Environmental Drivers of an Urban Hadeda Ibis Population

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Weather and habitat-use are key factors that influence the survival of a species. A central goal in conservation biology is to gain a mechanistic understanding of how these quantities limit a species' range. We examined how weather, season and geographic location influenced the demographic rates of an urban population of Hadeda Ibises *Bostrychia hagedash* on the leading edge of its expanding range in the Western Cape of South Africa. The Hadeda Ibis has increased its South African range 2.5 times within the last 50 years and is now a common urban resident throughout most of the country. Using capture–mark–recapture and generalized linear models, we build upon previous demographic analyses of this species. Our results show no significant influence of weather on demographic rates. Rainfall triggered the onset of the main breeding season (although breeding pairs were found at any time throughout the year), and Hadeda Ibises adjusted their breeding phenology according to the rainfall season of the areas into which they expanded. There was no evidence of spatial correlation within the study area. Hadedas have quickly adapted well to urban areas outside of their original range. Because weather had little effect on Hadeda demographics we suggest that urban areas may potentially buffer unfavourable effects of weather on Hadeda survival and are an important factor in the successful range expansion. This finding is consistent with the explanations of range expansions of other ibis species throughout the world.

Key words: capture–mark–recapture, Hadeda Ibis, range expansion, demography, climate change

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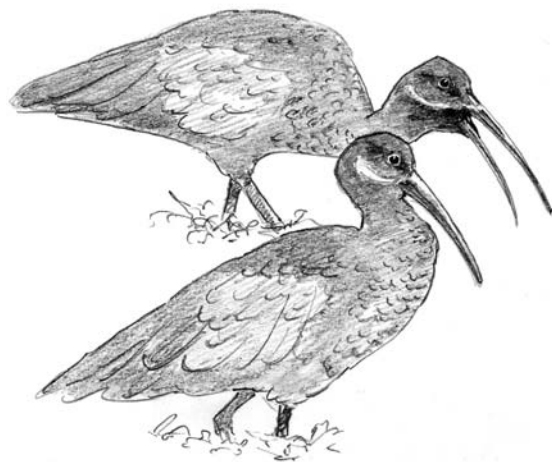
A species' range can be viewed as the geographic space where conditions allow a species to achieve positive population growth (Gaston 2003), i.e. additions through birth and immigration at least balance losses through death and emigration. Weather and habitat are two key quantities that affect the dynamics of a species' range (Sæther *et al.* 1996, Hughes 2000, Stenseth *et al.* 2002, Walther *et al.* 2002). One way these two quantities influence range dynamics is by affecting the demographic rates of populations that make up the edge of the range. Examining the drivers of demographic rates in populations at the range margin should therefore yield critical information for a better understanding of range dynamics.

In addition to weather and habitat, anthropogenic processes strongly affect the range boundaries (and range shifts) of species, due to fragmentation or loss of natural habitat as a result of rapid agricultural, commercial and housing pressure. This has been linked to substantial biodiversity loss (Fischer & Lindenmayer 2000, Kolar & Lodge 2001, Mcgarigal & Cushman 2002). What is less well appreciated is how human-modified landscapes have created suitable habitats for a range of species, such as doves and pigeons (Romagosa & Labisky 2000), insects (Thomas *et al.* 2001), foxes (Harris & Smith 1987), badgers (Harris 1984), and rodents (Ecke 1954, Lurz *et al.* 2001). Urban environments are attractive habitats for some species because they potentially buffer the effects of weather and may provide a year-round source of food (Duckworth *et al.* 2010).

One species that has profited from human-modified landscapes is the Hadeda Ibis *Bostrychia hagedash*, hereafter 'Hadeda'; see Duckworth *et al.* (2010) for a

detailed account of this species. In South Africa, Hadedas were originally confined to the eastern, wetter parts of the country that receive annual rainfall in excess of 1000 mm (Macdonald *et al.* 1986, Vernon & Dean 2005). As of the 20th century, Hadedas progressively expanded southwards and westwards into areas that are naturally hot and dry, increasing their South African range from 31,000 km² in 1910 to 1,300,000 km² in 1985 (Macdonald *et al.* 1986).

