J Ornithol (2015) 156:903–913
DOI 10.1007/s10336-015-1199-0

ORIGINAL ARTICLE

Black Sparrowhawk brooding behaviour in relation to chick age and weather variation in the recently colonised Cape Peninsula, South Africa

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Received: 10 June 2014 / Revised: 18 February 2015 / Accepted: 4 March 2015 / Published online: 18 March 2015

Abstract Understanding the effects climate change may have on animal populations relies on establishing which environmental conditions shape their behaviour and subsequent reproductive output, fitness or survival. South Africa has seen significant warming trends and changes in precipitation over the last few decades; however, the ways in which these trends are likely to influence animal populations are still relatively poorly understood. The Black Sparrowhawk (*Accipiter melanoleucus*) has expanded its range in South Africa and recently colonised the Cape Peninsula in the Western Cape, a region that experiences a Mediterranean climate. In this study, we examined the brooding behaviour of this species, a vital trait for reproductive success, in the Cape Peninsula breeding population. We examined the influence of chick age as well as temperature, rainfall and wind speed on parental brooding. Additionally, the effect of prey provisioning on brooding was investigated. In our analyses, we used data on brooding from nest cameras together with weather data collected at a fine temporal scale (1 h). The variable with the strongest influence on parental brooding was chick age. This variable showed a non-linear relationship. Initially chicks were brooded >50 % of the time; however after 3 weeks brooding declined rapidly. The proportion of time spent brooding increased with decreasing temperatures, while rainfall and wind speed showed a positive correlation with the amount of brooding. Our model predicted that in common winter conditions of the Western Cape (15 °C, 10 km/h wind speed, 1 mm/h rainfall) *A. melanoleucus* breeding pairs spent nearly 100 % of their time brooding young chicks (7 days old) to protect them from detrimental weather. Our results highlight measurable effects of weather patterns on avian behaviour at a key stage of the life cycle. Changes in weather conditions predicted for this region will likely further benefit this range-expanding species.

Keywords Black Sparrowhawk · *Accipiter melanoleucus* · Brooding · Climate · Weather · South Africa

Zusammenfassung

Der Einfluss von Nestlingsalter und Wetterschwankungen auf das Brutverhalten des Mohrenhabichts auf der kürzlich besiedelten Kap-Halbinsel, Südafrika

Um die möglichen Effekte des Klimawandels auf Tierpopulationen zu ergründen ist das Verständnis der Umweltfaktoren die ihr Verhalten und die darauffolgende Reproduktion, Fitness und das Überleben bestimmen von grundlegender Bedeutung. In welcher Weise die Klimaerwärmung und Niederschlagsveränderung der letzten Jahrzehnte in Südafrika Einfluss auf die Tierpopulationen hat ist noch nicht vollständig erforscht. Der Mohrenhabicht (*Accipiter melanoleucus*) hat sein lokales Verbreitungsgebiet in der letzten Zeit erheblich vergrößert und auch die

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Communicated by O. Krüger.

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durch ein mediterranes Klima geprägte Kap-Halbinsel in der Provinz Westkap besiedelt. In dieser Studie haben wir das Brutverhalten der Art, ein unverzichtbarer Aspekt für die erfolgreiche Reproduktion, an der Kap-Halbinsel Population erforscht. Untersucht wurde der Einfluss des Nestlingsalters sowie von Temperatur, Niederschlag und Windgeschwindigkeit auf das Brüten der Elternvögel. Zusätzlich wurde geprüft ob die Bereitstellung von Nahrung das Brüten beeinflusste. Für unsere Analysen nutzten wir Aufnahmen von Nestkameras zusammen mit Wetterdaten auf einer sehr detaillierten Zeitskala von einer Stunde. Den stärksten Einfluss hatte das Alter der Nestlinge, welches in einem nichtlinearen Zusammenhang mit dem Brüten der Elternvögel stand. Anfangs wurden die Nestlinge durchschnittlich >50 % der Zeit bebrütet aber nach drei Wochen fiel dieser Wert rasch ab. Der Anteil der stündlichen Brutzeit war höher bei niedrigeren Temperaturen, während Niederschlag und Windgeschwindigkeit eine positive Korrelation mit dem stündlichen Brutanteil zeigten. Unser Modell prognostizierte, dass bei üblichen Wetterkonditionen im Winter des Westkaps (15 °C, 10 km/h Windgeschwindigkeit, 1 mm/h Niederschlag) Brutpaare von *A. melanoleucus* nahezu 100 % der Zeit mit dem Bebrüten von jungen Nestlingen (7 Tage alt) verbringen müssen, um diese vor schädlichen Wettereinflüssen schützen zu können. Unsere Ergebnisse ziehen Aufmerksamkeit darauf wie Wettereffekte das Verhalten von Vögeln in einer entscheidenden Stufe ihres Lebenszyklus beeinflussen und wie diese Effekte quantifiziert werden können. Die vorhergesagten Klimaveränderungen in der Region werden der weiteren Ausbreitung des Mohrenhabichts voraussichtlich zuträglich sein.

Introduction

The prospect of global change caused by human activities has major implications for worldwide biodiversity and threatens animal and plant populations with extinction (Root et al. 2003). The extent of global extinctions will depend on future trends in greenhouse gas emissions and rates of anthropogenic habitat degradation, but also on the adaptability of populations to novel climatic circumstances (Visser 2008; Butchart et al. 2010; Hoffmann and Sgrò 2011). Birds have been proposed as model organisms to study the effects of climate change on animal behaviour (Crick 2004); consequently, understanding these effects will enable us to reconcile and refine our predictions about global change pressures on biodiversity (Studeny et al. 2013).

