

Behavioral Ecology (2024), 35(3), arae023. https://doi.org/10.1093/beheco/arae023

Original Article

Small-scale land-use change effects on breeding success in a desert-living social bird

Krista N. Oswald, a,b,o Oded Berger-Tal,b and Uri Rollb

^aJacob Blaustein Center for Scientific Cooperation, The Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, 849900 Midreshet Ben-Gurion, Israel and bMitrani Department of Desert Ecology, The Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, 849900 Midreshet Ben-Gurion, Israel

Received 23 July 2023; revised 19 March 2024; editorial decision 20 March 2024; accepted 30 March 2024

Human villages in deserts can provide resources in an otherwise stark environment, potentially buffering against extreme environmental conditions. It is thus expected that breeding within these villages would result in higher fitness. However, choosing to raise offspring in these resource-rich environments may have unintended negative consequences. Here, we studied the breeding success of a cooperative breeding bird nesting in habitats with different levels of human disturbance—the Arabian babbler (Argya squamiceps), in the Negev desert of Israel. We recorded 42 breeding attempts from 15 groups between March and July 2022. We examined overall breeding success, brood size, and causes of nest failure. When nestlings were 6 days old, we also calculated daily change in body mass and adult provisioning rate. We found that despite higher resource abundance in villages, proximity to villages did not affect provisioning rate, and nestlings gained less mass at higher temperatures for all nests. Currently, there is no evidence that human villages are providing oases of resources for nesting babblers. Further, various conservation interventions (e.g., encouraging residents to keep cats indoors) could improve babblers' overall fitness. Ultimately, we highlight how, for some desert specialists, additional resources provided by humans may not do enough to counter potential negative effects.

Key words: ecological trap, human-modified habitat, nest success, predation, provisioning rate, urban ecology.

INTRODUCTION

Our world is facing a climate and biodiversity crisis due to human actions (Chapin et al. 2001; Bellard et al. 2012). Species across the globe are threatened by land-use change, habitat fragmentation, pathogens, climate change, invasive species, and other anthropogenic disturbances (Sala et al. 2000; Jetz et al. 2007; Hoffmann et al. 2010; Yom-Tov et al. 2012). While land-use change is considered the single largest threat to biodiversity (Davison et al. 2021), threats to biodiversity do not act in isolation but often exacerbate one another (Oliver and Morecroft 2014), and are not trivial to disentangle (Pärtel et al. 2016; González-M et al. 2018; Redlich et al. 2022). Moreover, our knowledge of threats to biodiversity is often biased toward specific taxa and geographic areas (Davison et al. 2021), for example, xeric ecosystems are facing extreme losses in habitat and biodiversity (Reynolds et al. 2007; Ren et al. 2022), yet are neglected in ecological and conservation research (Roll et al. 2017; Davison et al. 2021).

Desert systems are unique in the stark difference they exhibit between human-altered habitats and natural habitats (Sullivan et al. 2013). In desert environments, human-altered habitat can provide

there may be obvious benefits to taking advantage of the increase in reliable resources but these require species to be able to live alongside humans and human-altered habitats. Yet, desert endemics that can live in modified environments will not only obtain the benefits from the increase in resources but may also face an increase in competition or predation due to an increase in invasive species in these regions (Yom-Tov et al. 2012; Sullivan et al. 2013; Salomon et al. 2022). Invasive species pose the second greatest threat to species survival globally (Schmitz and Simberloff 1997; Dueñas et al. 2021). Human-altered desert habitats can promote the establishment of invasive species

additional and (perhaps more importantly) reliable sources of food and water that benefit those desert-dwelling species (Shochat 2004;

Anderies et al. 2007). Further, this increased resource availability

can significantly alter behavioral traits by allowing organisms to re-

duce time spent foraging in favor of other behaviors (e.g., seeking

shade during hotter parts of the day; Tieleman and Williams

2002). Consequently, human-altered habitats in deserts could po-

tentially act as refugia during climate change-driven drought and

heat waves and generally reduce the impacts of climate change and

desertification (Reynolds et al. 2007; McKechnie and Wolf 2010;

Conradie et al. 2020; McKechnie et al. 2021). For desert endemics,

Address correspondence to K.N. Oswald. E-mail: knoswald@gmail.com.

Page 2 of 8 Oswald et al.

(Roll et al. 2008), as well as encourage range expansion of species from nearby non-desert habitats as resources become more plentiful (Lewin et al. 2021). When these invaders are predators, there can be a direct negative effect on the native desert specialists (e.g., Salomon et al. 2022).

Urbanization can have equivocal impacts on avian breeding success. Generally, nests in urban areas have smaller nestlings (reviewed in Chamberlain et al. 2009). However, the effects of urbanization on predation and brood size are more ambiguous (Chamberlain et al. 2009; López-Flores et al. 2009). Currently, there are only a few studies of how urbanization and increased resources in and around human-altered habitats may affect desert specialist birds. Here, we examine the effects of human-altered habitats on the breeding success of the Arabian babbler (Argya squamiceps) in the Negev desert in Israel. The Negev has seen an extreme expansion of human villages and agriculture since the 1950s, resulting in an increase in water and organic waste, and therefore, an increase in arthropod prey items for those species able to live commensally with humans (Efrat 2004; Ostrovsky et al. 2009; Yom-Tov et al. 2012). This has been specifically studied in desert villages where they found an increase in the abundance of food resources available for babblers following a prolonged study (Ostreiher 2013). Our work centered on two main objectives: first, examine differences in breeding success across a mosaic of human-modified habitats, and second, test whether increased resource availability near/inside humanmodified habitats can mitigate the potential negative effects of increasingly high temperatures (due to climate change) in hyperdesert habitats.