Reasons for their range expansion include the planting of mostly large-growing alien trees which provide roosting and nesting locations, and the artificial creation and irrigation of fields and lawns, that create excellent year-round foraging grounds (Macdonald *et al.* 1986, Duckworth *et al.* 2010). Hadedas are now common birds within urban areas throughout South Africa and are frequently observed foraging on parks, gardens, open fields and sports fields.

Here we examine a population of Hadedas on the edge of their expanding range, living in mostly human-modified landscapes, i.e. urban areas, in the Western Cape of South Africa. Duckworth *et al.* (2012) presented basic demographic information for this population. We investigate in detail potential climatic drivers of survival, reproductive success and breeding phenology.

Of all climatic factors, we expected rainfall to be the most important. Hadedas mostly prey on soil-living invertebrates, and do so more efficiently at relatively high soil moistures (0.7 cm³ of water for every cm³ of soil), whilst in areas of low soil moisture, for example <0.2 cm³/cm³, they struggle to find food. In the core area of our study there is a steep rainfall gradient, going from in excess of 1000 mm per year on the slopes of Table Mountain, to 400 mm per year over the flatter regions of Cape Town Cape Flats (Kruger 2004). We hypothesise that if the Hadedas' survival in the Western Cape is mostly dependent on weather, individuals and nests in areas that receive more rainfall would be more successful than those in areas of less rainfall. If Hadeda survival was maintained by human-modified landscapes, then individuals and nests throughout the study area would be equally successful.

METHODS

Species

The Hadeda is a large wading bird (adults 76 cm, 1.3 kg; Vernon & Dean 2005). Its original range was confined to wet areas of Southern Africa, but it has since colonised hot and dry areas and is now a common urban bird throughout South Africa (Macdonald *et al.*

1986, Duckworth *et al.* 2012). Its success in these areas may partly be attributed to human-induced land-use changes (for example, the creation of gardens, parks, and sports fields; Duckworth *et al.* 2010). The main breeding season coincides with the rainy season, but it is able to breed at any time of the year and produce multiple broods per year, given suitable conditions. Hadedas generally raise between 1 and 3 fledglings per brood. There is an age-effect on reproductive success: older breeding pairs raise more fledglings per year than do younger pairs. Incubation is typically 28 days, and after hatching, nestlings remain in the nest for a further 28 days.

Study Area

This study was conducted in the Western Cape of South Africa over the period 2003 to 2010. This region experiences a typical Mediterranean weather: cold, wet winters, and hot, dry summers (Kruger 2004). The core study area was the greater Cape Town area, roughly covering 3200 km².

Climatic variables

Climatic data was obtained from the South African Weather Service (SAWS), who recorded weather data via stations situated throughout the country. For our analyses it would have been ideal to use weather data from the weather station closest to each observation. Unfortunately, this was not possible due to limitations in the weather data. Therefore, we used the average values across the study area, which were more reliable and consistent.

Five climatic variables (hereafter called covariates) were chosen to investigate the effect of weather on Hadeda demographic rates and were obtained from the SAWS. These were: total rainfall (measured in mm), temperature (minimum and maximum, °C), and wind speed (average and maximum, km/h). Data spanned from 2003 until November 2011.

Covariates were chosen because of their hypothesised influence on Hadeda demographics. Rainfall has been shown to influence Hadeda foraging success through its effect on soil moisture (Duckworth *et al.* 2010). Hadedas construct nests on exposed branches in trees making wind speed a potential factor affecting reproduction. During the winter, maximum wind gusts can reach high speeds (over 60 km/h). Hadedas are only absent from exceptionally hot and dry places of South Africa (such as the Northern Cape; Harrison *et al.* 1997, Duckworth *et al.* 2010), and therefore the hot, dry summers experienced in the Western Cape may affect their survival and reproduction.

In exploring the effect of weather on Hadeda demographics, we built on earlier analyses of a subset of the present data (Duckworth *et al.* 2012). More detail on the methods can be found there but a brief description is presented in the next section.

