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Iberian Lynx *Lynx pardinus* Temminck, 1827 (Mammalia: Carnivora: Felidae) in central Spain: trophic niche of an isolated population

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Abstract: Understanding predator-prey relationships is fundamental to develop effective conservation plans. Between 2015 and 2018, we combed 21 transects, each 7km long, searching for Iberian Lynx *Lynx pardinus* scat within the province of Madrid in central Spain. In order to minimise inherent subjectivity of visual identification as much as possible, we performed a double specific nested polymerase chain reaction (PCR) followed by a primer extension assay addressed to two Iberian Lynx diagnostic single nucleotide polymorphisms. Forty-six scat samples were positively identified as belonging to Iberian Lynx through genetic analysis. From these, we extracted remains of consumed prey, which we determined to the lowest possible taxonomic level, mainly through hair identification. Identified prey was divided into four types: lagomorphs, small mammals, birds, and ungulates. The species’ diet composition was described based on the frequency of occurrence (FO) of each prey and niche breadth, and also compared with prior knowledge of the species using four prior studies as a comparative reference through the calculation of the niche overlap value. The FO of lagomorphs (39%) was the lowest, while the FO of small mammals (54%) was the highest recorded to date. The niche breadth (0.36) was higher than recorded in prior studies, but still showing the specialist character of the Iberian Lynx. Niche overlap was low (C = 0.49), showing differences in trophic niche between the population in our study area and the one studied in southern Spain. This indicates that the Iberian Lynx is adept at switching its main prey, an ability that has previously been firmly rejected. It is, however, capable of adapting to alternative prey more often than recorded to date, which could be a behavioural response to the patchy distribution of European Rabbit *Oryctolagus cuniculus* in the study area.

Keywords: Diet, lagomorphs, niche breadth, niche overlap, single nucleotide polymorphism.
INTRODUCTION

The Iberian Lynx *Lynx pardinus* is endemic to the Iberian peninsula (Rodríguez & Delibes 1992), and is regarded as a trophic super specialist (Ferrer & Negro 2004). Since the 1950s, the Iberian Lynx population has declined continuously (Valverde 1963; Cabezas-Díaz et al. 2009). Only 93 individuals were recorded in 2002 (Guzmán et al. 2004). Following conservation measures such as reintroductions of captive-bred Iberian Lynxes in southern Spain, this population experienced a constant growth (Simón et al. 2011; Rodríguez & Calzada 2015), reaching 589 individuals in 2017 (Simón 2018). Furthermore, Cruz et al. (2019) confirmed the presence of Iberian Lynxes outside the currently known range of the species in the southern Iberian peninsula, suggesting the continued existence of a stable population in central Spain within the province of Madrid.

The diet of a species is a fundamental aspect of its ecology that depends mainly on the abundance and availability of prey types (Terrabe & Arroyo 2011), but also on learning and experience of individuals (Shipley et al. 2009). A widespread phenomenon in many vertebrate and invertebrate taxa (Bolnick et al. 2003) is the so-called ‘niche variation hypothesis’. This occurs when some co-occurring individuals of a species actively select different prey types in their shared environment (Araujo et al. 2011). The niche variation could be a response to two main factors: (i) change in environmental conditions that affects prey availability and prompts all individuals of a population to use a larger spectrum of resources, or (ii) each individual continues to use a narrow range of resources that diverges from conspecifics, thus minimizing the interspecific competition (Costa et al. 2008).

Understanding predator-prey relationships is fundamental to identify conservation priorities, prior to the design of conservation programmes for vulnerable or endangered species (Popp et al. 2018). Lacking information on these relationships could result in ill-informed conservation strategies that lead to a failure of reaching conservation goals and at the same time to a gross waste of resources, as occurred in the Doñana National Park and in Sierra Morena showed that the European Rabbit is its main prey, being present in 70–99% of analysed samples (Delibes 1980; Beltrán & Delibes 1991; Palomares et al. 2001; Gil-Sánchez et al. 2006). The Iberian Lynx, however, also consumes other prey species in lower proportions, but their relative importance increases when the availability of Rabbits decreases (Beltrán et al. 1985; Beltrán & Delibes 1991). Therefore, Iberian Lynxes also prey on small mammals, e.g., Wood Mouse *Apodemus sylvaticus* and Garden Dormouse *Eliomys quercinus* (Aymérich 1982; Gil-Sánchez et al. 2006), wild ungulates like Red Deer *Cervus elaphus*, Fallow Deer *Dama dama* (Delibes 1980; Beltrán et al. 1985; Beltrán & Delibes 1991; Gil-Sánchez et al. 2006), European Mouffon *Ovis orientalis musimon* (Gil-Sánchez et al. 2006), and birds such as Red-legged Partridge *Alectoris rufa*, Mallard *Anas platyrhynchos* and Eurasian Magpie *Pica pica* (Delibes 1980; Aymérich 1982; Beltrán & Delibes 1991; Gil-Sánchez et al. 2006).

