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A blessing and a curse: Human resources are beneficial but human presence is detrimental for the growth and development of *Argya squamiceps* (Arabian Babbler)

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ABSTRACT

Human modifications to the environment are having a dramatic effect on biodiversity, but in desert habitats the high abundance of resources near human villages may be beneficial to breeding birds. By collecting high-throughput tracking data on *Argya squamiceps* (Arabian Babblers), we examined whether nesting and foraging in a village increased nestling growth and development in this social, desert-dwelling species. We placed tags on 10 individuals representing 8 groups of *A. squamiceps* and 16 nests with nestlings, collecting 191,087 localizations (average = 1,504.6 ± 1,067.4 SE localizations per day). Contrary to our predictions, we found that it was more beneficial for *A. squamiceps* to have nests farther away from villages — groups nesting farther from villages covered less area when foraging and yet had heavier nestlings. The heaviest nestlings were from nests where groups spent the highest proportion of time foraging in orchards. This suggests that some level of human resources (i.e., orchards) was beneficial but only if combined with otherwise low levels of human presence. Detailed movement data of wild birds, particularly in the context of reproductive success as used here, can further uncover the effects of human disturbance on breeding individuals. This is particularly important in dryland areas, where human impact may elicit nontrivial responses from local wildlife, and which are under-represented in such basic and applied research.

Keywords: breeding success, drylands, habitat use, movement ecology, tracking

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LAY SUMMARY

1. Humans continue to modify natural landscapes, with potentially detrimental effects on wildlife. Understanding how animals are responding to our changing world is key for our ability to protect them.
2. Deserts are under-researched and present a unique system to look at human disturbance, where human-modified habitat increases the presence of food and water.
3. Here, we examined how living in a mosaic of villages, orchards, and semi-natural desert affected nestling growth in a cooperative-breeding desert bird. We asked whether groups that use the more plentiful resources around human areas had higher quality nestlings.
4. We tracked 10 individuals from 8 groups of *Argya squamiceps* (Arabian Babbler) with nests that had nestlings, collecting ~1,000 locations per individual per day.
5. We found the best place for a nest was where individuals could take advantage of resources while remaining apart from people—the heaviest nestlings and higher nest success were close to orchards and far from villages.

UNA BENDICIÓN Y UNA MALDICIÓN: LOS RECURSOS HUMANOS SON BENEFICIOSOS PERO LA PRESENCIA HUMANA ES PERJUDICIAL PARA EL CRECIMIENTO Y DESARROLLO DE ARGYA SQUAMICEPS

RESUMEN

Las modificaciones humanas al ambiente están teniendo un efecto dramático sobre la biodiversidad, pero en hábitats desérticos la alta abundancia de recursos cerca de poblados humanos puede ser beneficiosa para las aves reproductoras. Al recopilar datos de seguimiento de alta resolución en Argya squamiceps, examinamos si anidar y forrajear en un poblado aumentaba el crecimiento y desarrollo de los polluelos en esta especie social, habitante del desierto. Colocamos dispositivos de seguimiento en 10 individuos que representaban 8 grupos de A. squamiceps y 16 nidos con polluelos, recolectando 191.087 localizaciones (promedio = 1.504,6 ± 1.067,4 EE localizaciones por día). Contrario a nuestras predicciones, encontramos que era más beneficioso para A. squamiceps tener nidos más alejados de los poblados: los grupos que anidaban más lejos de los poblados cubrían menos área al forrajear y, sin embargo, tenían polluelos más pesados. Los polluelos más pesados provenían de nidos donde los grupos pasaban la mayor proporción del tiempo forrajeando en huertos. Esto sugiere que cierto nivel de recursos humanos (i.e., huertos) fue beneficioso, pero solo si se combinaba con niveles bajos de presencia humana. Los datos detallados de movimiento de las aves silvestres, particularmente en el contexto del éxito reproductivo como se utilizó aquí, pueden revelar más información sobre los efectos de la perturbación humana en individuos reproductores. Esto es particularmente importante en áreas áridas, donde el impacto humano puede generar respuestas no triviales en la fauna local, y que están sub-representadas en este tipo de investigación básica y aplicada.

Palabras clave: ecología del movimiento, éxito reproductivo, rastreo, tierras áridas, uso de hábitat

INTRODUCTION

Humans are changing the environment at a more intense and rapid rate than has occurred in the last several million years, leading to the current biodiversity crisis (Chapin et al. 2001, Bellard et al. 2012). Land-use change has a dramatic negative impact on biodiversity, mainly through habitat destruction and modification (Newbold et al. 2015, Davison et al. 2021). How land-use change affects biodiversity can vary based on ecosystem type (García-Vega and Newbold 2020), yet most research fails to account for this variation, which has led to a significant geographic bias (Davison et al. 2021). For example, despite facing extreme losses in habitat and biodiversity (Reynolds et al. 2007, Ren et al. 2022) deserts continue to be neglected in conservation research (Roll et al. 2017, Davison et al. 2021).