Climate change is likely to impact bird populations via cumulative responses to weather variables that affect life cycles and behaviour (Carey 2009). For example, rainfall or temperature can have a significant impact on the reproductive success of birds (Wingfield 1984), either directly by changing metabolic costs or indirectly by altering food availability, and may differ in their effect across geographic regions (Redpath et al. 2002; Sergio 2003). Strong rainfall and cold temperatures have been linked to decreased productivity in reproduction (Redpath et al. 2002; MCDonald et al. 2004; Lehikoinen et al. 2009; Amar et al. 2011, 2012). Parental brooding is a vital behaviour for successful breeding, particularly for altricial species where young chicks are unable to thermoregulate and are therefore highly vulnerable to adverse weather conditions (Elkins 1983). Increased metabolic cost for nestlings and adult birds, triggered by low temperatures during the breeding season, may therefore cause a trade-off for the adult bird between foraging, to satisfy increased metabolic demand, and brooding, to protect nestlings from hypothermia (Redpath et al. 2002). Therefore, understanding how such behaviours vary in relation to local weather conditions will help inform predictions about how climate change may influence a key stage of the breeding cycle.

The last decades have seen significant warming trends in southern Africa, and the western part of the region is predicted to experience the most rapid change in the future (Midgley et al. 2003; Kruger and Shongwe 2004; Hockey et al. 2011). Within South Africa, many species have shown westward range shifts, and although the exact cause of these shifts remains unclear, many have been linked with changes in climate (Hockey and Midgley 2009; Hockey et al. 2011; Madden 2013). The Black Sparrowhawk (*Accipiter melanoleucus*) is one species that has expanded its range westward in the last few decades (Hockey and Midgley 2009; Amar et al. 2013) and now breeds throughout much of the Western Cape, including the Cape Peninsula, where the first breeding attempt was recorded in 1993 (Oettlé 1994). Within South Africa the species breeds during winter with most clutches being laid between May and November (Allan 1997; Curtis et al. 2004; Martin et al. 2014). The species now experiences two very different climatic regimes, dry winters in its traditional eastern range and wet winters in the newly colonised Mediterranean climate of the west (Amar et al. 2014; Martin et al. 2014). However, despite this novel environment, the Black Sparrowhawk has been shown to be very productive in the west and even led to the first recordings of multiple-brooding in the species, possibly because of the abundant sources of prey found within this human-modified environment (Curtis et al. 2004).

In this study we explore the brooding behaviour of Black Sparrowhawks in the recently colonised Mediterranean climate of the Cape Peninsula, South Africa. We examine how the proportion of time adults spend brooding changes as chicks age and according to local weather conditions, including temperature, rainfall and wind speed. Specifically, we hypothesise that in this winter rainfall region the time spent brooding will increase with detrimental weather (low temperatures, high rainfall and high wind speed) to protect nestlings from hypothermia.

Methods

Study area and data collection

Data on breeding behaviour of Black Sparrowhawks were collected in the 2012 breeding season from six nests on the Cape Peninsula, Western Cape Province, South Africa (Table 1). The nests were located by searching for calling individuals, prey remains, whitewash and nest structures in suitable stands of trees. If a pair was found actively breeding, a remote camera was installed 1.5–2 m above the nest before or during the nestling stage. The camera units were set to record on a daily duty cycle from 1 h before sunrise until 1 h after sunset, adjusted for seasonality. Two different camera types were used in monitoring nests. First, solar-powered remote trail cameras (Ltl Acorn Model: Ltl-6210MC) were used, which recorded images at regular 3-min intervals; second, images were taken by motion-triggered cameras, developed by the Royal Society for the Protection of Birds (Bolton et al. 2007). The recorded images from the six nest cameras were analysed visually to evaluate the percentage of time within each hour period that adults spent brooding their chicks. In case of the system recording every 3 min, this was the percentage of images showing brooding activity. With motion-triggered cameras this was the percentage of minutes per hour with brooding, derived from the digital timestamp of the images. We established that the two approaches were comparable by deploying both systems at a single nest. From a sample of hours ($n = 35$), examined throughout the nestling period, this comparison produced near identical results in the percentage of time spent brooding ($R^2 = 0.99$), which was unsurprising given that the average length of brooding bouts (mean ± SE 58.2 ± 8.69 min) was considerably longer than the 3-min interval of the camera system. Our brooding measures included parental brooding activities (shading or physical contact with the chicks) but not times where adult birds stayed idly on the nest. As with many other raptor species, and particularly accipiters, the female undertook the vast majority of brooding (Newton 1986; Redpath et al. 2002; Kross et al. 2012). However, the male would occasionally also brood the young chicks, and this behaviour was also included in our brooding measures. For each hour of observation we obtained data on the local weather conditions using information from a nearby weather station installed by the South African Environmental Observation Network (SAEON). This station was set up on Rhodes Memorial game camp (33.952°S, 18.459°E), which was located on average 11.07 km (range 0.44–22.94 km) from the nest sites studied. Weather variables used in this study were the average temperature per hour (°C), average wind speed during the hour (km/h) and total rainfall per hour (mm). Prey items brought to the nest by the Black Sparrowhawk pairs were noted within each hour. From these data we constructed a measure of prey provisioning in the prior 24 h by calculating a moving average to match each hour of parental brooding. Because of battery changes or malfunctioning of some cameras we did not have continuous footage for most of our nests, meaning the moving average was not always consistent in the number of hours covered to reflect the amount of prey provisioning. We also recorded brood size and the age of the chicks, which was determined from video footage, with chicks aged according to the date when the first chick hatched (day after hatch date = age 1 day). For older chicks where the hatch date was unknown, age was determined by comparing the relative plumage development and size of the chick to a reference collection of photographs of chicks 0–45 days old. To further confirm the age of the chicks, we backdated their age from the day they fledged, where on average they fledged at 45 days old.