In this article, we report the diet composition of Iberian Lynx, based on analysis of scat collected in a study area in central Spain. We discuss the trophic niche breadth of this population in the light of research conducted on the species’ diet in southern Spain.
STUDY AREA

The research was performed in the western region of the province of Madrid (Figure 1), which is delimited by boundaries with the community of Castilla–León in the north and northwest, the community of Castilla–La Mancha in the south, and the Manzanares River basin in the east. The study area ranges in elevation from 440 to 2,320 m. It represents three main landscape regions: (i) the Guadarrama Mountains, a mountainous granitic zone, (ii) the foothills with a gradient of siliceous sand and soft slopes, and (iii) the depression, a terrain characterised by interfluvial hills (Rivas-Martínez 1982; Zabía & del Olmo 2007).

The meso-Mediterranean zone is the dominant bioclimatic belt within the study area, but the oro- and supra-Mediterranean zones are also present in the Guadarrama Mountains (Rivas-Martínez 1982). The main climatic features of the study area are the seasonal variation in temperature between -8°C and 44°C, summer drought and irregular precipitation ranging from 400 to 2,000 mm per year (Zabía & del Olmo 2007).

The landscape in the study area is a mosaic of pastures with scrub and Holm Oak Quercus ilex groves interspersed with villages and patches of agricultural land (Schmitz et al. 2007; Image 1). Local people use pastures traditionally during the summer for grazing transhumant cattle, periodically perform selective logging in the forests and clean the understorey (Arnaiz-Schmitz et al. 2018).

MATERIAL AND METHODS

Sample collection

Evidence of the presence of Iberian Lynxes within the study area was collected between January 2015 and May 2018. We designed 21 transects of 7 km each that were combed by at least two researchers. We searched for scat on foot along pathways and firebreaks, since both Iberian Lynx and European Wildcat Felis silvestris usually move along such linear structures (Lozano et al. 2013; Garrote et al. 2014). Sometimes, we also combed other less regular landscape features such as the bases of large rocks, around Rabbit holes and near rivers, where scat was more likely to be found (Martín et al. 2007). Along these transects, we searched for scat that...
is morphologically compatible with scat of the Iberian Lynx. This ranges in length from 5cm to 9cm and in width from 1.5cm to 2cm, and is divided into several fragments (Rodríguez 1993). It ranges in colour from ash-grey to dark-brown, and is entirely covered by a mucous patina when fresh (Iglesias & España 2010).

The probability of an erroneous identification of the scat of Iberian Lynx, however, is high (Boshoff & Kerley 2010, Molinari-Jobin et al. 2012; Garrote & de Ayala 2015). It has been often misidentified due to its similarity with the scat of European Wildcat and Red Fox Vulpes vulpes (Palomares et al. 2002). To reduce this probability as much as possible, we performed a specific genetic identification analysis designed by Cruz et al. (2019). This genetic analysis consists of a double specific nested PCR followed by a primer extension assay addressed to two Iberian Lynx diagnostic single nucleotide polymorphisms (SNPs). The product of the double nested PCR is already specific for the Iberian Lynx since we used the primer DL7F [5’-CTT AAT CGT GCA TTA TAC CTTGT-3’] developed by Palomares et al. (2002), which was aligned to sequences of orthologue carnivores including Eurasian lynx Lynx lynx, Canada lynx L. canadensis, European Wildcat, and Domestic Cat Felis catus in order to select diagnostic positions. Then we identified two SNPs specific of the Iberian Lynx. These SNPs were marked with fluorescence and detected through a capillary electrophoresis. This method of analysis provides an increase of sensitivity and straightforward verification of the belonging species through the diagnostic SNPs, being strongly protected against false positive results. For further details see Cruz et al. (2019).

**Content analysis**

Subsequent to positive genetic identification of scat samples as belonging to the Iberian Lynx, we analysed the contents of these samples. We used a stereomicroscope to identify and remove remains of consumed prey like broken bones, teeth, feathers, and hair. Teeth and bone remains were identified with a stereomicroscope, while feathers and hair required the use of a 40x microscope. We washed hairs, first with distilled water and detergent, and then with 70% alcohol as described in Teerink (1991). After drying hairs, we poured a thin layer of transparent nail varnish over a slide and let it dry for 30 seconds. Then we put each hair on the slide for 30 minutes and covered it with a cover glass. That way, we obtained a hair cuticle mould with a scale pattern showing a certain, although limited, taxonomic value (Short 1978).

