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COMMUNICATION

BREAKING BARRIERS: IBERIAN LYNX *LYNX PARDINUS* TEMMINCK, 1827 (MAMMALIA: CARNIVORA: FELIDAE) COLONIZING OLIVE GROVES

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Breaking barriers: Iberian Lynx *Lynx pardinus* Temminck, 1827 (Mammalia: Carnivora: Felidae) colonizing Olive groves

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Abstract: In recent years, the Andújar-Cardeña Iberian Lynx *Lynx pardinus* population has grown both in number and in occupied surface area. This feline has spread into areas surrounding existing population nuclei and occupied new habitats including human-dominated areas and tree crops. Here we describe this colonization process and the evolution of the Iberian Lynx populations in the Olive *Olea europaea* groves that surround typical Lynx scrub habitats in Andújar-Cardeña. Our findings were obtained through radio-tracking, camera trapping and European Rabbit *Oryctolagus cuniculus* monitoring. Two colonized areas—Zocueca and Marmolejo-Montoro—were identified in which Olive cultivation is predominant. Since 2011, a total of 45 and 50 different individuals have been detected in Zocueca and Marmolejo-Montoro, respectively. At present, 19 individuals are known to live in Zocueca and 29 in Marmolejo-Montoro. The main cause of mortality is road-kills. Our results suggest that the Iberian Lynx is capable of colonizing human-modified areas such as agricultural land provided that they can support high-density Rabbit populations and the causes of non-natural mortality are minimized.

Keywords: Agricultural land, camera trapping, human-dominated habitat, radio telemetry, Sierra Morena.

Resumen: En los últimos años, la población de lince ibérico de Andújar-Cardeña ha crecido tanto en número como en superficie ocupada. Este felino se ha extendido a áreas que rodean los núcleos de población existentes y ha ocupado nuevos hábitats, incluyendo áreas dominadas por humanos y cultivos arbóreos. En este trabajo se describe este proceso de colonización y la evolución de las poblaciones de lince ibérico en los olivares *Olea europaea* que rodean sus hábitats típicos de matorral mediterráneo en Andújar-Cardeña. Nuestros hallazgos se obtuvieron mediante radioseguimiento, fototrampeo y seguimiento de la población de conejos. Se identificaron dos áreas colonizadas, Zocueca y Marmolejo-Montoro, en las que predomina el cultivo del olivo. Desde 2011, se han detectado un total de 45 y 50 individuos diferentes en Zocueca y Marmolejo-Montoro, respectivamente. En la actualidad, se sabe que 19 individuos viven en Zocueca y 29 en Marmolejo-Montoro. La principal causa de mortalidad son los atropellos. Nuestros resultados sugieren que el lince ibérico es capaz de colonizar áreas modificadas por humanos, como tierras agrícolas, siempre que existan poblaciones de conejos de alta densidad y se minimicen las causas de la mortalidad no natural.

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Author contribution: Germán Garrote designed the study, conducted the field surveys, compiled the data and wrote this manuscript. Bueno, Ruiz, Lillo, Martín and Moral conducted the field surveys. M.A. Simón wrote this manuscript.

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INTRODUCTION

The global expansion of human activities has had profound consequences for wildlife (Gaynor et al. 2018). Human-induced habitat degradation and loss, prey depletion and poaching are widely recognized as the main threats to carnivores (Karanth et al. 2004; Groenendijk et al. 2015; Wolf & Ripple 2016), causing widespread declines in their populations (Carter & Rosas 1997; Lodé et al. 2001; Ripple et al. 2014). Nevertheless, in recent decades a certain stabilization or even increase in the abundance of some carnivore populations has taken place owing foremost to protective legislation, greater public concern and a variety of policies that encourage co-existence between humans and carnivores (Recharte & Bodmer 2010; Chapron et al. 2014). Some carnivore species can now settle in and use human-altered landscapes if there are no human activities that act as impediments (Dellinger et al. 2013; Garrote et al. 2013). Thus, understanding and then managing carnivore responses to landscape heterogeneity and to the human-driven changes occurring therein are now two main priorities in ecological research and applied conservation techniques (Fahrig et al. 2011).

