# Population Viability Analysis for a vulnerable ground-nesting species, the Cape Rockjumper *Chaetops frenatus*: assessing juvenile mortality as a potential area for conservation management

Krista N Oswald & Alan TK Lee

View supplementary material ↗

Published online: 24 Oct 2021.

Submit your article to this journal ↗

View related articles ↗

View Crossmark data ↗

*Short Note*

# Population Viability Analysis for a vulnerable ground-nesting species, the Cape Rockjumper *Chaetops frenatus*: assessing juvenile mortality as a potential area for conservation management

**Krista N Oswald[1]*** (iD) **and Alan TK Lee[2,3,4]** (iD)

[1] *Department of Zoology and Entomology, Rhodes University, Grahamstown, South Africa*
[2] *FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, South Africa*
[3] *Centre for Functional Biodiversity, University of KwaZulu-Natal, Scottsville, South Africa*
[4] *BirdLife South Africa, Pinegowrie, South Africa*
*\*Correspondence: knoswald@gmail.com*

As an endemic bird to the Fynbos biome, prominently featured in literature and marketing material for the avifauna of the continent, the Cape Rockjumper *Chaetops frenatus* is an iconic species of South Africa. Building on studies from the past decade, recent publications all point to a vulnerability to climate change due to temperature-related effects on their behaviour, physiology, and life history. Here we present a population viability analysis for the species based on knowledge of recent declines and making use of recently available information on their life history. We combined recent breeding success data (2016–2018) with that of a population monitored approximately two decades ago (1998–2000) and modelled the probability of extinction for four scenarios where the principal change was in juvenile (more accurately, nestling) mortality. We focused on juvenile mortality as there are previously identified areas of vulnerability that present potential areas for mitigation. With juvenile mortality set at the recently recorded rate of 80% there is a 49.1% chance of population extinction within 100 years, despite optimistic adult survival and breeding parameters used in the models. We then provide insights into factors that mediate juvenile mortality as potential avenues for the management of the species.

## Analyse de la viabilité de la population d'une espèce vulnérable nichant au sol, le Rockjumper du Cap *Chaetops frenatus* : évaluation de la mortalité juvénile comme domaine potentiel de gestion de la conservation.

En tant qu'oiseau endémique du biome du Fynbos, figurant en bonne place dans la littérature et le matériel de marketing sur l'avifaune du continent, le Rockjumper du Cap *Chaetops frenatus* est une espèce emblématique de l'Afrique du Sud. S'appuyant sur les études de la dernière décennie, les publications récentes indiquent toutes une vulnérabilité au changement climatique en raison des effets liés à la température sur leur comportement, leur physiologie et leur cycle de vie. Nous présentons ici une analyse de la viabilité de la population de l'espèce basée sur la connaissance des déclins récents et utilisant les informations récemment disponibles sur leur histoire de vie. Nous avons combiné des données récentes sur le succès de la reproduction (2016–2018) avec celles d'une population suivie il y a environ deux décennies (1998–2000) et nous avons modélisé la probabilité d'extinction pour quatre scénarios où le principal changement était la mortalité des juvéniles (plus précisément, des oisillons). Nous nous sommes concentrés sur la mortalité juvénile car il existe des zones de vulnérabilité identifiées précédemment qui présentent des zones potentielles d'atténuation. Si la mortalité juvénile est fixée au taux de 80% récemment enregistré, le risque d›extinction de la population dans les 100 ans est de 49.1%, malgré les paramètres optimistes de survie et de reproduction des adultes utilisés dans les modèles. Nous fournissons ensuite des informations sur les facteurs qui interviennent dans la mortalité juvénile comme pistes potentielles pour la gestion de l'espèce.

