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RESEARCH PAPER

Ocellated lizard predation patterns on red-legged partridge nests in olive groves

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Abstract. In this study, we evaluated predation of the ocellated lizard on red-legged partridge nests in an olive grove in southern Spain over three consecutive years. The microhabitat characteristics of prey nests are analysed through comparison with successful nests. We found only 13 nests predated by lizards during the study period. This number was three times lower than that of nests that failed due to causes related to agricultural practices or human activity in the same period and study area. A few of the nests were predated by mammals more than they were preyed upon by lizards. The nests preyed on by lizards were associated with proximity to their refuge areas (e.g. stone piles, old buildings with holes, or rabbit burrows). The characteristics of the olive grove (e.g. drip irrigation and absence of vegetation under the olive trees) may favour the ocellated lizards' search-and-hunt strategy, which allows a lizard to readily find a nest if it is inside the lizard's territory and close to its refuge. We propose management strategies for reducing lizard-related nest losses. However, we argue that olive grove intensification is a major cause of partridge nest failure rather than predation by lizards and other predators.

Key words: *Alectoris rufa*, egg predation, nesting success, *Timon lepidus*, habitat management

Introduction

The red-legged partridge (*Alectoris rufa*) is a ground-nesting bird of high ecological and economic interest due to its hunting value (Díaz-Fernández et al. 2012), and it partly comprises the diet of most of the Mediterranean predators (Ferreras et al. 2022). Consequently, most are concentrated in the Iberian Peninsula. However, this species is present in the south of France and the north of Italy, and it has been introduced in the British Isles and some Atlantic islands (Farfán et al. 2022).

It is considered a typical species of open environments as it occupies pseudo-steppes, herbaceous crops, and mixed environments, including Mediterranean scrubland (Vargas et al. 2006). It is also present in hollow forest masses, such as *dehesas* (open oak woodland), and wooded crops, such as olive groves (Duarte et al. 2014). The species favours mixed landscapes in which diverse environments predominate, allowing it to satisfy its different trophic and habitat requirements during its annual cycle (Casas et al. 2022).

Landscape changes due to agricultural intensification have created a delicate situation for the species (Viñuela et al. 2013). The red-legged partridge has suffered a marked decline in recent decades (Escandell et al. 2011, Blanco-Aguiar et al. 2012), estimated at more than 50% of its population in Spain in the last 30 years (Farfán et al. 2022). In addition to the loss

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of habitat, a series of factors threaten populations of this species. Among them are hunting pressures that are not realistic (Casas et al. 2016), toxicity due to the use of pesticides and herbicides (López-Antia et al. 2013, 2015, 2021), the deterioration of the species' genetic pool due to hybridisation with farm-raised partridges (Casas et al. 2012), and factors that reduce the species' reproductive success (i.e. habitat loss, landscape changes, agricultural intensification and nest or chick predation conditioned by habitat simplification, Casas et al. 2022).

In addition to factors related to reproductive failures, there are agricultural practices that directly destroy nests, cause their abandonment, or lead to nests being increasingly detected by predators due to a reduction in vegetation cover (Buenestado et al. 2009, Casas & Viñuela 2010). Another factor is predation itself. Whether predation is a limiting factor for a species such as the red-legged partridge has been extensively discussed (Ferreras et al. 2022). Many species feed on their eggs, chicks, and adults (Duarte et al. 2008). However, the species' population dynamics have evolved in these scenarios, and its strategy against predators is adaptive (Lebreton 1982). Nevertheless, in low-quality habitats where generalist predators are abundant or in situations where other factors already compromise reproductive success, predation may act as an additive factor limiting recovery (Roos et al. 2018).

