**Title:** Living fast, dying young: Anthropogenic habitat modification influences the fitness and life history traits of a cooperative breeder

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**Abstract**

Anthropogenic habitat modification is especially detrimental to social species. Apart from direct fitness effects, it can destroy group structure and affect social interactions crucial for reproduction and survival. Here, we assessed the impact of habitat modification on the fitness and life history traits of a cooperative breeder, the Arabian babbler (*Argya squamiceps*). We collected spatial, reproductive, and social data on 572 individuals belonging to 21 social groups over six years and combined it with remote sensing to characterize group territories. Groups in modified habitats bred more and had greater productivity during dry years. Males living in modified habitats dispersed and acquired dominance at a younger age, showing a faster pace of life. However, group performance and total fitness were higher in natural habitats during average years. Habitat modification indirectly affected fitness by altering social structure, whereby younger males who lacked experience became dominant, leading to reduced nesting success.

**Main Text**

**Introduction**

Humanity's impact on Earth's ecosystems has been so extensive that it is now defined as a geological era - the Anthropocene (Steffen *et al.* 2011). Approximately 75% of the Earth is now dedicated to crop or livestock production (Brondízio *et al.* 2019), and this significant alteration of natural habitats has led to biodiversity decline and wildlife extinction (Dirzo *et al.* 2014; Spalding & Hull 2021). While habitat modification is well studied in temperate and tropical ecosystems, its consequences on arid ecosystems remain less studied (Emmerson *et al.* 2016; Haddad *et al.* 2015; Matuoka *et al.* 2020; Raven & Wagner 2021). The impact of agriculture on arid environments may be exceptionally profound due to significant increases in resource availability (Fardila *et al.* 2017). Such an increase in resource abundance may attract native species at the cost of reduced fitness (Catto *et al.* 2021; Cereghetti *et al.* 2019; Evans & Gawlik 2020) due to threats such as roadkill (Mumme *et al.* 2000; Sillero *et al.* 2019), predation (Chalfoun *et al.* 2002; Lewin *et al.* 2021), and chemical exposure (Boatman *et al.* 2004; Fry 1995).

Environmental changes can also indirectly impact social species’ fitness by altering group composition or size, which are crucial for reproductive and survival-related social interactions (Blumstein *et al.* 2023). Obligately social species, such as cooperative breeders, are particularly vulnerable to changes that affect group size (Blumstein *et al.* 2023). The ecological constraint hypothesis (Emlen 1982; Hatchwell & Komdeur 2000; Koenig & Walters 2015) suggests that helpers in cooperatively breeding species delay their dispersal since their habitat lacks suitable territories, dispersal carries low survival rates, followed by low mating probabilities, and reproductive success (Emlen 1982; Hatchwell & Komdeur 2000; Jetz & Rubenstein 2011; Koenig *et al.* 1992; Koenig & Dickinson 2004). Habitat modification has been shown to have detrimental demographic effects on cooperative breeders, including reduced group size, fewer dispersers, lower breeding success, and higher mortality (Beck & Heinsohn 2006; Brooker & Brooker 2002; Courchamp *et al.* 2000; Leon *et al.* 2022; Mumme *et al.* 2000). Additionally, declines in group density and/or population size can lead to a demographic Allee effect (Angulo *et al.* 2013, 2018; Keynan & Ridley 2016), where small populations or those with low density are more likely to become extinct (Angulo *et al.* 2018).

In this study, we explore the relationship between habitat modification and life history traits, group size, and overall fitness in the Arabian Babbler (*Argya squamiceps*), a territorial and desert-dwelling, obligately cooperative breeding bird. Over the past ~ 50 years, intensive agriculture has significantly increased resource availability in the hyper-arid habitat where Arabian babblers live (Zahavi & Zahavi 1997). This transformation has modified areas and increased access to resources compared to natural habitats that predominantly consist of native vegetation. We expected that modified habitats rich in resources would positively affect breeding season length and productivity but compromise individual survival by the associated risks that these habitats bring (e.g., non-native predator pressure; Lewin *et al.* 2021). In turn, survival rates might affect group social structure indirectly by altering group sizes, dispersal rates, or dominance acquisition, which can impact group fitness (e.g., by changing the number of helpers, which are crucial for fledgling survival in Arabian babblers; Ridley 2007). To test our hypotheses, we analyzed six years of data (2016-2021) collected from 570 individuals belonging to 21 distinct groups, comprising 211 breeding events within our study population of Arabian babblers. To evaluate the effect of habitat on fitness we assessed breeding events, annual reproductive output and success, juvenile and adult survival rates, and their effect on group size. Additionally, we compared two life history traits: age at dominance acquisition and age at dispersal. Remote Sensing (RS) software and images were employed to identify and characterize habitats, allowing us to evaluate anthropogenic impacts on fitness and life history traits (Fig.1).

**Materials and Methods**

**Study area, study species, and field data collection**

The Sheizaf Nature Reserve (30° 43 'N, 35° 15 'E) is found in the hyper-arid Arava Valley desert, Israel (Fig. 2A). The reserve size is 52.5 km2, divided by a road into the north (6.5 km2) and the south (46 km2) protected areas. The reserve consists of numerous dry riverbeds (i.e., wadis) that support natural vegetation such as Umbrella thorn acacias (*Vachellia tortilis*) and Christ’s thorn jujube (*Ziziphus spina-christi*) as main tree species, and shrubs such as Arabian boxthorn (*Lycium shawii*) and saxauls (*Haloxylon sp.*). After floods, grasses and other annual flowering plants bloom (e.g., *Matthiola longipetala, Colchicum palestinum,* and *Rumex cyprius*) in the wadis (Ridley 2007). Near the four human settlements at the reserve’s borders, the landscape has been intensively transformed into farmland, most of the natural vegetation has been removed, and the wadis have been canalized. The scarce vegetation near these modified areas include shrubs such as tamarisks (*Tamarix sp.*), and Arabian boxthorn, or trees such as naturalized date palms (*Phoenix dactylifera*) and isolated thorn acacias. Two kinds of cultivation techniques are used in the modified areas: open-air crops (mainly date and mango plantations) and greenhouses (Lewin *et al.* 2021). See Supporting Information Fig. S1 for more details and habitat characteristics.