---

Population Viability Analysis (PVA) is a stochastic systems model intended to assess the likelihood an individual population will become extinct within a certain timeframe, and under specific circumstances (Possingham et al. 1994; Beissinger and McCullough 2002). As such, PVAs are used to help inform conservation strategies and management for threatened species (Possingham et al. 1994; Fantle-Lepczyk et al. 2018,), by taking into

account landscape-based factors (e.g. habitat type; Verboom et al. 2001; Bonnot et al. 2013), as well as the specific life history traits of a population (Verboom et al. 2010). The Cape Rockjumper (*Chaetops frenatus*; 'Rockjumper') is a medium-sized passerine, endemic to the Cape Fold Mountains of southwest South Africa, which presents an ideal candidate species for assessing areas for conservation management. Rockjumpers are an evolutionary relict and part of an ancient lineage of early passerines (Oliveros et al. 2019) with strong economic ties to the African birding industry (Crowe 1993).

Recently, Rockjumper population estimates (herein referring to total population of the species) were re-evaluated due to re-assessment of their realised niche within the Fynbos ecoregion (i.e. being found solely in mountain fynbos) as well as their relatively low-density estimate (0.56–1.02 individuals per km$^2$; Lee and Barnard 2016). Warming temperatures are likely to result in shrinking of their suitable habitat as their mountain fynbos islands are pushed to higher altitudes; similar sky island extirpations have already been recorded in Latin America (Freeman et al. 2018). Their population re-assessment, along with their decreasing reporting rates in warmer parts of their distribution (Milne et al. 2015), resulted in the placement of the Rockjumper as Near Threatened by the International Union for Conservation of Nature in 2017 (IUCN 2017). Despite being the focus of research over the past few years, the Rockjumper has yet to be evaluated in terms of its population dynamics. This lack of knowledge is problematic, given that population viability is a criterion used by the IUCN in assessing global extinction risk status, and is crucial for informing policy (Possingham et al. 1994; Fantle-Lepczyk et al. 2018).

Aside from the above-mentioned studies examining broad-scale changes in Rockjumper population abundance and distribution, recent studies have identified several mechanisms where individual birds are sensitive to climate change, all of which may be affecting population viability and recruitment: (1) despite no evidence of drinking (Lee et al. 2017) and living in a semi-arid environment, birds depended on evaporative water loss as their main physiological cooling mechanism (Oswald et al. 2018a), (2) juvenile birds had potentially unsustainable water needs at high temperatures (Oswald et al. 2018b), (2) nest predation increased with increasing temperature (Oswald et al. 2020a), (3) birds spent less time foraging at high temperatures (where they switch to shaded microsites; Oswald et al. 2019), (4) adults provisioned less at increasing temperatures (Oswald et al. 2021), and (5) nestlings gained less mass at higher temperatures (Oswald et al. 2021). Here, we use recently available broad scope of ecological data to create a model PVA for the Rockjumper to better understand where the Rockjumper population is most vulnerable.

We used Vortex 10.5.5 (Lacy and Pollack 2021) to simulate population viability scenarios given the current state of knowledge of Rockjumper biology. All terminology used here is based on specific data parameter types used in Vortex as opposed to generally accepted ornithology terms (e.g. 'broods' instead of 'nest attempts'). As Vortex does not differentiate between juvenile mortality and that of earlier life history stages (i.e. nestling mortality), here we consider juvenile mortality as that for individuals <1 year old. The specific life history data used here came from birds at two localities of different altitudes ~500 km apart, representing a southwestern locality of ~600 m asl (Kogelberg mountains) and an eastern locality of ~1 200 m asl (Blue Hill Nature Reserve).

Currently there are no long-term study data providing adult (birds of age >1 year) survival rates, so we used adult survival rates of 0.70 for both sexes; this value was based on survival rates of Olive Thrush *Turdus olivaceus* (0.65) and Cape Robin-chat *Cossypha caffra* (0.72; Collingham et al. 2014). The Thrush and Robin-chat are species of similar size and life-histories found in the range of the Rockjumper, and a survival rate of 0.70 closely matched our incidental observations of family groups, where most adults were found between three seasons based on five family groups followed for behavioural studies (actual = 0.74, *n* = 20/27 birds resighted; Oswald et al. 2018c). For survival parameters we added 10% variation.

