Importance of Mesohabitat for Nest-Site Selection in Breeding Eagle Owls (Bubo bubo): A Multi-Scale Model

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Abstract: Apex predators make excellent bioindicators of habitat quality and anthropogenic changes. Eagle owls (Bubo bubo) are such apex and keystone predators, who show preferential nest-site selection, usually away from human activities and habitation. However, Israel is a small country with a burgeoning human population. Hence, in order to understand the habitat requirements of eagle owls in central Israel, we conducted a multi-scale model analysis on their existing nest sites between 2006 and 2010. We identified 203 successful breeding attempts at 73 different sites. Our data suggested that the breeding population of the eagle owls was limited by the availability of quality nest locations, i.e., quarries, and caves. The probability of an eagle pair breeding increased with the presence of both quarries and caves, but was not related to mesohabitat properties. In addition, eagle owl breeding densities were positively related to the number of nest localities and to the planted woodlands. Furthermore, we found that eagle owls successfully raised their young regardless of the surrounding mesohabitat and sought the presence of other potential nest sites in the vicinity of the active nest sites, most likely due to the owls’ opportunistic and generalist hunting behavior, which facilitated the consumption of a wide prey base. Appropriate nest sites (quarries and caves) appeared to increase population numbers and, therefore, should be protected Further studies should determine whether increasing artificial nest sites and reclaiming abandoned quarries could increase eagle owl numbers in a sustainable manner.

Keywords: nest site; limiting factors; quarry; cave; mesohabitat; eagle owl

1. Introduction
Apex predator populations are important for biodiversity conservation and for regulating the effect of competition by mesopredators on prey availability [1]. As human populations expand and habitats are destroyed, apex predator population numbers—which were small to begin with—and the predators’ ecological function are at risk [2,3].

Different factors such as nest-site availability and diet limit the populations of birds of prey [4,5]. To protect keystone species such as eagle owls (Bubo bubo), it is important to determine what factors affect their nest-site selection and breeding success. Previous studies reported that the occupation of a nest site by eagle owls may be affected by the proportion of specific mesohabitat properties surrounding the nest site, such as open landscapes [6], forests [7], protected areas [6], the distance to the road [7,9], intra-specific competition [7,10] and the elevation of the locality [11]. Similarly, eagle owl breeding success (i.e., the number of young fledged/pair) was also affected by surrounding mesohabitat properties such as [6,12] latitude [13] and elevation [14].

Even though mesohabitat properties/categories are important for some eagle owl populations, it is still unclear whether a lack of availability of nest sites can limit population
Eagle owls do not build nests, but lay eggs in a wide variety of nest sites and frequently breed on the ground in many mesohabitat types (forests, cliffs, caves and quarries), but also avoid areas where human activity is high. We assumed that just as nest cavities limit second-cavity bird breeding, specific nest sites may limit eagle owl breeding success and may therefore influence the persistence of breeding populations even more than the mesohabitat properties around the nest site themselves.

Protecting and conserving cryptic and elusive apex predators such as eagle owls are sometimes not prioritized in many conservation schemes. In the case of eagle owls, this may result from the fact that their direct and indirect predatory ecosystem effects are difficult to observe and measure, due to their nocturnal lifestyles. To conserve the owls, it is of high importance to determine what factors limit the number of pairs, breeding success and the subsequent persistence of the population in the wild.

We studied a breeding population of eagle owls in Israel that utilized two types of habitats—quarries and caves—as nest sites that were not distributed evenly throughout the study region and therefore potentially limited breeding numbers. Specifically, we studied whether the availability of nesting sites and presence of different mesohabitats affected breeding densities, the probability of breeding and breeding success in eagle owls. We hypothesized that both nest-site types, but not mesohabitat availability around the nest sites, would affect the number of breeding pairs, but not the breeding success, due to the eagle owls’ opportunistic and generalist hunting behavior.

2. Materials and Methods

2.1. Study Area

The study was conducted in a 2644 km² area of the Judea region of Israel (central-southern Israel, 31°44’44.47″ N, 34°59’11.93″ E) during the 2006–2010 breeding seasons, because of a preliminary, unpublished survey conducted in the region and because it is the work area of Ezra Hadad—the ranger for the Israel Nature & Parks Authority (Figure 1). The area is semi-arid, with the average annual rainfall during the 2006–2010 breeding season from 15 February to 15 July each year measuring 439 mm (N = 5 years, SE = 44.3 mm), with a mean daily maximum temperature of 27.2 °C (N = 3 years, SE = 0.5) and a mean daily minimum temperature of 12.5 °C (SE = 0.7; Israel Meteorological Center).