The Iberian Lynx *Lynx pardinus* is an Iberian endemic specialist predator whose staple prey is the European Rabbit *Oryctolagus cuniculus* (Fedriani et al. 1999; Gil-Sánchez et al. 2006). Its populations dropped dramatically in the 20th century (Gil-Sánchez & McCain 2011) to the point that at the beginning of the 21st century, less than 100 Lynx were estimated to remain in just two isolated populations in eastern Sierra Morena and Doñana (Simón et al. 2012; Guzmán et al. 2004). This decline was attributed to the combined effects of habitat destruction and fragmentation, declines in European Rabbit abundance, and hunting and/or poaching (Guzman et al. 2004; Rodríguez & Delibes 2004). As a result, the species was listed as Critically Endangered in 2002 (Cat Specialist Group 2002). Since then, the Iberian Lynx population increased significantly in size due to measures carried out as part of conservation projects (Simón et al. 2012) designed to increase the carrying capacity of occupied habitats by enhancing European Rabbit populations, reducing known causes of mortality, and creating new populations through reintroductions (Simón et al. 2012). These actions succeeded in population recovery, so that the Iberian Lynx was downlisted to Endangered in 2015 (Rodríguez & Calzada 2015). By 2017, the minimum number of Iberian Lynx detected in the wild was estimated at 589 individuals (Simón 2018). Specifically, the population in

Andújar-Cardeña rose from 79 individuals in an area of 153km² in 2004 to 195 individuals detected in 520km² in 2017. During the period of 13 years, the Lynx has spread to areas surrounding its main remnant population nuclei that contain apparently suboptimal habitats such as humanized areas and tree crops (Garrote et al. 2013, 2016).

On the southeastern edge of the range of the Andújar-Cardeña Lynx population, the Mediterranean scrubland borders vast swathes of intensively cultivated Olive *Olea europaea* groves. The first Lynx to establish territories here were detected in 2012, and the first breeding attempt in this type of habitat was recorded in 2013 (Garrote et al. 2015). Thereafter, more Lynx began to occupy this area and a new Lynx subpopulation was established 8km to the south of the main population in an area dominated by Olive groves. Below, we describe the colonization process and evolution of the Iberian Lynx populations that now thrive in these new habitats.

STUDY AREAS

Andújar-Cardeña in eastern Spain's Sierra Morena (Figure 1) is an area with low mountains covered by well-preserved Mediterranean forests and scrublands where most of the land is occupied by large hunting reserves. It is located between Guadalmellato (25km to the west) and Guarrizas (30km to the east), where Iberian Lynx were reintroduced since 2010. By 2017, the minimum number of individuals detected in Guadalmellato and Guarrizas were 82 and 85 individuals, respectively (Simón 2018). On the southern to southeastern edge of Andujar-Cardeña, the Mediterranean scrubland borders two large areas of intensive Olive cultivation consisting of old trees set in parallel lines, Marmolejo-Montoro and Zocueca. Due to the intensive management of these groves, few patches of shrubs or meadows still exist, the only exceptions to this uniformity being small rocky outcrops that cannot be managed, scattered stands of Mastic Tree *Pistacia lentiscus* and Holly Oak *Quercus coccifera*, and narrow (< 2m) gullies lined with Giant Cane *Arundo donax* and young White Poplar *Populus alba*. To the south of both areas flows the Guadalquivir River, which is surrounded by a gallery forest consisting mainly of White Poplar.