Statistical analysis

Data on the percentage of time spent brooding per hour were arcsine square root transformed prior to analysis to improve their normality. After transformation, model residuals were assessed with histograms and quantile-

Table 1 The six Black Sparrowhawk nests monitored in this study with geographical coordinates, timeframe recorded, chick age, brood size, hours of footage and camera type (*MT* motion triggered, *RI* regular interval)

Territory	Latitude (°S)	Longitude (°E)	Start date	End date	Chick age (days)	Brood size	Hours footage	Camera type
Chart Farm	34.004	18.445	28/06/2012	18/08/2012	1–49	2	242	MT
Glen Cairn	34.153	18.416	1/10/2012	19/10/2012	23–41	1	248	RI
Newlands Picnic	33.965	18.454	1/08/2012	23/08/2012	23–45	2	162	MT
Rhodes Mem	33.946	18.460	14/09/2012	11/10/2012	10–37	3	150	MT
Stone Church	34.055	18.424	10/11/2012	20/12/2012	1–41	2	558	RI
Sunnycroft	34.134	18.394	19/10/2012	7/11/2012	26–45	2	286	RI

quantile plots, which conformed to the assumption of normality. Data were analysed using a general linear mixed model (GLMM) fitted within R, version 3.0.3 (R Core Team 2013), using the lme4 package (v. 1.1-5), specifying a normal distribution and an identity link function. Our GLMMs fitted the transformed proportion of time spent brooding (in each hour) as the response variable with the fixed effects of rainfall, temperature, wind speed and chick age. Additionally, two-way interactions between fixed effects were specified and quadratic and cubic polynomials to test for non-linear effects of predictor variables (Schielzeth 2010; Kross et al. 2012). We had repeated measures from each territory and within the different hours of the day, and these variables (territory and hour of day) were therefore specified as random effects to control for their non-independence. GLMMs were fitted by maximum-likelihood estimation to facilitate comparison of differing fixed effect structures. Akaike's information criterion corrected for small sample size ($\mathrm{AIC_C}$) was used to select the model of best fit, and evidence for the strength of model support was assessed by Akaike weights (w_{AICc}). Brood size was not used as a predictor in the analysis because of the low variation and therefore low predictive power evident in our data set (i.e. 75 % of data had a brood size of 2; Table 1). Goodness of fit was judged with the conditional R^2 method proposed by Nakagawa and Schielzeth (2013) describing the variance captured by fixed and random effects. To aid interpretation and facilitate intra-model comparison of regression coefficients from complex GLMMs, the model with the lowest $\mathrm{AIC_C}$ value was refitted on a standardised data set (Schielzeth 2010). Standardisation of input variables was achieved by centring (subtracting sample mean) and scaling (dividing by sample standard deviation) and thereby converted to units of phenotypic standard deviations (Schielzeth 2010).

Review of raptor brooding behaviour

We were interested to explore the brooding behaviour of the Black Sparrowhawk monitored in this population in the context of the brooding behaviour of other raptor species. Specifically, we were interested to see whether the period with intensive brooding changed in relation to the average size of a species. We searched for brooding behaviour data for other raptor species using the following keywords "brooding", "breeding" and "parental care" together with raptor taxon names (e.g. "accipiter") in the literature database "Web of Science". We only used studies that provided information on the percentage of time spent brooding in relation to chick age and extracted the age of the chicks when brooding dropped below 20 %. Raptor size was chosen to reflect the general developmental time needed by nestlings after hatching. The Black Sparrowhawk *Accipiter melanoleucus* is size dimorphic, with a mean weight of 460 g for males and 815 g for females (Del Hoyo et al. 1994). To compare the different raptor species we used the mean weight taken from Del Hoyo et al. (1994); for size dimorphic species the average between male and female weight was used.

Results

Our best fitting model included the fixed effects of chick age (linear, quadratic and cubic polynomials), rainfall, temperature and wind speed, and the interactions of chick age × temperature and rainfall × wind speed (model no. 1, Table 2). This model had the lowest $\mathrm{AIC_C}$ and received the highest support with $W_{\mathrm{AICc}} = 0.261$ (Table 2). Also, model no. 1 appeared to fit the data very well, as nearly 70 % of the variance was captured by fixed and random effects (conditional $R^2 = 0.68$). The marginal R^2 value (variance captured by fixed effects only) for model no. 1 was 0.59. Further model combinations that included other two-way interactions received less support with higher $\mathrm{AIC_C}$ values (Table 2). The comparison of regression coefficients derived from fitting an identical model on the standardised data showed that the strongest effect on time spent brooding was due to the negative linear term of chick age (Fig. 1). The strongest effect of the weather predictor variables was found for temperature, which negatively impacted time spent brooding (Fig. 1). Wind speed and rainfall had a positive but less strong effect on the amount of brooding per hour (Fig. 1). Chick age had a non-linear influence on the brooding behaviour of Black Sparrowhawks, evident by the quadratic and cubic polynomials for chick age (Table 2; Fig. 1). During the first and second week after hatching usually more than 70 % of available time was spent brooding (Fig. 2). In the third week, average brooding declined, but this average value was strongly influenced by the anomaly in brooding behaviour seen on days 18 and 19, when much lower values (<20 %) were observed (Fig. 2). These anomalies at days 18 and 19 occurred in two separate nests and corresponded with atypically warm temperatures. It was not until after the third week that the percentage of brooding by Black Sparrowhawks declined rapidly (Fig. 2). Percentage of time spent brooding increased when temperatures were low and with increasing rainfall (Fig. 3). The interaction of chick age and temperature reflected greater brooding as temperatures declined when the chicks were younger. The interaction between rainfall and wind speed reflected that in wetter conditions brooding decreased more rapidly with increasing wind speed. Candidate models including the effect of prey provisioning and its two-way interactions showed $\mathrm{AIC_c}$ values with delta <2 compared to our best