Deserts present an ecosystem with one of the most dramatic contrasts between human development and the natural environment (Sullivan et al. 2013). In natural deserts, the timing and quantity of resources (both water and food) are unpredictable (Noy-Meir 1973), with human-altered habitats providing additional and (perhaps more importantly) reliable "oases" of food and water (Shochat et al. 2004, Anderies et al. 2007). Thus, while urbanization may be considered a threat to overall global biodiversity, there may be some environments or species that find certain aspects of urbanization beneficial. For example, urbanization can have equivocal and species-specific impacts on avian breeding success (reviewed in Chamberlain et al. 2009). Generally, nests in urban areas have smaller nestlings; possible explanations for this include less diverse food (Marussich and Faeth 2009), less nutritious food (see Knapp et al. 2013; Murray et al. 2018; Stofberg et al. 2022), or higher nestling stress levels (Almasi et al. 2015). While there have been several studies examining the effects of urbanization on general bird communities in deserts (e.g., Mills et al. 1989, Green and Baker 2003, Shochat et al. 2004, Walker and Shochat 2010), these studies are generally limited in their geographic representation (Diamant et al. 2025), and only a few recent studies have specifically examined the effects of urbanization on desert specialists (Alamán et al. 2024, Oswald et al. 2024).

Argya squamiceps (Arabian Babblers) have been studied in the Arava valley in eastern Israel since the 1960s (Zahavi and Zahavi 1997). *Argya squamiceps* are social cooperative breeders, ostensibly to increase overall fitness by having multiple adults and sub-adults (both male and female, related and unrelated) forage and provide food for nestlings of a single breeding pair in a harsh environment with limited resource availability (Carlisle and Zahavi 1986, Cockburn 1998). Average group size is generally 8–12 individuals, although this likely varies based on many environmental and social conditions, and so groups can be as small as a single breeding pair or as large as 24 individuals (Zahavi and Zahavi 1997). Previous work has provided insights into many aspects of this complex breeding ecology including but not limited to 3 major findings: (1) group size can be equivocal in regard to provisioning rate, either resulting in an increased rate (albeit with smaller prey; Wright 1998a) or an unchanged rate (Oswald et al. 2024); (2) brood size does not always affect provisioning rate (Wright 1998b, Oswald et al. 2024); and (3) there is little evidence for an effect of relatedness among helpers on provisioning effort (Wright 1997).

With consistently increasing land development in the area, recent studies have begun to examine the effect of urbanization (from expanding villages and agriculture) on the fitness of *A. squamiceps*; these studies have found that in modified habitats *A. squamiceps* face new challenges that include higher mortality (Alamán et al. 2024) and a new array of nest predators (Oswald et al. 2024). Oswald et al. (2024) also examined provisioning rate, which did not differ among habitat types despite previous research showing a higher level of resource abundance closer to human presence (Efrat 2004). However, previous studies on *A. squamiceps* have relied on traditional observational data from the nest and so were unable to quantify parental effort, which can be higher for birds in poorer habitat (Tremblay et al. 2005). Recently, a population of *A. squamiceps* were fitted with high-throughput tracking tags, making use of an established Advanced Tracking and Localization of Animals in real-life Systems (ATLAS; see Methods) array. Tracking individuals from each group of *A. squamiceps* has enabled a detailed understanding of how groups use each habitat type seasonally (Oswald et al. 2025), and may also be used to determine potential impacts of using the various habitat types on each groups' reproduction.

The advanced tracking system has been deployed in the Negev Desert near Sde Boker, Israel, on a plateau with a variety

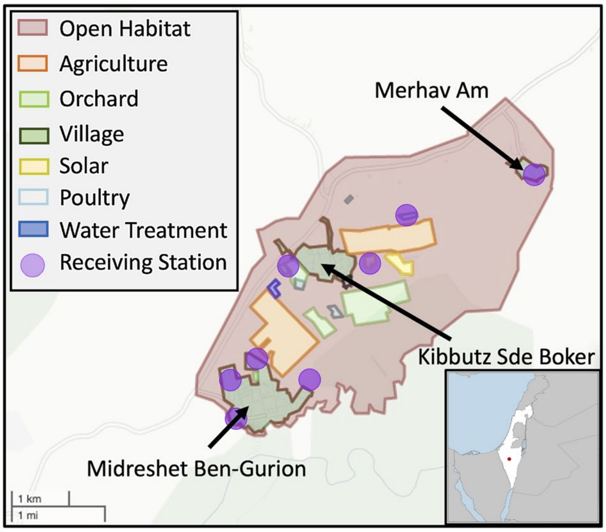

FIGURE 1. Overview of the area covered by the ATLAS around Sde Boker, Israel, including breakdown of habitat types and location of ATLAS receiving stations. Inset: Red dot indicates the study site location within Israel.

of different habitat types (consisting of varied vegetation and human presence; see below for habitat type designations) representing different levels of human modification and development (Figure 1). The Negev desert has seen significant expansion in the number and amount of both human villages and agriculture since the 1950s. This expansion has increased amounts of water and organic waste, and therefore an increase in arthropod prey items for species that are able to live commensally with humans (Efrat 2004, Ostrovsky et al. 2009, Yom-Tov et al. 2012). While adult and sub-adult *A. squamiceps* are generalist feeders (Anava et al. 2000), and will eat available berries and fruit alongside protein-rich items, *A. squamiceps* provision nestlings solely with protein-rich foods — mainly invertebrates and occasionally also vertebrates (Wright 1998b). The generalist feeding of *A. squamiceps* may suggest that foraging in villages can increase the food available to provision their nestlings.