The lithology in the study area consists mainly of karstic carbonates as well as shales of the Cretaceous Judea group and is characterized by artificial bell-cave structures, particularly in the shale formations. In a research survey, the caves were discovered as occurring in clusters and were formed under shallow phreatic conditions prior to the major uplift of the terrain of central Israel during the late Cenozoic. The artificial bell caves are the result of the quarrying of blocks of chalk, used for building during the late Roman, Byzantine and early-Islamic periods.

The study area was visited from March to August each year during the 2006–2010 breeding seasons, at a frequency of once to twice a week. Nests were found by searches on foot for related signs such as the presence of adults, fresh pellets, vocalizations, etc. We assumed that all abandoned historical nest sites were unused for that season and those with either eggs or nestlings were assumed to be occupied sites. Because eagle owls are evenly spaced over a landscape to avoid territorial conflict, we conducted optimal stratified surveys based on field experience and many years of field work at the study site. To prevent any disturbances to the breeding pairs, initial observations were conducted from a distance, using binoculars (Swarovski 10 × 42, Absam, Austria). The nests were visited weekly on foot after the nestlings hatched in order to determine breeding success, i.e., the number of young fledged/pair. All active quarries, caves and the location of active nest sites were recorded in the field using the Israel TM Grid coordinate system and uploaded to ARCMAP 10.4 (ESRI, Redlands, CA, USA) layer for the 2006–2010 breeding seasons (Figure 1).
Figure 1. Map of the study site, the Judea region, in central Israel. The black squares denote the locations of all the quarries including those not occupied, the elliptical line denotes the bell caves and the colored blocks the relative densities of eagle owl (*Bubo bubo*) nest sites. The inset map shows the study area in relation to the region; each grid is 15 km$^2$. Not all the quarries and caves were occupied.

2.2. Statistical Analysis

For the 2006–2010 breeding data, we used a one-way ANOVA to compare the number of nestlings fledged throughout the years as well as a $\chi^2$ test to compare the occupation of quarries and caves by the breeding pairs. We analyzed the number of potential nest localities (i.e., quarries or caves available but not occupied) around active nests and the proportion of different mesohabitat land cover categories around active nests (Table 1) to
predict the use of nest localities, occupation of nest sites, and breeding success. We analyzed the 2006–2010 agglomerated breeding data both generally and for each year separately.

Table 1. Average proportion of land cover categories in spatial scales of 1000–5000 m radius around nest sites of eagle owls (Bubo bubo).

| Scale (km) | 1000 | 2000 | 3000 | 4000 | 5000 |
|-----------|------|------|------|------|------|
| Built     | 8.4  | 9.1  | 10.4 | 11.4 | 12.1 |
| Disturbed | 2.3  | 1.5  | 1.1  | 1.1  | 1.1  |
| Grasslands| 0.8  | 1    | 1.1  | 1.2  | 1.3  |
| Maquis    | 10.5 | 9.8  | 9.2  | 8.6  | 8.2  |
| Shrub     | 12.4 | 10.9 | 10.2 | 9.9  | 9.6  |
| Grove     | 22.4 | 21.7 | 22.1 | 22.2 | 21.9 |
| Woods     | 19.4 | 18   | 16.6 | 15.9 | 15.5 |
| Agriculture| 18.3 | 21.5 | 22.5 | 23   | 23   |
| Orchards  | 5.4  | 6.5  | 6.7  | 6.6  | 7.1  |
| Water     | 0.1  | 0.1  | 0.1  | 0.2  | 0.2  |

The size of the home ranges is still uncertain. This may be because home ranges can vary yearly and most studies of eagle owl home ranges used VHF tracking [26–28], which typically underestimated the ranges, due to a low number of localizations as well as biased overestimations for both the locations close to the nest site and the locations of last sightings [29]. We therefore suggested increments of up to 5 km in distance (a 1–5 km radius) around active nests [30,31] that eagle owls could easily fly to during nocturnal foraging trips.

The mesohabitat land cover around the nest sites was defined as the proportion of each type of the land-use category (data from Israel’s National Ecosystem Assessment Program, HaMaarag, Tel Aviv, Israel), using ARCMAP 10.4 (ESRI, Redlands, CA, USA). The mesohabitat land-use categories used for this analysis were anthropogenic-disturbed areas (including quarries and landfills), built areas (villages, industrial areas and buildings), water sources, grassland, agricultural field crops, planted woodlands, shrub lands, maquis and agricultural orchards (Table 1). All the caves and quarries were identified by geographical information systems (GIS) and ground-proofed in the field.