Arabian babblers are found along the Arabian desert and the Sinai Peninsula (Zahavi & Zahavi 1997). In our study area, Arabian babbler groups range from 2 - 20 individuals of both sexes. Individuals delay dispersal for an average of 1 - 3 years, assisting their parents in caring for siblings until they acquire dominance, disperse, or die. Reproductive skew is high; each group usually contains a single breeding pair (> 96% of groups, hereafter the dominant individuals) and can attempt to breed up to four times a year, with an average clutch size of four eggs (Ostreiher 1999). Dominance hierarchies are linear, based on age, and are separate for males and females. Dispersal is female-biased and can be solitary or in a group (Ridley 2007, 2012), with individuals either joining an existing group, establishing a new group, or becoming a floater (without a fixed territory; Ridley *et al.* 2008). We classify individuals into five age classes: nestlings (from hatching to fledging), fledglings (< 90 days old), juveniles (90 to 240 days old), subadults (< 1 year old), and adults (> 1 year old). Mortality rates are highest during the first year of life (Ridley 2007).

Our Arabian babbler population has been continuously studied since 1971 when Amotz & Avishag Zahavi initiated the research (Zahavi & Zahavi 1997). All individuals in the study groups are habituated to the presence of observers and are ringed with unique combinations of color rings, allowing individual recognition. Once mature (> one year old), birds are sexed based on iris color (yellow in males, dark brown in females). Daily monitoring includes group location and size, which are recorded using the Anecdata.org application (Bailey *et al.* 2021). All changes to individual status (e.g., hierarchy, dispersal, disappearance, or death) are recorded. Breeding season monitoring includes nest searches and tracking of active nest data, such as the number of eggs, nestlings, and nest condition. In cases where direct nest observations are not possible, egg-laying dates are inferred from dominant pair incubation activity, and egg-hatching dates are estimated by the start of food provisioning by the group to nestlings. Nestlings are ringed nine to ten days after hatching (Lundy *et al.* 1998; Ostreiher 1999). Additional details about the research population, habituation, and ringing protocols can be found in Dragić *et al.* 2022. Permits for this study were granted by the Israel National Parks Authority (permit numbers: 2016/41453, 2018/41848, 2020/42538, 2022/43151).

**Habitat characterization**

The study includes 4665 locations collected during the 2020 (1499 locations, Fig. 2B) and 2021 (3166 locations, Fig. 2C) breeding seasons (March-August) for 21 different groups. We selected the breeding season for habitat characterization because the group territories are most stable during this period (Zahavi & Zahavi 1997). Only groups with at least 30 locations collected during the study period were included. Identifying habitat preferences involved two steps: (i) Species distribution modelling and (ii) Environmental characteristics of the territories and classification.

*Species Distribution Models*

A series of Species Distribution Models (SDM) was constructed to characterize the spatial distribution of the suitable areas used by the study groups, considering a series of environmental variables derived from freely available remote sensing images from the Copernicus Earth Observation program of the EU (https://land.copernicus.eu/, accessed on 15/04/2022).

First, Sentinel 1 (S1) imagery

(<https://developers.google.com/earth-engine/datasets/catalog/COPERNICUS_S1_GRD>) was used to retrieve information regarding soil humidity in the study area (Geudtner *et al.* 2014), via the Synthetic Aperture Radar backscatter VH as a proxy for soil moisture (Dabrowska-Zielinska *et al.* 2015) (Fig. 2D). Secondly, Sentinel 2 (S2) imagery

(<https://developers.google.com/earth-engine/datasets/catalog/COPERNICUS_S2_SR_HARMONIZED>) was used to assess vegetation density using Normalized Vegetation Index (NDVI) calculated with bands 4 (red) and 8 (near infrared; Amiri & Pourghasemi 2022). We used Google Earth Engine (Gorelick *et al.* 2017) to calculate per pixel monthly average values of both variables (Soil moisture and NDVI) for months corresponding to the Arabian babbler breeding season between 2016 and 2021.

We used the maximum monthly values of NDVI to identify the cultivated areas (i.e., agriculture) and the anthropogenic vegetated areas (i.e., gardens) in the study region. We considered a threshold value higher than 0.7 for densely vegetated areas (Mutiibwa & Irmak 2013) corresponding to cultivated and anthropogenic patches (hereafter modified habitats). Visual interpretation of the NDVI spatial structure allowed the extraction of regular spatial patterns associated with crops to determine modified areas, which was corroborated by observations on the ground. Then, we calculated the Euclidean distance to these modified areas using QGIS v3.22 Białowieża (QGIS Development Team 2022; Fig. 2E).

Finally, the environmental variables (soil moisture, NDVI, and distance to modified habitats) were extracted for each group location and used to build the SDM for each group during the study period (hereafter, territories). A single spatial projection was carried out for each group, month, and year. These projections describe the spatial distribution of the preferred areas of study groups by providing per-pixel suitability values. These values range from 0 (no suitability) to 1 (complete suitability). The spatial data was projected to WGS 84/UTM zone 36N Coordinate Reference System, with a final spatial resolution of 10 m x 10 m.

*Environmental characteristics of the territories and classification*

The environmental characteristics of the groups’ territories were calculated using weighted average values of soil moisture, distance to modified habitats, and NDVI based on the previously calculated per-pixel suitability. Finally, based on this environmental characterization, all groups’ territories were classified into (i) modified habitats and (ii) natural habitats by performing a k-means analysis (Lloyd 1982).

**Climatic variables**

We included two climatic variables in our analysis: rainfall and temperature. Both influenced breeding success and survival in other cooperative breeder species in extremely arid habitats (Bourne *et al.* 2020). We calculated the total yearly rainfall in millimeters as the accumulated rainfall from October of the previous year to April, corresponding with the region's wet period. We also calculated monthly average temperatures in Celsius for the study period. Climatic data were extracted from the Israeli meteorological services for the Hazeva meteorological station (<https://ims.gov.il/en/data_gov>).

**Fitness**

*Breeding variables*

To assess the effect of habitat on breeding, we first analyzed the number of breeding events by group per year (Box 1). A total of 211 breeding events were included in this dataset. For nesting success, each breeding event was categorized as 1 (succeed) or 0 (failure). To test whether the number of breeding events was related to nesting failure, we evaluated whether 125 renesting events (Box 1) occurred after a successful or an unsuccessful breeding event. We used the annual reproductive output (ARO; Box 1) to measure group productivity per year. We used two different datasets for ARO analyses. In the first one, we calculated for all study groups the total amount of fledglings raised per group per year. In total, 97 group/year entries were included. The second dataset was calculated for all the couples with at least one individual with a known age as the total amount of fledglings raised per dominant couple per year. In total, 107 couple/year entries were included. We used the annual reproductive success (ARS; Box 1) as a measurement of the actual breeding success of the groups per year. For each year, we included only groups where all fledglings of all breeding events were ringed to avoid overestimating mortality due to unnoticed dispersal. We also prepared two separate datasets: one with the ARS of all the groups (76 group/year entries) and one for all the couples with at least one individual of a known age (82 couple/year entries). The age of individuals was calculated in days to the beginning of the year (January 1st).