While adult Arabian babblers are generalist feeders (Anava et al. 2000), they provision nestlings solely with foods rich in protein—mainly invertebrates and occasionally also vertebrates (Wright 1998). This indiscriminate behavior in prey choice suggests that babblers nesting in villages have increased food available to provision nestlings. Increased resource availability may offset potential

decreases in reproductive success, commonly seen at high temperatures (i.e., adult provisioning rates are negatively correlated with increasing temperature; Hoset et al. 2004; Cunningham et al. 2015; Carroll et al. 2018; Barras et al. 2021; Oswald et al. 2021). We hypothesized babblers building nests near villages would have greater reproductive success due to higher resource availability. Specifically, babblers that build nests nearer to villages would have 1) higher rates of provisioning food to their nestlings, 2) higher nestling growth rates (i.e., greater mass gain), and 3) less predation—since urban environments often have fewer predators (Anderies et al., 2007), leading to 4) greater overall breeding success for babblers nesting in or near human-modified habitats compared to those nesting further away.

METHODS

Study site and species

This study took place from 1 March 2022 to 31 July 2022 on the Sde Tzin plateau around Kibbutz Sde Boker, Israel (30.873, 34.793). Babblers are territorial (territories of 0.2–1 km²), groupliving birds (generally 6–13 individuals per group) that are resident to the Negev desert. The tight-knit social structure of babblers makes them a model system to understand fundamental questions in evolutionary biology and behavioral ecology, as group living is theorized as an adaptation to coping with harsh environments (Zahavi and Zahavi 1999; Keynan et al. 2015; and see work on Southern Pied babblers Turdoides bicolor—Ridley 2016). We collected breeding data for 15 groups of babblers whose territories made use of habitats with different levels of anthropogenic presence. The Sde Tzin plateau consists of a mosaic of humanmodified habitats, including 1) human villages ("village"), 2) agricultural fields and orchards ("orchard"), and 3) interspersed areas of semi-wild desert plateau ("plateau"; Figure 1).

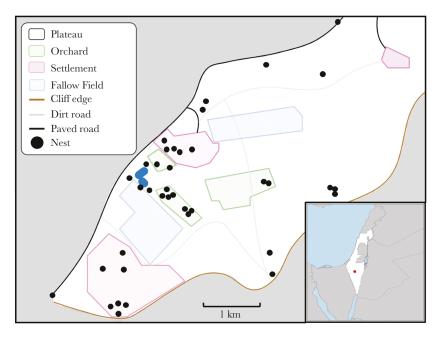


Figure 1 Map of the study area around Sde Boker, Israel, showing locations of the Tzin plateau ("plateau"), human villages ("village"), and orchards ("orchard"), and nest locations of Arabian babbler nests monitored during this study ("nest"). Also shown are fallow fields that were not used by babblers in this study ("fallow fields"; image created using BioRender.com). Location of the study area is marked with a red dot on the inset map.

Thus, we studied babbler groups that live predominantly amidst constant human presence (village), groups near highly modified environments with occasional human presence (orchard), and groups with far less (although intermittent) human presence (plateau; Figure 2).

Nest searching

We began searching for nests in early March 2022. Initially, nest searching was done ad hoc as we became familiar with the different groups and their general territories. Once we identified established territories and began marking individuals with unique colored ring combinations (see below), nest-searching became more systematic, and we began spending 2–3 h per group every 2–3 days until a nest was located. Nests were found by first locating a group (generally through vocalizations), and then looking for traditional signs of nesting (e.g., carrying material, carrying food). Babblers have opencup nests, with nests placed in shrubs or trees—during this study nests were between 0.25–6 m above ground. Birds were observed through binoculars at 10–30 m distance—while not directly habituated, these birds were used to human activity and did not react to humans as a direct threat.



Figure 2 Photos of typical representations of the three main distinct habitat types around Sde Boker, Israel, including A—village, B—orchard, and C—plateau.

Individual/Group identification

Starting at the end of March 2022, we made one main trapping effort per group with a goal of ringing $\sim 50\%$ of the adult individuals to help identify separate groups and ensure the correct group was being observed when searching for nests. Birds were caught using both standard mist-net techniques and with 40×40 cm baited flap-traps (see Oswald et al. 2018 for further trapping details). Captured adult birds were given a standardized aluminum ring, two plain colored rings, and one plastic numbered white ring. During this study, we captured and ringed 69 adults (35 females and 34 males). Altogether, the study area had > 150 babblers from 15 groups ranging in size from 2 to 14 adults per group.

Nest monitoring

Nests were monitored daily using remote motion-activated security cameras with 4G uplink via a SIM card (Reolink Go Plus 4G, Reolink USA) directly through the Reolink smartphone app (©Reolink). Nest cameras were placed on nests found at any stage (building, eggs, nestlings) and were left in place until a few days after the nest reached completion (either failing or succeeding). The cameras used wide-angle lenses and so needed to be placed close to nests (~30 cm), but initial observations showed that babblers spent < 5 min investigating the camera before resuming normal activity (e.g., brooding, incubating, feeding). We masked the cameras' infrared lights to reduce/eliminate attention to the nest when cameras were triggered by motion at night.