We applied logistic regression to assess the spatial distribution and location of the 73 nest sites found during the study, in relation to the quarries, caves and the mesohabitat land cover. We compared the spatial properties in relation to the location of the nest localities and the mesohabitat around the observed nest sites, to 73 randomly generated nest locations, utilizing the same buffer sizes (a 1–5 km radius) within the boundaries of the studied landscape.

Nest-site occupancy (binary response variable = nest sites occupied/not occupied) were compared during each of the study years, in relation to the number of nest localities and mesohabitat land cover. We used logistic regression to determine whether nest occupancy, during each year and at each of the scales, exhibited statistical dependence with respect to the above-mentioned explanatory variables.

We used a linear, mixed-model analysis [32] to determine whether nest density (the number of active nest sites in a 5 km radius, 78.54 km²) was related to the number of potential nest localities (i.e., quarry and caves) and mesohabitat land uses. We first generated a random series of eight five km radius random buffers and repeated the procedure 10 times for each year, separately. We then calculated the number of potential nest localities, number of active nest sites and mesohabitat land cover within each buffer. We repeated the same buffer randomizations per year and added them as random factors, together with the year, to avoid overlap among the buffers and thus avoid pseudo-replication issues.

We performed statistical analyses using JMP 13.0, North Carolina, USA and SPSS version 22, Chicago, IL, USA.
3. Results

During the 2006–2010 breeding seasons, we located a total of 203 breeding attempts in 73 different nest sites (mean = 40.6 nest per year, SE = 0.3, N = 5, Figure 1) and found that the number of nestlings fledged per breeding pair (mean 2.81 = nestlings per year, SD = 0.83, N = 203 nests) did not significantly vary between the years (F_{4,198} = 0.25, p = 0.91; Figure 2). During 2006, we studied 35 EO breeding pairs; in 2007, we found 39 pairs; in 2008, we found 46 pairs; in 2009, there were 42 pairs and in 2010, we followed the breeding attempts of 41 pairs. The number of fledglings per breeding pair was: 2006—2.49 fledglings (SD = 0.92), 2007—2.44 (SD = 0.68), 2008—2.59 (SD = 0.83), 2009—2.57 (SD = 0.80) and 2010—2.59 (SD = 1.0) and found that the number of nestlings fledged (mean 2.81 = nestlings per year, SD = 0.83, N = 203 nests) did not significantly vary between the years (F_{4,198} = 0.25, p = 0.91; Figure 2).

Throughout the study period, eagle owls preferentially occupied a higher percentage of quarries than caves (2006 − χ^2 = 11.5, df = 1, p < 0.001; 2007 − χ^2 = 7.3, df = 1, p = 0.007; 2008 − χ^2 = 15.0, df = 1, p < 0.001; 2009 − χ^2 = 14.2, df = 1, p < 0.004; 2010 − χ^2 = 9.0, df = 1, p = 0.003; Figure 3).

The spatial distribution and location of the 73 nest sites found, compared to the 73 randomly selected locations, suggested that nest locations were significantly associated with quarries and caves (Table 2). The number of caves and/or quarries around each observed nest was higher compared to the randomly generated locations. For example, the mean number of observed caves at the 1 km buffer scale was 0.72, compared to the randomly simulated caves, which averaged 0.068. Similarly, at the five km buffer, the mean number of observed caves was 5.45, compared to a mean of 2.42 randomly simulated caves. Consistently, the association of the nest locations was stronger with quarries as compared to caves at all spatial scales. While being significant at all scales, the significance tended to decrease with the increase in scale. For example, the significance of the number of surrounding caves decreased from p = 0.012 at the 1 km radius scale to p = 0.037 at the 4 km radius scale and 0.029 at the 5 km radius scale. The probability that an eagle owl nest would occur at spatial scales within a 1–5 km radius increased with the increase in the number of quarries and caves (Table 2). None of the mesohabitat cover types were significantly associated with the nest locations (Table 1). The most abundant land use surrounding the nests was planted fruit groves, which accounted for approximately 22% of the land cover. Planted woodlands were the next most common land cover, accounting for about 15–19%.
of the land cover, and water bodies were the least abundant and accounted for <1% of the cover (Table 1).