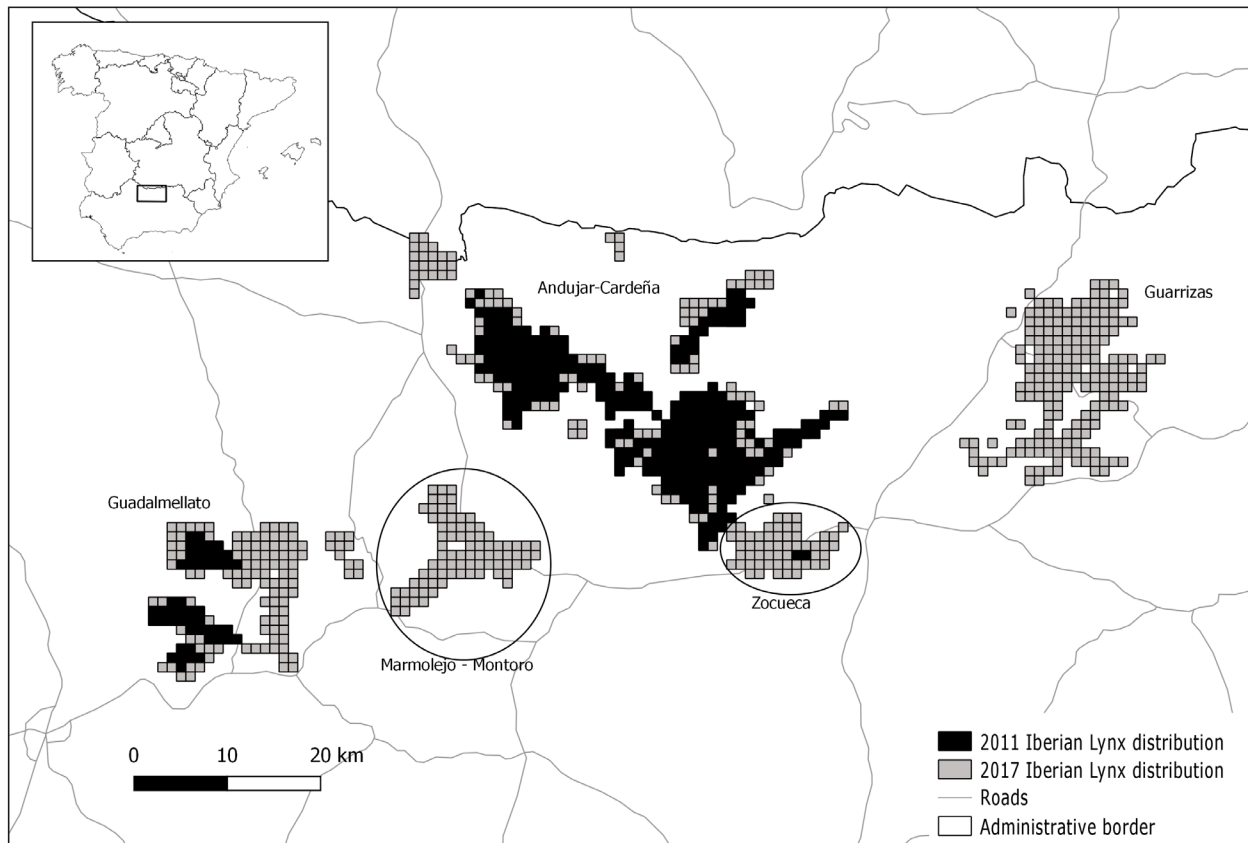


Figure 1. Iberian Lynx distribution in Sierra Morena, Andalucía. Guarrizas and Guadalmellato populations, created by reintroduction, are included. The study areas of Marmolejo-Montoro and Zocueca are shown by an ellipse.

MATERIALS AND METHODS

Our findings were obtained as part of the Iberian Lynx population-monitoring program carried out within the framework of the Iberian Lynx Life Project (see Simón 2012; Simón et al. 2012). This monitoring program employs radio-tracking, camera trapping and Rabbit population monitoring. Radio-tagged Lynxes were captured using double-entrance, electro-welded mesh box traps (2×0.5×0.5 m) baited with Rabbits where Lynx were trapped and then fitted with VHF radio collars (Wagener Collar, Brenaerham, Germany). The VHF radio-tracking routine consisted of obtaining 1–5 locations by triangulation each week. We used the Locate extension of the QGIS 2.2.0 (QGIS Development Team, 2014) program to obtain locations from the field data. Camera traps were deployed across the entire Iberian Lynx distribution area (Gil-Sánchez et al. 2011). During the year, signs of Lynx presence like tracks and excrements were searched for in the known distribution area and in its periphery. When such signs were detected in a new area, camera traps were installed to confirm