For each nest, we recorded its GPS location, habitat type (village, orchard, plateau; see Figure 1), brood size (number of nestlings in the nest; from 2 to 8), group size (from 2 to 14 adults), nest attempt (from 1 to 6), the group identification ("Group ID"), and the number of previously successful nests in that group (from 0 to 3). We calculated the distance (*m*) of each nest to the nearest village's perimeter fence. For nests inside villages, this distance was set as negative values to indicate how far into the village the nest was built.

We visited the nests on two days during the nestling period. On our first visit, we measured nestling $M_{\rm b}$ (g) in the morning and evening when nestlings were 6 days old to measure the daily change in body mass (Δ $M_{\rm b}$; day 1 = hatch day of first nestling). We chose 6 days old as Anava et al. (2001) found that nestling babblers gain the most $M_{\rm b}$ when they are 5.74 days old. Consequently, choosing this age would allow the most precision in identifying any effects on $M_{\rm b}$. The second day we visited the nests was to give each nestling an identifying colored ring combination and record their pre-fledge $M_{\rm b}$ when nestlings were 10 days old. We chose 10 days old as this is the same age nestling babblers are ringed at the long-term research site in the Arava valley \sim 50 km east of Sde Tzin (Ostreiher 1999; Dragić et al. 2022), and this is a few days before the average fledging age (i.e., the age nestlings leave the nest; 12–14 days; Zahavi 1990).

Adult behavioral data and nestling development

We collected adult behavioral data at the nest (provisioning rate, time spent brooding, time spent shading) from the 19 nests that had 6-day-old nestlings (n=3 village, n=7 orchard, n=9 plateau). We measured nestling daily Δ $M_{\rm b}$ by subtracting each nestling morning mass measurement (average time = 0800, range = 0742–0830 IST) from that measured in the evening (average time = 1755, range = 1727–1828 IST). To capture all activities at the nest during days of behavioral and nestling $M_{\rm b}$ measurements, we increased

Page 4 of 8 Oswald et al.

the nest-camera's motion-detection sensitivity to medium (level 60). Due to technical difficulties with four cameras, we obtained daily $\Delta~M_{\rm b}$ data from 19 nests but behavioral data from just 14 nests. Nestling daily $\Delta~M_{\rm b}$ (%) was then standardized to a 10-h period (Equation 1).

$$\Delta M_b = \left[\left(M_{b2} - M_{b1} \right) / \left(\left(t_2 - t_1 \right) / 600 \right) \right] / M_{b1} \times 100$$

When adult babblers visited nests, we recorded their sex (identifiable via iris color), ID (via ring color combination, when possible), and occurrence of provisioning. We then calculated a provisioning rate—the number of times an adult brought food for the nestlings per hour. When possible, we also recorded the size of prey item delivered to nestlings, based on a rough division of "small" (less than 1 cm³, almost imperceptible, no effort to place in nestlings' mouth), "medium" (2–4 cm³, takes some effort to place into nestlings' mouth), "large" (>4 cm³, adult struggles and tries multiple times to place the item in nestlings' mouth).

Temperature measurements

We obtained temperature data from the Israeli Meteorological Service's weather station at Sde Boker (ims.data.gov.il), which records air temperature ($T_{\rm air}$) at 10-min intervals. During the study period, daytime (0600–2000 IST) $T_{\rm air}$ ranged from 1.2 °C to 38.5 °C, with an average $T_{\rm air}$ of 23.4 °C.

Data analysis

Statistics were carried out in the R statistical environment v. 4.2.1 (R Core Team 2022) in RStudio v. 2022.07.1 (R Studio Team 2020). Packages used included lme4 (Bates et al. 2015), car (Fox and Weisberg 2019), multcomp (Hothorn et al. 2008), and dplyr (Wickham et al. 2020). Visuals were created using packages ggplot2 (Wickham 2016) and reshape2 (Wickham 2017). Descriptive statistics are presented as mean \pm SD. Significance was inferred when P-values were < 0.05. We used post hoc (Tukey's) tests on significant multilevel factors (i.e., habitat type) to assess the source of the variance.

We first modeled overall nest success as predicted by distance to the nearest village ("distance"), and group size, fitting a generalized linear mixed-effects model (GLMER) and specifying a binomial distribution, with Group ID as a random effect. For brood size analysis, we included only nests that reached the egg-laying stage (n = 35 of the 42 total nest attempts). We also removed one nest where the dominant male disappeared and the group social hierarchy was in flux (the resultant 8-egg nest indicated multiple laying females, exceeding the normal 3 - 5-egg brood size; O. Keynan personal communication; Wright 1998). We modeled brood size as predicted by distance and group size, fitting a linear mixed-effects model (LMER) and specifying a Poisson distribution, with Group ID as a random effect.

Adult provisioning rate and nestling daily Δ $M_{\rm b}$ (%) were averaged across all nestlings per nest. We used daily maximum air temperature ($T_{\rm max}$) as our temperature predictor variable, since daily $T_{\rm max}$ is likely to correlate with a range of environmental temperatures (Bakken 1989) and has been shown to correlate with behavioral changes at the nest (du Plessis et al. 2012; Cunningham et al. 2013; Oswald et al. 2021).

We then modeled nestling daily Δ $M_{\rm b}$ and adult provisioning rate separately, creating global LMERs that included potential predictor variables of $T_{\rm max}$, distance, group size, brood size, the interaction of distance, and $T_{\rm max}$, with Group ID as a random effect. We then applied an information theoretic approach (Burnham et al. 2011)

to compare all competing models using the *dredge* function in the *MuMIn* package (Barton 2020), ranked by AICc (Akaike's information criterion adjusted for small sample size; lowest to highest). We discuss all competing models within 2 AICc of the top model (i.e., the model with the lowest AICc).