![Figure 2](image_url)

**Figure 2.** The number of fledglings of the eagle owl (*Bubo bubo*) during the years 2006–2010 in the Judea region of central Israel.

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![Figure 3](image_url)

**Figure 3.** Comparison between the percentage of quarries (black, n = 30) and caves (white, n = 63) occupied by eagle owls (*Bubo bubo*) during 2006–2010. The preference for quarries is evident from the difference in nest placement between the two potential habitats.

**Table 2.** The probability of an eagle owl (*Bubo bubo*) nest in area (1–5 km radius) decreases with spatial scale, as expressed by lower significance values. Combined = number of caves and quarries. AIC denotes the Akaike Information Criterion.

| Radius | Cave | Quarry | C + Q | Observed Mean | Simulated Mean | p-Value Model | p-Value Variable |
|--------|------|--------|-------|---------------|----------------|---------------|------------------|
| 1000   | 191.664 | 0.73 | 0.069 | 0.0001        | 0.012          |
|        | 176.457 | 0.60 | 0.04  | <0.0001       | 0.0004         |
|        | 153.781 |       |       |               |                |
| 2000   | 192.633 | 1.67 | 0.26  | 0.0002        | 0.0130         |
|        | 178.548 | 1.05 | 0.12  | <0.0001       | 0.0005         |
|        | 159.405 |       |       |               |                |
| 3000   | 194.437 | 2.77 | 0.60  | 0.0005        | 0.0137         |
|        | 190.323 | 1.29 | 0.36  | <0.0001       | 0.0006         |
|        | 175.112 |       |       |               |                |
| 4000   | 201.343 | 3.81 | 1.66  | 0.0234        | 0.0373         |
|        | 191.845 | 1.73 | 0.59  | 0.0001        | 0.0006         |
|        | 192.764 |       |       |               |                |
| 5000   | 200.991 | 5.45 | 2.42  | 0.0191        | 0.0290         |
|        | 190.916 | 2.18 | 0.85  | <0.0001       | 0.0003         |
|        | 193.841 |       |       |               |                |

The probability that a specific nest site would be occupied during the study period (Table S1) and the number of nestlings fledged from the site were not significantly associated with the number of quarries and caves, nor the mesohabitat land around the nest site at any spatial scales (1–5 km radius; Table S2).

The linear mixed model (F₁,389 = 29.04, p < 0.001) including year, buffer group and buffer number as random factors found that the number of breeding pairs (mean = 0.73 active nests per buffer, range 0–7 nests) was positively correlated with the number of quarries (F₁,389 = 135.18, p < 0.001; mean = 0.50, range 0–6), number of caves (mean = 1.23, range 0–30; F₁,389 = 84.26, p < 0.001) and percentage of planted woodlands (mean = 517.75 Ha, range 0–3, 454.13 Ha; F₁₀,389 = 9.99, p = 0.002). They were not, however, related to the
percentage of built-up areas ($F_{1,389} = 0.04, p = 0.85$), disturbed areas ($F_{1,389} = 0.49, p = 0.48$), grasslands ($F_{1,389} = 0.24, p = 0.63$), maquis ($F_{1,389} = 0.05, p = 0.82$), crop fields ($F_{1,389} = 11, p = 0.74$), orchards ($F_{1,389} = 0.22, p = 0.64$) nor water bodies ($F_{1,389} = 0.55, p = 0.50$). Areas that had more quarries, caves and planted woodlands also had higher breeding densities.

4. Discussion

Our data suggested that the breeding population of the eagle owls in the Judea region of central Israel was limited by the lack of available nesting sites, i.e., quarries and caves. We found that the probability of an eagle pair breeding increased with the presence of both quarries and caves but was not related to mesohabitat land-use structure. Further, eagle owl breeding densities were related to the number of appropriate nest substrates and mesohabitat, mainly to planted woodlands. Furthermore, we found that eagle owls successfully raised their young regardless of the surrounding mesohabitat or the lack of additional nest sites around their nests, most likely due to the owls’ opportunistic and generalist hunting behavior which allows them to prey upon a varied prey base. Interestingly, our results concurred with [33], who concluded that cost–benefit evaluations regarding the cost of optimal-foraging, distance and height of nest sites on cliffs dictated site choice. Human disturbance was considered to be a prominent consideration in nest placement by eagle owls [9]. Our results concurred with some of the studies from Europe, where a shortage of nest sites was not found to affect breeding density [6,19].

