

Demography and population ecology of the Hadedda Ibis (*Bostrychia hagedash*) at its expanding range edge in South Africa

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Abstract A mechanistic understanding of species' geographic range dynamics requires an understanding of the dynamics of populations at the edge of that range. Several ibis species are currently expanding their ranges, and the Hadedda Ibis (*Bostrychia hagedash*) has increased its southern African range more than 2.5 fold over the past century. We studied the demography of a Hadedda population near the expanding range edge. Estimating survival on a quarterly time interval we found that it was lowest over the first 3 months of life, and then slightly higher over the rest of the 1st year (annual survival: 0.27, SE = 0.04). After the first year, survival was constant (0.75, SE = 0.09). Breeding success increased from 1.5 to 3 fledglings per year with increasing experience of the breeding pair. A matrix population model showed that the growth rate of this population was most sensitive to changes in adult survival and least sensitive to variation in reproduction. Hadeddas in our study population thus showed characteristics of long-lived birds but were also able to achieve a high reproductive output in good conditions.

Together with their ability to take advantage of a human modified landscape, this may explain the remarkable success of this species in expanding its range.

Keywords Capture-mark-resighting · Hadedda Ibis · Matrix population model · Range expansion · Reproduction · Survival

Zusammenfassung

Demographie und Populationsökologie des Hagedadsch-Ibises (*Bostrychia hagedash*) an der Front seines expandierenden Verbreitungsgebietes in Südafrika

Für ein mechanistisches Verständnis der Dynamik von Verbreitungsgebieten braucht es Kenntnis der Dynamik von Populationen am Rande des Verbreitungsgebietes. Mehrere Ibis-Arten erweitern momentan ihr Verbreitungsgebiet und das des Hagedadsch-Ibises (*Bostrychia hagedash*) hat sich in Südafrika im Laufe der letzten hundert Jahre um das 2.5 fache vergrößert. Wir untersuchten die Demographie einer Hagedadschpopulation am Rande des Verbreitungsgebietes. Die Überlebensrate je Quartal ist in den ersten drei Lebensmonaten am niedrigsten; für das gesamte 1. Lebensjahr beträgt sie $0,27 \pm 0,04$ (s.e.). Nach dem ersten Lebensjahr war die Überlebensrate altersunabhängig $0,75 \pm 0,09$. Mit wachsender Erfahrung des Brutpaares erhöhte sich der Bruterfolg von 1.5 flüggen Jungen pro Jahr auf 3. Ein Matrix- Populationsmodell zeigte, dass die Wachstumsrate dieser Population am empfindlichsten auf Veränderungen in der Überlebensrate von erwachsenen Vögeln reagiert und am wenigsten empfindlich auf Veränderungen im Bruterfolg ist. Der Hagedadsch in unserem Studiengebiet zeigte deshalb Eigenschaften von langlebigen Vögeln, war aber auch in der Lage, gute

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Bedingungen durch hohen Bruterfolg auszunutzen. Diese Eigenschaften, zusammen mit der Fähigkeit, von Menschen veränderte Landschaften auszunutzen, könnten den beachtlichen Erfolg dieser Art in der Ausdehnung ihres Verbreitungsgebietes erklären.

Introduction

Over the last 50 years, numerous species have altered their ranges as a result of rapid global climate change and land-use change (Thomas and Lennon 1999; Hughes 2000; Parmesan and Yohe 2003; Jepsen et al. 2008). A species' range can be defined as the area where reproduction plus immigration at least balances mortality plus emigration (Gaston 2009) such that the population growth rate (λ) is at least equal to 1 (Holt et al. 2005). Where $\lambda > 1$, the population is expanding, and where $\lambda < 1$, a population will eventually become locally extinct, in isolation from other populations (Holt et al. 2005). Therefore, species' ranges either contract or expand through changes in their demographic rates.

Species ranges are the result of demographic responses to varying conditions through space and time (Bahn et al. 2006). Conceptually, the centre of a range has optimal conditions, which in turn supports the highest population density (Whittaker 1956). Moving outwards from the core, conditions deteriorate such that the range edge has minimal conditions for population persistence (Whittaker 1956). However, empirical data show that this simple model does not generally apply (Sagarin and Gaines 2002), thus highlighting the need for detailed demographic studies in different parts of a species' range. For a species expanding its range, it is particularly important to understand the demographic mechanisms at the range edge that have facilitated the transformation from maintenance to expansion (Case and Taper 2000; Holt et al. 2005), as this in part determines how fast species can react spatially to climate or land use change. Because the range edge defines the shape of the range for the whole species, understanding range edge populations is central to understanding the overall dynamics of a species' range.

The Hadedda Ibis (or Hadedda for short: *Bostrychia hagedash*) has expanded its range in South Africa over the last 100 years (Macdonald et al. 1986). Hadeddas were confined originally to the wetter eastern and south-eastern parts of the country (Macdonald et al. 1986; Vernon and Dean 2005), but since 1910 they have increased their range consistently southwards and westwards (Macdonald et al. 1986).