RESULTS

Overview of nests

Nests were considered successful if at least one nestling fledged. A few nests experienced partial predation (n = 4, where some but not all eggs/nestlings were predated), one of these nests was successful, the other three experienced complete predation within 4 days of the initial partial predation. Of the 42 total nest attempts, we observed 16 successful nest attempts and 26 failed nest attempts (n = 40 individuals fledged and n = 18 individuals predated). Of the 26 failed nests, 12 failed due to predation, and for these, we recorded the species of predator. For the other 14 nests, two nests hatched and were abandoned, one nest had eggs rendered nonviable due to cold weather, seven nests were abandoned during nest building, and in one nest, both nestlings were fed a large prey item that caused them to suffocate, and for two nests the cause of failure was unknown.

Nest success and predation

Babblers in villages and orchards each had 27.3% success (3 of 11 nests), and those on the plateau had 50.0% success (10 of 20 nests), but these differences were not significant ($\chi^2 = 0.507$, P = 0.776). There was no significant difference in success correlated with distance to the villages (estimate = 0.001, SD = 0.001, z = 1.007, P = 0.314) or group size (estimate = 0.052, SD = 0.159, P = 0.743). Babblers in orchards had larger broods (mean = 3.3) compared to those in villages (mean = 2.6) and on the plateau (mean = 2.8), but these differences were not significant ($\chi^2 = 2.421$, F = 1.853, P = 0.176). There was also no significant difference in brood size correlated with distance to the villages (estimate = 0.000, SD = 0.000, t = 0.104, P = 0.917) or group size (estimate = 0.014, SD = 0.046, t = 0.307, P = 0.759).

Different predator species were identified in our three habitats. Predation in villages was solely from non-native species introduced to the region due to human activity—Golden Jackals (*Canis aureus*, n = 1) and domesticated cats (*Felis catus*, n = 3; Figure 3). The sole predator of nests in orchards was the native Red Fox (*Vulpes vulpes*; n = 5; Figure 3). Nests on the plateau were predated by Jackals (n = 2) and Foxes (n = 1; Figure 3).

Nestling development, temperature, and habitat

For nestling daily Δ $M_{\rm b}$ (%), there was one additional model within 2 AICc of the top model (see Supplementary Table S1 for full model output). The top model included brood size, and the next best model included brood size and $T_{\rm max}$ (Supplementary Table S1). Nestling daily Δ $M_{\rm b}$ was significantly related to brood size (χ^2 = 14.531, P = 0.002) with nests with four nestlings gaining more daily Δ $M_{\rm b}$ compared to those with two (four–two: estimate = 23.844, SD = 6.794, t = 3.510, P = 0.014), with no other paired relationship showing significance (Supplementary Table S2). Nestling daily Δ $M_{\rm b}$ was significantly lower on days with higher temperatures (estimate = -0.835, SD = 0.410, t = -2.033, P = 0.042; Figure 4).

For the adult provisioning rate, there was one additional model within 2 AICc of the top model (see Supplementary Table S3 for

full model output). The top model included brood size, while the next best model was our null model, without significant interactions (Supplementary Table S3).

DISCUSSION

For animals that can overcome their fear of humans, human villages may appear to be a bonanza of resources. Here, we examined overall breeding success in a desert-living bird within a mosaic of human-altered habitats. Our hypothesis was that babblers nesting

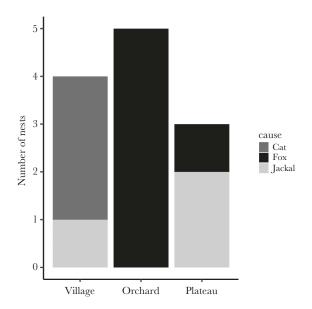


Figure 3 Cause of nest predation from nests of Arabian babblers (Argya squamiceps) from nests in either high human presence ("village"), highly modified environments with occasional human presence ("orchard"), or low (although intermittent) human presence ("plateau"). Predator types included domestic cat (Felis domesticus; "Cat"), Golden Jackal (Canis aureus; "Jackal"), or Red Fox (Vulpes vulpes; "Fox").

in villages would have greater fitness (e.g., higher breeding success) due to greater access to resources and potentially fewer predators. However, this was not the case. In general, we found no significant difference from birds closer to villages, although we did identify a few potential trends for nests within villages: breeding success was lower, brood sizes were smaller, predation was higher, and nestlings gained less mass. In addition, contrary to our prediction, the increase in resource availability in the villages did not mitigate the negative effects of higher temperatures on nestlings. While it remains unclear whether villages act as any kind of ecological trap for nesting babblers, it is clear that nesting in villages does not present an oasis from the outside desert environment.

Predation

During this study we only recorded babbler nest predation by three species, all of which were mammals—cats, foxes, and jackals. This is despite the presence of other potential predators such as the native Brown-necked raven *Corvus ruficollis*, the recently expanding Hooded crow *Corvus cornix*, and snakes such as *Spalerosophis diadema* or *Psammophis schokari*, although for *P. schokari*, we did record one unsuccessful predation attempt. In addition, our nest predation by cats is somewhat under-represented. We had two nests in villages experience partial predation from cats (i.e., ≥ 1 nestling survived the event), before the nest experienced full predation from different cats within the next few days. We determined nest success as fledgling of at least one individual; consequently, these events were counted as two predation events as opposed to four.