Breeding phenology

Breeding phenology of Hadedas was examined in relation to the seasonality of rainfall in two separate analyses. The first analyses examined the onset of breeding in relation to annual rainfall in the Western Cape. Hereafter we refer to this analysis as 'Western Cape phenology'. This analyses aggregated the mean number of nests from which nestlings fledged (hereafter, referred to as 'active nests'), and the average total rainfall per month over the period 2005–2011. We fitted two trigonometric curves (equation shown below); one fitted to the mean number of active nests per month and the second to the average total monthly rainfall. This allowed us to determine the annual peak in number of active nests and rainfall.

The second set of analyses compared Hadeda breeding phenology between areas of Southern Africa with either winter (defined as June, July and August) or summer (December, January, February) rainfall regimes. Hereafter we refer to this analysis as 'Southern Africa phenology'. We collected breeding data in this study within the Western Cape over the period 2003–2011 and compared it to Nest Record Cards (NERCs) which represented breeding data from southern Zimbabwe and eight provinces within South Africa. NERC data spanned from 1940 to 1994 (although not every year within this range was represented). Data were categorised depending on the main rainy season for each area: winter (Western Cape – data collected mostly from this study, but also included NERCs), summer (Gauteng, Mpumalanga, Limpopo, Free State, southern Zimbabwe and KwaZulu-Natal – NERCs) or year-round (Eastern Cape – NERCs). The mean number of active nests was aggregated per month, as with the first analyses. Unfortunately, there were few data points for summer and year-round rainfall regions. Winter rainfall areas totalled 261 observations, summer rainfall 35 observations and year-round rainfall areas 28. Observations for summer rainfall data spanned across 12 months, whereas observations for year-round rainfall data spanned across only 5 months. For this reason, year-round rainfall was omitted from the second analysis. Due to the large difference in sample size between winter and summer rainfall areas ($n = 261$ and 35, respectively) the proportion of total observations per month ($\frac{Month_i}{\sum Month_i}$) was used for each area, rather than

counts. This ensured that data from both areas were constrained to sum up to one and were comparable. We modelled the proportion of active nests per month for nests from each rainfall regime. We therefore had two curves: one for nests within summer rainfall areas and for nests within winter rainfall areas. As with the 'Western Cape Phenology', we fitted trigonometric curves.

Trigonometric curves for both analyses were fitted using a linear model in the form:

$$y = \sin(2 \times \pi \times \left(\frac{x}{12}\right)) + \cos(2 \times \pi \times \left(\frac{x}{12}\right))$$

In the Western Cape phenology analyses, x was the mean number of fledged nests per month, and the average total monthly rainfall. In the Southern Africa phenology analyses, x was the mean number of active nests per month for each rainfall regime. Once fitted, a spline interpolation smoother was used to smooth the curve.

Survival

Capture–Mark–Recapture (CMR) methods (Lebreton *et al.* 1992, White & Burnham 1999) were used to examine survival between August 2006 and December 2011 on a three month time interval using program MARK (v. 6.1). In total, 243 nestlings were ringed using colour rings with an individual two-letter code in addition to the standard metal ring. We collected 1155 resightings in total. The CMR models accounted for heterogeneity in resighting probability by employing a multi-state model defining three strata within the study area to account for areas of high, moderate and low resighting probabilities. Survival distinguished between three age classes, juveniles (0–3 months), sub adults (3–12 months), and adults (12+ months). This model structure was found to describe the structure in our data the best (Duckworth *et al.* 2012) and we use it as a starting model to examine the relationship between covariates and survival. This model is referred to as 'age' in Table 1. See Duckworth *et al.* (2012) for more detail on model selection and goodness of fit.

To examine in detail the effects of weather on the age classes described above, the survival model used a three month time period. This approach allows us to examine direct weather effects on survival at an intra-annual scale. We averaged the climatic variables over 3-month periods, except for rainfall and wind for which the average total and average maximum values were used respectively, and added as covariates to the CMR analysis.