By 2010, Hadeddas had completely colonised the south western regions of South Africa, as well as parts of the west coast and even as far north as the Namibian-South African border (see Macdonald et al. 1986 for a map of the range

expansion from 1910 to 1985; a map of their current distribution obtained from the second South African Bird Atlas Project is available at <http://sabap2.adu.org.za/>, select 'Species' and search for Hadedda). Between 1910 and 1985, their range increased 2.5-fold from 531,000 to 1,300,000 km².

Reasons proposed for the range expansion include artificial watering, by way of irrigated fields, which converted previously arid areas into year-round foraging grounds; and the plantation of mostly alien trees in which Hadeddas roost and nest (Macdonald et al. 1986). Artificial watering seems especially important, because this allows Hadeddas to persist in areas where they otherwise would not be able to do so (Duckworth et al. 2010).

Although research has focussed on the recent range expansion of the Hadedda, surprisingly little is known about their population ecology. Yet, knowledge of the demography of this species would not only help understand this expansion but would also shed light on the Hadedda's life history. Thus, the goals of this study were (1) to examine, for the first time, age-specific survival and reproduction in Hadeddas. These are key demographic rates to assess their life history. And (2) we develop a matrix population model to assess Hadeddas population growth rate in the greater Cape Town area.

Methods

Species and study area

The Hadedda is a large wading bird of the family Threskiornithidae of the order Pelecaniformes. Adults are on average 76 cm tall and weigh 1.3 kg (Vernon and Dean 2005). They occur naturally in moist grasslands, savannas, and well vegetated river courses, but have colonised urban areas successfully. The age at which Hadeddas start to breed is around 3 years (G.D.D., unpublished data). Hadeddas are solitary nesters and their nests are constructed from sticks attached to branches 5–20 m high up in trees. They lay between one and four eggs per breeding attempt. Their main breeding season coincides with the rainy season, which is during the southern hemisphere winter in the Western Cape (May–September), although a few active nests can be found at any time during the year. The same pair can raise up to four broods in a single year. Hadeddas show a high fidelity to their nest site and partner (Skead 1951). Incubation lasts 25–28 days (Vernon and Dean 2005), and nestlings fledge after 33–40 days (Vernon and Dean 2005). After fledging, the chicks are dependent on their parents for food for about 3 months, during which time they increasingly forage for food by themselves.

This study was conducted between 2003 and 2010 in the Western Cape province of South Africa. This area experiences a typical Mediterranean climate; winter rainfall, and hot, dry summers (Kruger 2004). The core study area was the greater Cape Town area, but data were also collected from the east (to Paarl, Stellenbosch and Somerset West) and south (to Noordhoek), roughly covering 3,200 km² (Fig. 1). Hadedas first colonised our study area in the early 1980s. The population increase since then is documented by three atlas projects (1982–1986, 1987–1993, and 2007–2011, Harrison et al. 1997) where Hadedas were recorded on 4% ($n = 1,219$), 10% ($n = 1,172$), and 86% ($n = 2,187$) of the checklists collected during each project in our study area.

We located Hadedas nests throughout our study area and recorded the number of fledglings produced. If possible, we ringed the nestling between 2 and 3 weeks of age, but we

could not reach all nests for which we have information on fledgling production. The nestlings were ringed with a numbered metal ring (South African Bird Ringing Unit, SAFRING) and an engraved colour-ring (Pro-Touch Engraving, Saskatoon, Canada), the latter with a unique double letter combination that could be read from a distance using binoculars or a spotting scope.

Survival analysis

We estimated local survival from capture-mark-resighting data collected between August 2006 and April 2011. Over this period, 237 nestlings were ringed and 1,110 resightings collected. Survival (ϕ) and resighting probability (P) were estimated using capture-mark-recapture (CMR) methods (Cormack 1964; Jolly 1965; Seber 1962). These methods allow for a separate estimation of the local survival rate and the probability that a ringed bird is resighted, given that it is alive in the study area at the time (Lebreton et al. 1992). We used a survival interval of 3 months. Since all birds were ringed as nestlings, we were able to look at age-specific survival in detail.

CMR methods assume that all individuals within a group have similar recapture and survival probabilities. In our study, resighting effort varied spatially. To account for this heterogeneity, we distinguished between three regions within our study area that received homogenous field effort, and used multistate models allowing for different resighting probabilities and movement among regions (Spendelov et al. 1995; Lebreton and Pradel 2002).

A further assumption of the CMR approach is that resightings are made instantaneously, whereas our data were collected continuously. This causes heterogeneity in apparent survival, but Hargrove and Borland (1994) estimated that this only leads to small bias of less than 5%, and we therefore continued with this approach.

We tested goodness-of-fit (GOF) for a general multistate model using programme U-CARE v. 2.3.1 (Choquet et al. 2009). None of the tests were significant (Test 3G: $\chi^2 = 37.75$, $P = 0.91$, $df = 52$; Test M: $\chi^2 = 4.39$, $P = 0.62$, $df = 6$, overall GOF Test: $\chi^2 = 43.14$, $P = 0.93$, $df = 58$), which suggests that the data sufficiently met the assumptions of the model. Since there appeared to be no overdispersion ($\chi^2/df = \hat{c} = 0.75$), \hat{c} was kept at 1.