*Fledgling survival to adulthood*

Only ringed individuals with a known age that hatched during the study period were included in the survival analysis. We calculated the age of individuals when they died, dispersed, or when the study ended (31/08/2022). Individuals were considered dead if they were not observed in the study area. Since long distance dispersal cannot be distinguished from death, the surroundings of the study area were also monitored to minimize mortality overestimation (Nelson-Flower *et al.* 2018). We calculated the average number of adults and subadults that were present in the group at the month of hatching, the juvenile-adult ratio at the time of hatching, brood size, number of breeding events in the breeding season, and average NDVI of the territory during the month of hatching. Sex was not included because it cannot be determined visually in individuals younger than one year. A total of 345 juveniles (modified habitats: 246; natural habitats: 99) were included in the analysis.

*Adult survival*

We used two datasets to test the influence of habitat on adult survival. The full dataset included 182 adults (modified habitats: 112, 65♂, 47♀; natural habitats: 70, 34♂, 36♀) who were present during the study period, regardless of when they were born. Only individuals who remained in their natal groups were included. The restricted dataset included 134 adults (modified habitats: 80, 45♂, 35♀; natural habitats: 54, 27♂, 18♀) who fledged and reached adulthood during the study. Individuals were only included if they remained in the same group from birth to dispersal or last sighting. The status of individuals that disappeared in the last two months of the study (n = 6) was labelled as unknown to avoid overestimation of mortality.

**Life history traits**

*Dominance acquisition*

We included 28 individuals (19♂, 7♀) who hatched in the study site and attained dominance (Box 1) during the study period. We created an additional full dataset (N = 44; 29♂, 15♀), including all dominant individuals present during the study period, regardless of when they attained dominance.

*Delayed dispersal*

We included 37 individuals (12♂, 25♀) who dispersed for the first time during the study period (Box 1). We excluded individuals who dispersed in coalitions or individuals who were actively chased away from a group. We repeated the analysis with a full dataset that included all individuals that dispersed (57 individuals: 16♂, 41♀).

**Statistical analysis**

All statistical analyses were performed in r v4.0.3 (R Core Team 2022). K-means analysis was performed with the package ‘stats’ v4.0.3 (R Core Team 2022). We used packages ‘lme4’ v1.1.27 (Bates *et al.* 2015) for Generalized Linear Mixed Models (GLMMs; Mcculloch & Neuhaus 2013) analysis and ‘survival’ v3.3 (Therneau 2022) for multivariate survival analysis (Cox proportional-hazards models, CPHMs; Cox *et al.* 2014). We used package ‘effects’ v4.2 (Fox & Hong 2009) to display the variables’ effect in our models. For drawing survival curves, we used package ‘survminer’ v0.4.9 (Kassambara 2017). Maps were drawn with QGIS v3.22. All other figures were drawn with ‘ggplot2’ v3.3.5 (Wickham 2016). To construct SDM, we used Maxent, as it is robust when no absence records are available for a species (Phillips *et al.* 2006). A five-fold cross-validation technique with 25% test samples was used (Hastie *et al.* 2001). Model performance evaluation criteria were based on area under the curve (AUC, Hastie *et al.* 2001) and model specificity and sensitivity (Pottier *et al.* 2013).

For breeding events analysis, we constructed a GLMM with a Poisson distribution of errors, with the interaction between habitat and rainfall (included in all models because we expected that the effect of rainfall would be lower in resources-rich modified habitats), and the average number of adults and subadults as explanatory variables. The yearly number of breeding events was the response variable. Group identity nested within year was set as a random effect. We used a GLMM with a binomial distribution of errors to assess the effect of habitat on nesting success. The model included the interaction between habitat and rainfall, the average number of adults and subadults, and the month's average temperature as explanatory variables, with nesting success as the response variable. Group nested within year was included as a random factor. We repeated the model, adding the ages of dominant individuals as an explanatory variable and couple nested within year as random effects. We tested whether the renesting attempt type (after a successful or failed breeding event) was independent of habitat using a Chi-Square test. A GLMM with a Poisson distribution of errors was used to test the effect of habitat on ARO. The model included the interaction between habitat and rainfall, and the average number of adults and subadults as explanatory variables. Group nested within year was included as a random effect. We constructed a second model that included the age of dominant individuals and couple nested within year as a random effect. In both models, the ARO was the response variable. For the ARS, we repeated the same model structures as for the ARO.

For juvenile and adult survival, we used CPHMs to explore the payoffs from different habitat choices on a local scale. Though observation-based survival analysis on wild populations might overestimate mortality rates due to permanent long-distance dispersals considered deaths, it was still an accurate tool to estimate the payoffs from different habitat choices (Nelson-Flower *et al.* 2018). For each individual, we included the number of days it was observed and whether it died during this period. If we stopped following an individual before the period of study ended (e.g., if the individual dispersed or had an unknown status), it was included as censored data so that the model considered these individuals for calculating the survival likelihood. For adult survival analysis, we also included habitat and sex as explanatory variables. For juvenile survival analysis, we included the following variables: habitat, the average number of adults and subadults, the juvenile-adults ratio, brood size, number of breeding events, and average NDVI. We used the *cox.zph* function in the package *survminer* to test if our models fit the proportional hazards assumption. The function correlates the scaled Schoenfeld residuals of each variable with the time. The non-significative results of this test refuted the assumption of a relationship between time and the variables (Supporting Information Table S1).

We used GLMM to assess whether habitat type affected group size. We included habitat type as the explanatory variable with group identity and month nested within year as random effects. For the analyses of the effect of habitat type on the age of dominance acquisition and first dispersal, we built separated GLMMs for males and females, with habitat type as the explanatory variable and the age at first attaining dominance or dispersal as the response variable. For dominance analysis, the number of same-sex adults in the group was also included as an explanatory variable in the restricted datasets as a proxy of the length of the dominance queue. Group identity was included as a random effect. The complexity of the GLMMs was reduced by removing non-significative variables, and model fit was assessed by AICc values (Supporting Information Tables S2, S3, S4; Anderson & Burnham 2002).

**Results**

**Habitat characterization**

*Species distribution models (SDM; Group spatial distribution) and habitat classification*

The SDMs exhibited strong predictive capabilities (with a mean AUC value of 0.946) while mean sensitivity and specificity reached 0.93 and 0.916, respectively (Supporting Information Table S5; Fig. S2a). Employing k-means clustering analysis, we categorized the 21 study groups into two clusters (compactness = 81 %, average silhouette width = 0.73; Supporting Information Fig. S2b), with 13 groups in the first (average ± SE, distance to modified habitats: 145.67 ± 36.18 m; soil moisture: -20.50 ± 0.31) and 9 groups in the second (distance to modified habitats: 886.67 ± 87.92 m; soil moisture: -20.03 ± 0.46). The average distance to modified habitats was the differential environmental factor in the characterised territories, so groups from the first cluster could be labelled as groups from modified habitats and groups from the second cluster as groups from natural habitats.