The small sample size of nests in villages and orchards made drawing conclusions on breeding success difficult as a power analysis showed our sample sizes were too small to detect significant differences (n = 37 to achieve power = 0.80 at $\alpha = 0.05$; package pwr, Champely et al. 2018). What is clear, for villages at least, is that a relatively straightforward conservation measure could have curbed babbler nest predation events (and likely that of many other species)—applying methods to control the domestic and feral cat population (e.g., encouraging residents to keep cats indoors, enforcing sterilization, and limiting access to waste). Unfortunately, despite

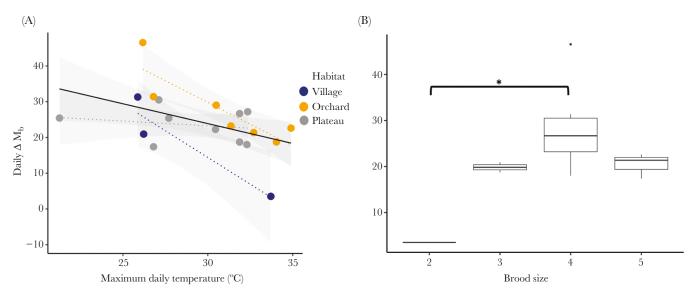


Figure 4 Nestling daily Δ M_b (%) collected from 19 nests of Arabian babblers (*Argya squamiceps*) A—correlated with maximum daily air temperature (°C) by habitat type (village, orchard, plateau) with black line showing trendline for all habitats combined, and B—in relation to brood size (i.e., number of nestlings in a nest; asterisk indicates significant difference).

Page 6 of 8 Oswald et al.

numerous studies providing evidence regarding the negative impacts of outdoor domestic cats (Baker et al. 2005; Dickman 2009; Loss et al. 2013; Trouwborst et al. 2020), such measures in Israel are seldom fully enforced and receive push-back from particular sectors of the Israeli public (Brickner-Braun et al. 2007). Moreover, the population of cats in the villages is maintained and possibly increasing due to intentional food supplementation by people (Gunther et al. 2022; pers. obs.).

Nestling development and provisioning rate

Contrary to our predictions, there was no difference in provisioning rate associated with distance to villages, and nestlings in villages did not gain greater M_b than those on the plateau. In addition, all nests experienced lower nestling mass gain on hotter days (Figure 4a). This was particularly surprising for nests in villages, where we found no evidence that increased resource availability helped mitigate the negative effects of higher temperatures (i.e., provisioning rate decreased with temperature across all habitats). Furthermore, access to additional resources in villages did not result in greater nestling growth (i.e., nestlings closer to villages gained similar M_b). It is further surprising that proximity to villages did not result in a buffering affect from higher temperatures as small villages in the Negev often remain cooler than the surrounding desert due to increased shade and water (Saaroni et al. 2004). So, while lowered mass gain at high temperatures could be more pronounced in urban areas that experience a "heat island" effect (Oke 1995), this would not be the case in our particular study system.

Like Wright (1998), we found that the overall provisioning rate was not correlated with group size. Wright (1998) attributed this to compensatory feeding, where a larger group size means all members do less work for the same net benefit to nestlings. We also suggest the possibility that group size may have been confounded by the presence of multiple successful broods—our two largest groups (one of 14 and one of 11 at the beginning of the breeding season) both had a successful nest early in the season, and so were provisioning nestlings at new nests while continuing to provide for recently fledged young. While we had few such nests with fledglings as well as a nest with nestlings, a simple post hoc linear model fitting provisioning rate to the presence of fledglings showed that provisioning rate was significantly lower in groups with two or more previous successful nests (estimate = -4.730, SD = -2.659, P = 0.022).

Conclusions

We examined the impact of small-scale villages and agriculture on breeding success for a year-round territorial desert bird. Our study site gave us a unique opportunity to examine specific behavioral and reproductive outcomes of desert birds that reside in habitats with different levels of human disturbance and proximity to villages. While we expected the increase in water and food availability in villages to help buffer against the negative effects of high temperatures on food provisioning, this was not the case. Contrary to presenting an oasis of resources in the desert, we found that babblers nesting closer to human disturbance (i.e., villages) tended toward lower breeding performance. The lack of fully "natural" habitat around Sde Boker could be considered a limitation of our study but may, in fact, be beneficial for applied conservation applications as it presents a more realistic situation being faced by many species-studies occurring in natural areas present a bias against the 75% of the terrestrial world where humans live and work (Martin et al. 2012).

Currently, villages are presenting what may be a mixed blessing for babblers, as they seem to be attracted to the villages' high resource availability but are not seeing this transform into greater breeding success. Instead, nests in more natural areas continue to have higher nest success. Consequently, increasing development in the babbler's desert habitat may pose a threat to this species. Human development not only alters the physical landscape but can also change other factors such as the predator landscape, and resource type and availability. Here, we highlighted how the effects of these changes do not exist in a vacuum and should be examined in relation to one another as they present potentially unexpected (and often unintended) interactions. As our world undergoes fundamental climatic and landscape-level changes, more focus should be given to desert habitats and the unique fauna and flora that inhabit it, that could find themselves facing trade-offs in a no-win situation.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

AUTHOR CONTRIBUTIONS

Krista Oswald (Conceptualization [Equal], Data curation [Equal], Formal analysis [Equal], Investigation [Equal], Methodology [Equal], Writing—original draft [Lead], Writing—review & editing [Equal]), Oded Berger-Tal (Conceptualization [Equal], Methodology [Equal], Resources [Equal], Supervision [Equal], Writing—review & editing [Equal]), and Uri Roll (Conceptualization [Equal], Funding acquisition [Lead], Methodology [Equal], Supervision [Equal], Writing—review & editing [Equal])

FUNDING

The authors have no funding to declare.