We started with a model where survival, resighting and movement differed among strata (the three regions of different field effort), but was constant over time, and then added effects to this model. All models were run in program MARK 6.0 (White and Burnham 1999), and model selection was based on the sample-size adjusted Akaike's Information Criterion (AICc; Akaike 1974).

The main focus of this analysis was on age-specific survival, and we distinguished among three main age

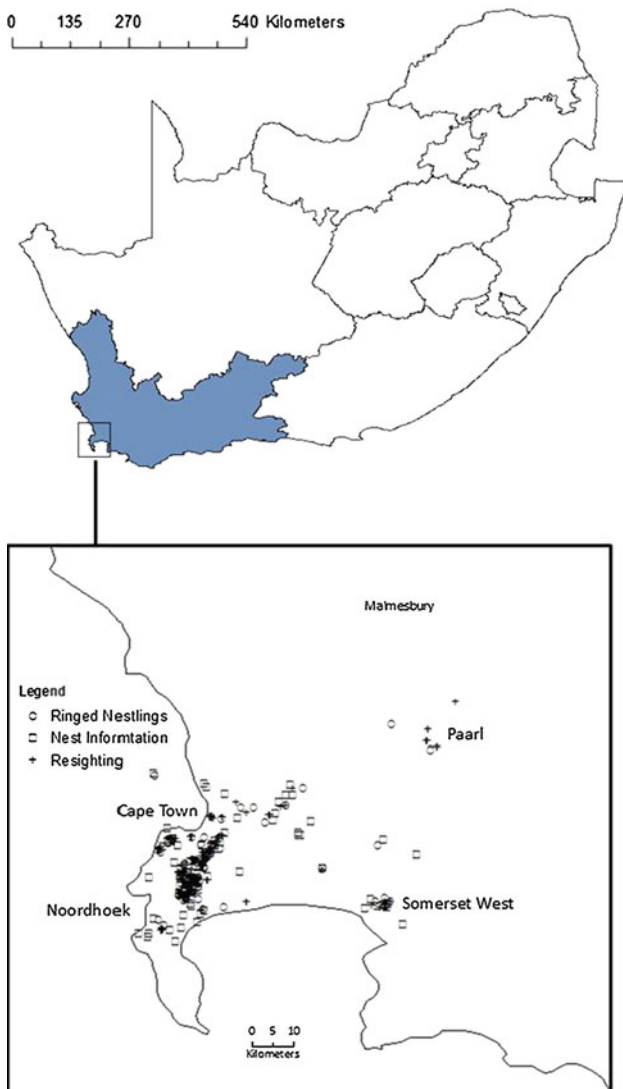


Fig. 1 Location of the study area in relation to South Africa, and a map showing the sites at which data were collected (inset)

classes: juveniles (0–12 months), immatures (12–24 months), and older (24+ months). Since our analysis was based on a 3-month interval, we were able to examine juvenile survival in more detail, by distinguishing among the ages 0–3, 3–6, and 6–12 months post fledging. The reasoning for this choice is that fledglings remain close to their parents, and are being fed by them for the first 3 months after fledging. For the next 3 months, they become increasingly independent, until they are totally independent around 6 months post fledging.

We also considered an effect of age on resighting probability. We expected younger birds to be resighted more easily because they remain near their nest for a few months after fledging, and we would be more likely to find them. We increased our resighting effort markedly in one of the three regions in 2008 and considered models that allowed for this structure in the resighting probabilities.

The multistate models used here involve parameters for movement among the regions, but these were not of principal interest since we used the multistate approach primarily to account for spatial heterogeneity in resighting effort. However, because of the relative size of the regions, we allowed movement between two of them to differ from movement to the third region. More details on the multistate model, including a map of the areas, are provided in the Electronic Supplementary Material.

Reproduction

Between September 2003 and February 2010, we monitored and recorded the number of fledglings in 404 broods from 198 different nests. Hadedas pairs remain faithful to their nest sites (Skead 1951) and, once a tree is chosen, nests are rebuilt on the same branch for many consecutive breeding attempts. Assuming that a particular nest was used by the same pair of birds over time, we recorded the number of breeding attempts per year, and used the number of years for which a nest had been active as a measure of breeding experience (referred to as “nest age” below). The latter also requires that we detected nests in their 1st year, which is a reasonable assumption given that Hadedas are conspicuous and vocal birds (since the 2010 soccer World Cup, they have been known locally as “flying vuvuzelas”), and most of our nests were near people’s homes.

The number of nestlings raised increases with experience in many bird species (Forslund and Pärt 1995). We therefore examined whether the number of fledglings produced per pair per year depended on nest age, considering three potential age-structures describing such an effect. Structure 1 distinguished between three nest-age classes: age 0 (i.e. no previous nesting experience), 1, and 2+. Structure 2 also distinguished between three nest-age

classes: age 0, 1–3, and 4+. Structure 3 distinguished between four age classes: age 0, 1, 2–3, and 4+. We examined which age structure could best explain variation in the number of fledglings produced per year, the number of broods per pair per year, and the number of fledglings per brood by fitting models describing each of the hypothesized age structures and evaluating them with AIC.