The ocellated lizard (*Timon lepidus*) is a saurian reptile closely linked to Mediterranean habitats. It is a thermophilic species that occupies North-West Italy, southern France, and the Iberian Peninsula (Salvador & Pleguezuelos 2002). It is scarce or absent in wetter or colder climates (Busack & Visnaw 1989). The species exhibits high ecological plasticity as it can adapt to habitats as diverse as dune systems, crops, and montane habitats (Mateo 2011). Ocellated lizards reach their highest densities in Mediterranean shrublands (Castilla & Bauwens 1992) but are relatively scarce within cereal monocultures (Martín & López 2002). In shrublands, ocellated lizards prefer structurally complex areas with open patches, enabling them to switch between basking in the sun and moving to shade. Therefore, tree and shrub cover is not a major limiting factor for this lizard. Still, shelter availability (Díaz et al. 2006, Gálvez-Bravo et al. 2009) among rocks, holes, or crevices such as trees or rabbit warrens is important for the species (Grillet et al. 2010).

The ocellated lizard is relatively common in Mediterranean open oak woodlands (Martín & López 2002), which are multifunctional agro-sylvo-pastoral systems that share a series of structural characteristics with olive groves, which is another habitat favoured by this lizard species (Mateo 2011). Olive groves currently occupy areas originally covered by natural Mediterranean *Quercus* spp. scrubland communities (Nieto et al. 1991) in which wild olive trees (*Olea europaea* var. *sylvestris*) were understory species. Olive groves are widespread throughout the Mediterranean basin (European Commission 2023). In the Andalusia region (Southern Iberian Peninsula), this crop covers over 16,700 km^2 (Ministerio de Agricultura, Pesca y Alimentación 2021), at least 19% of the region's surface area, which signifies the relevance of this habitat.

Ocellated lizards are primarily insect feeders, actively searching for their prey. Their preferred prey is large (12-25 mm) insects (e.g. Coleoptera, Hymenoptera, Heteroptera), but they will also consume Lepidoptera, caterpillars, gastropods, and a variety of other invertebrates (Mateo 2011). The species also consumes fruits (Hodar et al. 1996), small vertebrates, carrion, and birds' eggs (Pleguezuelos et al. 2000). The species has a reputation for being an active egg-eater of game species that are popular with hunters, particularly red-legged partridge. For this reason, ocellated lizards have been persecuted before and subjected to eradication campaigns in hunting estates in which the species is found (Salvador 1974, Corbett 1989), and it is in decline throughout its range in recent times (Mateo 2002, Cheylan & Grillet 2005).

Although lizard predation on partridge eggs has been confirmed (Calderón 1977, De Juana & De Juana 1982, Llandrés & Otero 1985), it is considered rare since eggs represent a low proportion of their diet (Mateo 2011). However, ocellated lizard predation amounts to a significant cause of clutch loss for the red-necked nightjar (*Caprimulgus ruficollis*) in agricultural landscapes, which is a ground-nesting species that shares their habitat with partridges (Cuadrado & Domínguez 1996). These results show some uncertainty concerning the lizard species' potential impact on partridge nests, thereby encouraging new studies on this issue. Furthermore, improving this knowledge is relevant for conserving these lizard and partridge species.

Here, we studied the ocellated lizard's predation of red-legged partridge nests in a game estate in southern Spain, covered mainly by olive groves. The estimated red-legged partridge density in the estate during the pre-breeding period was approximately

50 partridges per square kilometre, with the densities ranging between 44 and 59 partridges per square kilometre in October (Duarte & Vargas 2001a). Although ocellated lizards are frequently observed in the estate, there are no data on lizard densities in the study area. In other Iberian environments, ocellated lizard densities range between 52 and 67 individuals per hectare, depending on habitat complexity (Mateo 2011).

We assess the impact of ocellated lizard predation on the nesting success of the red-legged partridge. We hypothesise that some nesting habitat features may be associated with lizard nest predation. Ultimately, the study's main aim is to explore possible habitat management strategies that simultaneously allow the conservation of both species and reduce the predation rate.

Material and Methods

Study area

The present study was conducted between 1997 and 1999 in a 16.4 km^2 estate located in Antequera (Málaga Province, southern Spain; Fig. 1). The climate in the area is typically Mediterranean (Capel-Molina 1981), with warm summers and mild winters. The average temperature is 25 °C in August and 10 °C in January.