**Fitness**

*Breeding variables*

We found strong evidence that breeding events were fewer in groups from natural habitats compared to those from modified habitats (average ± SE, natural: 1.54 ± 0.18 events/year, modified: 2.54 ± 0.15 events/year; Table 1; Fig. 3a). There was no interaction between habitat and rainfall. However, we found that rainfall positively affected the number of breeding attempts (Table 1, Supporting Information Fig. S3a). There was no relationship between nesting success and habitat, rainfall (and its interaction), or temperature, but groups with a higher average number of adults and subadults had greater nesting success (Table 1; Supporting Information Fig. S3b). In the analysis of nesting success by couples, we found moderate evidence that the age of dominant males positively affected nesting success (Table 1; Fig 3b), but no relationship between habitat and type of renesting event (χ2= 0.067, p= 0.795, Supporting Information Fig S3c). We found very strong evidence that groups and couples from modified habitats produced more fledglings per year than groups from natural habitats (average ± SE, groups: natural: 2.92 ± 0.54 fledglings/year, modified: 4.68 ± 0.44; couples: natural: 2.84 ± 0.54, modified: 4.07 ± 0.40; Table 1; Fig. 3c; Supporting Information Fig. S3d). In both datasets, we also found very strong evidence that the number of adults and subadults positively affected fledgling productivity (Table 1, Fig. 3d, Supporting information, Fig S3e). We found moderate evidence for the positive effect of total rainfall and its interaction with habitat on productivity in the groups dataset (Table 1, Fig. 3c) and strong evidence of the positive effect of rainfall on productivity in the couples dataset (Table 1, Supporting Information Fig. S3d. We found strong evidence of a negative effect of habitat on the ARS in the groups' dataset but no evidence of the effect of habitat on the ARS in the couples dataset (average ± SE, groups: natural: 1.81 ± 0.45 fledglings/year, modified: 1.3 ± 0.22; couples: natural: 1.75 ± 0.44, modified: 1.16 ± 0.21; Table 1; Fig. 3f, Supporting Information Fig. S3f). In both datasets, we found moderate evidence that rainfall and its interaction with natural habitats, and the number of adults and subadults positively affected the number of fledglings that survived (Table 1; Supporting Information Figs. S3f, S3g).

*Fledgling survival to adulthood*

We found very strong evidence that fledglings in natural habitats were more likely to survive to their first year of life than those in modified habitats (Table 1; Fig. 3h). While 57 out of 99 fledglings (57.57%) survived to adulthood in natural habitats, only 80 out of 246 (32.52%) survived in modified habitats. We did not find an effect of any other variables included in the model on fledgling survival to adulthood.

*Adult survival*

Our findings strongly indicate that adult babblers in natural habitats lived longer than those in modified habitats in both the restricted (Table 1; Fig. 3i) and the full dataset (Table 1; Fig. 3i). We found no sex differences in adult survival. In the restricted dataset, adults in natural habitats had higher survival rates in the second (predicted, confidence interval: 0.880, 0.811 – 0.955), third (0.772, 0.658 – 0.906), and fourth year (0.603, 0.430 – 0.846) compared to modified habitats (second year: 0.605, 0.507 – 0.720; third year: 0.360, 0.256 – 0.506; fourth year: 0.135, 0.052 – 0.349). Similar results were found in the full dataset: second year (natural: 0.882, 0.826 – 0.941; modified: 0.717, 0.641 – 0.802), third year (natural: 0.794, 0.711 – 0.887; modified: 0.544, 0.456 – 0.649), and fourth year (natural: 0.749, 0.653 – 0.858; modified: 0.466, 0.374 – 0.580).

*Group size*

Groups from modified habitats were smaller than groups from natural habitats (average number of individuals ± SE, natural: 5.19 ± 0.12; modified: 3.85 ± 0.07; Table 1; Fig. 4a).

**Life history traits**

*Dominance acquisition*

In the restricted dataset, males in natural habitats attained dominance later in life than those in modified habitats (Table 1; Fig. 4B). Males from natural habitats reached dominance at an average age (± SE) of 1171.33 (± 175.10) days, while males from modified habitats achieved dominance at an average age (± SE) of 807.53 (± 65.46) days. The number of adult males in the group delayed the age of dominance acquisition in both habitats (Table 1). In the full dataset, similar results were found for the habitat differences in age of dominance acquisition (Table 1; Fig. 4b; average age ± SE: natural: 1113.30 ± 130.11, modified: 780.10 ± 50.98 days). In the restricted dataset, there was no evidence of the effect of habitat or the number of adult females in the group (Fig. 4b) on the female age when first attaining dominance. In the full dataset, there was moderate evidence that females from modified habitats attained dominance at a younger age than those from natural areas (Table 1; Fig. 4b; average age ± SE: natural: 976.00 ± 28.04 days, modified: 691.14 ± 53.13 days).

*Delayed dispersal*

The analysis of the restricted dataset provided weak evidence that males in natural habitats dispersed later than males from modified habitats (Table 1; Fig. 4c; average age ± SE: natural: 943.14 ± 122.35 days, modified: 521.20 ± 148.05 days). Similar results were found in the full dataset, where males in natural habitats dispersed later than males from modified habitats (Table 1; Fig. 4c; average age ± SE: natural: 994.55 ± 114.69 days, modified: 521.20 ± 148.05 days). In both datasets, there was no effect of habitat on the age of first dispersal in females (Fig. 4c).

**Discussion**

Anthropogenic habitat modification has a strong influence on Arabian babblers’ fitness, both directly, by the change of habitat conditions, and indirectly, due to social structure alterations (Blumstein *et al.* 2023). In dry years, we found direct effects such as higher reproductive success but lower fledgling and adult survival in modified habitats. However, we also found indirect effects on modified habitats via changes in group social structure, resulting in smaller groups that induced earlier male dominance acquisition and dispersal. Our study showed that these differences in social structure and life history traits were associated with lower nesting success and lower productivity of younger, inexperienced dominant males. Our findings provide empirical evidence of the fitness costs of habitat modification via changes in key social parameters in social, cooperatively breeding species. These social changes may be responsible for the negative effects of anthropization on fitness.

