IBIS
BOU international journal of avian science
Ibis (2020) doi: 10.1111/ibi.12846

Short communication

Increasing temperatures increase the risk of reproductive failure in a near threatened alpine ground-nesting bird, the Cape Rockjumper *Chaetops frenatus*

KRISTA N. OSWALD*[1,2] ELIZABETH F. DIENER,[3]
JOHN P. DIENER,[3] SUSAN J. CUNNINGHAM[4]
BEN SMIT[1,2] & ALAN T. K. LEE[4,5]
[1]*Department of Zoology and Entomology, Rhodes University, Grahamstown, 6139, South Africa*
[2]*Department of Zoology, Nelson Mandela University, Port Elizabeth, 6031, South Africa*
[3]*Chattanooga, TN, 37410, USA*
[4]*Fitzpatrick Institute of African Ornithology, DST-NRF Centre of Excellence, University of Cape Town, Cape Town, 7701, South Africa*
[5]*Centre for Functional Biodiversity, School of Life Sciences, University of KwaZulu-Natal, Private Bag X01, Scottsville, 3209, South Africa*

A major cause of reproductive failure in birds is nest predation. Predation risk depends on predator type, as predators vary in their ecology and sensory modalities (e.g. visual vs. olfactory). Snakes (generally olfactory predators) are a major nest predator for small birds, with predation strongly associated with higher temperatures. We investigated nest survival in a ground-nesting alpine species, the Cape Rockjumper *Chaetops frenatus*, endemic to alpine fynbos in southwestern South Africa. We collected 3 years of nest data, testing whether nest survival was related to (1) habitat stage (early post-fire vs. late post-fire habitat, ≤ 3 and > 3 years since fire respectively), (2) nest concealment and (3) temperature. We found that nests had better survival at lower temperatures, with snake predation (our main source of predation) increasing in higher temperatures.

Keywords: landscape ecology, nest concealment, predator landscape, predator–prey interactions, reproductive success.

For birds, the probability of successfully fledging young is influenced by both intrinsic and extrinsic factors. Intrinsic factors may include individual thermoregulatory capabilities, female and nestling body mass, and group size (Blums *et al.* 2002, Ridley & Van den Heuvel 2012). Extrinsic factors may include nest-site selection, weather, food availability and predation risk (Martin 2001, Cox *et al.* 2013a, Carroll *et al.* 2018). Predators of avian nests include mammals, birds and snakes, all of which respond differently to nest-sites depending on their hunting strategy (Martin 1987); thus, identifying predator species is necessary for understanding the relationship between predation and nest concealment (Kleindorfer *et al.* 2005, Thompson 2007).

For visual predators, nest predation is often negatively correlated with vegetative concealment in the area directly surrounding the nest (hereafter 'nest concealment'; Ricketts & Ritchison 2000, Little *et al.* 2015; although see Li & Martin 1991). However, predation by olfactory predators is generally unrelated to nest concealment (Colombelli-Négrel & Kleindorfer 2009, Conover *et al.* 2010). Predation may also be related to concealment within the broader predator landscape (i.e. the openness of the overall breeding habitat, containing multiple potential predators; hereafter 'habitat openness'). Greater habitat openness may increase adult birds' ability to detect nest predators and so increase their ability to drive off or distract predators before they reach the nest (Amat & Masero 2004, Magana *et al.* 2010), although in some instances more open habitat can lead to increased predation (Ricketts & Ritchison 2000, Little *et al.* 2015).

While mammal predation often occurs irrespective of temperature (Cox *et al.* 2013b), both snake and avian predation often increase with higher temperatures (Weatherhead & Hoysak 1989, Cox *et al.* 2013b, DeGregorio *et al.* 2014). For snakes, this is likely to be due to increased activity at higher temperatures (Nelson & Gregory 2000, Brown & Shine 2002). With increasing temperatures resulting from climate change, it is thus likely that reproductive success for species with high rates of avian or snake predation may be acutely sensitive to temperature-related predator abundance, distribution and behaviour.

We collected nest data in a ground-nesting alpine bird, the Cape Rockjumper *Chaetops frenatus* (hereafter 'Rockjumper'). Rockjumpers are endemic to the alpine fynbos of South Africa. Alpine fynbos is characterized by sparsely vegetated open scree slopes with regularly occurring natural fire (Lee & Barnard 2016), and

*Corresponding author.
Email: knoswald@gmail.com
Twitter: @krista_natasha

progressively denser vegetation (i.e. less open habitat) with increasing numbers of years since fire. Rockjumpers build open-cup nests under rocky overhangs (Holmes *et al.* 2002), with varying amounts of short fynbos providing varying amounts of nest concealment. Ground-nesters that are also territorial residents, such as Rockjumpers, may retain knowledge of local predator activity (Lloyd 2004), allowing for nest placement in areas that combine the optimal balance of habitat openness and nest concealment.