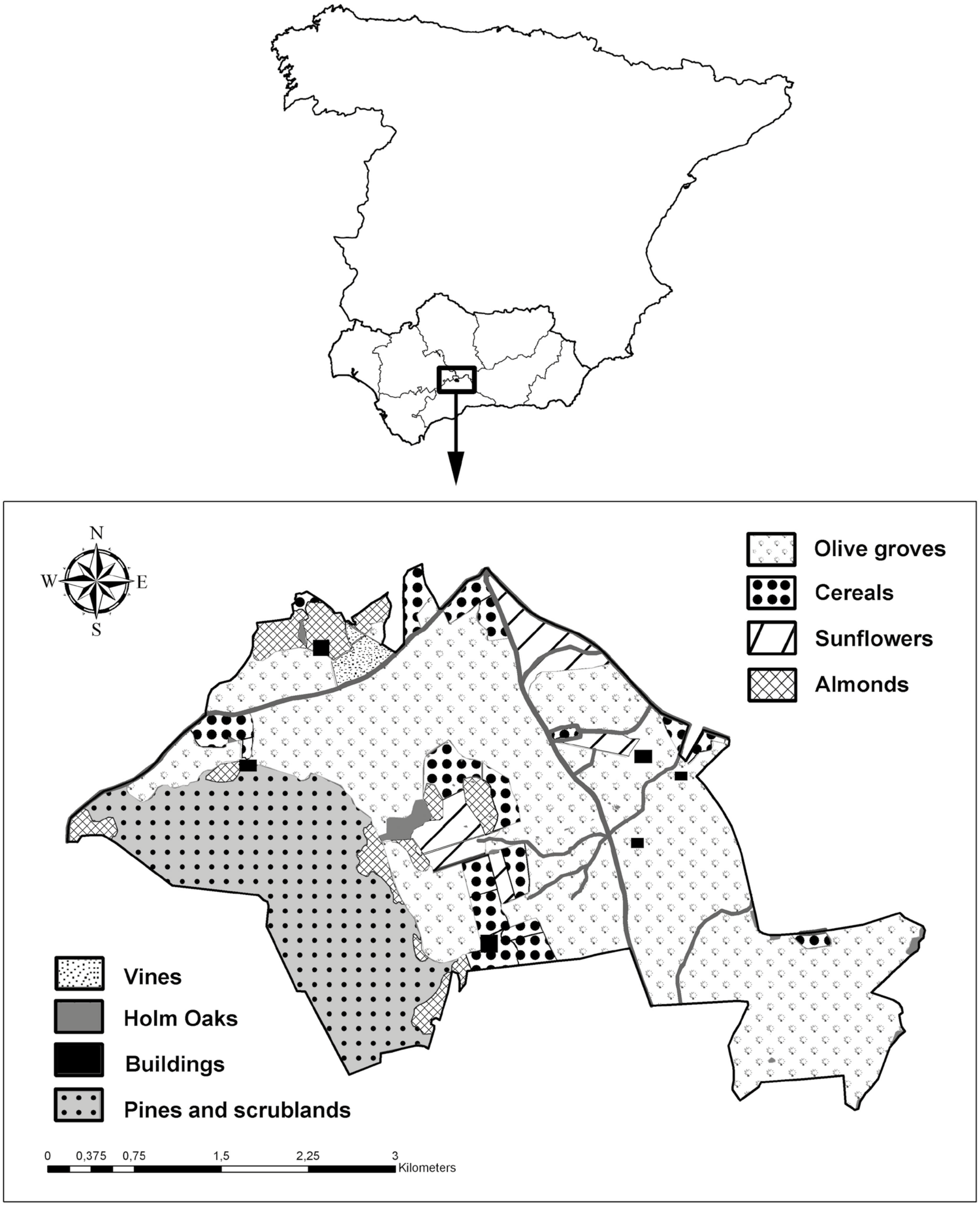

Fig. 1. Location of the study area in the south of Spain (Málaga Province), land uses, and main roads or tracks inside the game estate.