Also using data for the Thrush and Robin-chat (Collingham et al. 2014) we based a maximum longevity value of 15 years. Again, this agreed with observations in the field: while we currently do not have complete data on Rockjumper longevity, five of 13 birds ringed as adults at Blue Hill Nature Reserve in 2014 were resighted or captured as late as 2018 (ATKL, unpubl. ringing data). None of the colour-ringed individuals captured during Holmes et al. (2002); birds captured and ringed between 1998 and 2000) in the Kogelberg region were resighted; however, no specific resighting effort was made after this study, and it is possible the habitat underwent a change making it unsuitable for Rockjumpers as none have been recorded at that site in recent years. We specified an age of breeding initiation as two based on Holmes et al. (2002). We assumed 90% of females breed every year based on regular breeding activity at all family groups observed over a four-year period at Blue Hill Nature Reserve, but tempered by observations of non-breeding pairs from the Kogelberg site (Holmes et al. 2002; Oswald et al. 2019; Oswald et al. 2020a). We then specified the following: 10% attempt no broods, 30% attempt one brood, 30% attempt two broods, and 30% attempt three broods. These values were based on nest data collected in 2018, where a concerted effort was made to find all renesting attempts at specific territories (*n* = 14 territories) resulting in actual values of 29% attempting one or two broods (*n* = four territories each), and 43% attempting three or more broods (*n* = two territories each with three attempts, four attempts, and five attempts; unpublished data). All instances of more than three nest attempts occurred in groups with no successful attempts; territories with a successful nest attempt only made up to two further nest attempts in each season. These parameters resulted in a stable population scenario, to which we fitted elements of variation (see alternative models, Supplementary Figure S1).

At no point did we observe more than two juveniles per family group, and although three eggs were laid by some females in 2018 (*n* = 5 females; Table 1), all three-egg nests were unsuccessful. As such, we imposed a maximum brood size value of two based on average data and allowed a

**Table 1:** Breeding data collected for Cape Rockjumpers *Chaetops frenatus* during two three-year periods (1998–2000, Holmes et al. 2002; 2016–2018, KNO, unpubl. data). Data includes: 'Year' = the year of the study; 'Nests' = the number of nests found; 'Clutch Size' = the number of eggs laid per nest; 'Total Eggs' = the total number of eggs laid per year; and 'Proportion Failed' = the proportion of eggs that did not result in fledged young (calculated per study)

| Year | Nests | Clutch Size | | | Total Eggs | Fledglings | Proportion failure | Reference |
|------|-------|---------|---------|-----------|------------|------------|------------|-----------|
| | | one-egg | two-egg | three-egg | | | | |
| 1998 | 8 | | 8 | | 16 | 7 | 0.61 | Holmes et al. 2002 |
| 1999 | 10* | | 10 | | 20 | 4 | | |
| 2000 | 12 | | 12 | | 24 | 16 | | |
| 2016 | 2 | | 2 | | 4 | 0 | 0.81 | KNO, unpubl. data** |
| 2017 | 20 | 6 | 14 | | 34 | 5 | | |
| 2018 | 43 | 8 | 23 | 12 | 90 | 20 | | |

*The number of nests found in 1999 reported by Holmes et al. 2002 for 1999 was given as *n* = 15, 10, and 16 at different points in the article. We have used *n* = 10, as we believe this was the number on which their percentages were based.

** Data were collected concurrent with Oswald et al. (2020a) and Oswald et al. (2021)

mean of two with standard deviation of one as the distribution of offspring per brood. We specified the breeding system as monogamous, again based on stability of observed family groups at Blue Hill Nature Reserve, although we did not specify 'strict monogamy' as an option given knowledge of repairing and extra-pair copulations in passerines in general (Griffith et al. 2002). Other parameters that could be introduced in Vortex included scenarios involving catastrophes and inbreeding depression. However, we ran models for the global known population, whereas local catastrophes such as snow events may reduce survival only for subpopulations (Oswald et al. 2020a), and would not affect the entire population. In addition, some catastrophic events such as wildfire can have a beneficial effect on survival (Oswald et al. 2020a); 2018 fledging success in territories two years post-fire was 57% compared to 14% in territories six years post-fire (KNO, unpubl. data). These catastrophes were also already included in juvenile mortality rates. In addition, populations are currently large enough that inbreeding depression is not yet a concern for the species: there is currently no evidence for inbreeding depression (Oswald et al. 2020b). We set the starting population as 40 000, with a carrying capacity of 90 000 (based on population estimates; Lee et al. 2015; see sensitvity analysis in Supplementary Material for more details on effects of specific parameters).