The most natural way of analysing these data would be by generalised linear models (GLM) assuming a Poisson distribution and log link function. However, the data appeared to contain an excess of zeros in comparison to what is expected under a Poisson process. Furthermore, broods from the same nest may not be independent of each other. Accounting for both of these complications in a single analysis was not straightforward, and so we analysed our data using three different approaches.

First, we accounted for excess zeros using hurdle models implemented in the package “pscl” (Zeileis et al. 2008) in program R v. 2.11.1 (R Development Core Team 2010). Hurdle models consist of two parts. The first part separates the process of either getting a positive count (i.e. $x > 0$) or a zero (i.e. $x = 0$) and was modelled using a binomial distribution. The second part employs a zero-truncated Poisson distribution to model the positive counts. The hurdle models we used treat each brood as an independent data point.

Second, we accounted for possible non-independence among broods from the same nest using generalised linear mixed effects model (GLMM) where nest identity was added as a random effect. We fitted these models using package “lme4” (Bates and Maechler 2010) in program R.

Third, we fitted simple GLMs and compared them to the more complex models using AIC and by examining the variance components in the GLMMs to see whether the data supported the added complexity.

Matrix population model and population growth

The population growth of Hadedas was examined using a matrix population model (Caswell 2001). We assumed a pre-breeding census and a yearly time step. The matrix entries were the age-specific survival rates estimated from the best CMR model, converted from a quarterly time period to a yearly one using the delta method. The reproductive rates were taken from the best model analysing the reproductive data.

We assumed that Hadedas bred at the age of 3 years. The model is:

$$n_{t+1} = An_t \quad (1)$$

where n_t represents the number of individuals in each age class, and A is the population projection matrix:

$$A = \begin{bmatrix} 0 & 0 & F_1 & F_2 & F_3 & F_4 & F_5 \\ S_2 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_3 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_4 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_5 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & S_6 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & S_7 & S_8 \end{bmatrix} \tag{2}$$

where

$$F_i = R_i \times S_1 \times 0.5 \tag{3}$$

R_i is the number of fledglings produced from nests that are i years old. S_i is the survival probability of birds in their i th year. Only females were considered in this analysis, and therefore the number of fledglings was multiplied by 0.5, assuming an equal sex ratio in the nest.

The dominant eigenvalue of matrix A is the asymptotic population growth rate, λ (Caswell 2001), assuming a stable age distribution is reached. We explored the sensitivity and elasticity of λ to variation in mean values for the fitness components. The sensitivity analysis estimated the effect of absolute changes in demographic rates on λ , whereas the elasticity analysis estimated the effect of relative changes in demographic rates on λ (Caswell 2001). We calculated 95% confidence intervals (CI) for λ and sensitivity based on 10,000 bootstrap replicates following Caswell (2001). The bootstrap describes the uncertainty in the mean estimate of λ and sensitivity as a function of the uncertainty in the entries of matrix A . All matrix calculations were performed in R 2.11.1 (R Development Core Team 2010).

Results

Survival

Model selection favoured a model that distinguished only between three age classes in survival, 0–3, 3–12, and 12 months and older (Model 1, Table 1; Fig. 2). Adding extra parameters to distinguish between the 3–6 and 6–12 month age classes reduced the deviance only marginally (Models 2, Table 1) and we thus have no evidence that these age classes differed in survival from each other. Similarly, estimating survival of the 24+ age class separately led to a poorly supported model (Model 5). However, since all birds were ringed as nestlings, we may not yet have enough data to reliably estimate survival of the oldest age class. On the other hand, setting survival constant above 6 months (Model 3) or 3 months (Model 4) of age resulted in considerably less well supported models.

Converting from quarterly to yearly survival, Model 1 estimated annual 0–12 months survival to be 0.27 (SE = 0.04), and annual survival of birds older than 12 months to

be 0.75 (SE = 0.09). The resighting probabilities ranged from 0.03 (SE = 0.01) to 0.83 (SE = 0.07). Movement rates ranged from 0.002 (SE = 0.007) to 0.09 (SE = 0.02) per 3-month period.

Reproduction

A simple Poisson GLM of the number of fledglings produced in relation to nest age was better supported than a comparable hurdle model; $AIC_{\text{hurdle}} : 891.1$, $AIC_{\text{glm}} : 889.0$ ($\Delta AIC = 2.10$). This indicates the excess of zeros was not severe enough to justify the need for the more complex hurdle model. Nest ID was then included as a random effect and the number of fledglings per year as a function of nest-age was modelled with a Poisson GLMM. The variance estimate for the random effect was small ($\sigma^2 = 0.05$), indicating that repeat broods by the same pair were somewhat independent in terms of their success. Nonetheless, estimates from GLMM models with nest ID added as random effects were used in the remaining analyses.