Annual accumulated rainfall during the study period ranged from 315-1,215 mm, while monthly rainfall ranged from 0-325 mm (Duarte 2012). Natural shrubland covers 24.1% of the estate, which is concentrated on a calcareous hill and consists of degraded holm oak (*Quercus rotundifolia*) woodland, with an understory of *O. europaea* var. *sylvestris* and lentisc (*Pistacia lentiscus*) (Nieto et al. 1991). The arable area accounts for 12.3 km^2 (75.2%) and hosts diverse natural vegetation patches of different sizes. The remaining 0.7% comprises farmhouses and agricultural buildings. The primary agricultural use of the estate is olive production (olive groves cover 77% of all of the farmland and 57.9% of the total estate surface area), but there are other crops, including cereals, sunflowers, almonds, and vines. Several visits were made to the study area during 2006 and the period 2019-2021 to carry out additional research (Duarte et al. 2021), which allowed us to verify that the environmental conditions remained similar to those of the study period.

Olive trees were planted 10-15 m apart in linear squares. The average distance between the olive trees is 11.5 ± 0.1 m (n = 223), and the olive tree density ranges between 70 and 80 trees per hectare. The space between two rows of olive trees is called a lane, and the space below the canopy of an olive tree is called the ring. An olive tree may develop multiple trunks (between two and four, but three is the most common configuration), known as olive tree legs. There is often an abundant herbaceous layer dominated by *Diplotaxis* spp., *Raphanus* spp., *Amaranthus* spp., *Heliotropium* spp., and *Convolvulus* spp. (García & Cano 1995) in the ring of the trees and along the lanes. The herbaceous layer is mechanically and chemically managed in mid-spring. Soils are usually exposed between April and September to reduce competition for water between the trees and the herbaceous layer.

Data collection

The study period included three breeding seasons between April 1997 and August 1999. We detected partridge nests by intensively searching the study area. Olive groves are generally subject to intensive agricultural management, especially during spring and summer. During this period, every olive tree and the lanes between tree rows and the grove edges are weeded manually or with tools, and herbicides are applied. This level of management required the deployment of many workers who inevitably discovered most of the existing partridge nests in the grove. When a nest was discovered, the workers left it undisturbed by not cutting the surrounding vegetation. All the nest locations were reported to the estate gamekeeper, who also regularly monitored the nest and informed us of any hatching, nest loss, or clutch desertion. To avoid further disturbance to the nesting birds, nest monitoring was carried out only by this person, who kept a safe distance from them and used a 60× telescope (ATS Swarovski optic). We only visited the nests once the eggs had hatched or

Fig. 2. Red-legged partridge nests with eggshells cleanly separated into two halves because of the hatching process.

Fig. 3. Red-legged partridge nests in which broken eggs were found, which suggests predation.

failed. Nests with hatched eggs were easily identified since the eggshells were cleanly separated into two halves because of the hatching process (Fig. 2), while eggs disappeared, were broken (possible predation; Fig. 3), were unhatched, and were found cold much later than their expected hatching time in the failed nests.

To identify possible egg breakage patterns and relate them to lizard predation events, we kept some ocellated lizards in captivity in a farmhouse in the same study area. We used wooden reptile terrariums (150 × 50 × 50 cm) with glass fronts and a bottom with a steel grid that ensured good airflow. The wood was resistant to heat and humidity, and the glass allowed observation. The terrarium had a bed of soil, dry leaves and olive branches that recreated the outside olive grove habitat. The lizards were caught live by the gamekeeper and confined in the terrariums. We supplied partridge eggs to these caged predators and found that ocellated lizards exhibited an unmistakable pattern of egg breakage (Fig. 4), signified by the appearance of a distinct pattern of teeth marks on the eggshell (Herranz 2000), which provided a method for identifying partridge nests that were predated by lizards (see Green et al. 1987 for a similar procedure). The lizards' captivity did not last more than a week as they were released in perfect condition at the same point of capture in this period. During their captivity, the relevant animal welfare requirements were observed.