We then explored various models but focused on four principal models that differed principally in juvenile mortality (<1 year; 60%, 65%, 70%, and 80%) based on reporting values of nest failure (Table 1; Supplementary Figure S1). We chose to focus on juvenile mortality as this was an area that presented possible avenues for management (see discussion below). Using the more recent data collected at Blue Hill Nature Reserve (Table 1), we ran one additional model with 80% juvenile mortality, where all females breed, and 40% of females attempt a minimum of three broods (model '80% b'). With given knowledge, at 70% juvenile mortality the Rockjumper population is relatively stable, and with <70% juvenile mortality we even see an increase (Figure 1). However, with juvenile mortality >70% the population decreases and at 80% juvenile mortality there is 49.1% chance the Rockjumper population will go extinct in 82.3 years (Figure 1; Table 2).
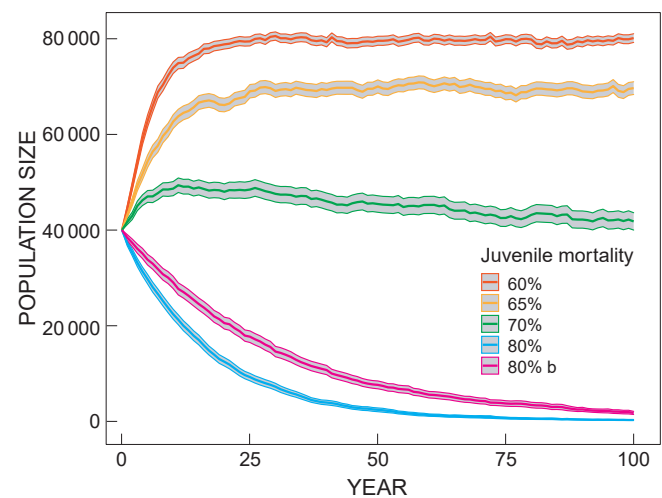


**Figure 1:** Year-on-year population estimates for Cape Rockjumper based on population viability scenarios with variation in juvenile mortality (60%, 65%, 70% and 80%), where 10% of adults attempt no broods, and 30% attempt one, two and three broods. Scenario 80% b is juvenile mortality set to 80%, where 30% of adults attempt one and two broods, and 40% attempt three broods. Initial carrying capacity was set to 90 000 and the starting population was set to 40 000. Error bars represent 95% confidence intervals of the mean, based on 1 000-model run iteration

The PVA we constructed indicated a potentially tenuous existence for the Rockjumper with increased juvenile mortality (Figure 1). Potential management strategies could include controlling predation at Rockjumper nests to increase fledging success (i.e. decrease juvenile mortality; based on Oswald et al. 2020a). The most recent studies of Rockjumper life history indicated surprisingly high levels of nest predation, driven specifically by snakes (Oswald et al. 2020a). This was particularly unexpected given the lack of alarm calls by adult Rockjumpers at the presence of snakes in the nonbreeding season (Oswald 2016) suggesting that while snakes are successful nest predators, they are not a threat to adult birds. Alternatively, this may mean that high levels of snake predation on nests is a relatively new development and may be increasing in intensity due to