The amount of temporal variation in survival explained by the covariates was calculated using an analysis of deviance (Skalski *et al.* 1993):

$$\text{Explained variation} = \frac{Dev(\text{constant model}) - Dev(\text{covariate model})}{Dev(\text{constant model}) - Dev(\text{timedependent model})}$$

where Dev stands for the deviance of the model in parentheses. 'Constant model' refers to a model that is constant over time, but with the age effects as described above. 'Covariate model' refers to a constant model to which covariates were added. 'Time dependent model' refers to a model that has one parameter for each time period.

Reproduction

DATA

Hadeda breeding data between 2003 and 2011 in the Western Cape of South Africa were collated. Hadeda pairs remain faithful to their breeding sites (Skead 1951) and construct nests in the same location each breeding attempt. Nests were monitored by either project team members or by individuals from a network of project volunteers. Many Hadedas constructed nests in private gardens. Excrement beneath their nests and their loud, signature call (after which they are named), makes their nesting presence within gardens obvious. Thus, homeowners were often able to note the breeding outcome accurately. Nests with at least one egg were considered to be active and were monitored through short visits roughly every 3–7 days until the nest became inactive (classified as successful, unsuccessful or abandoned). A nest was considered to be successful if it raised at least one fledgling and nests for which the outcome was uncertain were not included.

As of November 2011, 223 nests had been observed, making up 474 broods. In order to understand Hadeda reproduction throughout Southern Africa we supplemented this data set with Nest Record Cards (NERCs). These cards were compiled by volunteers who monitored Hadeda nests throughout South Africa and the southern parts of Zimbabwe and were submitted to a database, curated by the Animal Demography Unit at the University of Cape Town. These cards range from 1940 to 1994, although 50% of the data were collected after 1972. Only NERCs that definitively stated the outcome of the nestling attempt, or made a statement about large chicks (which were assumed to have fledged), were used. In total the NERCs made up 99 broods.

RANDOM EFFECTS

Generalized linear models (GLMs) were used to analyse Hadeda reproduction. Nestlings from a particular brood may share the same fate and some nests contributed several broods to the reproduction database over the course of the study. This potentially violates the assumption of independence required by standard GLMs. To account for this non-independence, each breeding pair was considered as a random factor. In terms of the analyses, this regards Hadeda siblings from the same nest as more likely to share the same fate than those from other independent nests. 'Brood' was nested within 'Nest'. Function lmer of package 'lme4' (Bates & Maechler 2010) was used to run this analyses, in program R (v. 2.13.2; R development Core Team 2011).

Table 1. Proportion of temporal variance in Hadeda survival explained by age, wind, temperature and rainfall by means of an analysis of deviance (ANODEV) within the Western Cape of South Africa between 2006–2011. The term 'Age' refers to the age structure of the models (see 'Methods' for more information). The proportion of total deviance explained by each covariate was calculated using analysis of deviance, as shown by '% deviance explained'. *w* is the Akaike weight and assesses the support that a given model has from the data relative to the other models in the set. *F* and *P*-values were calculated from ANODEV and *K* is the number of parameters. Only the 8 top-ranking models are shown.

	Model	ΔAIC	*w*	*K*	Deviance	% deviance explained	*F*	*P*
1	Age	0.00	0.24	11	890.14			
2	Age+Rain+Max temp+Avg wind	0.15	0.22	14	883.95	23.18	1.21	0.35
3	Age+Avg wind	1.23	0.13	12	889.27	3.28	0.64	0.43
4	Age+Rain	1.36	0.12	12	889.40	2.80	0.55	0.47
5	Age+Max temp	1.69	0.10	12	889.73	1.54	0.30	0.59
6	Age+Min temp	1.75	0.10	12	889.79	1.33	0.26	0.62
7	Age+Max wind	1.86	0.09	12	889.90	0.91	0.17	0.68
8	Age+Time	17.22	0.00	31	863.43			

NUMBER OF FLEDGLINGS PRODUCED IN RELATION
TO WEATHER

Modelling the number of fledglings per brood was done using a GLM with a Poisson distribution and a log-link function. The environmental conditions during the period over which the nestlings were nest-bound were considered as potentially affecting fledging success.