K.N.O. is supported by postdoctoral fellowships from the Jacob Blaustein Center for Scientific Cooperation and the Zuckerman Postdoctoral Scholars fund. We would like to thank the Arabian Babblers Research Project (specifically Oded Keynan, Alex Alaman, and Nikola Dragić) for their willingness to answer any and all questions related to what babblers "normally" do. We would also like to thank Yael Lenhardt and Ron Efrat for general bird advice, as well as helping secure appropriate permissions and logistics for trapping and ringing. We further thank Darren Burns for for help with catching and ringing birds. In addition, on many occasions members from the Conservation Behavior Research and the Conservation & Biodiversity labs made themselves available to help carry ladders and various other random tasks in the field. Lastly, we would like to thank the Israeli National Parks Authority, as well as the communities of Sde Boker and Midreshet Ben-Gurion for allowing us to setup cameras for nest monitoring.

ETHICS APPROVAL

Ethics for this research were approved by the Israeli National Parks Authority (permit number: 2022/43033).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY

Analyses reported in this article can be reproduced using the data provided by Oswald (2024).

Handling Editor: Robin Tinghitella

REFERENCES

- Anava A, Kam M, Shkolnik A, Degen AA. 2000. Seasonal field metabolic rate and dietary intake in Arabian Babblers (*Turdoides squamiceps*) inhabiting extreme deserts. Funct Ecol. 14(5):607–613. doi:10.1046/j.1365-2435.2000.t01-1-00461.x
- Anava A, Kam M, Shkolnik A, Degen AA. 2001. Growth rate and energetics of Arabian Babbler (*Turdoides squamiceps*) Nestlings. Auk. 118(2):519–524. doi:10.1093/auk/118.2.519
- Anderies JM, Katti M, Shochat E. 2007. Living in the city: resource availability, predation, and bird population dynamics in urban areas. J Theor Biol. 247(1):36–49. doi:10.1016/j.jtbi.2007.01.030
- Baker PJ, Bentley AJ, Ansell RJ, Harris S. 2005. Impact of predation by domestic cats Felis catus in an urban area. Mammal Rev. 35:302–312.
- Bakken GS. 1989. Arboreal perch properties and the operative temperature experienced by small animals. Ecology. 70(4):922–930.
- Barras AG, Niffenegger CA, Candolfi I, Hunziker YA, Arlettaz R. 2021. Nestling diet and parental food provisioning in a declining mountain passerine reveal high sensitivity to climate change. J Avian Biol. 52(2):1–12.
- Barton K. 2020. MuMIn: Multi-Model Inference. R package version 1.43.17. https://CRAN.R-project.org/package=MuMIn
- Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. J Stat Softw. 67(1):1–48.
- Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F. 2012. Impacts of climate change on the future of biodiversity. Ecology Lett. 15(4):365–377.
- Brickner-Braun I, Geffen ELI, Yom-Tov Y. 2007. The domestic cat as a predator of Israeli wildlife. Israel J Ecol Evol. 53(2):129–142.
- Burnham KP, Anderson DR, Huyvaert KP. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behav Ecol Sociobiol. 65(1):23–35.
- Carroll R, Davis CA, Fuhlendorf SD, Elmore RD, DuRant SE, Carroll JM. 2018. Avian parental behavior and nest success influenced by temperature fluctuations. J Therm Biol. 74:140–148.
- Chamberlain DE, Cannon AR, Toms MP, Leech DI, Hatchwell BJ, Gaston KJ. 2009. Avian productivity in urban landscapes: a review and meta-analysis. Ibis. 151(1):1–18. doi:10.1111/j.1474-919X.2008.00899.x
- Champely S, Ekstrom C, Dalgaard P, Gill J, Weibelzahl S, Anandkumar A, Ford C, Volcic R, De Rosario H, De Rosario MH. 2018. Package "pwr." R package version. 1(2). [accessed 29 November 2023]. http://14.63.219.55/web/packages/pwr/pwr.pdf
- Chapin FS, Sala OE, Huber-Sannwald E. 2001. Global biodiversity in a changing environment: scenarios for the 21st century. 2nd ed. New York (USA): Springer Science & Business Media.
- Conradie SR, Woodborne SM, Wolf BO, Pessato A, Mariette MM, McKechnie AE. 2020. Avian mortality risk during heat waves will increase greatly in arid Australia during the 21st century. Conserv Physiol. 8(1):coaa048.
- Cunningham SJ, Kruger AC, Nxumalo MP, Hockey PA. 2013. Identifying biologically meaningful hot-weather events using threshold temperatures that affect life-history. PLoS One. 8(12):e82492.
- Cunningham SJ, Martin RO, Hockey PA. 2015. Can behaviour buffer the impacts of climate change on an arid-zone bird? Ostrich. 86:119–126.
- Davison CW, Rahbek C, Morueta-Holme N. 2021. Land-use change and biodiversity: challenges for assembling evidence on the greatest threat to nature. Global Change Biol. 27(21):5414–5429. doi:10.1111/gcb.15846
- Dickman CR. 2009. House cats as predators in the Australian environment: impacts and management. Human-Wildlife Conflicts. 3(1):41–48.
- Dragić N, Keynan O, Ilany A. 2022. Protocol to record multiple interaction types in small social groups of birds. STAR Protocols. 3(4):101814. doi:10.1016/j.xpro.2022.101814
- du Plessis KL, Martin RO, Hockey PA, Cunningham SJ, Ridley AR. 2012. The costs of keeping cool in a warming world: implications of high temperatures for foraging, thermoregulation and body condition of an aridzone bird. Global Change Biol. 18(10):3063–3070.
- Dueñas M-A, Hemming DJ, Roberts A, Diaz-Soltero H. 2021. The threat of invasive species to IUCN-listed critically endangered species: a systematic review. Global Ecol Conserv. 26:e01476. doi:10.1016/j.gecco.2021.e01476
- Efrat E. 2004. Man and the environment in Israel geographical essays. Tel Aviv University, Tel Aviv, Israel: Ramot Publishing.
- Fox J, Weisberg S. 2019. An R Companion to Applied Regression, Third Edition. Thousand Oaks, CA: Sage (Vienna: R Foundation for Statistical Computing). https://socialsciences.mcmaster.ca/jfox/Books/ Companion/