the species' presence and to attempt to identify the individuals present. In this way, we were able to identify the areas into which the species was expanding, which were then incorporated into the annual population-monitoring program. We designed a camera trapping grid system each year, with a mean distance between cameras of 1.36 ± 1.03 km. Surveys lasted from June to July until October to November to maximize detection of kittens. The camera stations were kept active for a period of two to five months, depending on efficiency and redundancy of captures. Cameras were baited with Lynx urine or with live bait, either Rabbits or Rock Pigeons *Columba livia* in wire cages inaccessible by Lynxes. Each camera trap was visited once a week allowing to download pictures, to replenish urine or batteries and to care for live bait. Due to high levels of human frequentation and unrestricted access, only Lynx urine was used as bait in the Olive groves to avoid camera theft. Two camera trap models were used in this study: Moultrie M880 and Covert II Assassin. Lynxes were individually identified on the basis of their spot pattern (Garrote et al. 2011). Fecundity was assessed

yearly by camera trapping through counting the number of kittens that accompanied each adult female after the breeding season. Therefore, our measure of fecundity is in regards to the number of kittens per territorial female detected during the period of post-weaning dependence (Monterroso et al. 2016). We identified a Lynx as territorial if the individual had breeding status, determined through detection of kittens, and/or if the camera trapping results or radiotracking data supported a non-overlapping surface (Gil-Sánchez et al. 2011). The information obtained from the camera traps and radiotracking enabled us to delimit the species' annual area of presence in a grid of 1x1 km².

European Rabbit populations were monitored using latrine counts (> 20 pellets in a circle with an area > 30cm²) along transects. Latrine counts are an indirect method that is frequently used to estimate relative Rabbit abundance over large areas (Virgós et al. 2003), which is calculated as a kilometric abundance index (KAI) of latrines. The complete Iberian Lynx distribution area was divided into 2.5x2.5 km² squares. Latrine counts were carried out along 4.5–7 km transects in each square. Sampling was conducted once a year in June and July at the end of the Rabbits' breeding season (June–July) when the populations reached their greatest density (Beltrán 1991).

RESULTS

Two areas dominated by Olive cultivation were identified as having been colonised by Iberian Lynx. The first, Zocueca, is located on the southeastern edge of the main population (Figure 1). A total of 56 camera traps were installed in this area from 2011 to 2017, yielding a sampling effort of 2,017 trap nights. A total of 46 different individuals were identified throughout the study period. The first Lynx was detected in 2011. In 2017, a minimum of 19 individuals were detected in an area of 53km² (Table 1).

The second area, Marmolejo-Montoro, lies 8km to the south-west of the main Andújar-Cardeña Lynx population. The first two Lynx were sighted and radio-detected here in 2013; one was a radio-collared individual from the main Andújar-Cardeña population (Table 1). A total of 58 camera traps were installed in this area from 2013 to 2017, yielding a sampling effort of 7,474 trap nights. A total of 50 different individuals were identified throughout the study period. In 2017, a minimum of 29 individuals had been detected in an area of 82km².

Nine Lynx with radio-collars were monitored in Zocueca and seven in Marmolejo-Montoro. Of these 16 individuals, seven were captured and radio-marked in



Image 1. Iberian Lynx in an Olive grove in Sierra Morena, Spain.

Table 1. Results of the Iberian Lynx population-monitoring in our study area.