Since nests were monitored very closely either by project team members, volunteers or home owners, the date of outcome (defined as either death or fledging) was often known. It turned out to be much easier to determine the date of outcome than the date incubation began, and consequentially we did not have the exact period over which nestlings were nest-bound for each brood. To account for weather conditions over the nest-bound period we added covariates for the average period of time Hadedas are nest-bound (28 days, Macdonald *et al.* 1986, Vernon & Dean 2005) prior to the date of outcome.

Another covariate that was hypothesised to strongly influence reproduction was the breeding age effect. Duckworth *et al.* (2012) found an age effect for Hadeda reproduction and found that the best fitting age effect distinguished between three age classes: age class 1 (their first attempt at breeding), age class 2 (2nd, 3rd and 4th year of breeding) and age class 3 (breeding for the 5th+ year). However, in our dataset, only a few nests were in age class 3 relative to the other two classes. This resulted in large confidence intervals around mean estimates for the effect of covariates on reproduction. To overcome this issue, we pooled age class 2 and 3. As a result, this model had two age classes (first attempt at breeders and those with more than one year's breeding experience) rather than the three as

reported by Duckworth *et al.* (2012). We set this model as our constant model, to which we added environmental covariates. This model is termed 'age' in Table 2.

SPATIAL CORRELATION

Hadeda breeding data collected during this study were analysed for spatial correlation. As a result of the age-effect on reproduction (Duckworth *et al.*, 2012), a pair that appears to be constantly producing more nestlings than other pairs may just be older than other pairs. To account for this, a regression with a Poisson distribution that predicted the number of fledglings as function of the best age effect constraining reproduction (see 'Reproduction') was run. The residuals from this model and coordinates for each nest were used to assess spatial correlation by means of a variogram, using R package 'gstat' (Pebesma 2004). They were also used to statistically test for spatial autocorrelation using Morans I test (Moran 1950), implemented in R package 'ape' (Paradis *et al.* 2004). Four nests lay far outside of the study area and were omitted from this analysis.

RESULTS

Breeding Phenology

We examined Hadeda breeding phenology in two separate analyses (see methods): (1) a 'Western Cape Phenology' analysis, which examined breeding phenology in relation to annual rainfall in the Western Cape and (2) a 'Southern Africa Phenology' analysis, which compared the breeding phenology of nests in winter and summer rainfall areas. Trigonometric curves fitted to these two analyses fit well and allowed for clear