Here, we used high spatio-temporal resolution tracking data to examine the relationship between adult foraging behavior, nest location, and nestling growth for *A. squamiceps* living in a mosaic of human-modified habitats. We did so by placing high-throughput tracking tags on adult and sub-adult individual *A. squamiceps* during the breeding season, when they were provisioning food to nestlings. We hypothesized that since villages have more plentiful and denser resources, nesting and foraging in villages would positively alter nestling growth compared to nests outside villages. Specifically, we expected one of two situations: (1) adults with nests farther from villages would cover more area to find food, leading to similar growth in nestlings across all nests, or (2) adults with nests farther from villages would cover the same amount of area to find food, leading to smaller nestlings compared to nestlings in nests closer to villages.

METHODS

Study Site and Details of Tracking System

This study took place from February 18 to July 8, 2023 on the Sde Tzin plateau around Kibbutz Sde Boker, Israel (30.874°N, 34.793°E). The site is covered by an ATLAS array (Toledo et al. 2014, 2020) consisting of 8 receiving stations placed around the Sde Tzin plateau in locations that maximized the ability to trilaterate (i.e., using distances to determine the coordinates of a point of interest) and record localizations of tag transmissions (using UHF) based off reception by 3 or more stations (Figure 1). The ATLAS system provides localization data with similar accuracy and precision to traditional GPS (within ~5 m of traditional GPS), at a faster sampling rate (~1–8 s), while being comparatively inexpensive (Beardsworth et al. 2022, Nathan et al. 2022). ATLAS technology is already yielding novel insights into how wild animals interact with their environments through quantitative tracking resulting in copious amounts of data across a variety of species and ecosystems (Corl et al. 2020, Lourie et al. 2021, Vilk et al. 2022, Roeleke et al. 2022, Luisa Vissat et al. 2023, Heathcote et al. 2023). The reverse-GPS technology of the ATLAS relies on installation of a system of receivers usually limited to a regional scale (25–1,600 km^2). The technology allows for simultaneous remote tracking of multiple animals, with tags small enough and light enough to place on ~20 g organisms (Nathan et al. 2022).

To understand the effects of habitat type on the reproduction of *A. squamiceps*, we first classified the area covered by the ATLAS system into different habitat types. We divided the plateau into 7 main habitat types based on high-resolution satellite imagery (https://govmap.gov.il; Figure 1): (1) plateau: the habitat type covering most of the area on the Sde Tzin plateau, with low human presence and no agriculture or irrigation, including degraded land and more natural vegetation adjacent to the nearby National Park; (2) agriculture: areas with seasonal produce (e.g., cabbage, lettuce, etc.) grown by Kibbutz Sde Boker; (3) orchard: predominantly olive groves with a small argan grove near Kibbutz Sde Boker; (4) village: the three regions with permanent human habitation including Midreshet Ben-Gurion, Kibbutz Sde Boker, and Merhav Am; (5) solar: fenced regions of solar panels; (6) poultry: fenced-in industrialized sheds for poultry production; and (7) water treatment: a fenced region with 3 open water treatment pools (see Supplementary Material Figure S1 for representative photos of our 3 main habitat types: village, orchard, and plateau).

Trapping and Tagging

We focused on the 8 groups of *A. squamiceps* (average group size = 7.1, range = 4–11) whose territories and nest sites were known to occur solely within the area covered by the ATLAS based on previous studies (Oswald et al. 2024, 2025). We aimed to have at least one individual per group with an active tracking tag throughout the breeding season. Previous research on this same species showed that with few exceptions, individuals in a group generally stay within ~20 m of one another throughout the day (Dragić et al. 2021, 2022; Alamán et al. 2024), so at our spatial scale, tracking a single individual from a group should represent the movement of the group itself. The main exception to this behavior included the dominant female, who often stayed closer to the nest (K. N. Oswald personal observations), so we avoided putting a tracking tag on dominant females. Adult individuals were captured using baited spring-traps (a spring-loaded nylon net that closes over individuals to trap them quickly and safely by bait on a hairpin trigger) or mist-nets. Seven of the captured individuals were banded as part of previous studies (Oswald et al. 2024, 2025), while 3 captured individuals were unbanded and so first given a standard aluminum band and an identifying combination of color bands. For all captured individuals, we attached ATLAS tags which weighed <3.4% of individual's body mass using a leg-loop harness made of 0.8-mm silicone thread (Supplementary Material Figure 2; for more information on the system and tagging, see Oswald et al. (2025) and Supplementary Material: Further information on ATLAS and individual tagging). In total, we used data from 13 tagged individuals for this study: 4 females (average body mass = 78.4 g), 6 males (average body mass = 74.6 g), and 3 sub-adults (offspring from the previous breeding season; average body mass = 71.1 g).