| | 2011 | 2012 | 2013 | 2014 | 2015 | 2016 | 2017 |
|------------------------------------|--------|---------|---------|-----------|-----------|-----------|-----------|
| ZOCUECA | | | | | | | |
| Individuals | 1 | 4 | 12 | 11 | 10 | 14 | 19 |
| Breeding females | 0 | 0 | 2 | 3 | 3 | 4 | 4 |
| Breeding events | 0 | 0 | 1 | 2 | 1 | 3 | 4 |
| Kittens | 0 | 0 | 2 | 5 | 2 | 6 | 10 |
| Kittens/breeding females | 0 | 0 | 1 | 1.7 | 0.7 | 1.5 | 2.5 |
| Surface | 2 | 12 | 27 | 47 | 44 | 54 | 53 |
| Rabbit abundance | - | - | 22.5 | 18.8 | 18.9 | 26.2 | 19.5 |
| Radio-tagged individuals | 0 | 1 | 2 | 3 | 5 | 4 | 5 |
| Camera-trap stations (trap nights) | 2 (62) | 2 (175) | 5 (225) | 5 (246) | 20 (433) | 11 (446) | 11 (430) |
| MARMOLEJO-MONTORO | | | | | | | |
| Individuals | | | 2 | 9 | 24 | 28 | 29 |
| Breeding females | | | 0 | 2 | 5 | 5 | 6 |
| Breeding events | | | 0 | 1 | 5 | 3 | 4 |
| Kittens | | | 0 | 2 | 13 | 9 | 8 |
| Kittens/breeding females | | | 0 | 1.0 | 2.6 | 1.8 | 1 |
| Dead | | | 0 | 0 | 0 | 3 | 2 |
| Surface | | | 8 | 19 | 73 | 85 | 82 |
| Rabbit abundance | | | - | 9.1 | 29.6 | 25.4 | 23.2 |
| Radio-tagged individuals | | | 1 | 1 | 1 | 6 | 6 |
| Camera-trap stations (trap nights) | | | - | 11 (1068) | 14 (1146) | 16 (2289) | 17 (2971) |

Olive groves in the study area; 10 were individuals that had been marked in other areas and had dispersed into the study area. These Lynx originated from the Andújar-Cardena population ($n=4$), and from the individuals reintroduced into Guarrizas ($n=3$) and Guadalmellato ($n=3$) (Figure 1). One of the Lynx radio-marked in Marmolejo-Montoro established itself in Zocueca.

Rabbit abundances in the two areas are similar, with an annual average of 20.92 ± 3.59 latrines/km in Zocueca (years 2013–2017) and 21.84 ± 8.90 latrines/km in Marmolejo-Montoro (years 2014–2017).

A total of 11 Lynx breeding attempts were detected in Zocueca and 13 in Marmolejo-Montoro. Average fecundity was 1.46 ± 0.70 and 1.68 ± 0.69 kittens/year/territorial female in Zocueca and Marmolejo-Montoro, respectively.

In all, 22 Lynx deaths were reported (Table 2), with road accidents being the most frequent cause of death in both populations (63%). Disease was the second commonest cause of death (18%); of the four known cases, one was a five-year-old territorial female that died of tuberculosis; and the other three were old animals that had lost their territories and had wandered into this area.

Table 2. Cause-specific mortality detected in the Zocueca and Marmolejo-Montoro Iberian Lynx populations in the period 2011–2017.

| | Zocueca | Marmolejo-Montoro |
|--------------|-----------|-------------------|
| Road-kill | 10 | 4 |
| Poaching | 1 | 0 |
| Disease | 4 | 0 |
| Fight | 2 | 0 |
| Total | 17 | 5 |

DISCUSSION

Our results show that the Iberian Lynx has colonized the Olive groves that border the Mediterranean scrub habitats in the mountains of Andújar and Cardena. When the Lynx's range was at its smallest and restricted to just Doñana and Andújar, the research showed that its preferred habitat was found to be Mediterranean shrublands (Palomares et al. 2000; Fernández et al. 2006). Specifically, Lynx showed a preference for areas with shrub cover of over 35%, rocky outcrops and high densities of European Rabbits (Palomares et al. 2000;



Image 2. Iberian Lynx in Zocueca, Spain.

Palomares 2001; Fernández et al. 2006), whereas arable areas and woody crops were identified as unsuitable habitats (Palomares 2001; Fernández et al. 2006). Nevertheless, our findings suggest that the ecology of the Iberian Lynx is more plastic than originally thought, and that it is able to use habitats including agricultural areas that were deemed unsuitable (Palomares et al. 2000). Although some patches of scrub must be present in the chosen agricultural areas, research shows that the Iberian Lynx can establish territories and even reproduce in areas with only 2% shrub cover as long as suitable Rabbit densities exist (Garrote et al. 2016).