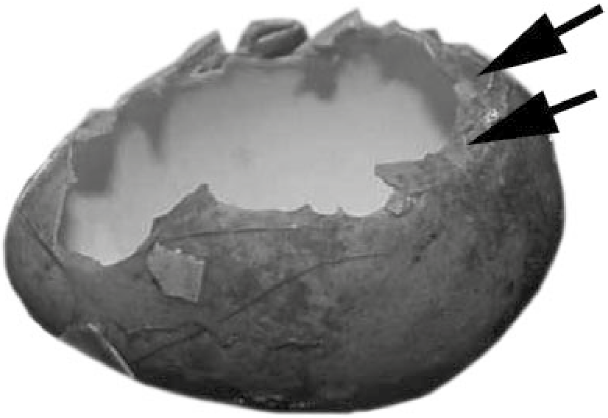

Fig. 4. Breakage pattern of red-legged partridge eggs by ocellated lizards, recorded using lizards in captivity. The arrows indicate the compression marks. Photo: Jesús Duarte.

Data analysis

We only considered nests estimated to have been predated by ocellated lizards and successful nests with hatched eggs. For both of these nest types, we recorded several microhabitat variables (hereafter "nesting site") surrounding the nest (Table 1). These variables were related to the olive tree under which the nest was found (e.g. age, trunk structure, ring, canopy, and nearby lane) and to the surrounding habitat features (e.g. vegetation coverage and height, distance to borders and crops, water, and ocellated lizard shelter availability). In addition, we considered possible lizard shelters, rabbit burrows, rock clumps, and holes in stone walls or old buildings or farmhouses.

The nesting site variables set were analysed to detect potential multicollinearity by developing a Spearman's rank correlation coefficients (rho) matrix for each pair of variables. Based on these values, the coefficient of determination (R^2) and the Variance Inflation Factor (VIF) were calculated, the latter as $1/(1 - R^2)$ (Kleinbaum et al. 2007). Variables with VIF > 5 were rejected from subsequent analyses (O'Brien 2007), thereby we only included variables that captured the effects of any set of highly correlated variables in the final models (Tischendorf 2001).

We generated predictive models using a generalised linear mixed model (GLMM) with binomial error distribution and a logit link function (Crawley 1993) to test if the probability of detecting a nest predated

Table 1. Variables used to study the microhabitat of the red-legged partridge nest sites.

Variable (Code)	Type	Biological justification
Age of the olive tree (Age)	Categorical* 1 (0-8), 2 (9-19), 3 (25-100), 4 (> 100 years)	Younger trees offer less protection against predators and less complexity than older
Presence of piled cut branches in the olive tree ring or lane (Branch)	Binomial**	Piled brunches support shelter to predators
Distance to the nearest border of the olive grove or strip inside it (any vegetation patch different from olive trees) (DBorder)	Continuous (m)	Edge effect, access of predators from other habitats
Distance to the nearest herbaceous crop (Dcrop)	Continuous (m)	Edge effect, access of predators from other habitats
Distance to the nearest water point (Dwater)	Continuous (m)	Food availability (insects) for ocellated lizards
Distance to the nearest ocellated lizard shelter (rabbit burrow, accumulations of stones, holes in stone walls or old buildings) (Dshelter)	Continuous (m)	Ocellated lizard refuge availability may increase predation risk
Height of the lower branches of tree canopy perimeter (from lower side of the base of branch to the ground) (Canopy)	Continuous (m)	Lower branches hide partridges and allow early detection of a predator. Associated to oldest and most complex trees
Presence of holes at ground or above ground level in the olive tree trunk (Holes)	Binomial	Nearby shelters for predators
Irrigation regime of the olive grove patch (dripping)	Categorical 1 (no irrigation, rainfed), 2 (dripping)	Water availability important for partridges but also for predators. It supports more vegetation and insects: attraction effect
Number of trunks (legs) of the olive tree (Nlegs)	Continuous (range: x-y)	More legs, more microhabitat complexity
Herbaceous vegetation cover in the olive tree ring (area below tree canopy) (Hcover)	Categorical 0 (0%), 1 (< 20%), 2 (20-40%), 3 (40-60%), 4 (60-80%), 5 (> 80%)	Shelter for predators or coverage for nests
Herbaceous vegetation height in the olive tree ring (Hheight)	Categorical 0 (0 cm), 1 (< 20 cm), 2 (20-50 cm), 3 (> 50 cm)	Shelter for predators or coverage for nests