**Table 2:** Model summary output for Cape Rockjumper PVA: 'det-r' = the deterministic rate of change; 'stoch-r' = the stochastic rate of change; 'PE' = probability of extinction; 'N-extant' = predicted population size after 100 years; 'SD(N-ext)' = standard deviation of N-extant; 'meanTE' = mean time (years) to extinction. All runs based on 1 000 iterations. Adult breeding scenarios are 10% no broods, and then 30% each for one, two, and three broods. Scenario 80%b assumes all females breed, 30% attempt one or two broods, and 40% produce three broods

| Juvenile mortality | det-r | stoch-r | SD(r) | PE | N-extant | SD(N-ext) | meanTE |
|---|---|---|---|---|---|---|---|
| 60% | 0.103 | 0.088 | 0.214 | 0 | 80 141.76 | 14 601.47 | 0 |
| 65% | 0.068 | 0.051 | 0.223 | 0 | 69 681.16 | 21 389.90 | 0 |
| 70% | 0.029 | 0.012 | 0.233 | 0 | 41 811.77 | 29 226.20 | 0 |
| 80% | −0.064 | −0.089 | 0.267 | 0.491 | 289.57 | 1 421.24 | 82.3 |
| 80%b | −0.031 | −0.051 | 0.271 | 0.107 | 2 093.36 | 6 491.50 | 85.0 |

changing climate; snake predation was positively correlated with higher temperatures (Oswald et al. 2020a). Here, the supposition is that while climate change may be restricting Rockjumpers' climate niche, it might well be facilitating the climatic niche of an efficient nest predator. For Rockjumpers to maintain a stable population they may need to offset nest predation rates by continued renesting attempts, or alternatively attempting to breed earlier in the year (i.e. through the colder winter months when snakes are not active), despite the risk of extreme cold weather events.

A secondary area of potential management of populations would be controlled burning (or more accurately, a cessation of human intervention in controlling natural fire) of mountain fynbos on a 5–6-year cycle, as Rockjumpers had greater nest success in territories with ≤3 years since wildfire (Oswald et al. 2020a). More critical levels of population declines may currently be offset by increased fire frequency in the biome (Kraaij and van Wilgen 2014). As stated, survival was highest in the territories we monitored in relatively recent burnt territories (Oswald et al. 2020a), where lower juvenile mortality in recently burned landscapes (43%) likely provides valuable population recruitment opportunities. However, fire at the wrong time of year (spring or summer) would of course also be catastrophic for nestlings, even if we assume adults can escape these unscathed. Further influence of fire on Rockjumper survival rates is required: a notable caveat of the parameterization used in this study is that it is based on life history monitoring at only two sites at disjunct time periods. Additionally, we add the caveat that such a fire regime may be detrimental for other species across taxa in the mountain fynbos, and further study would be needed before such a measure were undertaken.

We considered our initial parameters 'optimistic' in the base models: we had evidence to suspect that female survival rates may be lower than used in our models due to added vulnerability of brooding at night, a bias towards higher male counts during surveys, and the fact that extra-pair individuals in territories ('helpers') tended to be male (Oswald et al. 2021). Given the socially monogamous breeding system, the number of reproductive females was a major constraint on the population. Holmes et al. (2002) indicated higher levels of non-breeding than used here, as well as fewer renesting attempts compared to observational data collected as part of the more recent studies (Oswald et al. 2020a; Oswald et al. 2021). As mentioned, the high mortality rates used here were based on fledging success (i.e. nestling mortality), and do not include mortality for the remaining

~315 days of the year; there is likely higher mortality of <1 year-old birds before the higher survival rate of 70% assigned to 2nd year birds. By contrast, we included a higher nesting percentage based on observations in 2018, and a wide range of options for multiple brood attempts; these parameters were required to maintain the population at stable levels.

In essence, vulnerability of the Rockjumper population would result from low clutch sizes coupled with low survival probabilities in the first year from egg to adult. Introducing catastrophic events (e.g. snowfall) would simply increase the probability of extinction from the 'base' 70% mortality model. Survival of Rockjumpers additionally hinges on a high percentage of adult females breeding and having multiple successful nesting attempts per season, with all females continuing to renest even after one successful attempt in any given season. Rockjumpers may also be required to shift their breeding phenology to earlier in the season (e.g. beginning in early June instead of late July and August) and risk possible inclement winter weather to take advantage of the cooler months when snakes are less active. While insect productivity is highest in October (Lee and Barnard 2015), and timing of the current breeding season seems likely for birds to benefit from food availability, the benefit of decreased snake presence earlier in the year may offset this in the future. Given stable mortality rates, the population would recover slowly from any population-wide catastrophe, but even a small increase in juvenile mortality combined with small-scale catastrophic events puts the global Rockjumper population on a fast track to probable extinction. This is a very worrying scenario, and we suggest that intensive managing and monitoring of Rockjumper populations should be considered.