The presence of this feline is dependent on Rabbit abundance, which directly affects its demography and, above all, its breeding rates (Monterroso et al. 2016). The appearance in 2011 of a new variant of the Rabbit Haemorrhagic Disease Virus (RHDV2), also known as *Lagovirus europaeus* GI.2 (hereafter GI.2; Le Pendu et al. 2017) in European Rabbit populations led to a decline of 60–70% in Rabbit populations in Andújar-Cardeña, which was followed by a fall of 45.5% in Lynx breeding rates from 1.36 ± 0.12 kittens/year/territorial female before GI.2 to 0.13 ± 0.07 (2011–2013; Monterroso et al. 2016). Emergency management actions implemented to alleviate the effects of GI.2 (i.e., Rabbit restocking operations and the setting up of supplementary feeding stations) prompted a significant increase in Lynx fecundity (2012–2017: 0.82 ± 0.19 kittens/year/territorial female, unpublished data). Pre-GI.2 fecundity values,



Image 3. Iberian Lynx (kitten) in Zocueca, Spain.

however, have not yet been restored. In the Olive groves where Rabbit abundance was three times higher than in Andújar-Cardeña (07.13 ± 0.62 latrines/km; unpublished data), Lynx fecundity reached 1.46 ± 0.70 and 1.68 ± 0.69 kittens/year/territorial female in Zocueca and Marmolejo-Montoro, respectively. These values are higher than the fecundity detected in the Andújar-Cardeña Lynx population during the same period and similar to values during the pre-GI.2 period. Evidently, Lynx breeding rates are not impeded by the use of Olive grove habitat.

The recovery of the Iberian Lynx population in Andújar-Cardeña was due to two main factors: (i) the carrying capacity of the habitat was increased by improving Rabbit populations and (ii) non-natural mortality was reduced (Simón et al. 2012; López et al. 2014). In the most remote areas where the impact of human presence is minimal, the main strategy employed was the reinforcement of Rabbit populations. In more peripheral areas, where Rabbit populations are strong enough to sustain the territorial Lynx's, the emphasis was put on reducing non-natural mortality via an anti-poaching program, the identification of road black-spots and educational activities. As a consequence of these



conservation efforts, Lynx mortality (compared to figures from the 1980s and 1990s) has decreased significantly, not only in Andújar-Cardeña but throughout its whole range (Simón et al. 2012; Lopez et al. 2014). The highest abundance ($n = 202$ individuals) and density (0.72 individuals/km²) of the Lynx population in Andujar-Cardeña was reached between 2010 and 2011. This coincides with the completion of the conservation efforts to increase the carrying capacity of the Lynx. It was also during this time that the first Lynx was detected in the Olive groves. Almost simultaneously, the appearance of the aforementioned GI.2 caused a significant decline in Rabbit populations in areas of historical presence, reaching minimum densities in 2013 (Monterroso et al. 2016). Therefore, the process of colonization of Olive groves by the Lynx could be due to the search for new territories due to intraspecific competition, conditioned by demographic pressure, and subsequently exacerbated by the reduction in the carrying capacity of the medium due to the drastic decline of food. It is after the settlement of the first Lynx native to Andujar-Cardeña, when dispersing Lynx of the neighboring Guarrizas and Guadalmellato populations were detected.

It has become obvious that the Iberian Lynx can colonize areas such as Olive groves that have been altered by human activities, provided that good Rabbit populations exist and that mortality rates are kept to acceptable levels (López-Parra et al. 2012; Garrote et al. 2013; López et al. 2014). The colonization of these areas improved connectivity between Lynx populations in Andújar-Cardeña, Guarrizas and Guadalmellato, and stimulated a continuous exchange of individuals. Today, these populations can be considered a single metapopulation. The vast areas of agricultural land surrounding traditional Lynx habitats were always regarded as unsuitable and obstructing the species' expansion. Nevertheless, the historical absence of the Lynx in these areas could in fact be more closely tied to human-induced mortality than to any lack of habitat resources (Corsi et al. 1999; Gastón et al. 2016). Given the scarcity of European Rabbits in most Iberian habitats (Delibes-Mateos et al. 2014), agricultural areas with small patches of scrub could become the most Rabbit-rich habitat in the Lynx's range (Calvete et al. 2004). Therefore, management should be orientated towards allowing small shrubby patches to be conserved in Olive groves and other agricultural areas. Likewise, vigorous actions must be implemented to reduce non-natural mortality, which would notably increase the useful surface available for Iberian Lynx.

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