Table 2. Model selection for Hadeda reproduction in relation to age, wind, temperature and rainfall within the Western Cape of South Africa between 2003–2011. The term 'Age' refers to the age structure of the models (see 'Methods' for more information). *w* is the Akaike weight and assesses the support that a given model has from the data relative to the other models in the set and *K* is the number of parameters.
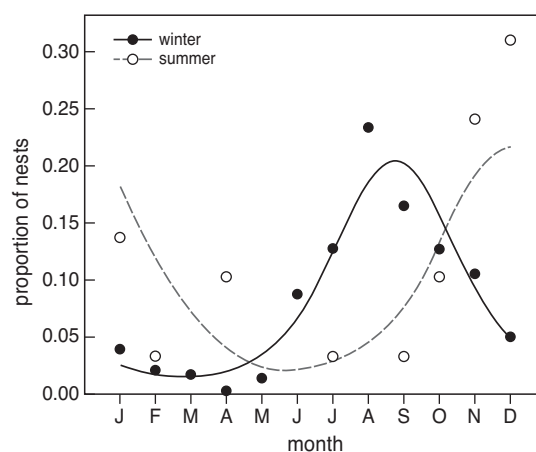
	Model	ΔAIC	*w*	*K*	Deviance
1	Age	0.00	0.20	2	174.35
2	Age + Avg wind	0.30	0.17	3	172.62
3	Age + Rain+ Max temp + Avg wind	0.30	0.17	4	168.64
4	Age × Avg wind	1.00	0.12	4	171.29
5	Age + Rain	1.40	0.10	3	173.67
6	Age × Max temp	1.50	0.09	4	171.83
7	Age + Max temp	2.00	0.07	3	174.27
8	Age + Min temp	2.00	0.07	3	174.33
9	Intercept	32.80	0.00	1	209.08
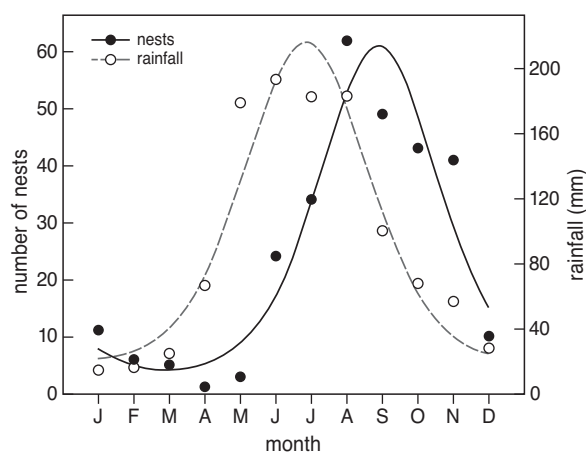
Figure 1. 'Western Cape Phenology' analysis. Aggregated number of nests per month from which Hadeda nestlings successfully fledged and aggregated total average rainfall per month within the Western Cape of South Africa between 2006–2011. The lines are the model predictions, as estimated by trigonometric analyses, and the dots are the actual data (solid line and dots: average monthly number of nests from which nestlings fledged; dotted line and open dots: average total rainfall). Only the sin term was significant for the number of nestlings ($df = 9$; sin: $z = -12.01$, $P < 0.001$; cos: $z = -0.73$, $P > 0.1$), whilst for rainfall both the sin and cos terms were significant ($df = 9$; sin: $z = -10.78$, $P < 0.001$; cos: $z = -20.12$, $P < 0.1$).

Figure 2. 'Southern Africa Phenology' analysis. Monthly proportion of total annual nests from which Hadeda nestlings fledged from two different rainfall regimes within South Africa and southern Zimbabwe. The lines are the model predictions, as estimated by trigonometric analyses, and the dots are the actual data (solid line and dots: nests from winter rainfall areas; dotted line and open dots: nests from summer rainfall areas). Only the cos term was significant for nests from summer rainfall areas ($df = 9$; sin: $z = -0.19$, $P > 0.1$; cos: $z = 2.62$, $P < 0.001$), whilst both sin and cos terms were significant for winter rainfall areas ($df = 9$; sin: $z = 0.11$, $P < 0.001$; cos: $z = -1.96$, $P < 0.05$).

determination of peaks and troughs in rainfall and the number of active nests per month (Figures 1 and 2). Using these curves for the 'Western Cape Phenology' analyses (Figure 1) we predict peak rainfall to be during July, whereas the peak number of active nests was in September; a difference of two months. Given that these birds incubate for 28 days and take about another 28 days from hatching to fledging, the delay between nest building and incubation (as gained from predicted date of hatching), and predicted rainfall was only a few days.

In the 'Southern Africa Phenology analyses', the seasonality of the average number of active nests per month in summer and winter rainfall regimes were also well fitted by trigonometric curves (Figure 2). It was possible to fit distinct breeding phenology curves for fledglings from summer and winter rainfall areas. From the curve's predictions, the peak of the proportion of active nests for the summer rainfall curve was during December (a proportion of 0.22), whereas the winter rainfall curve was low at this time (proportion of 0.047). Conversely, winter rainfall nests had the highest proportion of active nests during September (0.21), where proportion of total summer nests was low (0.07).

Survival

A model allowing for an age effect but keeping survival constant over time was better supported than any model with covariates (Table 1). Analysis of deviance suggested that none of the single or combination of covariates significantly influenced Hadeda survival (Table 1). Model 2 (Constant + total rain + max temp + avg wind) explained the most total deviance, but this was not significant ($P > 0.1$, Table 1). Regression coefficients on the logit scale for Model 2 suggest rainfall had a minimal effect on survival (model coefficient of 0.003), an increase in maximum temperature was related to an increase in survival (model coefficient 0.201), and an increase in average wind speed was strongly related to a decrease in survival (model coefficient –0.383). Of the single covariates, average wind explained the most deviance (Table 1, Model 3), followed by total rainfall (Table 1, Model 4).