Our study aimed to determine overall patterns of nest success by examining the effects of habitat openness, nest concealment, temperature and predation on nest survival. We predicted a positive correlation between nest survival and (1) greater habitat openness and (2) increased nest concealment. Additionally, we predicted that predation events would be best explained by nest concealment (if predominantly mammal) and temperature (if predominantly snake or bird).

METHODS

Study site and species

This study was conducted at Blue Hill Nature Reserve ('BHNR'), a *c.* 2000-ha reserve consisting of alpine fynbos at elevations of *c.* 1100–1600 m asl, which is suitable for Rockjumpers. Rockjumper family groups at BHNR generally consist of two to four individuals at comparatively low densities (1.54 individuals/km^2; Lee *et al.* 2015). Holmes *et al.* (2002) found Rockjumpers have a single two-egg nest per season, with an average incubation and nesting period both of *c.* 20 days, and a breeding season from August to December. Despite being facultative cooperative breeders (Holmes *et al.* 2002), 26 of the 30 territories in our study had a single pair of adult breeding birds.

Nest monitoring

Nests were located by spending 4–5 h in territories every 4–5 days, looking for signs of breeding (e.g. nest material in bill, food in bill, localized area fidelity). We observed birds by using binoculars or spotting scopes from 30 to 100 m distance to minimize observer disturbance. We collected observations over two complete breeding seasons (September–November 2017 and August–December 2018), with the inclusion of two nests found *ad hoc* in 2016. Only nests that reached the egg-laying stage were considered for the purpose of this study.

We placed trail cameras (Bushnell Corporation, Overland Park, KS, USA; various models) $\leq$ 1 m from every nest, set to record 3 photos per low-sensitivity motion sensor trigger. Additionally, we placed one to four infrared camera setups ('Handykams'; Handykam.com, Redruth, UK; 2017 n = 1, 2018 n = 4 cameras) $\leq$ 0.5 m from nests as available, set to record a 30-s video on low-sensitivity motion sensor trigger. Nests were checked every 4–5 days, with observers staying a maximum of 15 min within the territory per visit. We estimated hatch date with the following procedure: we estimated age of nestlings using a set of photographs collected from nestlings with known hatch date and, if a nest was found to have hatched between nest checks, we assigned a date halfway between the visits.

Habitat openness and nest concealment data

For habitat openness, we designated a Habitat Stage (early post-fire vs. late post-fire habitat) for each territory based on the following information: before 2017, all Rockjumper territories were in habitat that last burned in a 2012 wildfire ('late post-fire habitat', > 3 years since burned). In April 2017, the northern section of Blue Hill experienced a wildfire. Although the fire left the habitat denuded of vegetation, and exposed the sandy substrate, primary growth vegetation began to return within a few weeks ('early post-fire habitat', $\leq$ 3 years since burned). For nest concealment, we estimated the percentage of vegetative ground cover as viewed from *c.* 1.75 m height, within a 1-m radius ('Veg Cover'), using the nest as the centre point. The vegetation of the alpine fynbos at BHNR is typically *c.* 0.5 m tall, and all vegetation present within the 1-m radius was < 1 m tall.

Nest success

For each nest we recorded the territory designation 'Territory' (n = 30 territories based on unique colour-ring combinations; see Oswald *et al.* (2019)), individual nest identification number ('Nest ID'), number of eggs and/or nestlings in the nest ('Brood Size') and ordinal date ('Date'). In total, we collected data from 56 nests over 3 years (2016: n = 2; 2017: n = 17; 2018: n = 37). Forty-eight nests failed (2016: n = 2; 2017: n = 16; 2018: n = 30), with the remaining eight nests fledging at least one chick (2017: n = 1; 2018: n = 7). Nests were considered successful if one or more young fledged. Two nests were removed from predation analysis as their failure was attributed to an unusual late-season snow cover event in 2018 that rendered the eggs unviable, leaving a total of 54 nests. We found similar numbers of nests failed as eggs and nestlings (n = 24 and 22, respectively; Table 1) and thus have not included nesting stage in further analyses.

