsal disease is more prevalent in low-lying areas, as *Knemidocoptes* mites survive less well at higher altitudes (Latta and O'Connor 2001). Sites with lower rainfall were associated with increased tarsal disease and fault bars.

The findings we report here are particularly important in the face of climate change. The Cape Floristic Region is predicted to experience an increase in temperature and decrease in rainfall (Midgley et al. 2005). We predict that Cape sugarbirds may experience increased population

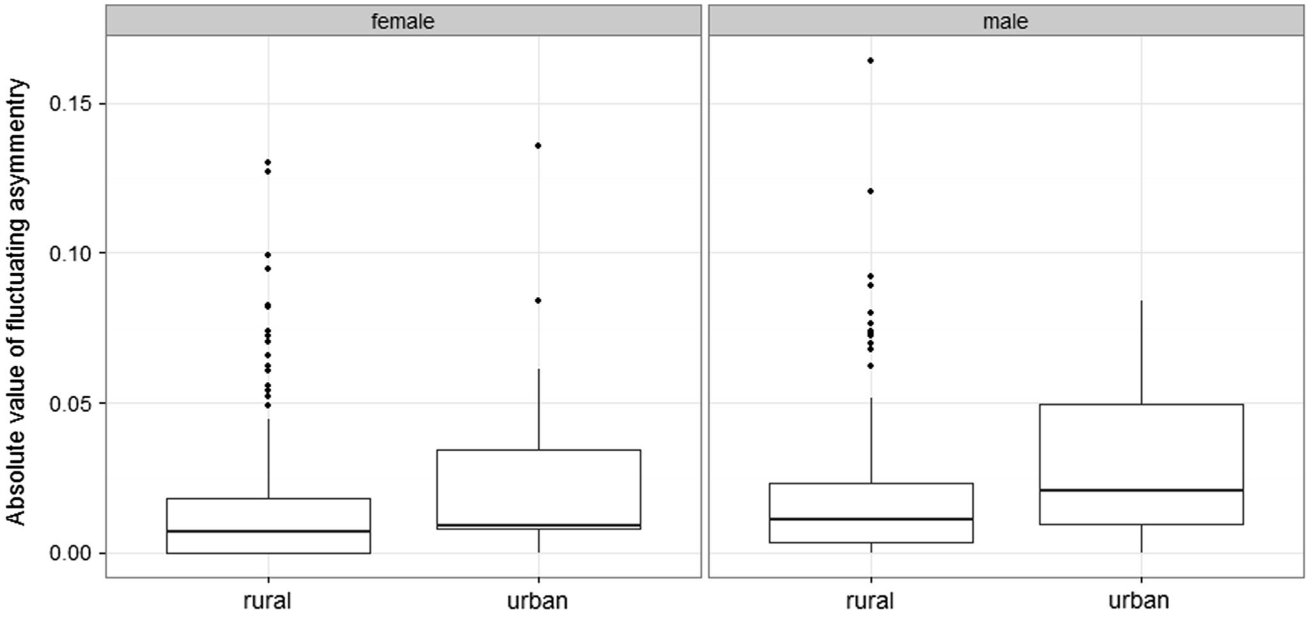

**Fig. 6** Boxplots of absolute values of fluctuating asymmetry of rectrices of Cape Sugarbird by sex and location (rural vs urban), indicating median, interquartile range, 5- and 95-percentile and extreme values. Probability of fluctuating asymmetry was best explained by habitat classification and sex

stress, and reduced fecundity and survival, if the climate continues to warm and dry.

Some aspects of urbanization appear correlated with fault bars and fluctuating asymmetry in Cape Sugarbirds. This may be due to urban-edge stressors such as poor nutrition derived from artificial feeders, predation, and habitat degradation and fragmentation, though more research is needed to explore the exact causal mechanisms.

The fynbos biome of the Cape Sugarbird is under severe threat from both urbanization and climate change. The findings of this study can help support conservation measures aimed at increasing persistence of the Cape Sugarbird and other fynbos endemics. For instance, nutritional and heat stress can potentially be reduced by encouraging urban planting of indigenous nectar-bearing and shade plants (Pauw and Louw 2012).

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