Table 2 Evaluation of GLMM fixed effects for Black Sparrowhawk brooding behaviour with Akaike's information criterion corrected for small sample size (AIC_C), model support by Akaike weights (w_{AICc}) and degrees of freedom consumed by each model (*df*)

No.	INT	CA	CA^2	CA^3	*R*	*T*	WS	CA × *R*	CA × *T*	CA × WS	*R* × *T*	*R* × WS	*T* × WS	*df*	AIC$_C$	ΔAIC$_C$	w$_{AICc}$
1	2.115	−0.0334	−0.0022	0.00004	0.3939	−0.0433	0.0107		0.0009			−0.0242		12	1111.81	0.00	0.261
2	2.084	−0.0333	−0.0022	0.00004	0.3943	−0.0429	0.0144		0.0009	−0.0001		−0.0243		13	1113.28	1.46	0.126
3	2.115	−0.0334	−0.0022	0.00004	0.4272	−0.0434	0.0107		0.0009		−0.0027	−0.0242		13	1113.83	2.02	0.095
4	2.116	−0.0335	−0.0022	0.00004	0.3864	−0.0434	0.0107	0.0003	0.0009			−0.0240		13	1113.83	2.02	0.095
5	2.113	−0.0334	−0.0022	0.00004	0.3944	−0.0432	0.0110		0.0009			−0.0242	−0.00002	13	1113.84	2.03	0.095
6	2.071	−0.0332	−0.0022	0.00004	0.3967	−0.0423	0.0163		0.0009	−0.0001		−0.0245	−0.00010	14	1115.27	3.46	0.046
7	2.086	−0.0334	−0.0022	0.00004	0.3818	−0.0430	0.0144	0.0005	0.0009	−0.0001		−0.0239		14	1115.28	3.47	0.046
8	2.085	−0.0333	−0.0022	0.00004	0.4360	−0.0429	0.0144		0.0009	−0.0001	−0.0034	−0.0242		14	1115.29	3.48	0.046
9	2.116	−0.0335	−0.0022	0.00004	0.4165	−0.0434	0.0107	0.0003	0.0009		−0.0024	−0.0240		14	1115.86	4.05	0.034
10	2.113	−0.0334	−0.0022	0.00004	0.4279	−0.0432	0.0110		0.0009		−0.0028	−0.0242	−0.00002	14	1115.86	4.05	0.034
11	2.114	−0.0335	−0.0022	0.00004	0.3870	−0.0433	0.0109	0.0003	0.0009			−0.0240	−0.00002	14	1115.87	4.06	0.034
12	2.071	−0.0332	−0.0022	0.00004	0.4401	−0.0423	0.0163		0.0009	−0.0001	−0.0036	−0.0245	−0.00011	15	1117.28	5.47	0.017
13	2.073	−0.0333	−0.0022	0.00004	0.3853	−0.0424	0.0162	0.0005	0.0009	−0.0001		−0.0242	−0.00010	15	1117.28	5.47	0.017
14	2.086	−0.0334	−0.0022	0.00004	0.4171	−0.0430	0.0145	0.0005	0.0009	−0.0001	−0.0028	−0.0240		15	1117.31	5.50	0.017
15	2.114	−0.0335	−0.0022	0.00004	0.4176	−0.0433	0.0110	0.0002	0.0009		−0.0024	−0.0241	−0.00002	15	1117.90	6.08	0.012
16	2.073	−0.0333	−0.0022	0.00004	0.4234	−0.0424	0.0163	0.0004	0.0009	−0.0001	−0.0030	−0.0243	−0.00010	16	1119.31	7.50	0.006
17	2.145	−0.0336	−0.0022	0.00004	0.1586	−0.0446	0.0093		0.0009					11	1120.13	8.32	0.004
18	2.154	−0.0342	−0.0022	0.00004	0.1062	−0.0450	0.0094	0.0031	0.0009					12	1121.28	9.46	0.002
19	2.116	−0.0334	−0.0021	0.00004	0.1583	−0.0443	0.0128		0.0009	−0.0001				12	1121.66	9.85	0.002

Random effects of territory and hour of day specified for all combinations. Precision of estimates given to max. 1e−5. Further model combinations with ΔAIC$_C$ > 10 not shown

INT Intercept, *CA* chick age, *CA^2* quadratic polynomial of CA, *CA^3* cubic polynomial of CA, *R* rainfall, *T* temperature, *WS* wind speed, × two-way interactions of fixed effects