Following Shaffer (2004), we calculated daily survival rate using a modified Mayfield method (Mayfield 1975). We implemented 'logistic exposure models' across nest

Table 1. Total number of nests ($n = 54$), including number of failed nests per nest stage ('egg stage' or 'nestling stage') and month in which they failed, as well as the number and percentage of successful nests (i.e. producing at least one fledgling) by month fledged, from Cape Rockjumper *Chaetops frenatus* nests observed during August to December in 2016–2018 from Blue Hill Nature Reserve, South Africa.

Month	Total nests	Failed at egg stage[a]	Failed at nestling stage	Fledged
August	2	1	1	0 (0.0%)
September	9	6	1	2 (22.2%)
October	15	10	4	1 (6.7%)
November	21	5	12	5 (23.8%)
December	7	2	4	1 (14.3%)
Total	54	24	22	8 (14.8%)

[a] Not including two nests which failed as eggs due to snow cover.

checks for all nests under observation using the following parameters: whether a nest had survived or failed for each exposure period ('Survival'; survived = 1, failed = 0) and the number of days the nest was exposed between nest checks ('Exposure'). Exposure period was 1 for all except four nests, where camera set-ups experienced equipment failure. At failed nests we examined camera footage for the cause of failure. If we identified a failure event, we recorded the date, time, cause (i.e. 'Type': mammal, snake, bird or other) and species of nest predator where possible. Additionally, we examined the area around failed nests for signs of predation that would help with identification of Type (nest disturbance, eggshell presence, etc.).

Weather data variables

Weather data were recorded every 30 min by a VantageVue weather station at BHNR (Davis Instruments Corp., Hayward, CA, USA). We recorded maximum daily air temperature (T_{maxday}) for each Exposure period, averaging T_{maxday} for Exposure periods of more than one.

Analyses

All analyses were performed in the R statistical environment version 3.5.3 (R Core Team 2016). Packages used included *lme4* (Bates *et al.* 2015), *dplyr* (Wickham *et al.* 2019) and *blme* (Chung *et al.* 2013) (see Table S1 for raw data). Due to general linear mixed-effects models resulting in issues of singular fit, we instead used Bayesian linear mixed-effects models (BLMERs), as BLMERs resolve issues of singular fit by applying weak priors to fixed parameters (Quiñones & Wcislo 2015, Franks *et al.* 2018). All models specified a binomial distribution and Nest ID as a random effect.

We first created a BLMER estimating Survival as a function of Year, but as this was not significant ($\chi^2 = 0.848$, $P = 0.654$) we removed it from further analysis. We then estimated Survival as a function of potential predictor variables Habitat Stage, Veg Cover and T_{maxday}, using the above-specified model but with a modified logit-link function that includes exposure as per Shaffer (2004). Model selection was based on the lowest Bayesian information criterion for small sample sizes (BICc), and we present model outputs for the top competing models within Δ2 BICc (see Tables A1 and A2 for competing models and model selection outputs). As predation events were primarily due to snakes (see below), we created a BLMER estimating Snake Predation (1 = snake predation, 0 = not snake predation) as a function of T_{maxday} (see Table A3 for model output).

RESULTS

Causes of failure

Throughout the 3-year study, we recorded nest failure at 46 of 54 nests (85.2%). For failed nests, the cause of failure could not be determined at 19 nests (41.3%). The majority of the 27 identified failure events were from predation, with Boomslangs *Dispholydus typus* the main predator ($n = 17$; 64.3%; $n = 2$ as eggs and 15 as nestlings; Fig. 1). Other causes of failure included Cape Grey Mongoose *Galerella pulverulenta* ($n = 6$), Honey Badger *Mellivora capensis* ($n = 1$), unidentified rat species *Otomys* spp. ($n = 1$), Common Egg-eater *Dasypeltis scabra* (identified from eggshell ejecta, $n = 1$) and unidentified ants/starvation ($n = 1$), with eight successful nests (Fig. 1).

Nest failure, habitat openness and nest concealment

Our top competing models (Δ2 BICc) explaining nest survival included T_{maxday} and Habitat Stage as the only predictor variables (Table A1). In both competing models, nest survival was explained predominantly by T_{maxday}, with higher probability of nest survival during exposure periods with lower temperatures (coefficient estimate = −0.09, se ± 0.03, $Z = 3.29$, $P < 0.001$; Table A2; Fig. 2). Habitat Stage had a smaller effect on survivorship, with higher nest survival in territories with more open habitat (coefficient estimate = −1.14, se ± 0.59, $Z = 1.95$, $P = 0.051$). More successful nests resulted from nests in early post-fire habitat (2018 fledge rates: early post-fire habitat = 45.5% ($n = 5/11$), late post-fire habitat = 8.3% ($n = 2/24$)).