- González-M R, García H, Isaacs P, Cuadros H, López-Camacho R, Rodríguez N, Pérez K, Mijares F, Castaño-Naranjo A, Jurado R, et al. 2018. Disentangling the environmental heterogeneity, floristic distinctiveness and current threats of tropical dry forests in Colombia. Environ Res Lett. 13(4):045007.
- Gunther I, Hawlena H, Azriel L, Gibor D, Berke O, Klement E. 2022. Reduction of free-roaming cat population requires high-intensity neutering in spatial contiguity to mitigate compensatory effects. Proc Natl Acad Sci USA. 119(15):e2119000119.
- Hoffmann M, Hilton-Taylor C, Angulo A, Böhm M, Brooks TM, Butchart SHM, Carpenter KE, Chanson J, Collen B, Cox NA, et al. 2010. The impact of conservation on the status of the World's vertebrates. Science. 330(6010):1503–1509. doi:10.1126/science.1194442
- Hoset KS, Espmark Y, Moksnes A, Haugan T, Ingebrigtsen M, Lier M. 2004. Effect of ambient temperature on food provisioning and reproductive success in snow buntings Plectrophenax nivalis in the high arctic. Ardea. 92(2):239–246.
- Hothorn T, Bretz F, Westfall P. 2008. multcomp: simultaneous inference in general parametric models. Biom. J. 50(3):346–363.
- Jetz W, Wilcove DS, Dobson AP. 2007. Projected Impacts of Climate and Land-Use Change on the Global Diversity of Birds. PLoS Biol. 5(6):e157. doi:10.1371/journal.pbio.0050157
- Keynan O, Ridley AR, Lotem A. 2015. Social foraging strategies and acquisition of novel foraging skills in cooperatively breeding Arabian babblers. Behav Ecol. 26(1):207–214. doi:10.1093/beheco/aru181
- Lewin A, Erinjery JJ, le Polain de Waroux Y, Tripler E, Iwamura T. 2021.

 Land-use differences modify predator-prey interactions and Acacia vegetation in a hyperarid ecosystem. J Arid Environ. 192:104547. doi:10.1016/j.jaridenv.2021.104547
- López-Flores V, MacGregor-Fors I, Schondube JE. 2009. Artificial nest predation along a Neotropical urban gradient. Landsc Urban Plann. 92(2):90–95. doi:10.1016/j.landurbplan.2009.03.001
- Loss SR, Will T, Marra PP. 2013. The impact of free-ranging domestic cats on wildlife of the United States. Nat Commun. 4(1):1–8.
- Martin LJ, Blossey B, Ellis E. 2012. Mapping where ecologists work: biases in the global distribution of terrestrial ecological observations. Front Ecol Environ. 10(4):195–201. doi:10.1890/110154
- McKechnie AE, Rushworth IA, Myburgh F, Cunningham SJ. 2021. Mortality among birds and bats during an extreme heat event in eastern South Africa. Austral Ecol. 46(4):687–691.
- McKechnie AE, Wolf BO. 2010. Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. Biol Lett. 6(2):253–256.
- Oke TR. 1995. The heat island of the urban boundary layer: characteristics, causes and effects. In: Cermak JE, Davenport AG, Plate EJ, Viegas DX, editors. Wind Climate in Cities. Berlin: Springer Dordrecht. p. 81–108.
- Oliver TH, Morecroft MD. 2014. Interactions between climate change and land use change on biodiversity: attribution problems, risks, and opportunities. WIREs Clim Change. 5(3):317–335. doi:10.1002/wcc.271
- Ostreiher R. 1999. Nestling Feeding-Space Strategy in Arabian Babblers. Auk. 116(3):651–657. doi:10.2307/4089326
- Ostreiher R. 2013. Influence of agricultural areas on the ecology and behaviour of the Arabian babbler. In: Giladi Y, editor. The Arava Landscape, Nature. and People in the Arave Valley. Ein Yahav, Israel (in Hebrew): Arava publishing. p. 262–273.
- Ostrovsky G, Kozer R, Garfinkel M. 2009. Garbage and Recycling in Israel: a Report and Recommendations. Tel Aviv: Adam Teva Din.
- Oswald K. 2024. Nesting data from 42 Arabian Babbler (Argya squamiceps) nests [Dataset]. Dryad. https://doi.org/10.5061/dryad.8cz8w9h01
- Oswald KN, Lee AT, Smit B. 2018. Comparison of physiological responses to high temperatures in juvenile and adult Cape Rockjumpers *Chaetops frenatus*. Ostrich. 89(4):377–382.
- Oswald KN, 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. J Avian Biol. 52(e02756).
- Pärtel M, Bennett JA, Zobel M. 2016. Macroecology of biodiversity: disentangling local and regional effects. New Phytol. 211(2):404–410. doi:10.1111/nph.13943
- R Core Team. 2022. R: A language and environment for statistical computing. https://www.R-project.org/
- Redlich S, Zhang J, Benjamin C, Dhillon MS, Englmeier J, Ewald J, Fricke U, Ganuza C, Haensel M, Hovestadt T, et al. 2022. Disentangling effects of climate and land use on biodiversity and ecosystem services—A