The agricultural settlements in the Arava Valley introduced abundant resources to the hyper-arid environment since the late 1960s. Arabian babbler groups responded to these changes by moving towards the modified areas and enhancing their breeding efforts. Environmental changes that increase resource availability extend breeding seasons and breeding attempts per season in various species (Beck & Heinsohn 2006; Catto *et al.* 2021; Rollinson & Jones 2002). In Arabian babblers, we found that groups in modified habitats attempted to breed more, yet nesting success rates were similar in both natural and modified habitats, and renesting events were independent of previous nest success. The agriculture acted as a buffer during dry years, leading to higher annual productivity in modified habitats. Nevertheless, natural habitats had higher annual productivity during years with average rainfall and temperatures. Annual recruitment rates were lower in the modified habitats due to lower fledgling survival in the first year of life when mortality rates peak (Ridley 2007). Fledgling survival to adulthood rates in natural habitats were comparable to those of other cooperatively breeding species (Brouwer *et al.* 2006; Covas *et al.* 2004; Sankamethawee *et al.* 2009), while those in modified habitats were lower. This difference might be based on a poorer adaptation to modified habitats, requiring more time to master foraging skills (Heinsohn 1991; Whiteside *et al.* 2015); young individuals are also more explorative and risk-prone (Keynan *et al.* 2015), leading to increased predation, poisoning, and risks in an unfamiliar hostile environment. Fledgling survival may also be lower due to the smaller groups and earlier dispersal in modified habitats (findings from this study), resulting in fewer helpers, a known cause of reduced fledgling survival in cooperative breeders (Langen 2000; Ridley 2007; Ridley & Raihani 2007).

Smaller groups produce fewer dispersing cohorts and may lead to lower dispersal success and/or lower survival rates, driving populations of cooperative breeders to extinction (Courchamp *et al.* 2000). Additionally, human interferences may reduce the availability of suitable colonization patches and their size, limiting the maximum group size per patch, potentially resulting in a demographic Allee effect (Courchamp *et al.* 2000; Keynan & Ridley 2016). Both empirical and theoretical studies support this hypothesis (Creel & Creel 1998; Woodroffe & Ginsberg 1998), and there is evidence of demographic declines in this population of Arabian babblers (Keynan & Ridley 2016). Our study confirms the significant negative effect of habitat modification on group size, which may be a consequence of the combined effects of reduced recruitment rates and adult survival. Although we do not know the cause of high adult mortality in modified habitats in our population, data on other cooperative breeders suggests predation (Beck & Heinsohn 2006) or roadkill (Mumme *et al.* 2000). These may apply to our study population since an increase of predation pressure in agricultural areas of the Arava Valley has been recently documented (Lewin *et al.* 2021). Although vehicle transit is generally more intense in modified than natural habitats, most observed mortality in our study population is associated with secondary poisoning and entrapment in greenhouses.

A consequence of lower adult survival in modified habitats is the availability of dominant positions, resulting in faster turnover and younger males attaining dominance. Younger and less experienced dominant males may negatively affect group nesting success and productivity, supporting the observations in other cooperatively breeding species (Hatchwell *et al.* 1999; Komdeur 1996). Dispersal is costly for cooperative breeders (Nelson-Flower *et al.* 2018; Ridley 2012), but the presence of smaller groups that accept new members and include available dominant positions may drive the early dispersal in modified habitats (Shen *et al.* 2017). Early dispersal may lead to reduced survival, as explained by the ecological constraints (Hatchwell & Komdeur 2000; Nelson-Flower *et al.* 2018) or the benefits of philopatry hypotheses (Nelson-Flower *et al.* 2018; Stacey & Ligon 1991). While these cues may favor dispersal in both sexes, we surprisingly found it only in males, although females in this species are the sex that disperses more often (Ostreiher *et al.* 2022). Our results suggest that dispersal-related decisions may be affected by increased breeding opportunities due to higher adult mortality rates in modified habitats. Similar results were found in pied babblers (*Turdoides bicolor*), where dispersal is not sex-biased (Raihani *et al.* 2010), but vacant breeding positions increased the probability of male dispersal, and not females’ (Nelson-Flower *et al.* 2018). In white-winged choughs (*Corcorax melanoramphos*), dispersal was female-biased only in years of drought, with increased mortality promoting female dispersal, but not males’ (Leon *et al.* 2022).

In conclusion, this study provides empirical evidence that cooperatively breeding species are vulnerable to habitat modification. Despite the apparent positive effects that an increase in resources might bring, habitat modification influences deeper aspects of sociality, such as the acceleration of life history traits. The indirect effects on social structures and group sizes enhance the detrimental consequences of habitat modification on survival and breeding success (Blumstein *et al.* 2023). Amid the unfolding global change scenario, which includes rapid and extreme ecosystem changes, features such as degree of sociality and life history traits should be considered when developing effective conservation plans.

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**Competing Interest Statement:**

The authors declare that they have no conflict of interest.

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**Tables**

**Table 1.** **Coefficients and significance values of the variables included in the models for breeding analyses.** Significance \* denotes < 0.05, \*\* < 0.01, \*\*\* < 0.001. 1: In Cox proportional hazard models, a positive sign in the coefficients means that the risk of death is higher and, thus, a negative correlation

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Model** | **Dataset** | **Parameter** | **Estimate** | **SE** | **p-value** |
| **Breeding events** |  | Habitat: natural | *-0.52* | *0.16* | *<0.001\*\*\** |
|  | Total rainfall | *0.01* | *0.00* | *0.013\** |
| **Nesting success** | Groups | Number of adults and subadults | *0.13* | *0.07* | *0.043\** |
| Couples | Age dominant male | *0.50* | *0.21* | *0.015\** |
| **Annual Reproductive Output (ARO)** | Groups | Habitat: natural | *-2.19* | *0.62* | *<0.001\*\*\** |
|  | Total rainfall | *0.02* | *0.01* | *0.010\** |
|  | Habitat:Total rainfall | *0.02* | *0.01* | *0.016\** |
|  | Number of adults and subadults | *0.16* | *0.03* | *<0.001\*\*\** |
| Couples | Habitat: natural | *-0.61* | *0.16* | *<0.001\*\*\** |
|  | Total rainfall | *0.58* | *0.18* | *0.001\*\** |
|  | Number of adults and subadults | *0.37* | *0.07* | *<0.001\*\*\** |
|  | Age dominant male | *0.21* | *0.08* | *0.004\*\** |
| **Annual Reproductive Success (ARS)** | Groups | Habitat: natural | *-2.57* | *1.14* | *0.006\*\** |
|  | Total rainfall | *0.02* | *0.01* | *0.023\** |
|  | Habitat:Total rainfall | *0.04* | *0.016* | *0.029\** |
|  | Number of adults and subadults | *0.17* | *0.07* | *0.010\** |
| Couples | Total rainfall | *0.50* | *0.20* | *0.012\** |
|  | Habitat:Total rainfall | *0.86* | *0.38* | *0.027\** |
|  | Number of adults and subadults | *0.42* | *0.15* | *0.006\*\** |
| **Fledgling survival** |  | Habitat: natural | *-0.751* | *0.20* | *<0.001\*\*\** |
| **Adult survival** | Restricted | Habitat: natural | *-1.381* | *0.34* | *<0.001\*\*\** |
| Wide | Habitat: natural | *-0.971* | *0.38* | *< 0.001\*\*\** |
| **Group size** |  | Habitat: natural | *1.99* | *0.81* | *0.025\** |
| **Dominance acquisition ♂** | Restricted | Habitat: natural | *456.07* | *98.82* | *< 0.001\*\*\** |
|  | Number of adult males | *261.40* | *41.32* | *< 0.001\*\*\** |
| Wide | Habitat: natural | *343.38* | *129.02* | *0.017\** |
| **Dominance acquisition ♀** | Wide | Habitat: natural | *28.91* | *122.03* | *0.025\** |
| **Dispersal ♂** | Restricted | Habitat: natural | *421.90* | *191.30* | *0.051·* |
| Wide | Habitat: natural | *473.40* | *197.90* | *0.031\** |