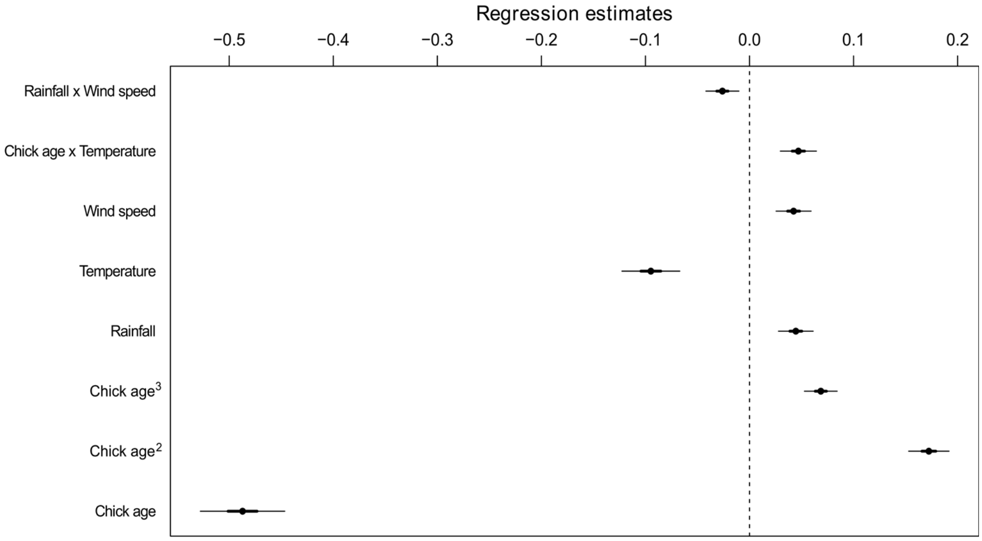

Fig. 1 Comparison of regression coefficients from a GLMM fitted on standardised data with the fixed effects of chick age, rain, temperature, wind speed, quadratic and cubic polynomials for chick age, interactions chick age × temperature and rain × wind speed and random effects hour of day and territory. Predictor units resemble phenotypic standard deviations and are on the same scale. Point shows mean estimate while *outer bars* denote a 95 % CI and *inner bars* 1SE

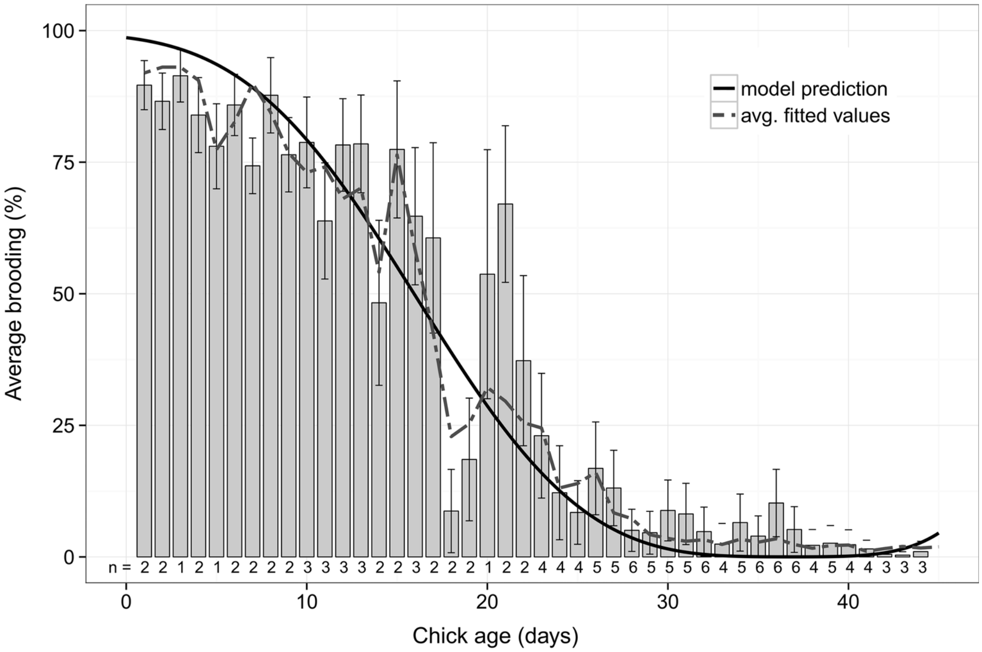

Fig. 2 Relationship between chick age and Black Sparrowhawk brooding behaviour. Note the rapid decline in time spent brooding (%) approximately 3 weeks after hatching. *Bars* display raw data with ±2 SE and *n* value below indicates number of replications for each day (see also Table 1). *Dashed line* shows average fitted values from a GLMM with the fixed effects of chick age, rain, temperature, wind speed, quadratic and cubic polynomials for chick age, interactions chick age × temperature and rain × wind speed and random effects hour of day and territory (model no. 1, Table 2). *Black trendline* represents the prediction from the same model for the relationship between brooding and chick age at mean values of other fixed effects. Brooding anomaly at days 18 and 19 caused by two nests with abnormally warm temperatures observed 3 months apart

fitting model no. 1 and a negative effect on parental brooding (Table 3, "Appendix"). Testing directly for the inclusion of prey provisioning did not support it as a fixed effect ($P = 0.173$, type III Wald chi square, Table 3, "Appendix").