* Age of olive trees according to Muñoz-Cobo & Purroy (1980). ** In binomial variables absence always coded as 0 and presence as 1.

by ocellated lizards was related to the nesting sites' microhabitats. Ocellated-lizard-predated nests (the dependent variable) were encoded as "1," while the successful nests were coded as "0." Covariables and the factors listed in Table 1, as well as the two-way interactions between distance to a possible lizard shelter and variables related to lizard concealment possibilities (herbaceous cover and height, canopy height, presence of piles branches or holes in the tree), were initially included in the model as possible explanatory effects. The year of sampling was considered a random effect in the model. We compared models using Akaike's Information Criterion corrected for small samples (AICc) and selected the model with the lowest AICc.

A chi-square analysis was used to test for differences in ocellated-lizard-predated nest frequencies between years (Fowler & Cohen 1992). All analyses were performed using SPSS 24.0 (IBM, USA). Means are provided with their standard errors.

Results

During the three nesting seasons, we identified 13 nests predated by ocellated lizards, and we recorded habitat features in these predated nests and the 78 successful red-legged partridge nests. Lizard predation on partridge nests was homogeneous during the three years under study: four nests in 1996, five in 1997, and four in 1998 (chi-square test = 0.153; df = 2; P = 0.925).

Of the nests predated by ocellated lizards, predation affected the number of laid eggs in only 38.5%. In the remaining 61.5% of the nests, predation was partial and only affected some eggs. In these cases of partial predation, the rest of the eggs hatched in two nests (25%), while the non-predated eggs were abandoned, and incubation stopped in the remaining nests (75%).

The mean clutch size of the nests predated by ocellated lizards was 11.6 ± 0.8 eggs. Ocellated lizards only preyed on one egg in the two cases of nests with partial predation and hatched eggs. Ocellated lizards predated on an average of 6.5 ± 1.3 eggs per nest, while 3.8 ± 1.4 eggs per nest failed after partial predation.

Tests for multicollinearity did not reveal any variables with VIF > 5. The best model (Table 2) correctly classified 100% of the successful nests and 61.5% of the nests predated by lizards. Nest predation was only significantly affected by the distance of the nest to a potential ocellated lizard shelter (Poisson GLMM: Wald χ^2 = 7.679; P = 0.007) as the predated nests were closer to lizard shelters (84.2 ± 11.6 m) than the successful nests (276.1 ± 15.4 m).

Table 2. Results of GLMMs explaining variation in red-legged partridge successful nests and those predated by ocellated lizards in the study area. All the valid models generated testing different combinations between the interactions and the set of variables and factors are presented. Dshelter – distance to the nearest ocellated lizard refuge, k – number of parameters, AICc – Akaike information criterion corrected for small sample sizes.

Model	k	AICc
Dshelter	2	462.463
Dshelter	2	464.533
Dshelter	2	472.561
Dshelter	2	473.581
Dshelter	2	478.719
Null	1	572.263

Discussion

There has been much discussion on whether predation is a significant cause of nest loss for the red-legged partridge and if it affects its reproductive success (Ferreras et al. 2022). In this study, we found 13 nests predated by ocellated lizards. However, in the same study area and period, Duarte (2012) found 18 nests predated by mammals and 45 nests that failed due to human interference (farming or nuisance) from a total sample of 165 nests.

Therefore, in the study area, farming- and human-related failures impacted red-legged partridge nests that were 3.5 times larger than that of lizards. These data suggest that the leading cause of nest failure in the olive grove studied is agricultural work, not predators. Among these predators, ocellated lizards had a slightly lower impact on the nests than other predators, mainly mammals responsible for partridge nest losses in olive groves (Duarte & Vargas 2001b).

Partridge nest predation by ocellated lizards represented a small portion of the large sample of nests that were predated during our three years of study, and they were predated at almost the same rate in every year studied (between four and five nests per year). However, ocellated lizard predation in olive groves is more common than previously reported in more northern Spanish localities (e.g. Herranz 2000, Herranz et al. 2002).