The only mesohabitat structure that was related to the number of breeding pairs was the amount of planted woodlands, which was also related to the number of quarries, but not to the number of caves. This is most likely because woodlands were frequently planted around the former as part of environmental reclamation projects [34]. The major line of thought is that unused quarries should be rehabilitated because, when left untreated, they can cause land disturbances, as well as safety and environmental problems. The problem, as we see it, is that most of the rehabilitation is focused on how to convert the unused quarries into recreational areas for humans; the importance of biodiversity is not a priority [34]. Based on our findings, the number of potential nest localities is more important than the amount of planted woodlands, because the probability that an eagle owl nest was located at a site was significantly associated only with quarries and caves, but not with the amount of planted woodlands or recreational areas. Interestingly, planted woodlands may still be a significant factor in this issue since, in Spain, it was found that the amount of forest around the cliffs used by eagle owls as nest sites increased the probability of occupation [7], but decreased with human disturbance [9,12].

Unlike this study, where the occupation of nest sites was not related to the mesohabitat structures, the occupation of nest sites in France was positively related to open-habitat availability [6] and to protected areas in Spain [8]. In Europe, the number of fledglings was positively correlated to the percentage of open land [35], forested landscape [6] and protected areas [36], but was negatively correlated to the cover of urbanized areas [12] and proportion of wooded areas [14] around the nests. This underlines the fact that the mesohabitat around nest sites may affect breeding in ways that we have not yet elucidated. For example, the quality of nestlings (i.e., their body mass) could differ between habitats [37] and influence recruitment as well as population sustenance. Further studies are needed to determine whether the fitness and diet of owls may vary in the different mesohabitats.

Even though the eagle owl population in Israel is stable [38], the owls’ dependence on quarries and caves for nest sites could be problematic locally, because the sites are not protected by law. As the human population of Israel is growing and habitat loss is becoming more prevalent [39], the carrying capacity and landscape continuity to sustain large predators, such as eagle owls, is impaired [40].

Furthermore, since eagle owls are large, attractive owls that breed in open areas on the ground and are easy to find, they are at risk of disturbance from recreational birders and wildlife photographers who frequently seek the owls out to watch and photograph them [41,42]. Anthropogenic disturbance was also found to affect nest-site occupancy by
eagle owls in Spain; they bred less in nest sites located near paved roads [7,43]. Now that we have determined that the presence of nest sites encourage eagle owl breeding, it is vital to implement conservation practices to protect the quarries and caves from human disturbance or “development” exclusively for human purposes [33]. This is especially important in light of the fact that the bell caves are historical, human-created structures from ca. 2000 years ago and can only be maintained as historical sites [22]. Future studies are needed to assess the possibility of preserving quarries that are not necessarily within the boundaries of nature reserves, in order to sustain the present breeding population and to facilitate their dispersal into areas where the species currently does not breed.

The finding that a lack of appropriate nest localities may be a limiting resource to eagle owls in Israel may differ from other studies, due to the sampling effort. Here, we sampled a large area where eagle owls are known to breed. In addition, unlike Europe, Israel is a much smaller country with a denser human population, made up of habitat that is frequented by humans (i.e., from intensive agriculture, villages, recreational activities, etc.), and lacks large, extensive forest areas and wildlife refuges [40]. This study highlights the importance of protecting not only larger habitats, but also potential nest-site localities, from future land-use changes in the guise of development, even if only for recreational activities (i.e., rock climbing, mountain bicycles, off-road vehicles, etc.).

Even though eagle owls are generalists who breed in a wide variety of nesting habitats throughout many parts of their range [19], locations that limit nest sites highlight the complexity of wildlife conservation for apex predator species between regions and countries, especially in species with a wide global distribution such as the eagle owl. Inappropriate nesting sites for eagle owls appear to limit population numbers just like cavities can limit secondary cavity-breeders [5,44,45]. Hence, further studies are needed to determine if, by increasing artificial nesting sites, we could naturally influence dispersal and increase eagle owl numbers in areas with limited nest sites, but with a diverse and abundant prey base to sustain such populations [46]. This is especially important when taking into consideration that the study species is susceptible to human disturbance, while the human density in the region continues to grow. Multi-scale insights are required to ensure the persistence of the eagle owl populations in central Israel.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/d14060438/s1: Table S1. Analysis of land use—land cover on nesting success of eagle owls (Bubo bubo) at 1–5 km scales. “Gadash” denotes low crop fields. Table S2. Analysis of land use—land cover on mean annual number of fledglings, at 1–5 km scales. “Gadash” denotes low crop fields.

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