In our study, parental brooding dropped below 20 % after the chicks were aged 24 days. Age at which brooding is rapidly reduced is likely to depend on when chicks are able to thermoregulate, and this timing may well be related to the size of the species and thus the overall development time of the chicks. To explore the evidence for such a relationship we reviewed the available data on raptors for when this rapid drop in brooding (<20 %) occurs in relation to the size (weight) of the species (Fig. 4). These data suggested a strong linear relationship between the length of intensive brooding and species average weight ($R^2 = 67.5$,

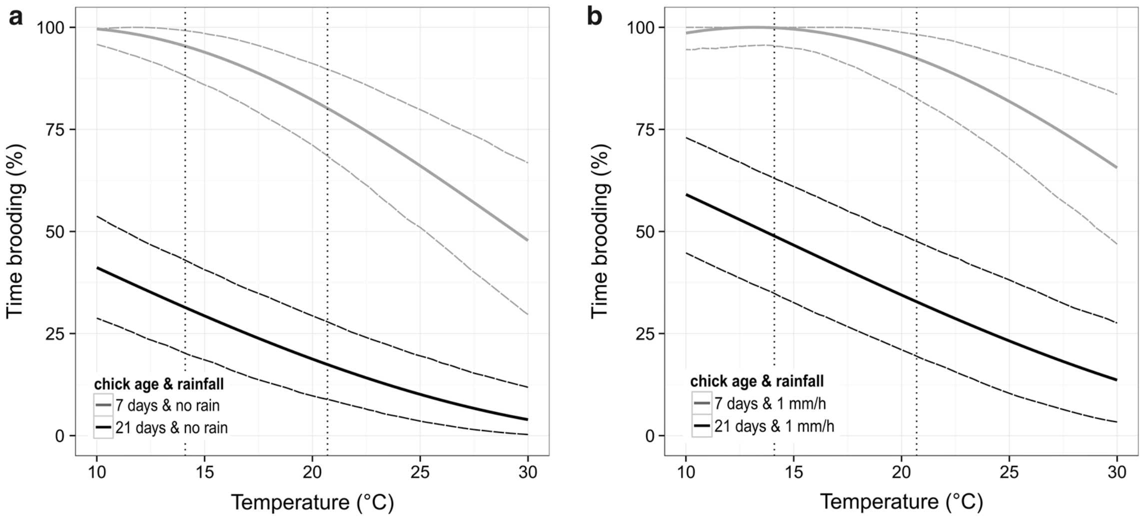

Fig. 3 Relationship between time spent brooding by Black Sparrowhawks and weather variation with young and old chicks. Time spent brooding (%) in relation to temperature (°C) with no rainfall and young (7 days old) or old chicks (21 days old) displayed in **a**. **b** Relationship between time spent brooding and temperature at high rainfall (1 mm/h) and with young or old chicks. Age of 21 days was chosen for old chicks because chicks start to self-thermoregulate more effectively afterwards (Hockey et al. 2005). Lines are predicted from the GLMM output with the fixed effects of chick age, rain, temperature, wind speed, quadratic and cubic polynomials for chick age and interactions chick age × temperature and rain × wind speed (model no. 1, Table 2). *Vertical dotted lines* represent 1 and 3 quartiles of the temperature data; *dashed lines* represent bootstrapped 95 % CIs (1000 replications)

$P < 0.001$), with brooding increasing by 1 day for each extra 330 g the species increases in weight. In comparison with other raptor species of similar size, the Black Sparrowhawks in our study area decreased their brooding activity considerably later (Fig. 4). Based on this relationship, the chick age of 24 days when brooding drops off <20 % would be expected for a species about three times the size of a Black Sparrowhawk (Fig. 4).

Discussion

The results of this study suggest measurable impacts of weather patterns on Black Sparrowhawk brooding behaviour. We found that low temperatures, higher wind speed and high rainfall during the nestling phase lead to Black Sparrowhawks increasing the amount of time they spend brooding their chicks, confirming the hypothesis of the study. Thus, within the Mediterranean climate of the Western Cape, the dominant weather conditions during winter appear to have a strong influence on an important behavioural trait, which is likely to be energetically costly (Dunn 1980; Martin 1987). Our results suggest that temperature is the most important weather variable explaining variation in brooding behaviour, whereas the effects of wind speed and rainfall were less influential. Testing for the inclusion of prey provisioning to explain variation of parental brooding showed weak evidence (based on the AIC_c) that brooding decreases with an increase in the amount of prey delivered in the previous 24 h. The inaccuracy of our provisioning measure, due to the discontinuous nature of our data, likely affects our analysis of prey provisioning and these results have to be viewed with caution. The interaction of rainfall and wind speed, suggesting a decrease in brooding with high rainfall and high wind speed, was the weakest of all variables and does not appear to be biologically sensible. It may simply be an artefact in the data as high rainfall events were relatively rare. Modelling the behavioural response to detrimental weather during breeding showed that conditions could easily occur where the female would spend more than 80 % of her time brooding the chicks. The increased brooding effort is important to protect the chicks from hypothermia, which is especially necessary at a young age when they are unable to effectively thermoregulate (Visser 1998). This was confirmed by the results in this study, where the interaction between chick age and temperature emphasised that young chicks are especially vulnerable to cold temperatures. We found a strong decline in brooding as chicks aged, with a major drop in brooding activity 3 weeks after hatching, a stage at which chicks develop substantial plumage and are probably better able to thermoregulate themselves. After 44 days no more brooding behaviour was recorded; this is in accordance with the previously described time of chicks fledging at 37–45 days old (Hockey et al. 2005). The anomalies at age 18 and 19 days, with very low percentages of brooding, were observed from two separate nests 3 months apart (territories Chart Farm and Stone Church, Table 1). These anomalies may be explained by the surprisingly warm