## ORCIDs

Krista N Oswald: https://orcid.org/0000-0001-8745-4432
Alan TK Lee: https://orcid.org/0000-0002-5858-9351

## References

Beissinger SR, McCullough DR. 2002. *Population viability analysis*. University of Chicago Press.

Bonnot TW, Thompson III FR, Millspaugh JJ, Jones-Farrand DT. 2013. Landscape-based population viability models demonstrate importance of strategic conservation planning for birds. *Biological Conservation* 165: 104–114. https://doi.org/10.1016/j.biocon.2013.05.010.

Collingham YC, Huntley B, Altwegg R, Barnard P, Beveridge OS, Gregory RD, Mason LR, Oschadleus HD, Simmons RE, Willis SG. 2014. Prediction of mean adult survival rates of southern African birds from demographic and ecological covariates. *Ibis* 156: 741–754. https://doi.org/10.1111/ibi.12195.

Cowling RM, Potts AJ, Bradshaw PL, Colville J, Arianoutsou M, Ferrier S, Forest F, Fyllas NM, Hopper SD, Ojeda F, et al. 2015. Variation in plant diversity in mediterranean-climate ecosystems: the role of climatic and topographical stability. *Journal of Biogeography* 42: 552–564. https://doi.org/10.1111/jbi.12429.

Crowe T. 1993. Evaluation for nature conservation: principles and criteria: news and views. *South African Journal of Science* 89: 2–5.

Fantle-Lepczyk J, Taylor A, Duffy DC, Crampton LH, Conant S. 2018. Using population viability analysis to evaluate management activities for an endangered Hawaiian endemic, the Puaiohi (*Myadestes palmeri*). *PloS ONE* 13: e0198952. https://doi.org/10.1371/journal.pone.0198952.

Freeman BG, Scholer MN, Ruiz-Gutierrez V, Fitzpatrick JW. 2018. Climate change causes upslope shifts and mountaintop extirpations in a tropical bird community. *Proceedings of the National Academy of Sciences of the United States of America* 115: 11982–11987. https://doi.org/10.1073/pnas.1804224115.

Griffith SC, Owens IP, Thuman KA. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Molecular Ecology* 11: 2195–2212. https://doi.org/10.1046/j.1365-294X.2002.01613.x.

Holmes RT, Frauenknecht BD, Du Plessis MA. 2002. Breeding system of the Cape Rockjumper, a South African fynbos endemic. *The Condor* 104: 188–192. https://doi.org/10.1093/condor/104.1.188.

IUCN. 2017. The IUCN Red List of Threatened Species, Version 2017-3. https://www.iucnredlist.org/species/22708094/118953543. [Accessed 10 May 2021].

Kraaij T, van Wilgen BW. 2014. Drivers, ecology, and management of fire in fynbos. *Fynbos: Ecology, Evolution, and Conservation of a Megadiverse Region*. Oxford: Oxford University Press. pp 47–72.

Lacy RC, Pollack JP 2021. Vortex: A stochastic simulation of the extinction process. Brookfield: Chicago Zoological Society.

Lee A, Barnard P. 2015. Spatial and temporal patterns of insect-order activity in the fynbos, South Africa. *Journal of Entomology and Zoology Studies* 3: 95–102.

Lee AT, Barnard P. 2016. Endemic birds of the Fynbos biome: a conservation assessment and impacts of climate change. *Bird Conservation International* 26: 52–68. https://doi.org/10.1017/S0959270914000537.

Lee AT, Barnard P, Hockey PA. 2015. Population metrics for fynbos birds, South Africa: densities, and detection and capture rates from a Mediterranean-type ecosystem. *Ostrich* 86: 179–187. https://doi.org/10.2989/00306525.2015.1021287.