In modelling the number of fledglings per year as a function of nest-age, structure 2 was better supported than either structure 1 ($\Delta AIC = 2.10$, just under three times less well supported as per evidence ratio based on Akaike weights) or structure 3 ($\Delta AIC = 4.05$; over seven times less well supported). According to structure 2, Hadedá pairs of nest-age class 0 (first attempt at raising a brood) raise 1.41 nestlings per year, nest-age class 1–3 (2nd to 4th breeding attempt) raised on average 2.07 nestlings per year, and the nest-age class 4+ (5th or more attempts) raised 3.02 nestlings per year (Fig. 3).

The number of fledglings raised per year is the product of the number of fledglings raised per breeding attempt and the number of successful broods raised per year. To examine the nest age effect in more detail, we analysed these two components separately. Structure 2 was also well supported in both the number of fledglings per brood and the number of broods per year (Fig. 4). The number of broods produced per year, and the number of fledglings per brood increase with nest age. Nest-age class 0 raised 1.09 broods per year, age class 1–3 raised 1.42 and age class 4+ raised 1.59 (Fig. 4a). Pairs of nest-age class 0 produced 1.33 nestlings per brood, age class 1–3 produced 1.56, and age class 4+ produced 1.89 (Fig. 4b).

Matrix population model and population growth

Following the most parsimonious representation of age-specific survival and reproduction suggested by our data, we set $F_2 = F_3 = F_4$ and S_i constant for all $i > 1$ (see Eq. 2; parameter values are given in Table 2). Using yearly survival estimates derived from Model 1 (Table 1), the population growth rate (λ) was estimated at 0.94 (95% CI:

Table 1 Summary of model selection analysis for survival over 3-months periods of Hadedas in the Western Cape, South Africa over the period 2006–2011

	Model ^a	Δ AIC	w	K	Deviance
1	$S(a_{0-3/3-12/12+})P(s \times a_{3-6/6+} + e)\psi(s)$	0.00	0.54	12	779.20
2	$S(a_{0-3/3-6/6-12/12+})P(s \times a_{3-6/6+} + e)\psi(s)$	2.08	0.19	13	779.16
3	$S(a_{0-3/3-6/6+})P(s \times a_{3-6/6+} + e)\psi(s)$	2.99	0.12	12	782.19
4	$S(a_{0-3/3+})P(s \times a_{3-6/6+} + e)\psi(s)$	4.01	0.07	11	785.32
5	$S(a_{0-3/3-6/6-12/12-24/24+})P(s \times a_{3-6/6+} + e)\psi(s)$	4.10	0.07	14	779.04
6	$S(a_{0-3/3-6/6-12/12-24/24+})P(s \times a_{3-6/6-12/12-24/24+} + e)\psi(s)$	9.01	0.01	20	770.94
7	$S(a_{0-3/3-6/6-12/12-24/24+})P(s \times a_{3-6/6-12/12-24/24+})\psi(s)$	14.29	0.00	19	778.41
8	$S(a_{0-3/3-6/6-12/12-24/24+})P(s + a_{3-6/6-12/12-24/24+} + e)\psi(s)$	17.84	0.00	14	792.78
9	$S(\cdot)P(s \times a_{3-6/6+} + e)\psi(s)$	31.11	0.00	10	814.53
10	$S(a_{0-3/3-6/6-12/12-24/24+})P(s + e)\psi(s)$	32.84	0.00	11	814.15

^a Each model consists of three parts; survival (S), resightings (P) and movement (ψ) among three regions that differed in field effort. The numbers and letters in brackets indicate which factors were included in a particular model. The focus was on age-specific survival (a), and the age classes (in months, e.g. 0–3 is the age class from fledging to 3 months old) between which a particular model distinguished are shown as subscripts. Resighting rates were a function of stratum (s), age (a), and effort (e). Movement was structured to allow for differences in distance and size among the three regions (s). See Supplementary Material for more information. Model selection was based on Akaike's Information Criterion, ($AICc$). A lower $AICc$ value indicates a better model. ΔAIC is the difference in AIC units between the current model and the best model. w (AIC Weights) is the support for a particular model in relation to other models. Dividing one model's AIC Weights by another's gives the number of times the first model is better supported (evidence ratio). K Number of parameters in the model, *Deviance* model deviance

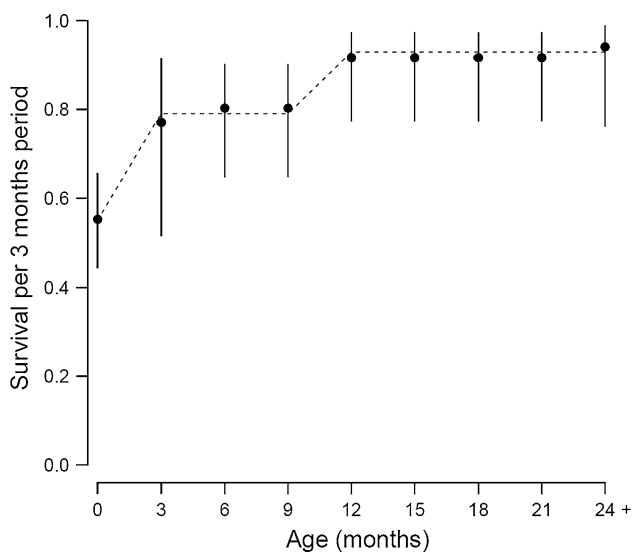


Fig. 2 Age-specific survival rates per 3-month period for Hadedas in the Western Cape, South Africa, between 2006 and 2011. The survival rates were estimated from capture-mark-resighting data aggregated into 3-monthly occasions for analysis with regular capture-mark-recapture models. *Data points* and *95% confidence intervals* (CI) are estimates from the model with the most flexible age structure (Model 5, Table 1), whereas the *dashed line* shows the most parsimonious age effect, from the Akaike's Information Criterion ($AICc$) selected model (Model 1, Table 1)