Nesting Ecology, Searching, and Monitoring

At this study site, *A. squamiceps* build open-cup nests almost solely in either trees or shrubs, with nest height and location (e.g., tree or shrub) similar among habitat types (K. N. Oswald personal observations). Average brood size is 3–4 eggs, with an average incubation period of 12–15 days, and a similar length of nestling period (Zahavi and Zahavi 1997). Predators in the different habitats do differ, with main nest predators in villages being *Felis catus* (domestic cats) and the occasional *Canus aureus* (golden jackals), in orchards being almost solely *Vulpes vulpes* (red foxes), and on the plateau being jackals and foxes (Oswald et al. 2024).

We began searching for nests in late February 2023. First, we remotely monitored group behavior using the real-time localizations of tagged individuals available through the ATLAS to see if the group was showing site fidelity that could indicate a possible nest site. We then located the nest by spending 2–3 hr observing the group from ~30 m distance using binoculars and looking for signs of nesting (e.g., carrying nesting material, a particular vocalization). Once a nest was located, we set up a motion-activated security camera on the nest to monitor activity throughout the nesting period (from nest initiation through nest completion). Nests were monitored remotely using 4G uplink via a SIM card (Reolink Go Plus 4G, Reolink USA) that upon being motion activated uploaded 30-s videos to the Reolink smartphone app. We masked the infra-red light of each camera using 4 overlaid pieces of masking tape to avoid drawing attention to nests at night. See Oswald et al. (2024) for further details on nest searching and camera setup.

Nests were visited on a single occasion after the initial camera setup, when nestlings were 10-days old (hatch day = day 1) to give each nestling a metal band and identifying combination of colored bands, and to record their pre-fledge body mass. We chose day 10 to remain consistent with pre-fledging mass taken in other studies on the same species (Ostreiher 1999, Dragić et al. 2022, Oswald et al. 2024). Mass measurements were taken at 09h00 IST (mean = 08h55 IST, range: 08h25–09h35 IST). We then returned to retrieve the cameras 3–5 days after the nest was no longer active (either depredated or fledged), confirmed through remote monitoring.

Data Analysis

All analyses were performed in the R Statistical Environment v 4.3.1 (R Core Team 2022) using RStudio 2023.06.2 (RStudioTeam 2020). Packages used included *toolsForAtlas* (Margalit 2021), *lme4* (Bates et al. 2015), *sp* (Bivand et al. 2013), *lmerTest* (Kuznetsova et al. 2017), *leaflet* (Cheng et al. 2023), *adehabitatHR* (Calenge and Fortmann-Roe 2023), with visuals made using *ggplot2* (Wickham 2016).

The ATLAS provides raw data that allow for a simple filter-smoothing process (Beardsworth et al. 2022). As we were interested in diurnal habitat use (i.e., when individuals were foraging), we filtered out nocturnal localizations for each day based on sunrise and sunset data for *Sde Boker*. Our motion-activated cameras showed no foraging activities during the night. Each localization was a result of an individual tag being recorded by a minimum of four (and often up to all eight) receiving stations. Following Gupte et al. (2022) we then performed initial exploratory analysis of data tracks, and minimized location error by filtering based on two location attributes added with *toolsForAtlas*: (1) we filtered the overall location quality for each localization (*traceNorm*; calculated from the variance in Easting and Northing) by creating histograms and removing the outliers (based on the "tail") using a standard deviation of 10, and (2) we filtered location error estimates (*stdVarY*; variance-covariance matrix of each position) using a standard deviation of 20. We further filtered unrealistic movement by assuming a maximum speed of 5 m s^{-1} based on the behavioral traits of *A. squamiceps* (e.g., mainly hopping or walking on the ground). We are further convinced 5 m s^{-1} is a realistic maximum speed as a study on *Sylvia atricapilla* (Eurasian Blackcaps) found tagged individuals had a maximum speed of 3 m s^{-1} during non-migratory periods (Tomotani et al. 2019).

To determine movement patterns for each day each group had nestlings, we calculated a 100% Local Convex Hull (T-LoCoH; km^2) per day per group. We chose to use T-LoCoH (hereafter referred to as "occurrence-area"), as this method of creating occurrence-area polygons incorporates time, focuses on the area where the tracked individuals specifically occurred during the breeding period, and more accurately represents habitat-use in a heterogeneous landscape (Getz et al. 2007, Scull et al. 2012, Lyons et al. 2013, Alston et al. 2022). Occurrence-areas were calculated only for days that had a minimum 100 localizations, specifying $k = 12$ (number of nearest neighbors to include) and setting duplicates to "random" (where duplicated points are moved slightly). We scaled group size to have a standardized mean of 0 and standard deviation of 1.