**Figures**

Figure 1

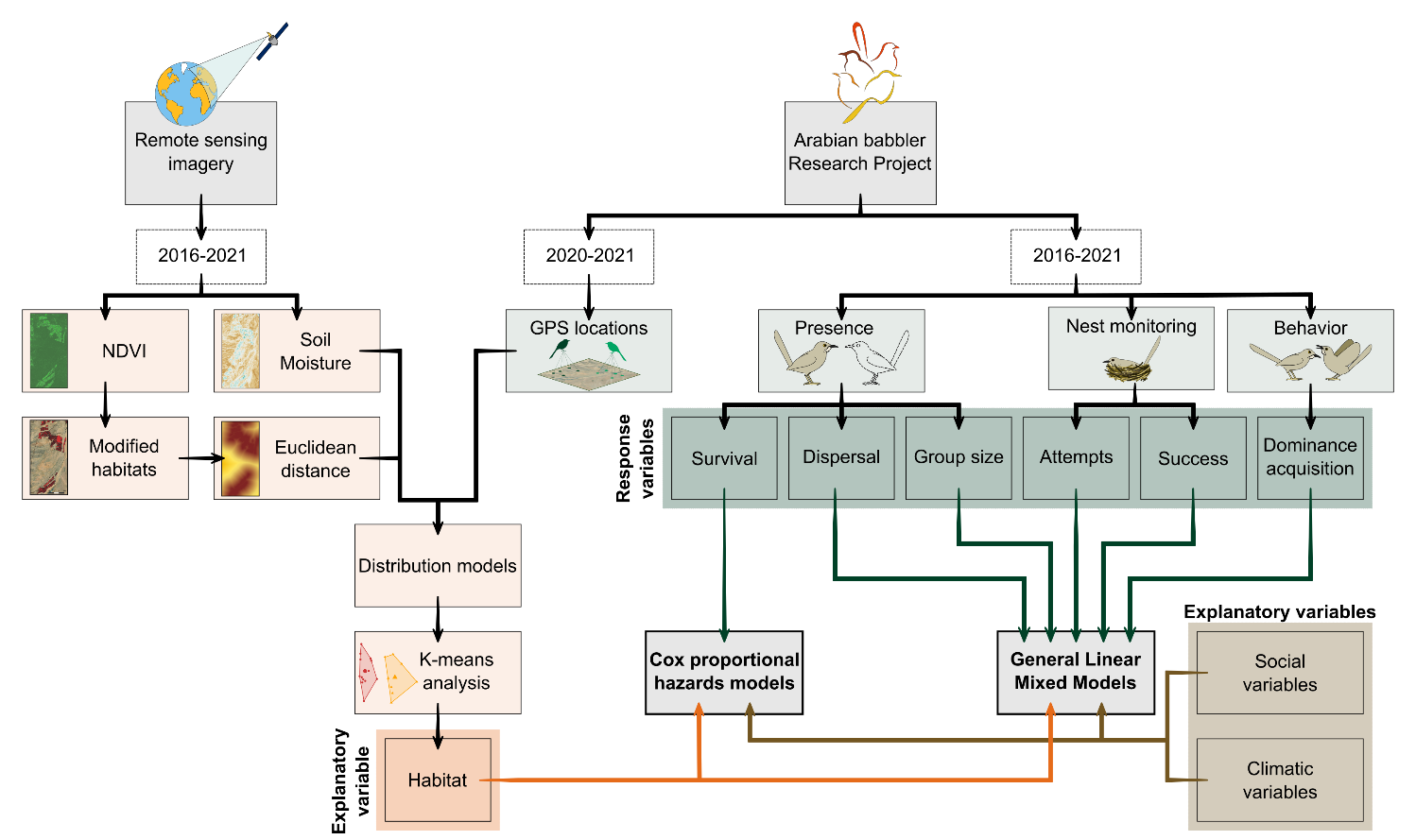


Figure 2

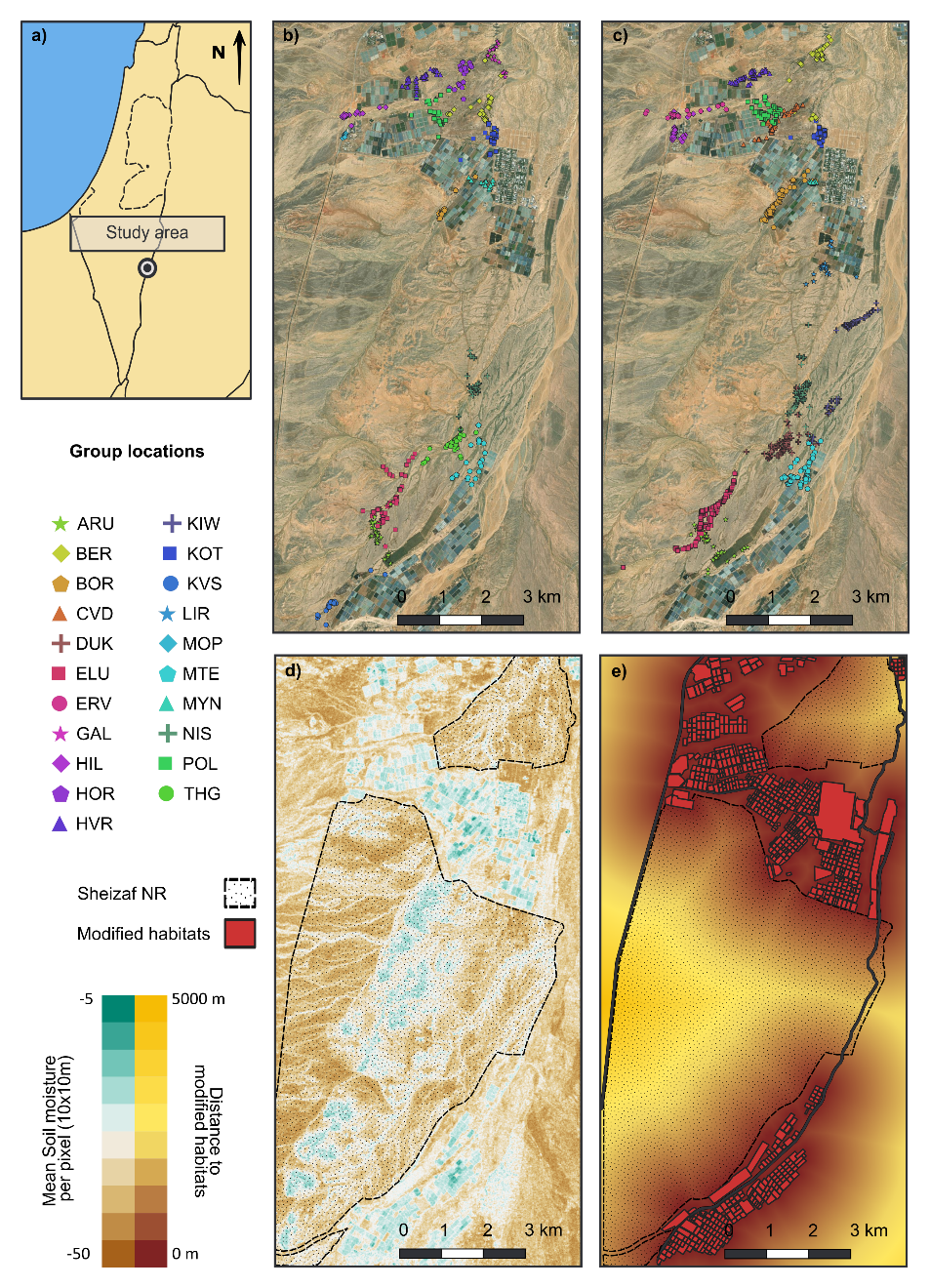


Figure 3