Lee AT, Wright D, Barnard P. 2017. Hot bird drinking patterns: drivers of water visitation in a fynbos bird community. *African Journal of Ecology* 55: 541–553. https://doi.org/10.1111/aje.12384.

Milne R, Cunningham SJ, Lee AT, Smit B. 2015. The role of thermal physiology in recent declines of birds in a biodiversity hotspot. *Conservation Physiology* 3: cov048. https://doi.org/10.1093/conphys/cov048.

Oliveros CH, Field DJ, Ksepka DT, Barker FK, Aleixo A, Andersen MJ, Alström P, Benz BW, Braun EL, Braun MJ, et al. 2019. Earth history and the passerine superradiation. *Proceedings of the National Academy of Sciences of the United States of America* 116: 7916–7925.

Oswald KN. 2016. Observed instances of alarm calling in the Cape Rockjumper. *Ostrich* 87: 285–288. https://doi.org/10.2989/00306525.2016.1206043.

Oswald KN, Diener EF, Diener JP, Cunningham SJ, Smit B, Lee AT. 2020a. Increasing temperatures increase the risk of reproductive failure in a near threatened alpine ground-nesting bird, the Cape Rockjumper *Chaetops frenatus*. *Ibis* 162: 1363–1369. https://doi.org/10.1111/ibi.12846.

Oswald KN, Edwards S, Lee AT, Cunningham S, Smit B. 2020b. No evidence of genetic structure in a sky island endemic: implications for population persistence under a shrinking thermal niche. *Authorea* (preprint). https://doi.org/10.22541/au.157901262.2442030.

Oswald KN, Lee AT, Smit B. 2018a. Seasonal physiological responses to heat in an alpine range-restricted bird: the Cape Rockjumper (*Chaetops frenatus*). *Journal of Ornithology* 159: 1063–1072. https://doi.org/10.1007/s10336-018-1582-8.

Oswald KN, Lee AT, Smit B. 2018b. Comparison of physiological responses to high temperatures in juvenile and adult Cape Rockjumpers *Chaetops frenatus*. *Ostrich* 89: 377–382. https://doi.org/10.2989/00306525.2018.1509905.

Oswald KN, Evlambiou AA, Ribeiro ÂM, Smit B. 2018c. Tag location and risk assessment for passive integrated transponder-tagging passerines. *Ibis* 160: 453–457. https://doi.org/10.1111/ibi.12558.

Oswald KN, Smit B, Lee AT, Cunningham SJ. 2019. Behaviour of an alpine range-restricted species is described by interactions between microsite use and temperature. *Animal Behaviour* 157: 177–187. https://doi.org/10.1016/j.anbehav.2019.09.006.

Oswald K, Smit B, Lee A, Peng C, Brock C, Cunningham S. 2021. Higher temperatures are associated with reduced nestling body condition in a range-restricted mountain bird. *Journal of Avian Biology* e02756. https://doi.org/10.1111/jav.02756.

Possingham H, Lindenmayer D, Norton T. 1994. A framework for the improved management of threatened species based on population viability analysis (PVA). *Pacific Conservation Biology* 1: 39–45. https://doi.org/10.1071/PC930039.

Verboom J, Foppen R, Chardon P, Opdam P, Luttikhuizen P. 2001. Introducing the key patch approach for habitat networks with persistent populations: an example for marshland birds. *Biological Conservation* 100: 89–101. https://doi.org/10.1016/S0006-3207(00)00210-X.

Verboom J, Schippers P, Cormont A, Sterk M, Vos CC, Opdam PF. 2010. Population dynamics under increasing environmental variability: implications of climate change for ecological network design criteria. *Landscape Ecology* 25: 1289–1298. https://doi.org/10.1007/s10980-010-9497-7.

Wisheu IC, Rosenzweig ML, Olsvig-Whittaker L, Shmida A. 2000. What makes nutrient-poor Mediterranean heathlands so rich in plant diversity? *Evolutionary Ecology Research* 2: 935–955.