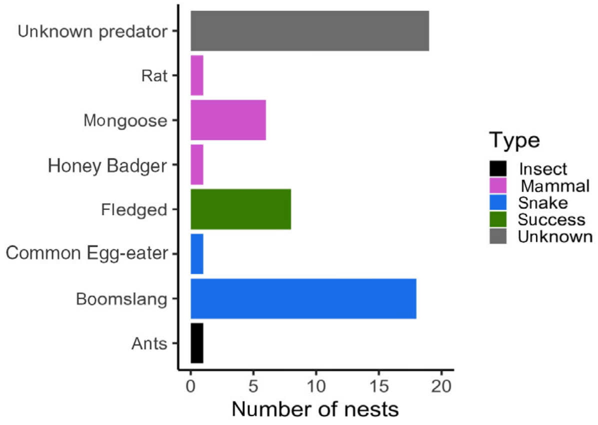

Figure 1. Total number of nests from three breeding seasons (2016–2018) of Cape Rockjumpers *Chaetops frenatus* at Blue Hill Nature Reserve, Western Cape, South Africa. Totals include the number of successful nests ('Fledged') as well as failed nests by cause of failure. Failure was from predation by Boomslang *Dispholydus typus*, Cape Grey Mongoose *Galerella pulverulenta*, Honey Badger *Mellivora capensis*, unidentified rat species *Otomys* spp., Common Egg-eater *Dasypeltis* spp., ants/starvation ('ants') or unknown predator.

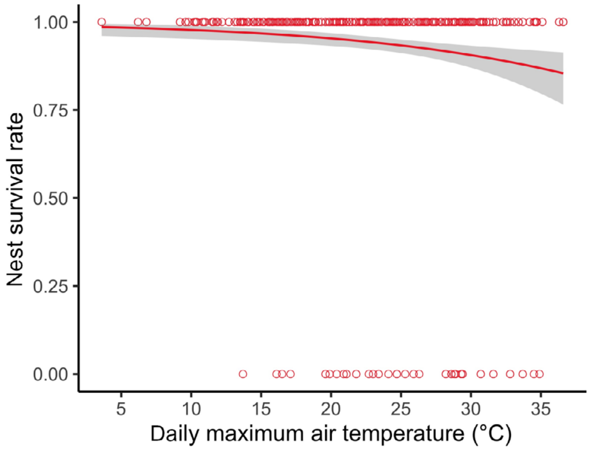

Figure 2. The relationship between nest survival (1 = survived, 0 = failed) and daily maximum temperatures (°C), recorded at all observed nests (n = 54) over three breeding seasons (2016–2018) for Cape Rockjumpers *Chaetops frenatus* at Blue Hill Nature Reserve, Western Cape, South Africa. Red lines show the predicted relationship from the GLM (Table A2) and shaded 95% confidence intervals.

Predation

Predation by snakes had significantly greater probability of occurring at higher T_{maxday} (coefficient estimate = 0.08, se ± 0.04, Z = 2.15, P = 0.031; Table A3). Boomslang predation during our study occurred between 14.2 and 31.6 °C (mean = 23.4 ± 5.0 °C). There was one recorded instance of partial predation when two of three nestlings were preyed on by a Boomslang, and then 5 days later the third nestling was also preyed on by a Boomslang. We observed Rockjumpers successfully deterring Cape Grey Mongooses *Galerella pulverulenta* from nests on three separate occasions through mobbing, all in early post-fire habitat, but as in Oswald (2016) we witnessed no instances of mobbing successfully deterring Boomslangs for any Habitat Stage (K.N. Oswald pers. obs.).

DISCUSSION

Our study highlights the need to investigate multiple ecological factors such as temperature and concealment for understanding predator–prey interactions in relation to reproductive failure. Although we found no relationship between nest concealment and predation, we did find that the probability of nest predation by snakes increased with increasing air temperature, beginning at the relatively low air temperature of *c.* 15 °C (Fig. 2). As Rockjumpers had lower nest survival on warmer days, probably due to increased snake activity, our study highlights potential vulnerability to increasing temperatures due to climate change in birds whose nests are most vulnerable to predation by snakes. A previous study by Milne *et al.* (2015) found that Rockjumper populations were declining in areas of their habitat experiencing the greatest warming, and we suggest it is possible that increased snake predation may be connected to these declines.