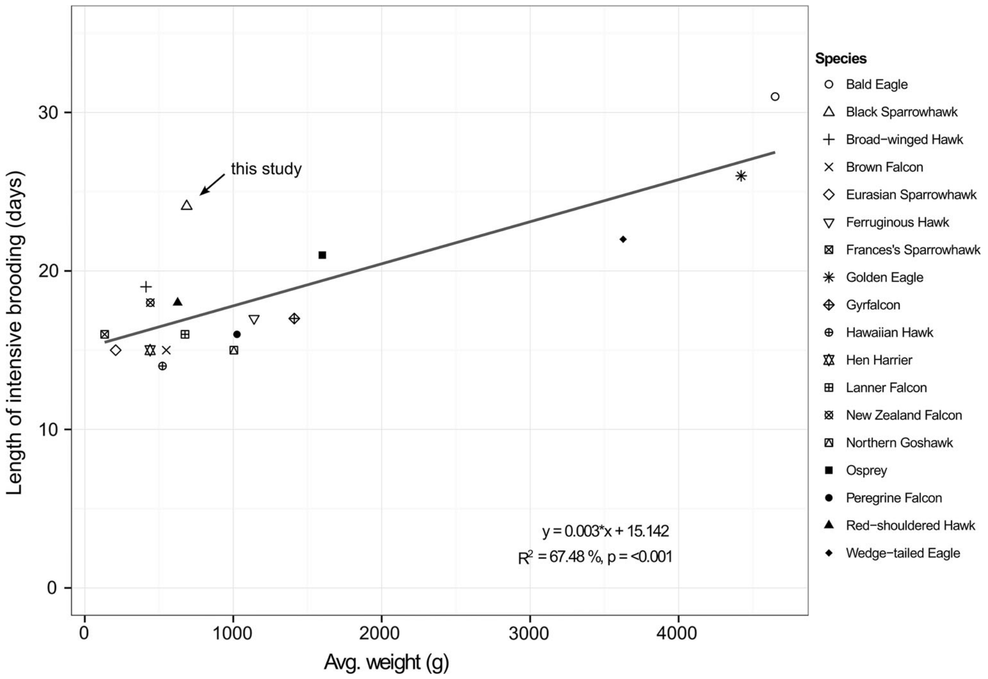

Fig. 4 Relationship between length of intensive brooding and average weight (g) of a raptor species derived from the literature. We suggest that the time where brooding rapidly drops off because of a sufficient ability of the chicks to thermoregulate is strongly related to the general size of the species and thereby the timeframe needed for chick development. Species weights are mean values taken from Del Hoyo et al. (1994); for sexually dimorphic species the average of male/female mean weight is displayed. Brooding drop-off age was defined as the number of days after hatching where parental brooding falls below 20 % of available time. A curvilinear trend line fitted the data less well, reducing the R^2 value to 49.25 % (not displayed). For references used for this review, see Table 5 in "Appendix"

temperatures on those days, with the temperature being 26.1 and 17.6 % warmer, respectively, than the mean over the whole nesting period.

Our mini review of brooding patterns and species size suggested that there was a strong significant linear relationship between the species weight and timing of reduced brooding. For most studied species, as in this current study, brooding tends to remain at relatively high levels and then rapidly declines, presumably when the chicks are able to thermoregulate for themselves. Our analysis suggests that the timing of this developmental stage in raptors is linked directly to the species size (weight). Data for the Black Sparrowhawk from this current study appeared to be an outlier with brooding declining 6 days later than predicted from our overall relationship. This might be because Black Sparrowhawks in our study area, unlike the rest of their South African range, are breeding during the wettest time of the year and in substantially colder temperatures (Martin et al. 2014). In contrast, Black Sparrowhawks breeding in Zimbabwe stopped parental brooding entirely as early as 22 days after chick hatching (Hartley and Hough 2004). Thus, the apparent higher brooding demands of this species on the Cape Peninsula, compared with other raptors and other regions, may therefore be the result of these constraining climatic conditions.

Weather conditions and Black Sparrowhawk breeding strategy

Detrimental effects of rainfall and low temperatures for breeding raptors arise by increasing the metabolic cost for adults and chicks (Redpath et al. 2002), but also by restricting foraging time and success (Newton 1978; Mearns and Newton 1988; Olsen and Olsen 1992; Sergio 2003). Behavioural mechanisms designed to cope with bad weather may not be able to compensate fully, as is evidenced by chick mortality recorded during periods of heavy rainfall in the Eurasian Sparrowhawk (Moss 1979; Watts 2014). Thus, Black Sparrowhawk breeding pairs face a trade-off in the Western Cape climate. They can only succeed in raising their offspring if they provide sufficient food to satisfy their broods increased demand, whilst at the same time providing sufficient protection and brooding of their nestlings. During the early stages of chick development, where chicks are most susceptible to predation and weather conditions (first 3 weeks), Black Sparrowhawk breeding behaviour may be described as females having complete dependency on the males, who actively hunt and provide food for chicks and females (Brown and Brown 1979). This partitioning of parental duties allows the females to focus their energy on the young chicks, protecting them and brooding them during detrimental weather conditions. This strategy therefore enables the species to successfully rear chicks despite harsh winter weather conditions in the Western Cape (Curtis et al. 2004). Thus, it would be very interesting to compare these behaviours between our study area and the historical eastern range where the species breeds during the dry season. No such data currently exist, but such a comparison would further our understanding of how populations adapt their breeding strategy to overcome the detrimental weather patterns that are more frequent in the newly colonised Western Cape.