We first examined daily adult behavior patterns throughout the nestling period for each nest. We fitted a generalized linear mixed-effects model (GLMER with an inverse gamma distribution) to daily occurrence-area (km^2) as predicted by the age of the nestlings, the brood size, and the scaled group size with nest ID as a random effect. We then examined daily patterns in habitat use by fitting GLMERs separately to the percentage of each habitat used (village, orchard, or plateau, with our response being the percentage of habitat used per day per nest) as predicted by the age of the nestlings, the brood size, and the scaled group size with nest ID as a random effect.

We further examined occurrence-area size, habitat use, and nestling day-10 mass averaged for each nest for the duration of its nestling period. Due to a small sample size of nests with nestlings ($n = 16$) and even smaller sample size of nests with nestling mass on day 10 ($n = 9$) alongside previous studies suggesting group size and brood size may not be significant factors (Wright 1998b, Oswald et al. 2024), we decided to use a non-frequentist method to determine significant factors (van de Schoot et al. 2021). For all models we applied an information theoretic approach (Burnham et al. 2011) to compare all competing models using the *dredge* function in the *MuMIn* package (Barton 2020). We considered models with AIC_c lower than the null model as those that included important predictive factors. We thus discuss results from all predictive factors in the top models, presented as means ± SE.

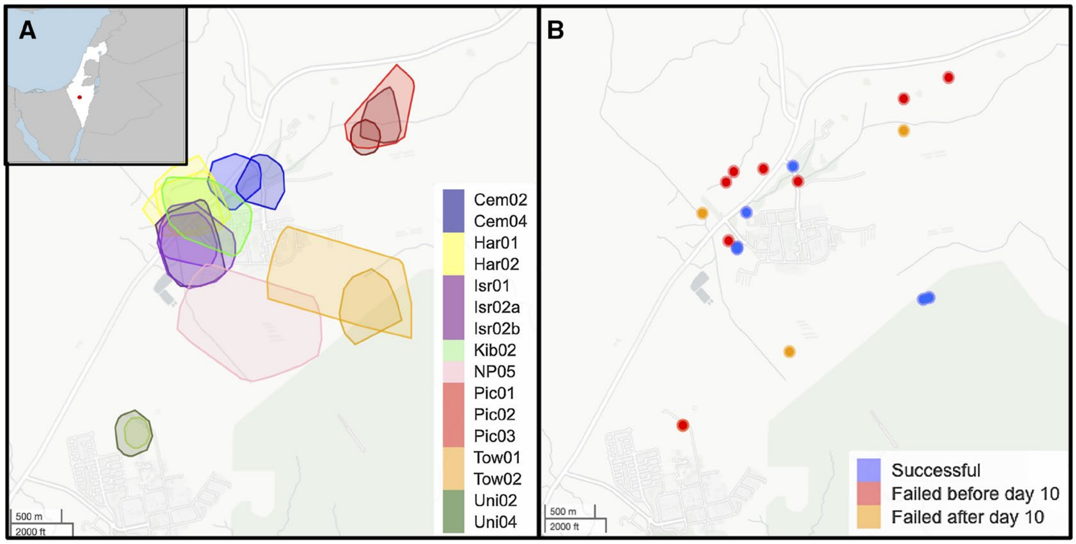

FIGURE 2. (A) Breeding occurrence-areas for 8 groups of *A. squamiceps* during the 2023 breeding season (groups identified by color, with occurrence-area of each nest given a different hue), and (B) location of each nest, with color indicating success (in blue) or failure (failed nests were colored separately to indicate if they failed after, in orange, or before, in red, the day of measuring nestling mass). Inset: Red dot indicates the study site location within Israel.

For all nests with nestlings ($n=16$), we fitted a global linear model to the average occurrence-area size (km^2) per nest as predicted by the distance the nest was from the nearest village (m) and scaled group size. For nests with nestlings where we collected day-10 mass (g; $n=9$) we fitted a global linear model to the average nestling mass per nest as predicted by the distance the nest was from the nearest village (m), occurrence-area size (km^2), brood size, and scaled group size. In this dataset, we did not include group as a random effect as only one group had more than a single nest with nestlings reaching day 10, with said group having two nests reach day 10. We then used the same model selection approach as above (top being the model(s) with AIC$_c$ lower than the null model) to determine important predictive factors.

Last, we added data on nest success from Oswald et al. (2024) to the current sample to re-assess whether nest success was related to the distance a nest was from the nearest village ($n=58$ nests total: $n=42$ nests from Oswald et al. (2024), and $n=16$ nests from the current study). For this analysis, we fitted a GLMER of nest success predicted by scaled distance, with group ID as a random effect.