0.71–1.09). The demography thus suggests a shrinking population, albeit with a large CI, while atlas data show that Hadedas are being recorded much more frequently now than in the early 1990s. Our survival estimate for the age class 24+ is based on few data and may well be biased low. Adult survival in other large-bodied wading birds or

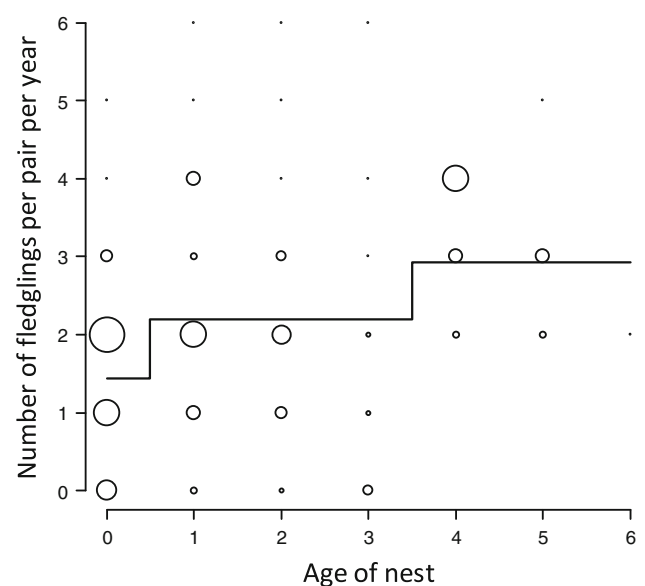


Fig. 3 Number of fledglings produced per pair per year in relation to nest age for Hadedas in the Western Cape, South Africa, between 2003–2010. *The bubbles* show the observations, and the size of the bubbles is proportional to the number of data points. The fitted line shows the best fitting relationship between the number of fledglings per pair per year and nest age (see “Methods” for details). The equation for this line is: $\log(\text{number of fledglings per year}) = 0.37 + 0.42 \times (x) + 0.74 \times (y)$, where the dummy variable $x = 1$ for age class 2 (y is necessarily 0 here), and $y = 1$ for age class 3 (x is necessarily 0 here), and $x = y = 0$ for age class 1. Both terms x and y were significant ($x: z = 4.43, P < 0.001, n = 276$; $y: z = 3.79, P < 0.001, n = 276$)

ibises is around 0.90–0.96 (Cézilly 1997; Cézilly et al. 1996; Li and Li 1998; Hafner et al. 1998). Using 0.81 as survival of the 24+ months age class to parameterise the

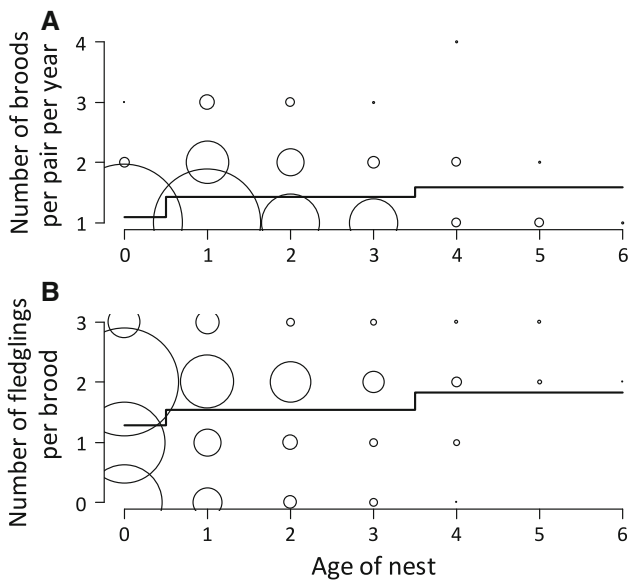


Fig. 4 **a** Number of broods produced per year, and **b** the number of fledglings produced per brood in relation to nest age for Hadedas in the Western Cape, South Africa, between 2003 and 2010. See legend to Fig. 3 for more details. The equation for the best fitting line in (a) is $\log(\text{number of broods per pair per year}) = 0.09 + 0.26 \times (x) + 0.37 \times (y)$. Only x was significant ($x: z = 2.64, P < 0.05; y: z = 1.53, P = 0.11$). The equation for the line in (b) is $\log(\text{number of fledglings per brood}) = 0.29 + 0.16 \times (x) + 0.35 \times (y)$. Both age terms were significant ($x: z = 1.69, P < 0.10; y: z = 1.98, P < 0.05$)

matrix population model (Eqs. 1–3) yielded a stable population ($\lambda = 1.00$), and setting this survival rate to 0.85 led to an increasing population ($\lambda = 1.04$) that was qualitatively consistent with the atlas data. Alternatively, Hadedas could start breeding earlier than we assumed. However, if all birds started breeding at 2 years old instead of 3, the population would still be shrinking ($\lambda = 0.98$).