Nest survival

Throughout our study the greatest numbers of failed nests were due to snakes – almost exclusively Boomslangs – with this predation more likely at higher temperatures. While Boomslangs are known to be present in fynbos (Holmes *et al.* 2002, Jacobsen & Randall 2013), the dominance of Boomslangs as a nest predator of a ground-nesting bird was surprising given their eponymous status as a primarily arboreal hunter (Marais 2011). Boomslang density in alpine fynbos may be underreported, partially from the difficulty of properly studying snake ecology due to their cryptic behaviour, habitat-use and activity patterns (Siegel *et al.* 1987).

Although generally increasing at higher temperatures, snake activity does reach upper limits at which they seek out shaded microsites (Huey & Kingsolver 1989). During this study, BHNR recorded no temperatures above 36 °C, which is lower than temperatures at which snake species experience physiological stress (Gangloff *et al.* 2016) and seek out shade (Webb & Shine 1998). Our lowest Boomslang predation temperature (14.2 °C) is below the temperature range recorded for Boomslang activity in the Kalahari (19.2 ± 1.7 to 31.4 ± 1.3 °C; G.J. Alexander, B. Maritz, T.F. Beck & R.A. Maritz, unpubl. data), possibly due to differences in operative temperatures (the thermal environment experienced by the animal), which can result in temperatures > 10 °C above standard measures of air temperature (Walsberg & Wolf 1996).

Our only other snake predator, the Common Egg-eater *Dasypeltis scabra*, is probably also an underreported cause of predation (Bates & Little 2013) and we suggest the lack of recorded Egg-eater predation events (full or partial) may be partly attributed to our lack of recorded nocturnal predation events in general. We also recorded no predation from Corvidae or Chacma Baboons *Papio ursinus* (which are prevalent at BHNR). Our camera traps recorded one instance of Baboons exploring a nest which had been depredated by a Boomslang 3 h previously, and as Baboons are known to opportunistically eat eggs (Devore & Washburn 1963), it is likely they would have depredated the nest if it had remained active.

The higher probability of nest success at lower air temperatures indicates that birds nesting earlier in the season (i.e. at lower temperatures) have a higher chance of avoiding nest predation. However, the two nests that failed due to snow show that this may come with an increased risk of failure due to inclement weather. We found no relationship between nest concealment (i.e. Veg Cover) and nest survival, but higher nest survival was associated with more open habitat. These results are contrary to previous studies in which both increased habitat openness (i.e. overall less vegetated habitat) and decreased nest concealment (i.e. less vegetation around the nest itself) resulted in increased predation (Ricketts & Ritchison 2000, Little *et al.* 2015). Multiple species choose nest-sites in open landscapes with good visibility, presumably to be able to more easily spot potential predators (Götmark *et al.* 1995, Magana *et al.* 2010).

We thus suggest two possibilities that might underlie greater nest survival in a more open predator landscape: (1) birds may benefit from more recent fire due to increased habitat visibility allowing adults to spot potential predators before the predators are within range to sense the nest or (2) recently burned areas may have fewer predators. As we recorded no instances of birds successfully deterring snakes, but did record birds in early post-fire habitat successfully deterring Mongooses from nests via mobbing, we suggest that the main benefit of nesting in an open habitat is detection and deterrence of mammalian predators. Fewer instances of snake predation in open habitat may be due to a decrease in either localized nest odour resulting in decreased instances of snakes locating nests, or in lower Boomslang numbers, as Boomslangs themselves would be more vulnerable to predation. While we did not record data on adult nest behaviour for this study, temperature can also affect bird incubation (i.e. fewer nest visits and more consecutive time on and off nests; Conway & Martin 2000), so the higher snake predation at higher temperatures that we recorded may result from adults spending less time at nests and thus detecting fewer predators.

Implications for population persistence

Past work has highlighted several potential negative effects of increasing temperatures on Rockjumpers that may explain temperature-related population declines, including high evaporative water loss rates (Oswald *et al.* 2018), foraging trade-offs at high temperatures (Oswald *et al.* 2019) and reduced mass gain in older nestlings at high temperatures (K.N. Oswald *et al.* unpubl. data). In this study, we found evidence that declining populations may also result from a relationship between increased temperatures and predation risk, resulting in reduced reproductive success.

CONCLUSIONS

Our findings emphasize the need for an integrative approach to assessing species vulnerability. While climate change will have many direct effects on reproductive success at both individual and population levels (Martin *et al.* 2017, Bladon *et al.* 2019, Van de Ven *et al.* 2019), these effects may also be mediated by indirect species interactions. We provide further evidence that examining indirect effects and ecological interactions is sometimes necessary to inform an accurate framework for determining species vulnerability (Williams *et al.* 2008).