RESULTS

We collected 191,087 localizations from 13 tagged individuals representing 8 groups and 16 nests with nestlings during the 2023 breeding season (Figure 2; see Supplementary Material Figure 3 for visualization of hourly localizations per nest). On day 10, we collected nestling mass from 9 of these 16 nests. The other 7 nests were depredated before day 10 (day 3 = 2, Day 5 = 1, day 6 = 2, and day 7 = 2). The average number of localizations collected per individual per day was 1,504.6 ± 1,067.4. The minimum number of daily localizations collected was 67 and the maximum was 4,990, although we only used days with ≥100 localizations in our analyses.

We found no difference in the daily occurrence-area (km^2) of groups in relation to age of nestlings, brood size, or adult group size, with our top model being the null model (see Supplementary Material Table 1 for ranking of competing models within 5 AIC$_c$ of the top model). As nestlings grew older, provisioning adults and sub-adults tended to decrease their use of the village habitat (–0.58 ± 0.30% per day) and increase the percent of the orchard habitat (0.65 ± 0.3% per day), with no difference in the percentage of the plateau habitat used in relation to nestling age (0.13 ± 0.41% per day; Figure 3).

The top model explaining occurrence-area size (km^2) per nest included distance, with groups having smaller average daily occurrence-areas when their nest was farther from a village (–0.00 ± 0.04 km^2 per m from a village; Figure 4A; see Supplementary Material Table 2 for ranking of competing models within 5 AIC$_c$ of the top model).

We obtained day-10 mass measures for 28 nestlings from nine of the 16 nests. The top model explaining day-10 nestling mass included how far nests were from the nearest village, with nestlings being heavier the farther they were from the nearest village (3.2 ± 1.1 g per kilometer from a village); Figure 4B; see Supplementary Material Table 3 for ranking of competing models within 5 AIC$_c$ of the top model).

There was no difference in nestling mass related to the percentage birds used either village or plateau habitat (village: –1.22 ± 0.68 g per % increase in village habitat use; plateau: –4.09 ± 0.92 g per % increase in plateau habitat use), although there was a decrease in mass for individuals using a higher percentage of village habitat (Figure 5). Nevertheless, groups using proportionally more orchard habitat tended to have nests with heavier nestlings (1.18 ± 0.52 g per % increase in orchard habitat use; Figure 5). Three groups with nests surviving to day 10 did not use any village habitat and two groups did not use any orchard habitat, but all groups made at least some use of the plateau habitat (Supplementary Material Table 4).

While there was a tendency for nests farther from villages to have higher success, model results showed that this could be due to individual groups (as the next highest ranked model was our null model). The distance of a nest from the nearest village was not related to nest success (Figure 6).

DISCUSSION

In this study, we monitored 8 groups of *A. squamiceps* to see whether foraging in different habitat types (village, orchard, or plateau) had a significant effect on nestling growth and development when provisioning nestlings. While many studies have examined how nestling growth is affected by the location of the nest among different habitats, to our knowledge, this study is the first to use fine-scale tracking data to directly link where individuals forage while provisioning nestlings to nestling condition. In general, it was more beneficial for groups to have nests farther away from villages, as they covered less area and yet had heavier nestlings. However, the heaviest nestlings were from nests where provisioning adults foraged mostly in orchard habitat. Therefore, some level of human resources (i.e., orchards) seems to be beneficial, but only if combined with otherwise low levels of human presence. While our low sample size of nests makes drawing conclusions on post-fledge success difficult to examine, our large sample size of localizations emphasizes the significance of our patterns in habitat use and occurrence-area effects on nestling growth.

We found no change in daily occurrence-area size associated with nestling age, group size, or brood size. The lack of difference associated with group or brood size was somewhat expected, as previous studies on *A. squamiceps* found group and brood size can have conflicting or even non-existent effects on various breeding dynamics (e.g., provisioning rate showing no change in relation to group size; Carlisle and Zahavi 1986, Zahavi 1990, Wright 1997, Wright 1998b, Wright 1998a, Oswald et al. 2024). Even outside the breeding season, occurrence-area is unrelated to group size (Oswald et al. 2025). While occurrence-area size does not change as nestlings age, there could be a change in the foraging behavior of *A. squamiceps* within these areas. Many studies have shown that individuals will bring larger prey items as nestlings age (Knapton 1984, García-Navas et al. 2012, Wiebe and Slagsvold 2014, Lee et al. 2016), and so instead of a change in daily occurrence-area size, provisioning individuals may search for larger prey within a similar-sized area.

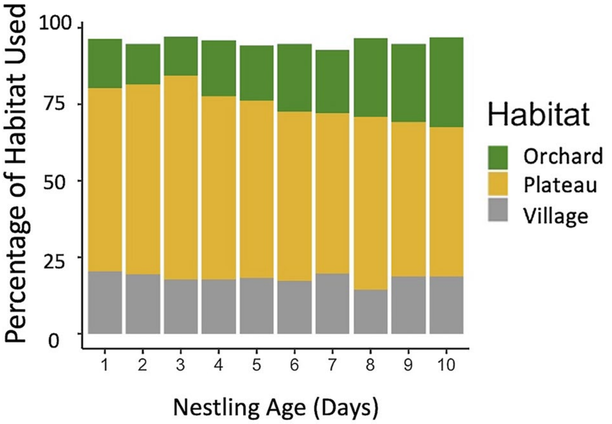

FIGURE 3. Percentage of habitat type (village, orchard, plateau) used by provisioning *A. squamiceps* in relation to the age of their nestlings.