Page 8 of 8 Oswald et al.

multi-scale experimental design. Methods Ecol Evol. 13(2):514-527. doi:10.1111/2041-210X.13759

- Ren Q, He C, Huang Q, Shi P, Zhang D, Güneralp B. 2022. Impacts of urban expansion on natural habitats in global drylands. Nat Sustain. 5(10):869–878. doi:10.1038/s41893-022-00930-8
- Reynolds JF, Smith DMS, Lambin EF, Turner BL, Mortimore M, Batterbury SPJ, Downing TE, Dowlatabadi H, Fernández RJ, Herrick JE, et al. 2007. Global desertification: building a science for dryland development. Science. 316(5826):847–851. doi:10.1126/science.1131634
- Ridley AR. 2016. Southern pied babblers: the dynamics of conflict and cooperation in a group-living society. In: Koenig WD, Dickinson JL, editors. Cooperative Breeding in Vertebrates: Studies in Ecology, Evolution and Behaviour. Cambridge (UK): Cambridge University Press. p. 115–132.
- Roll U, Dayan T, Simberloff D. 2008. Non-indigenous terrestrial vertebrates in Israel and adjacent areas. Biol Invasions. 10(5):659–672. doi:10.1007/ s10530-007-9160-7
- Roll U, Feldman A, Novosolov M, Allison A, Bauer AM, Bernard R, Böhm M, Castro-Herrera F, Chirio L, Collen B, et al. 2017. The global distribution of tetrapods reveals a need for targeted reptile conservation. Nat Ecol Evol. 1(11):1677–1682.
- RStudioTeam. 2020. RStudio: Integrated Development for R. Boston, MA: RStudio, Inc., http://www.rstudio.com/
- Saaroni H, Bitan A, Dor EB, Feller N. 2004. The mixed results concerning the 'oasis effect'in a rural settlement in the Negev Desert, Israel. J Arid Environ. 58(2):235–248.
- Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, et al. 2000. Global biodiversity scenarios for the year 2100. Science. 287(5459):1770–1774.
- Salomon A, Kozhoridze G, Shochat E, Magen I, Naveh I, Leader N, Tsoar A, Ovadia O. 2022. Bird eggs or wheat: assessing the impact of an overabundant crow species in a landscape mosaic in the Negev desert of Israel. J Nat Conserv. 70:126283. doi:10.1016/j.jnc.2022.126283

- Schmitz DC, Simberloff D. 1997. Biological invasions: a growing threat. Issues Sci Technol. 13(4):33–40.
- Shochat E. 2004. Credit or debit? Resource input changes population dynamics of city-slicker birds. Oikos. 106(3):622–626.
- Sullivan BK, Van Haverbeke DR, Chambers C. 2013. Wildlife and anthropogenic changes in the arid southwest. Design with the Desert: Conservation and Sustainable Development. CRC press, Boca Raton.:169–191.
- Tieleman BI, Williams JB. 2002. Cutaneous and respiratory water loss in larks from arid and mesic environments. Physiol Biochem Zool: PBZ. 75(6):590–599.
- Trouwborst A, McCormack PC, Martínez Camacho E. 2020. Domestic cats and their impacts on biodiversity: a blind spot in the application of nature conservation law. People Nat. 2(1):235–250.
- Wickham H. 2016. ggplot2: Elegant Graphics for Data Analysis. New York, NY: Springer-Verlag. https://ggplot2.tidyverse.org
- Wickham H. 2017. reshape2: flexibly reshape data: a reboot of the reshape package. R package version. 1(3).
- Wickham H, Francois R, Henry L, Muller K. 2020. dplyr: A grammar of data manipulation. R package version 085. https://CRAN.R-project. org/package=dplyr
- Wright J. 1998. Helpers-at-the-nest have the same provisioning rule as parents: experimental evidence from play-backs of chick begging. Behav Ecol Sociobiol. 42(6):423–429. doi:10.1007/s002650050456
- Yom-Tov Y, Hatzofe O, Geffen E. 2012. Israel's breeding avifauna: a century of dramatic change. Biol Conserv. 147(1):13–21. doi:10.1016/j.biocon.2012.01.005
- Zahavi A. 1990. Arabian babblers: the quest for social status in a cooperative breeder. In: Stacey PB, Koenig WD, editors. Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior. Cambridge (UK): Cambridge University Press. p. 103–130.
- Zahavi A, Zahavi A. 1999. The handicap principle: a missing piece of Darwin's puzzle. Oxford (UK): Oxford University Press.