This work was supported by a Nelson Mandela Metropolitan University Research Themes Grant (B.S.), a post-doctoral research grant from the South African National Biodiversity Institute (A.T.K.L.) and a grant from the DST-NRF Centre of Excellence at the FitzPatrick Institute for African Ornithology (S.J.C.). Funding was also provided by an Animal Behavior Society: student research grant (K.N.O.), and the Tygerberg Bird Club (K.N.O.). We would like to thank the Lee family for allowing the research to occur on their property in the Western Cape, South Africa. We would also like to thank our field assistants, without whom this work could not have occurred: Cameryn Brock, Ceili Peng, Olivia Venter and Jo Balmer. Lastly, we would like to give special thanks to Dr Tom E. Martin and Dr Zen J. Czene for commenting on an earlier draft and providing key insight and suggestions to improve our manuscript.

All applicable institutional and/or national guidelines for the care and use of animals were followed. Bird handling, welfare and observations procedures were approved by the University of Cape Town Animal Ethics Committee (2014/V19/AL; Dec-

2014 to Dec-2016); the Nelson Mandela Metropolitan University Research Ethics Committee (Animal; A15-SCI-ZOO-007; Jun-2014 to Feb-2016) and the Rhodes University Animal Ethics Committee (RU-DZE-2017-10-028; Jun-2014 to Feb-2016). Birds were captured with permission from the Western Cape Province: Cape Nature (permit #AAA041-00565).

Data availability statement

All relevant data of this article can be found in the Supplementary files.

REFERENCES

Amat, J.A. & Masero, J.A. 2004. Predation risk on incubating adults constrains the choice of thermally favourable nest sites in a plover. *Anim. Behav.* **67**: 293–300.

Bates, M.F. & Little, I.T. 2013. Predation on the eggs of ground-nesting birds by *Dasypeltis scabra* (Linnaeus, 1758) in the moist highland grasslands of South Africa. *Afr. J. Herpet.* **62**: 125–134.

Bates, D., Maechler, M., Bolker, B. & Walker, S. 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Soft.* **67**: 1–48.

Bladon, A.J., Donald, P.F., Jones, S.E., Collar, N.J., Deng, J., Dadacha, G., Abebe, Y.D. & Green, R.E. 2019. Behavioural thermoregulation and climatic range restriction in the globally threatened Ethiopian Bush-crow *Zavattariornis stresemanni*. *Ibis* **161**: 546–558.

Blums, P., Clark, R.G. & Mednis, A. 2002. Patterns of reproductive effort and success in birds: path analyses of long-term data from European ducks. *J. Anim. Ecol.* **71**: 280–295.

Brown, G.P & Shine, R. 2002. Influence of weather conditions on activity of tropical snakes. *Austral Ecol.* **27**: 596–605.

Carroll, R., Davis, C.A., Fuhlendorf, S.D., Elmore, R.D., Durant, S.E. & Carroll, J.M. 2018. Avian parental behavior and nest success influenced by temperature fluctuations. *J. Therm. Biol.* **74**: 140–148.

Chung, Y., Rabe-Hesketh, S., Dorie, V., Gelman, A. & Liu, J. 2013. A nondegenerate penalized likelihood estimator for variance parameters in multilevel models. *Psychometrika* **78**: 685–709.

Colombelli-Négrel, D. & Kleindorfer, S. 2009. Nest height, nest concealment, and predator type predict nest predation in superb fairy-wrens (*Malurus cyaneus*). *Ecol. Res.* **24**: 921–928.

Conover, M.R., Borgo, J.S., Dritz, R.E., Dinkins, J.B. & Dahlgren, D.K. 2010. Greater Sage-grouse select nest sites to avoid visual predators but not olfactory predators. *Condor* **112**: 331–336.

Conway, C.J. & Martin, T.E. 2000. Evolution of passerine incubation behavior: influence of food, temperature, and nest predation. *Evolution* **54**: 670–685.

Cox, W.A., Thompson, III, F.R. Reidy, J.L. & Faaborg, J. 2013a. Temperature can interact with landscape factors to affect songbird productivity. *Global Change Biol.* **19**: 1064–1074.

Cox, W.A., Thompson III, F. & Reidy, J. 2013b. The effects of temperature on nest predation by mammals, birds, and snakes. *Auk* **130**: 784–790.

Degregorio, B.A., Chiavacci, S.J., Weatherhead, P.J., Willson, J.D., Benson, T.J. & Sperry, J.H. 2014. Snake predation on North American bird nests: culprits, patterns and future directions. *J. Avian Biol.* **45**: 325–333.