We did, however, find shifts in the habitat type used by individuals in relation to the age of the nestlings. As nestlings grew older, *A. squamiceps* decreased the percentage of village habitat they used and increased their use of orchard habitat, while maintaining the same proportional use of plateau habitat (Figure 3). As groups that used proportionally more of the orchard habitat had heavier nestlings (Figure 5; also found for nests in orchards in Oswald et al. 2024), this suggests that orchard habitat has prey of either higher quality, size, or availability. Previous research found there were no obvious differences in prey size provisioned to nestlings from nests among the different habitats (K. N. Oswald personal observations). However, a more recent publication found *A. squamiceps* seem to preferentially forage in the more natural plateau habitat, spending more time in village habitat during the drier summer months, theoretically when resources in the plateau habitat are scarce, with no seasonal change in their use of orchard habitat (Oswald et al. 2025). Orchard habitat in this area consists mainly of organic olive orchards (i.e., orchards without use of pesticides or herbicides), and although they are watered regularly, watering is automated and there is little human presence or daily interference (K. N. Oswald personal observations). Notably, the increased use of orchard habitat is not reflected in increased overall breeding success, as a previous study found nests in orchard habitat had similar nest success (both number of successful nests and number of fledglings) and risk of depredation to nests in other habitat types (Oswald et al. 2024). However, heavier nestlings do lead to heavier fledglings, which can lead to higher post-fledge success (Thompson and Flux 1991, Berkeley et al. 2007, Greno et al. 2008, Cox et al. 2014, Evans et al. 2020). In all nests in our study, groups built their nests in the same habitat where they spent most of the time foraging. This suggests that fledglings from groups nesting and foraging in orchard habitat may have a higher chance of long-term survival.

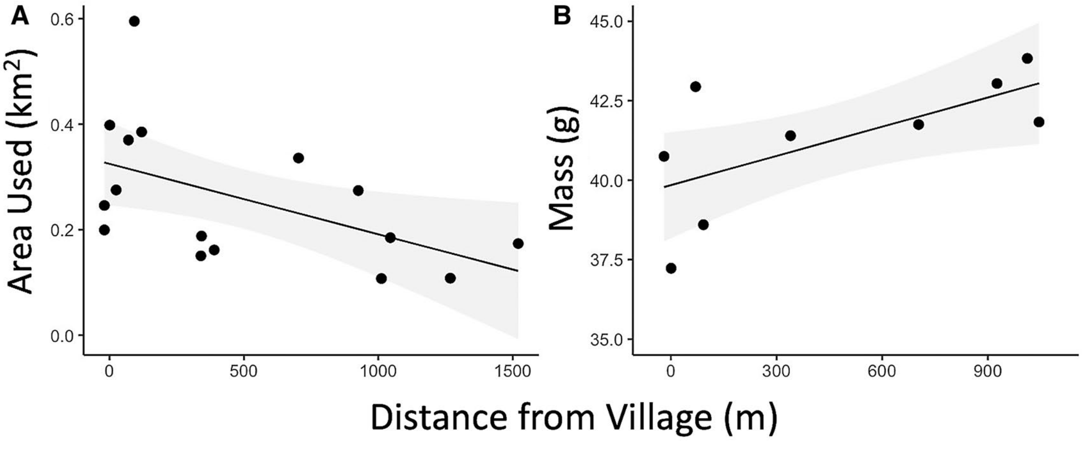

FIGURE 4. (A) Daily occurrence-area (km^2) of *A. squamiceps* with nestlings ($n = 16$), and (B) the average mass (g) of nestlings for nests with 10-day olds nestlings ($n = 9$), in relation to the distance the nest was from the nearest village (m); model fit is glm.

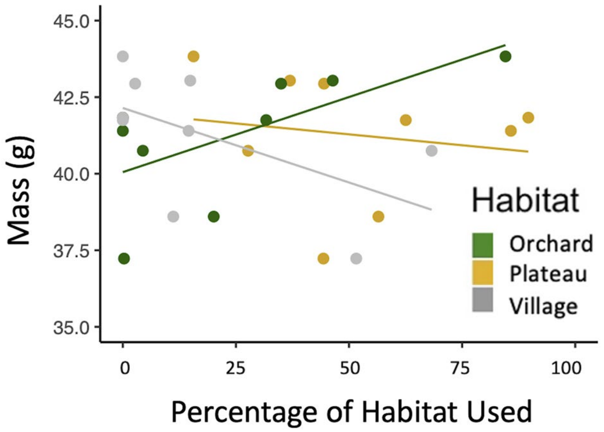

FIGURE 5. Average mass (g) per nest of *A. squamiceps* nestlings on day 10 in relation to the percentage of either village, plateau, or orchard habitat used by provisioning *A. squamiceps*.