However, the results show that the probability of a partridge nest being preyed on by an ocellated lizard is closely associated with microhabitats associated with the nests. Specifically, it is related to the existence of a shelter in which an ocellated lizard can hide (e.g. rabbit burrows and holes in the walls of old buildings, rocks, and piles of stones) being close to a nest rather than the characteristics of the vegetation or the olive tree next to the nest. These resources are not widely distributed throughout the olive grove, and their distribution seems to be associated with predated nests.

As proposed in the initial hypothesis, predation is related to habitat. Favourable habitat conditions for a predator allow it to reach an optimal population state, thereby enabling it to select its prey according to its requirements and increasing predation risk for the prey (Wheatley et al. 2020). The habitat of the ocellated lizard in the olive grove has not been specifically studied, but olive groves are considered a favourable habitat for reptiles (Carpio et al. 2016). There are several reasons for this. First, according to Busack & Visnaw (1989), ocellated lizards are active in ambient temperatures of 15-42 °C, which is typical in our study area. Second, olive groves are considered an open forested habitat with some structural complexity within habitat patches, but they have an open structure that allows for clearings, which are favoured by ocellated lizards for their insolation and search for prey (Mellado et al. 1975) as well as the existence of numerous crevices for shelter (Díaz et al. 2006). In the case of olive groves, these crevices are not rock cracks but holes in the tree trunks, as the ocellated lizard has a well-developed tree-climbing ability and often uses trunk holes as a refuge (Pérez-Mellado 1998). The holes in olive trees are so common, especially in trees of a certain age, that this variable proved insignificant in the developed model. This finding is probably because most olive trees in the study area have holes and are old.

The model does not analyse the significant effect of vegetation of the ring and lanes of the olive tree on ocellated lizard predation largely because this is a transient characteristic in the olive grove's partridge nests. However, this does not mean that the lizards may not favour the lack of vegetation in some way. On the contrary, farming practices tend to cause the disappearance of this vegetation, and although its presence and the existence of cover provide structural complexity to the olive tree (Muñoz-Cobo 1992), the removal of vegetation is favoured by anthropic predators (Duarte 2012), which prefer nests located in young olive plantations, olive patches of low structural complexity, or tree canopies far above the ground (Duarte & Vargas 2001b). Furthermore, the lack of vegetation may increase the lizards' ability to see and actively locate possible prey (Hernández et al. 1991).

Proximity to borders of herbaceous crops, which are some of the habitats of ocellated lizards (Busack & Visnaw 1989), or to water sources and hedges do not favour predation either. What is relevant and significant is the existence of optimal shelters for ocellated lizards near the nests. The mean distance between predated nests and ocellated lizard shelters is compatible with the mean daily movement of the ocellated lizards and the size of their territories (Salvador et al. 2004), and successful nests are out of reach of ocellated lizard territories that provide optimal shelter. Therefore, a partridge establishing a nest near one of these ocellated lizard shelters creates a predation risk. Moreover, rabbit burrows and refuges are critical habitat components for ocellated lizards (Grillet et al. 2010).

The ocellated lizards' hunting strategy involves actively searching for insects along long ground-level routes (Mateo 1988, Hernández 1990, Hernández et al. 1991), during which they may encounter partridge nests. This searching behaviour is usually performed on vegetated patches (as insects are guaranteed to be there) of low height, as this is what ocellated lizards can see. However, this hunting is also carried out in patches with cut vegetation whenever some factor attracts insects, such as water (Vasconcelos et al. 2022). Most of the olive trees in this study area are drip irrigated. Therefore, the natural water sources are insignificant as water is widely available throughout the olive grove.

Ocellated lizards consume prey according to their body size since they cannot break live prey into smaller pieces, so they are gape-limited (Mellado et al. 1975). Another critical factor is the energy provided by the prey. While these lizards reject prey below a minimum threshold (Castilla 1989), large prey is captured only when the effort is minimal while providing maximum energy production, such as eggs. The maximum prey size captured by an adult ocellated lizard (Castilla et al. 1991) is comparable to a partridge egg, which is a static item and requires little effort to capture beyond breaking the shell to access its contents. If there are any cracks or shelters that ocellated lizards can use as a refuge near the nest, the conditions that allow the lizard to find the partridge nest are optimum.