Reproduction

In 135 out of the 474 (28.5%) broods in this study at least one of the nestlings died prior to fledging. Of the 135 nest failures, the reason for failure was known in 96 (71.1%) of them. 43 (44.8%) were due to storms, 18 (18.8%) were abandoned for some reason, 24

(25%) were predated upon (birds of prey accounting for all but one observation) and 11 (11.4%) due to territorial disputes with other Hadedas.

No model that fitted only a single covariate was well supported (Table 2), nor was any model that included season (not shown in Table 2 as only the top models are shown). All models fitted with the age-effect (the age-effect on reproduction) were well supported. Of the models that included age and a single covariate, age + wind (Model 2) was the best supported model. Although not significant, this model log coefficient (wind: –0.032) shows a minimal effect of average wind speed on reproduction. A model that included each covariate and age was less well supported than a model that included just age (Models 3 and 1, respectively, Table 2).

Given that there was a rainfall gradient within our study area, we expected there to be a degree of spatial autocorrelation within the data. However, our results do not show this, and there was no spatial autocorrelation of reproduction throughout the entire study area (Moran's I test $P = 0.61$).

DISCUSSION

Potential sources of variation in the demography of Hadedas living in mostly urban areas in the Western Cape, South Africa were examined from 2003–2011. We assessed how survival and reproduction were affected by local weather, fine-scale spatial variation and seasonality. We used a short survival interval (3-month interval) in our survival models which allowed us to examine the direct effects of potential climatic drivers of survival in great detail. Overall, our analyses did not find an association between the covariates measured here and survival or reproduction within our study area. Rainfall triggered the onset of breeding, and Hadedas were able to adjust their breeding phenology to the rainfall seasonality in different areas. There was no evidence of spatial autocorrelation throughout the entire study area.

Breeding phenology
Hadeda breeding was triggered by rainfall, as we expected, despite the year-round availability of food. On average, Hadedas build their nests for 30 days and incubate for 28 days, and we show here that Hadedas begin to lay their eggs in response to the first rainfall events of the season (Figure 1). An evolutionary adaptation of many species is to begin breeding in response to environmental cues (Lack 1968, Breed & Clarke 1970, Aleksuik & Gregory 1974, McAllan *et al.* 2006, Altwegg & Anderson 2009) that indicate an upcoming period of high food availability. Hadedas time their breeding to coincide with the main rainy season (during which they will forage most efficiently). Such behaviour has been shown for other ibis species (del Hoyo & Matheu 1992). However, despite the clear seasonality in breeding, active Hadeda nests were found at any time of the year. This could possibly be breeding pairs building nests in response to light rains during the summer months, or a behavioural adaptation of breeding pairs with close access to irrigated fields.

Survival and reproduction
None of the measured covariates explained a great amount of variation in survival (Table 1) or reproduction (Table 2), suggesting that local weather was not a significant driver of Hadeda demographics in this mostly urban population. For the reproduction analyses we used average values across the entire study area rather than data from weather stations closest to each observation, because of data limitations. We acknowledge that ignoring the spatial pattern of weather data may potentially confound our results. However, Moran's I spatial autocorrelation test revealed that there was no spatial autocorrelation in reproduction throughout our study area. Any spatial effects of weather data on reproduction would have been detected by Moran's I test, and given that this test returned a non-significant result, we can be confident that there were no spatial effects of weather data on reproduction which validates our analyses approach. We used a short survival interval (3-month interval) in our survival models which allowed us to examine the direct effects of potential climatic drivers of survival in great detail.