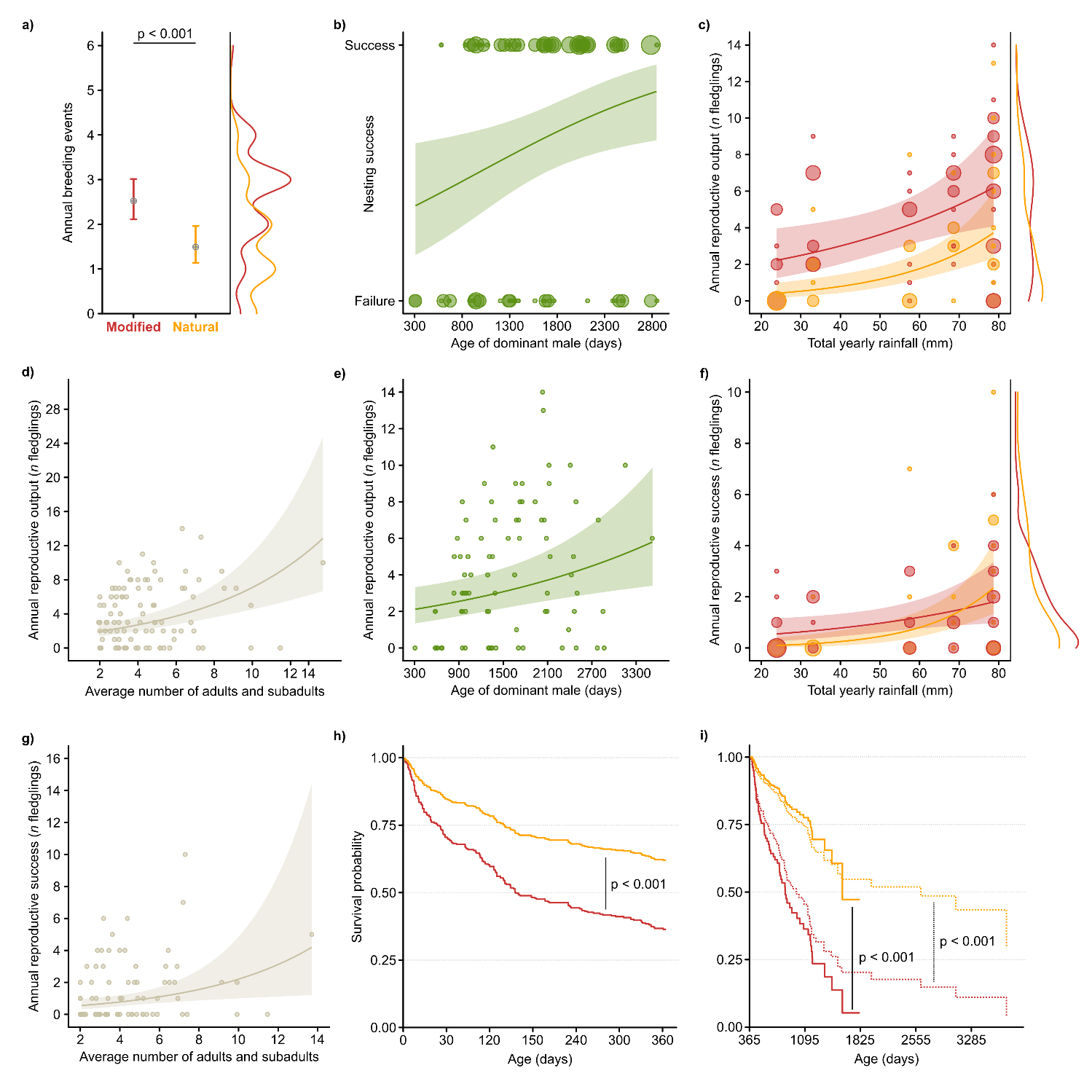
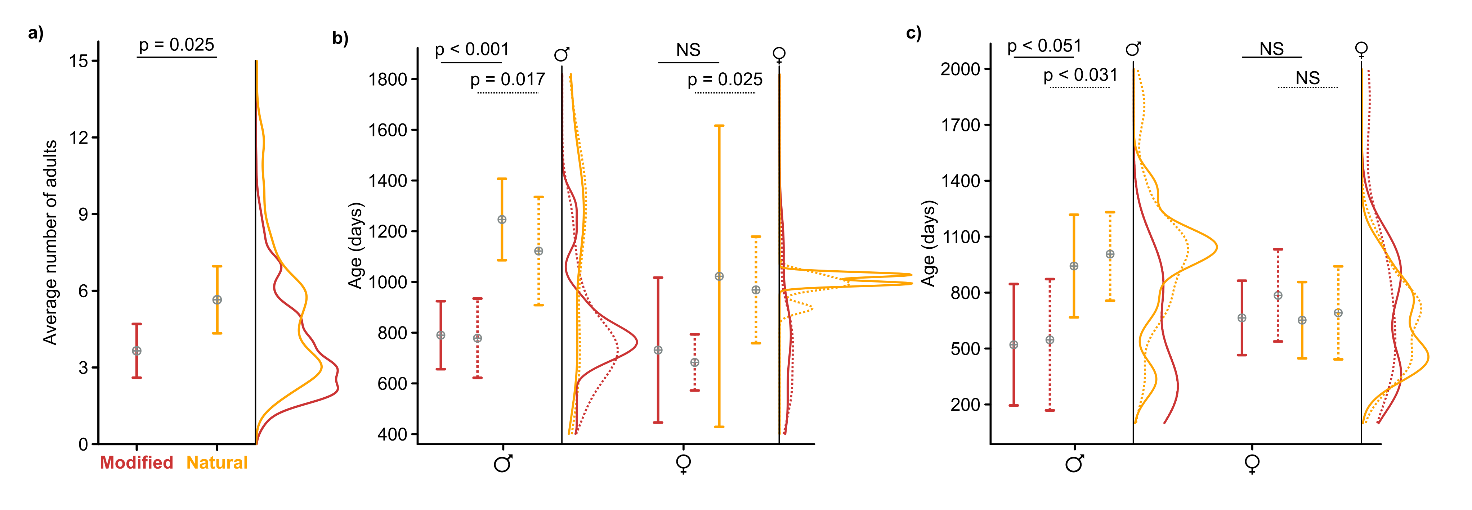
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Figure 4