Limitations of the study

This work has a series of limitations. Firstly, almost 25 years have elapsed since the fieldwork was carried out, so these results could be no longer valid. Certainly, red-legged partridge populations have decreased in this period. Moreover, ocellated lizard densities have decreased over the last few decades, even though they are frequently encountered in much of their current range (Mateo 2011). However, with both species' population numbers declining, we believe these results are valuable, even more so when the extension and intensification of olive groves continue to grow (Ministerio de Agricultura, Pesca y Alimentación 2021).

However, there may be concern about some of the methods used, such as the methods used to determine which nests were preyed on by lizards and those used to locate the nests in the study area. Regarding the second point, the manual or casual systematic search for nests has been used for this type of work both before and after this study (Cuadrado & Domínguez 1996). In farms subject to economic interest and without being able to use radio-tracking methods (see Buenestado et al. 2009, Mateo-Moriones et al. 2012), our approach was one of the few options available for studying red-legged partridges in olive groves. Therefore, we took advantage of the circumstances in this study to obtain the data. Nevertheless, the search (conducted by farmers in their daily work) and follow-up assessment were carried out with all possible precautions.

Secondly, applying currently available methods (e.g. camera trapping) would have been much better for monitoring nest success or confirming predation by ocellated lizards as they are more reliable and less intrusive. These methods would have even allowed for estimating more appropriate loss and success rates based on daily monitoring (Cox et al. 2012, Carpio et al. 2014). However, in the historical context of the study and considering these limitations, the results indicate the relationship between a predator (the ocellated lizard) and its prey (the eggs present in the red-legged partridge nests).

Conclusions and management implications

The results of this work should be considered an approximation, given the limitations inherent in the methods. However, although it can be argued whether the number of nests predated by ocellated lizards herein is representative, the results that link these predated nests to the characteristics of their nearest microhabitats are consistent with the ecology of the ocellated lizard.

Given ocellated lizards' protected status and worrying recent population trends, ocellated lizard conservation should take a more prominent role when applying management measures to reduce their predation on game species. This approach rejects any direct control campaign in favour of measures focusing on habitat management. For example, instead of removing vegetation from the olive grove, which has environmental consequences on the soil and its biodiversity (Rey et al. 2019, Tarifa et al. 2021), maintaining well-developed herbaceous vegetation in the olive rings (Bravo et al. 2022) would not only prevent ocellated lizards searching for prey in the areas in which partridges typically nest but would also benefit partridges by reducing the chances of nest abandonment and probably that of predation by other feral and domestic species (Castro-Caro et al. 2014). Furthermore, this simple measure could redirect ocellated lizards' foraging and searching behaviours, thus reducing their probability of finding a partridge nest.

However, the immediate removal of structures that can be used as shelters by ocellated lizards (e.g. accumulations of stones) or plugging holes in nearby olive trees, rabbit burrows, or holes in farmhouse walls and stone walls is not a realistic measure; there are hundreds of holes in the olive trees, and nothing guarantees that the ocellated lizards will not choose to use the trees if resources become scarce given their ease of climbing. Moreover, these measures could harm other species associated with the olive grove or may result in compensatory mortality, thereby facilitating other predators' access to the nests (Lyons et al. 2015) since nest failures caused by different predator guilds may not be independent (Ellis-Felege et al. 2012).

Given that lizards seem to be among the smallest causative agent of partridge nest losses in olive groves (Duarte & Vargas 2001b, Duarte et al. 2008, Ferreras et al. 2022), one should consider whether this predation rate is too high a price to pay by game managers as farming causes a much more significant impact (Casas & Viñuela 2010, Duarte 2012) and is much easier to manage. In any case, the intensification of the olive grove is damaging partridge populations much more than any of their natural predators.

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Author Contributions

J. Duarte designed the study. Both authors participated in fieldwork and data collection. J. Duarte analysed the data and led the writing. M.A. Farfán improved the manuscript with his valuable comments.

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