From the coefficients from the survival model 2 (Table 1, Model 2) it appears as though the strong winds during the winter months marginally affect Hadeda reproduction (although these were not statistically significant). During winter, Cape Town winds can reach exceptionally high speeds (Schumann & Martin 1991), and it can be assumed that such excessive wind speeds may cause mortality of individuals through collisions with objects. An increase in temperature was related to an increase in survival. This is probably due to an increase in foraging conditions during hot days, while it never gets excessively hot enough in our study region to directly cause mortality. It was surprising that rainfall did not affect demographic rates given the relationship between Hadeda survival and soil moisture.

The environment in the Western Cape differs in important ways from the area in which Hadedas have

occurred traditionally. The Hadeda's original range was typified by soft, moist soil and tall trees in which to nest (Vernon & Dean 2005). In the Western Cape, the dominant vegetation is fynbos, which lacks native tall trees (Midgley & Rebelo 2008) and soils are naturally hard and dry, interspersed with large boulders and rocks (Goldblatt & Manning 2002). Together these create challenging conditions for Hadeda's survival. It appears that the modification of the natural landscape in the Western Cape by humans has transformed this environment into one in which Hadedas have adapted to and in which they may persist. In urban areas, the indigenous fynbos has been converted into gardens, lawns, sports fields and parks. These are irrigated year round, and thereby create suitable foraging grounds. Large, mostly alien, trees have been planted by humans (Macdonald *et al.* 1986) and create roosting and nesting opportunities. It appears that urban development is buffering the effects of weather, and may have allowed Hadedas to persist in areas where they would not naturally do so.

Ibis expansion

Other ibis species have colonised urban areas and expanded their ranges in the last 50 years, such as the Glossy Ibis *Plegadis falcinellus* (Anderson 1997, Patten & Lasley 2000), the African Sacred Ibis *Threskiornis aethiopicus* (Kopij 1999) and the White Ibis *Threskiornis molucca* in Australia (Martin *et al.* 2007). In South Africa, Sacred Ibises were classified as a non-breeding winter visitor at the beginning of the 20th century (Anderson 1997), but are now regarded as common urban residents (Anderson 1997, Barnes 2005). They have also colonised parts of Europe and North America (Clergeau & Yesou 2006, Herring & Gawlik 2008). A notable trait shared by these expanding ibis species is that they have all rapidly colonised human-modified landscapes (Clergeau & Yesou 2006, Herring *et al.* 2006, Martin *et al.* 2007, Herring & Gawlik 2008). Our results are in agreement with this, and suggest that the expansion of Hadeda's range is facilitated by the urban environment which has buffered the harsh effects of weather.

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SAMENVATTING

De Hadeda-ibis *Bostrychia hagedash* komt in een groot deel van Afrika voor. In de afgelopen 50 jaar is het areaal in Zuid-Afrika meer dan verdubbeld. Tegenwoordig is deze ibis er in stedelijk gebied een regelmatig voorkomende soort. Om de veranderingen in verspreiding van de Hadeda-ibis te begrijpen, werd de invloed van het weer en het aanbreken van het regenseizoen op het voortplantingssucces en de overleving onderzocht. Het onderzoek vond plaats in de provincie West-Kaap aan de rand van het verspreidingsgebied. Er werden 243 vogels met kleurringen voorzien om overleving en voortplantingssucces te kunnen schatten. Het weer bleek op deze parameters geen aantoonbaar effect te hebben. Wel had regenval invloed op het begin van het broeden. De hoofdmoot van de vogels begon met de nestbouw nadat het regenseizoen (in de maanden mei tot augustus) was aangebroken. De Hadeda-ibis heeft zich buiten zijn oorspronkelijke verspreidingsgebied snel aan het stedelijk gebied aangepast. Verondersteld wordt dat de ibis daar profiteert van kunstmatig vochtige (besproeide) grasvelden (bijvoorbeeld sportterreinen), waardoor langdurige droogte de overlevingskansen niet nadelig beïnvloedt. Door te profiteren van door de mens geschapen leefomstandigheden lijkt de soort in staat het areaal uit te breiden. Een dergelijk opportunisme is ook waargenomen bij andere ibissoorten elders op de wereld. (PW)