**Figure legends**

**Figure 1. Overview of the study design.** The data for this study are from the Arabian Babbler Research Project, which has been ongoing since 1971, and from available remote sensing imagery extracted from Copernicus Sentinel 1 (S1) and Sentinel 2 (S2). Earliest image availability starts in 2016 for the study area; hence, this year was set as the starting point for this study. For the Arabian babbler Research Project, we collect individual GPS locations (since 2020), presence (from which we calculate survival, group size, and dispersal), nest data (from which we calculate attempts, success, and productivity) and behavior (from which we infer dominance). We obtained data for soil moisture (S1) and NDVI (S2) from the remote sensing imagery. NDVI was used to define modified habitats. We created distribution models for each group’s territory characterization using soil moisture, Euclidean distance to modified habitats, and group locations. We used K-means analysis to classify the groups into modified and natural habitats. We used habitat, social (group size and group structure) and climatic (rainfall and temperature) variables to analyze the effect of habitat on survival using Cox proportional hazards models. The effect of habitat on group size, dispersal, breeding attempts and success, and dominance acquisition was analyzed via generalized linear mixed models.

**Figure 2. A) Location of the study area within Israel**; **B, C) Study group locations during the 2020 and 2021 breeding seasons (respectively)**. Symbols and colors represent the GPS location for each study group; **D) Soil moisture per 10 m x 10 m pixel in March 2021 extracted from S1**. Blue represents higher and brown lower soil moisture; **E) Euclidean distances to modified habitats (crops, greenhouses, and settlements), derived from maximum NDVI extracted from S2 imagery**. The yellow-red gradient indicates the distance to modified habitats (yellow farther, red closer).

**Figure 3. a) Effect of habitat on the number of breeding events performed by groups per year.** Grey circles represent the model’s fitted values for each variable in response to habitat. Vertical lines represent the 95% confidence intervals for the fitted values; **b) Effect of age of dominant males on nesting success.** P = 0.015; **c) Effect of the interaction between habitat and rainfall on the groups’ annual reproductive output (ARO).** P = 0.016; **d) Effect of the number of adults and subadults on the groups’ ARO.** P < 0.001; **e) Effect of the age of dominant males on the couples’ ARO.** P = 0.004; **f) Effect of the interaction between habitat and rainfall on the groups’ annual reproductive success (ARS).** P = 0.029; **g) Effect of the number of adults and subadults on the groups’ ARS.** P = 0.010; **h) Cox hazard model for juvenile survival**; **i) Cox hazard model for adult survival.** The full line represents the model prediction with the restricted dataset, and the pointed line represents the model prediction with the full dataset. In all panels, natural habitats are in orange and modified habitats are in red. Raw data is shown as circles, and the circles' size refers to the frequency of observations. Shaded areas represent the 95% confidence interval of the models. The linear graphs on the right (panels a, c, and f) represent the frequency of observations in the raw data for each habitat. The p-values of the effects are shown.

**Figure 4.**

**a) Effect of habitat on the average number of adults in the group per month**; **b) Effect of habitat on the age of dominance acquisition in males and females in the restricted dataset (full line) and the full dataset (dashed line**); **c) Effect of habitat on the age of dispersal in males and females in the restricted dataset (full line) and in the full dataset (dashed line).** Grey circles represent the model’s fitted values for each variable in response to habitat. Vertical lines represent the 95% confidence interval for the fitted values. The linear graphs on the right represent the frequency of observations on the raw data for each habitat. The p-values of the effects are shown. Non-significant effects are marked as ‘NS’

**Text boxes**

**Text box 1. Definitions of breeding and social parameters:**

**Breeding event:** A breeding event begins when the first egg is laid in a nest. In Arabian babbler, nest construction (also referred to as a nesting event) is not necessarily followed by egg laying and multiple nests can be abandoned before the actual breeding.

**Nesting success:** A breeding event is considered successful when one or more nestlings fledge.

**Renesting event:** A successive breeding event. In Arabian babbler, it can occur after a successful and/or an unsuccessful breeding event.

**Annual reproductive output (ARO):** The total number of fledglings in a year (January - December).

**Annual reproductive success (ARS):** The total number of fledglings in a year (January - December) that survived at least a year (≥ 1 year old).

**Group size:** The average monthly number of adults in a group. An individual is considered a part of a group if it was observed roosting overnight with the group for at least three consecutive nights. Dates of entry and departure to and from a group are based on daily observations.

**Age of first dominance acquisition:** The difference between the date of hatching (in days) and the date that an individual replaced the previous dominant individual.

**Age of first dispersal:** The difference between the date of hatching (in days) and the date that an individual left its natal group and joined a new group or became a floater.