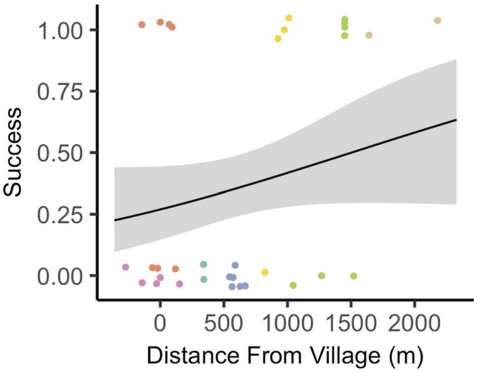

FIGURE 6. Nest success (1 = success, 0 = failure) in relation to the distance the nest was from the nearest village (m) for 58 nests recorded in 2022 ($n = 42$) and 2023 ($n = 16$) from 17 groups. Datapoints shown represent the 8 groups monitored in the current study, with each group represented by a different color.

Groups with nests farther from villages had smaller average occurrence-areas while provisioning nestlings (Figure 4), suggesting that our initial impressions and predictions on resource availability were incorrect. Tremblay et al. (2005) found that *Parus caeruleus* (Eurasian Blue Tits) had to travel twice as far to find food to maintain their nestlings' mass when nesting in poor-quality compared to high-quality habitat. In our case, not only did groups with nests farther from villages have smaller occurrence-areas, but they also managed to provide food that led to higher nestling mass (Figure 4). It could be that *A. squamiceps* with nests in villages have to travel farther to find better foraging grounds if the food type they are looking for is not available in the village; this has been found in other species such as urban nesting *Falco naumanni* (Lesser Kestrels) that nest in the city but forage outside (Liven-Schulman et al. 2004). This suggests that orchard habitat and the semi-natural plateau habitat may in fact be of higher quality than village habitat—at least regarding the high-protein prey items beneficial for raising *A. squamiceps* nestlings.

Here we again found that nesting in villages has either neutral or negative results on breeding for *A. squamiceps*. While villages are clearly presenting *A. squamiceps* with a habitat type they find appealing enough to claim as territories and nest sites, the villages may in fact be ecological traps (poor-quality habitat that nonetheless attract individuals; Robertson and Hutto 2006) or sinks (poor-quality habitat that attracts poor-quality individuals of a species; Kristan 2003). Previous research showed nesting in village habitat led to lower breeding success, smaller brood sizes, higher depredation, and smaller nestlings for *A. squamiceps* (Oswald et al. 2024). Since we continued to find no difference in nest success based on nest location in relation to habitat, the best reproductive strategy for *A. squamiceps* in the current study area seems to be ensuring they produce the heaviest nestlings with the greatest chance of long-term survival. While we continued to show no difference in nest success based on where *A. squamiceps* were choosing to build their nests and forage for prey, anything that leads to heavier nestlings is beneficial for those nestlings which do survive to fledge (Berkeley et al. 2007, Greno et al. 2008). In our study, heavier nestlings resulted when both nests and foraging adults were farther from villages.

CONCLUSIONS

Villages in desert environments have a higher abundance and predictability of food resources and water (Efrat 2004), which can increase breeding success. However, our study found that while a low level of human presence and resources (i.e., orchards) may be beneficial to raising heavier young, a higher level of human presence leads to predominately negative effects on nesting. Nests in villages had lower breeding success, smaller brood sizes, higher depredation, and smaller nestlings. Therefore, despite the common view that villages act as oases, desert species may have higher success out in the desert environment, for which they are well-adapted. Human villages may thus represent an ecological trap or sink for some desert specialists, potentially due to lower quality resources, or hidden costs from altered species' interactions and competitive dynamics in the village environment. With continued agricultural and urban expansion, successful groups of *A. squamiceps* will be those inhabiting the edges of human areas, where they can make use of resources (e.g., orchards) in the harsher late summer months (Oswald et al. 2025) while nesting in areas of their territories outside villages on the semi-natural plateau. Novel wildlife tracking technologies such as the ATLAS system used in this study, can continue to help uncover the effects of human development in dryland areas, which are under-represented in both basic and applied research.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Ornithological Applications* online.

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Ethics statement

Ethics for this research were approved by the Israeli National Parks Authority (permit number: 2022/43033). Ringing of birds was done with authorization from the Israel Bird Ringing Center (https://www.birds.org.il/en/birding-center/The-Israeli-Bird-Ringing-Center).

Conflict of interest statement

The authors have no conflicts of interest to declare.

Author contributions

KNO, OB, and UR conceived the idea, design, experiment. KNO and TR performed the experiments. KNO, OK, OB, and UR wrote the paper. KNO, ST, and RN developed or designed methods. KNO analyzed the data. ST, RN, OB, and UR contributed substantial materials, resources, or funding.

Data availability

Raw data are available in the supplementary materials.

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