Black Sparrowhawk range expansion

The colonisation of the Western Cape by Black Sparrowhawks has only occurred within the last few decades (Hockey and Midgley 2009). Simultaneously, annual mean temperatures have increased by 0.2 °C per decade from 1960 to 2003 on the Cape Peninsula (Kruger and Shongwe 2004) alongside declines in the average rainfall levels in the region of about 1 mm per annum from 1987 to 2010 (Madden 2013). These trends may have helped the establishment of Black Sparrowhawk populations since they would lead to a relaxation of the foraging trade-off discussed in this study. Even small-scale changes in these climate variables can lead to avian range shifts (Sekercioglu et al. 2008), but how such effects vary with species-specific traits is not yet fully understood (Tingley et al. 2012). Looking into the future, results from this study suggest that climate change is likely to directly affect Black Sparrowhawk populations in the Western Cape in a positive manner. Predictions of climate change scenarios over the next century in the Western Cape region suggest a warming trend of 2–4 °C of average temperatures and a decrease in precipitation, especially evident in the winter season (Christensen et al. 2007). This will therefore likely further relieve the constraint associated with winter breeding for Black Sparrowhawks in the Western Cape.

Conclusions

The colonisation of the Western Cape by the Black Sparrowhawk has been largely attributed to human alterations of landscapes by planting trees in formerly treeless Fynbos habitats and also by providing abundant foraging opportunities in and around human settlements and agricultural areas (Allan 1997; Curtis et al. 2007; Hockey and Midgley 2009; Hockey et al. 2011). Additionally, this study indicates that climate effects can have a strong influence on a vital behaviour, which is likely to be important in the future reproductive success of Black Sparrowhawks. It seems plausible that behavioural changes in the time spent brooding by Black Sparrowhawks have enabled the range expansion into the Western Cape, which coincided with both warming trends and declining precipitation. The Black Sparrowhawk may therefore be an example of a species modifying its behaviour according to the combined effects of anthropogenic habitat alteration and novel climatic conditions. Monitoring future population trends and range shifts is likely to help untangle the contribution of these effects on animal populations, thereby helping to predict opportunities and costs that may occur due to global change.

Acknowledgments We are grateful for help with data processing from Marina Wang, Tesray Linevee, Sarah Caine, Jacques de Satgé, Jess Suri and Tumelo Morapi. Jacques de Satgé and Susie Cunningham are also thanked for comprehensive discussions and their help in improving the manuscript. Two anonymous reviewers are thanked for their comments of on a previous draft of this manuscript. For the provisioning of weather data we acknowledge the support of the South African Environmental Observation Network (SAEON). We are also grateful to Nigel Butcher (RSPB) who helped develop some of the cameras used in this study. J.K. was funded by a Deutschlandstipendium scholarship of the University of Applied Sciences Bremen.

Appendix

See Tables 3, 4 and 5.

Table 3 GLMM model summary for effects of chick age and weather parameters on Black Sparrowhawk brooding behaviour, including prey provisioning as fixed effect

Fixed effects	Estimate	SE	Chi square	*P* value
Intercept	2.139	$1.286e^{-1}$	276.404	$<2.2e^{-16}$
Chick age	−0.033	$8.441e^{-3}$	15.639	$7.665e^{-5}$
Chick age^2	−0.002	$3.773e^{-4}$	34.593	$4.065e^{-9}$
Chick age^3	0.00004	$5.195e^{-6}$	73.907	$<2.2e^{-16}$
Rainfall	0.393	$8.035e^{-2}$	23.946	$9.910e^{-7}$
Temperature	−0.043	$5.646e^{-3}$	57.745	$2.984e^{-14}$
Wind speed	0.011	$2.030e^{-3}$	26.999	$2.035e^{-7}$
Prey provisioning	−0.070	$5.156e^{-2}$	1.861	0.173
Chick age × temperature	0.0009	$1.650e^{-4}$	26.968	$2.069e^{-7}$
Rainfall × wind speed	−0.024	$7.501e^{-3}$	10.524	0.001

Random effects	Variance	SD
Hour	0.018	0.132
Territory	0.015	0.122

Model AICc = 1112.0, *P*-values are from a type III Wald chi-square test

SD standard deviation

Table 4 Summary statistics of measured weather variables during monitored Black Sparrowhawk breeding

Variable	Min.	Max.	Average	SD
Temperature (°C)	7.7	32.9	17.6	4.65
Rainfall (mm/h)	0	4.8	0.04	0.25
Wind speed (km/h)	0	32.2	8.9	4.3

SD standard deviation

Table 5 References used for review of the relationship between length of intensive brooding and average weight of a raptor species (Fig. 4)

Common name	Scientific name	References
Bald Eagle	*Haliaeetus leucocephalus*	Cain (2008)
Black Sparrowhawk	*Accipiter melanoleucus*	This study
Broad-winged Hawk	*Buteo platypterus*	Lyons and Mosher (1987)
Brown Falcon	*Falco berigora*	Donald (2004)
Eurasian Sparrowhawk	*Accipiter nisus*	Newton (1978)
Ferruginous Hawk	*Buteo regalis*	Wakeley (1978)
Frances's Sparrowhawk	*Accipiter francesiae*	Lily-Arison (2000)
Golden Eagle	*Aquila chrysaetos*	Collopy (1984)
Gyrfalcon	*Falco rusticolus*	Jenkins (1978)
Hawaiian Hawk	*Buteo solitarius*	Griffin et al. (1998)
Hen Harrier	*Circus cyaneus*	Leckie et al. (2008)
Lanner Falcon	*Falco biarmicus*	Jenkins (2000)
New Zealand Falcon	*Falco novaeseelandiae*	Kross et al. (2012)
Northern Goshawk	*Accipiter gentilis*	Byholm et al. (2011)
Osprey	*Pandion haliaetus*	Levenson (1979)
Peregrine Falcon	*Falco peregrinus*	Jenkins (2000)
Red-shouldered Hawk	*Buteo lineatus*	Dykstra et al. (2003)
Wedge-tailed Eagle	*Aquila audax*	Debus et al. (2007)

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