Sensitivity analysis based on our best estimates of all fitness components revealed that λ was most sensitive to changes in the 24+ months age class survival (sensitivity 0.93, 95% CI: 0.90–0.97), then to 0–12 months survival

Table 2 Mean values and 95% confidence intervals (CIs) of demographic estimates used in the matrix population model (Eqs. 2, 3) to estimate population growth of Hadedas in the Cape Town area. Survival estimates were based on capture-mark-resighting data collected between 2006 and 2011, and reproduction was observed between 2003 and 2010

Parameter	Mean value (95% CI)
Survival 0–12 months (S_1)	0.27 (0.19–0.35)
Survival older age classes (S_2 – S_8)	0.74 (0.56–0.92)
Reproduction: age class 1 (R_1)	1.41 (0.31–2.51)
Reproduction: age class 2 (R_2 – R_4)	2.07 (0.97–3.17)
Reproduction: age class 3 (R_5)	3.02 (1.81–4.22)

(0.39, 0.28–0.52), then to 12–24 months survival (0.16, 0.14–0.21), and least sensitive to reproduction (age class 1: 0.022, 0.012–0.037, age class 2: 0.042, 0.026–0.059, age class 3: 0.040, 0.025–0.055). An elasticity analysis revealed the same pattern.

Discussion

Populations at the range edge define a species’ geographic distribution, and the dynamics of these populations makes a critical contribution to range changes, for example expansion into areas that have become suitable for the species (Kot et al. 1996). This study estimated age-specific survival and reproduction, and established a basic demographic population model for Hadedas on the leading edge of their expanding range in South Africa. Adopting a 3-month interval for the survival analyses allowed us to examine patterns in early-life survival in great detail. Clear age effects in survival and reproduction were found. Survival increased with age up to 12 months. Using estimates for all demographic rates, we found that the matrix population model returned a mean population growth rate that was inconsistent with the observation that this population is increasing. Either our survival estimates are biased low (likely survival of the 24+ month age class for which we had few data) or the population increase was driven by immigration. The age effect of reproduction was apparent: an increase in the number of fledglings per pair was associated with an increase in nest age (as a measure of experience of the breeding pair). This trend was evident in terms of both the number of fledglings per brood, and the number of broods per pair per year.

Survival

In most bird species, young birds survive less well than older ones (e.g. Ricklefs 2000). However, given the usual focus on annual survival, little is known about age-specific survival at a finer time scale. The first major change in the lifestyle of an altricial bird is when it fledges, and the period immediately after fledging could thus be particularly risky. Accordingly, we found that survival was lowest during the first quarter of the Hadedas’ life, and then increased until the age of 1 year.

Few studies have focussed on the demographics of water birds (Cézilly 1997; Hafner et al. 1998; Tavecchia et al. 2001; Balkiz et al. 2010), making comparisons to other waders and ibises difficult. We are aware of only one paper that studied the demography of ibises (Li and Li 1998). Li and Li (1998) estimated annual survival for an increasing population of Crested Ibis (*Nipponia nippon*) to be 0.57 for juveniles, 0.80 for immature, and 0.95 for adults. While our

estimate of survival for 1st-year Hadedas (0.27) is markedly lower than that for Crested Ibis, the immature life stages appear to have comparable survival rates. The Crested Ibis population was critically endangered and closely managed, which could explain the relatively high juvenile survival found in that study. Alternatively, our estimate may be biased low if Hadedas emigrated from our study area during their 1st year. However, our study area was large relative to the movement of the birds, and we had no record of any of our birds encountered outside the study area.

Our 1st-year survival estimate was more consistent with that of other related water birds. Juvenile survival for the Eurasian Spoonbill (*Platalea leucorodia*) was 0.32 (Bauchau et al. 1998), for Wood Storks (*Mycteria americana*) it was 0.44 (Hylton et al. 2006), and it ranged from 0.06 to 0.55 between years for Little Egrets (*Egretta garzetta*) (Hafner et al. 1998).

Few other studies on birds with a biology comparable to Hadedas report survival of the immature age class (Cézilly 1997). North (1979) found that 2nd year survival for the Grey Heron (*Ardea cinerea*) was 0.64, which is consistent with our estimate for Hadedas (0.74). Survival of immature Blue Cranes (*Anthropoides paradiseus*) was 0.73 (Altwegg and Anderson 2009).