Devore, I. & Washburn, S.L. 1963. Baboon ecology and human evolution. In Bourliè, F. & Howell, C.F. (eds) *African Ecology and Human Evolution*: 335–367. London: Routledge.

Franks, S.E., Roodbergen, M., Teunisson, W., Carrington Cotton, A. & Pearce-Higgins, J.W. 2018. Evaluating the effectiveness of conservation measures for European grassland-breeding warblers. *Ecol. Evol.* **8**: 10555–10568.

Gangloff, E.J., Holden, K.G., Telemeco, R.S., Baumgard, L.H. & Bronikowski, A.M. 2016. Hormonal and metabolic responses to upper temperature extremes in divergent life-history ecotypes of a garter snake. *J. Exp. Biol.* **219**: 2944–2954.

Götmark, F., Blomqvist, D., Johansson, O.C. & J Bergkvist, J. 1995. Nest site selection: a trade-off between concealment and view of the surroundings? *J. Avian Biol.* **26**: 305–312.

Holmes, R.T., Frauenknecht, B.D. & Du Plessis, M.A. 2002. Breeding system of the Cape Rockjumper, a South African fynbos endemic. *Condor* **104**: 188–192.

Hořák, D., Sedláček, O., Tószögyová, A., Albrecht, T., Ferenc, M., Jelínek, V. & Storch, D. 2011. Geographic variation in avian clutch size and nest predation risk along a productivity gradient in South Africa. *Ostrich* **82**: 175–183.

Huey, R.B. & Kingsolver, J.G. 1989. Evolution of thermal sensitivity of ectotherm performance. *Trends Ecol. Evol.* **4**: 131–135.

Jacobsen, N.H. & Randall, R.M. 2013. Survey of reptiles in the Wilderness section of the Garden Route National Park, South Africa. *Herp. Notes* **6**: 209–217.

Kleindorfer, S., Fessl, B. & Hoi, H. 2005. Avian nest defence behaviour: assessment in relation to predator distance and type, and nest height. *Anim. Behav.* **69**: 307–313.

Lee, A.T.K. & Barnard, P. 2016. Endemic birds of the Fynbos biome: a conservation assessment and impacts of climate change. *Bird Conserv. Int.* **26**: 52–68.

Lee, A.T.K., Barnard, P. & Hockey, P.A.R, 2015. Population metrics for fynbos birds, South Africa: densities, and detection and capture rates from a Mediterranean-type ecosystem. *Ostrich* **86**: 179–187.

Li, P. & Martin, T.E. 1991. Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. *Auk* **108**: 405–418.

Little, I.T., Hockey, P.A. & Jansen, R. 2015. Predation drives nesting success in moist highland grasslands: the importance of maintaining vegetation cover for bird conservation. *Ostrich* **86**: 97–111.

Lloyd, P. 2004. Variation in nest predation among arid-zone birds. *Ostrich* **75**: 228–235.

Magana, M., Alonso, J.C., Martin, C.A., Bautista, L.M. & Martin, B. 2010. Nest-site selection by Great Bustards *Otis tarda* suggests a trade-off between concealment and visibility. *Ibis* **152**: 77–89.

Marais, J. 2011. *A Complete Guide to the Snakes of Southern Africa*. Johannesburg: Penguin Random House South Africa.

Martin, T.E. 1987. Artificial nest experiments: effects of nest appearance and type of predator. *Condor* **89**: 925–928.

Martin, T.E. 2001. Abiotic vs. biotic influences on habitat selection of coexisting species: climate change impacts? *Ecology* **82**: 175–188.

Martin, K., Wilson, S., Macdonald, E.C., Camfield, A.F., Martin, M. & Trefry, S.A. 2017. Effects of severe weather on reproduction for sympatric songbirds in an alpine environment: Interactions of climate extremes influence nesting success. *Auk* **134**: 696–709.

Mayfield, H.F. 1975. Suggestions for calculating nest success. *Wilson Bull.* **87**: 456–466.

Milne, R., Cunningham, S.J., Lee, A.T. & Smit, B. 2015. The role of thermal physiology in recent declines of birds in a biodiversity hotspot. *Cons. Physiol.* **3**: cov048.

Nelson, K.J. & Gregory, P.T. 2000. Activity patterns of garter snakes, *Thamnophis sirtalis*, in relation to weather conditions at a fish hatchery on Vancouver Island, British Columbia. *J. Herpetol.* **34**: 32–40.

Oswald, K.N. 2016. Observed instances of alarm calling in the Cape Rockjumper. *Ostrich.* **87**: 285–288.

Oswald, K.N., Lee, A.T. & Smit, B. 2018. Seasonal physiological responses to heat in an alpine range-restricted bird: the Cape Rockjumper (*Chaetops frenatus*). *J. Ornithol.* **159**: 1063–1072.

Oswald, K.N., Smit, B., Lee, A.T. & Cunningham, S. 2019. Behaviour of an alpine range-restricted species is described by interactions between microsite-use and temperature. *Anim. Behav.* **157**: 177–187.

Quiñones, A. & Wcislo, W.T. 2015. Cryptic extended brood care in the facultatively eusocial sweat bee *Megalopta genalis*. *Insectes Soc.* **62**: 307–313.

R Core Team 2016. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Ricketts, M.S. & Ritchison, G. 2000. Nesting success of Yellow-breasted Chats: effects of nest site and territory vegetation structure. *Wilson J. Ornithol.* **112**: 510–517.

Ridley, A. & Van den Heuvel, I. 2012. Is there a difference in reproductive performance between cooperative and non-cooperative species? A southern African comparison. *Behaviour* **149**: 821–848.

Shaffer, T.L. 2004. A unified approach to analyzing nest success. *Auk* **121**: 526–540.

Siegel, R.A., Collins, J.T. & Novak, S.S. (Eds) 1987. *Snakes: Ecology and Evolutionary Biology*. New York, NY: Macmillan Publishing Company.

Thompson III, F.R. 2007. Factors affecting nest predation on forest songbirds in North America. *Ibis* **149**: 98–109.

van de Ven, T.M., Mckechnie, A. & Cunningham, S. 2019. The costs of keeping cool: behavioural trade-offs between foraging and thermoregulation are associated with significant mass loss in an arid zone bird. *Oecologia* **191**: 205–215.

Walsberg, G.E. & Wolf, B.O. 1996. A test of the accuracy of operative temperature thermometers for studies of small ectotherms. *J. Therm. Biol.* **21**: 275–281.

Weatherhead, P.J. & Hoysak, D.J. 1989. Spatial and activity patterns of black rat snakes (*Elaphe obsoleta*) from radiotelemetry and recapture data. *Can. J. Zool.* **67**: 463–468.

Webb, J.K. & Shine, R. 1998. Using thermal ecology to predict retreat-site selection by an endangered snake species. *Biol. Conserv. Int.* **86**: 233–242.

Wickham, R.F., Henry, L. & Müller, K. 2019. *dplyr: a Grammar of Data Manipulation. R package v.0.8.1*. Available at: https://CRAN.R-project.org/package=dplyr (accessed 10 September 2019).

Williams, S.E., Shoo, L.P., Isaac, J.L., Hoffmann, A.A. & Langham, G. 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biol.* **6**: e325.

Received 11 October 2019;
revision accepted 28 April 2020.
Associate Editor: Catriona Morrison.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Raw data for three breeding season (2016–2018) for Cape Rockjumpers *Chaetops frenatus* at Blue Hill Nature Reserve, Western Cape, South Africa, including: territory designation ('Territory'), individual nest identification code ('Nest ID'), number of nestlings in the nest ('Brood Size'), ordinal date ('Date'), whether a nest had survived or failed for each exposure period ('Survival'; survived = '1', failed = '0'), the number of days the nest was exposed between nest checks ('Exposure'), total number of nest checks by observer ('Visits'), predator type ('Type'; 'mammal', 'snake', 'other', or 'none'), species of predator ('Species'), daily maximum temperature (°C; 'T_{maxday}'), stage of habitat growth ('Habitat Stage', > 3 years since fire = 'late', < 3 years since fire = 'early'), and percentage vegetative ground cover within a 1-m radius of the nest ('Veg Cov').

Table A1. Competing model outputs for all models explaining nest survival as a function of habitat stage ('late post-fire habitat' or 'early post-fire habitat'), vegetative concealment ('veg cover') and daily maximum temperatures ('T_{maxday}').

Table A2. Model coefficient summary table for top competing models ($\Delta 2$ BICc, $n = 2$) explaining nest survival ('Survival') as a function of habitat ('Habitat Stage'; 'late post-fire habitat' or 'early post-fire habitat'), vegetative concealment ('Veg Cover') and daily maximum temperatures ('T_{maxday}').

Table A3. Model coefficient summary table for model explaining snake predation ('1' = snake, '0' = not snake) as a function of daily maximum temperature ('T_{maxday}').