Reproduction

A clear breeding-experience effect was found for Hadedas. Nests that had been used for more years produced more fledglings. Since Hadedas are faithful to their nesting site, we interpret this result as an effect of experience and age of the breeding pair. The capacity for older birds to breed more successfully is well-known and occurs within many species (Forslund and Pärt 1995; Komdeur 1996; Reid et al. 2003; Altwegg et al. 2007; Limmer and Becker 2010).

Three key hypotheses have been proposed to account for such observations. (1) Heterogeneity in quality among individuals and non-random mortality results in poor quality individuals dying early and an increase in mean performance among the survivors (Vaupel and Yashin 1985). (2) Increased reproductive effort with age as the residual reproductive value decreases and individuals increasingly favour investment in reproduction over their own survival (Williams 1966). (3) Improved life-skills efficiency with age may allow older individuals to raise more nestlings than younger individuals do (Curio 1983).

The first hypothesis may be tested using random effects. Differences in inherent quality of breeding birds are accounted for by the random effects term added as nest ID within the reproduction model. As a result, if the observed trend of older birds producing more fledglings was dependent solely on the inherent quality of breeding birds,

the breeding age effect would disappear. This was not observed, and thus, this hypothesis was not supported by our data.

It is difficult to tease apart which of the remaining hypotheses drive the observed breeding age effect (Newton 1989). The present study gathered insufficient data to definitively support one theory over the other. To understand which is more applicable in this instance, future research should aim to quantify the levels of reproductive efforts and daily energetic expenditures of older and younger birds, as has been done in other studies (D'Amico and Hémery 2007; Green et al. 2009). This will shed light on whether older birds perform life skills more efficiently than do young birds, thereby distinguishing which of the remaining two hypotheses is more likely.

Life histories

Sæther et al. (1996) propose that birds cluster around three life history strategies: high-reproductive, survivorship, and bet-hedging species. The latter are characterised by having a larger clutch size than survivors but they also have a high reproductive potential, including the ability to breed more than once per year under good conditions.

The data from this study suggest that Hadedas fit into the bet-hedger strategy. Our results showed that Hadedas are relatively long-lived, but are able to reproduce at a high rate. They have a relatively large clutch size (typically three to four eggs are laid per brood), and are able to breed up to four times per year (see Fig. 4a). Several pairs observed during this study fledged five or six chicks in a single year. Moreover, if a particular brood failed, the adult pair was often able to breed again immediately. Even though the Hadedas' reproductive output is less than that of typical bet-hedger species such as some galliformes and some anseriformes (Sæther et al. 1996); they reproduce at a higher rate than representatives of the survivor species group like, for example, Blue Cranes (Altwegg and Anderson 2009).

Active Hadedas nests were found at any time throughout the year in our study population, which suggests that, like other wading birds, Hadedas can take advantage of good conditions (Sæther et al. 1996). Lack (1968) proposed that levels of food supply during the breeding season limit reproductive output. The many artificially irrigated fields and lawns throughout the study area may provide Hadedas with a constant source of food (Duckworth et al. 2010), and, as a result, food appears not to be limiting reproduction, and hence Hadedas are able to reproduce year-round.

Range expansion

Our demographic estimates and population model led to a shrinking Hadedas population even though the confidence

interval around the estimated population growth rate included values consistent with an increasing population. Nevertheless, the most likely values for the fitness components appear inconsistent with the observed range expansion and increased reporting rates of these birds in the atlas projects, from 4% in the late 1980s to 86% towards the end of our study. There are two possible explanations for this discrepancy: either we underestimated some of the demographic rates, or the expansion is driven by immigration from other sources. Little is known about the movement of these birds, but given that our estimate for the 24 + months age class was based on little data (19 individuals were observed in this age class, and only at the end of the study), we think that this survival rate could be biased low. Assuming adult survival rates that are in line with estimates from the literature on similar birds leads to an increasing population.

Our estimates of age-specific survival and reproduction, and a matrix population model showed two characteristics of this population. On the one hand, Hadedas appear to be relatively long-lived birds, a trait that makes their populations less susceptible to intermittent breeding failure. On the other hand, breeding success was on average high and variable for a bird of this size. This trait allows Hadedas to take advantage of favourable conditions, like irrigated fields and lawns throughout the Western Cape, which supply them with a year-round food source (Duckworth et al. 2010). This may allow them to breed successfully, often more than once per year, which in turn allows them to persist and expand (Macdonald et al. 1986). Other ibises expanding their ranges have also been reported to quickly take advantage of good conditions provided by humans, which has been suggested as a causal factor in their range expansion. Examples include the Australian White Ibis in Australia (Martin et al. 2007, 2010), the African Sacred Ibis in Europe (Clergeau and Yesou 2006) and the Glossy Ibis in North America (Patten and Lasley 2000). Perhaps the ability to quickly take advantage of good conditions, a trait of a bet-hedging life strategy, makes the family prone to expanding their ranges, given the right conditions.

For Hadedas, improved foraging success on irrigated land (Duckworth et al. 2010) likely resulted in higher breeding success and population growth. Our study provides a baseline against which demographic studies at the core of the range can be compared. It also highlights the need to better understand the movement patterns of these birds, since range expansions are determined both by local population growth and dispersal (Kot et al. 1996).

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