Removed remains were identified up to the family level, except those belonging to Wild Boar Sus scrofa, because of their easy identification. We identified hair using Teerink (1991) and Valente et al. (2015), teeth using Dueñas et al. (1985), and feathers using Dove & Koch (2011).

**Diet composition**

Hutchinson (1957) defined the niche as an n-dimensional hypervolume where distribution of environmental variables and/or factors would allow a certain species to exist indefinitely. This approach provides a quantitative perspective of the niche concept and, therefore, established the conceptual basis for the performance of studies in many different fields of ecology (Smith 1982). We defined the trophic niche as the n-dimensional hypervolume, n being the number of prey types consumed by the target species, constrained by used trophic resources that would allow the species to exist indefinitely.

For diet description we grouped consumed prey into four categories: birds, lagomorphs, small mammals and ungulates. We calculated the frequency of occurrence (FO) for each category regarding total analysed scat samples, and also the niche breadth using Levins Index (Levins 1968):

\[
B = 1/(\sum [p_i^2])
\]

where \(p_i\) is the proportion of occurrence of the prey category \(i\), regarding the total consumed prey. To compare this with other populations, we used the standardisation suggested by Colwell & Futuyma (1971),

\[
B_{\text{std}} = (B-1)/(n-1)
\]

where \(n\) is the number of prey categories consumed. This index shows the degree of specialisation of a certain species; a value close to 0 is indicative of a specialist predator, while a generalist predator shows values close to 1 (Colwell & Futuyma 1971).

Both FO and \(B_{\text{std}}\) calculated from analysed scat samples were compared with prior knowledge of the trophic ecology of the Iberian Lynx. For that, we selected four relevant studies as a comparative reference (Table 1), and regrouped their results to our four prey types. This was not possible in regard to the study by Fedriani et al. (1999) who used a broad classification of prey items, e.g., other vertebrates, referring to all non-lagomorph vertebrates. Therefore, we calculated the FO of each prey category and \(B_{\text{std}}\) for all four reference studies, and compared results with those obtained in our study area.

We compared the trophic niche of the Iberian Lynx population in the province of Madrid (M) with that described in prior studies (A). For the latter, we
calculated the average FO of each prey category in the reference studies. Then we used the index formulated by Schoener (1970) for calculating the niche overlap between both populations, M and A:

\[ C = 1 - \frac{1}{2} \sum |p_{iM} - p_{iA}| \]

where \( p_{iM} \) is the proportion of occurrence of the category \( i \) within population M, and \( p_{iA} \) is the same but within population A. C takes a minimum value of 0 when there is no overlap, and a maximum of 1 when the proportions of consumed resources are the same in both populations.

Lastly, we compared FO and \( B_{stand} \) obtained in the province of Madrid between the two periods when samples were collected, i.e., spring–summer and autumn–winter. We used Fisher’s exact test, which is suitable for small sampling sizes.

RESULTS

Between January 2015 and May 2018, we collected 98 scat samples along 21 transects that were each combed twice, once in spring–summer from May to July and once in autumn–winter from October to February. Through genetic analysis we identified 46 of these samples positively as belonging to Iberian Lynx, with 31 collected in the spring–summer season and 15 collected in the autumn–winter season. As our genetic method allows only for identifying scat of Iberian Lynx, we did not attempt to identify the remaining 52 scat samples to other species.

The content analysis of the 46 scat samples revealed an overall niche breadth \( B_{stand} \) of 0.36, with small mammals constituting the majority of prey categories. Fisher’s exact test shows the existence of marginally non-significant (\( p = 0.07 \)) differences in diet composition between both seasons of the year considered (Figure 2). Details are provided in Table 2.

DISCUSSION

The \( B_{stand} \) (0.36) calculated for the population in our study area shows the specialist character of the Iberian Lynx. However, this value is higher than those obtained for comparative reference studies in Table 1. Furthermore, the obtained C value of 0.49 shows the trophic niche shift of this population, with regard to that known so far. Figure 3 shows that the trophic niche of the Iberian Lynxes within the study area is directed towards predation on small mammals.

The Iberian Lynx is regarded as a trophic specialist, strictly dependent of the European Rabbit (Delibes 1980; Aymerich 1982; Beltrán et al. 1985; Beltrán & Delibes 1991; Calzada & Palomares 1996; Palomares

Table 1. Previous studies used as comparative references, with authors, sample size (n), sample periods (years), studied population and niche breadth (\( B_{stand} \)) of respective populations.

| Authors | n  | Years         | Population     | \( B_{stand} \) |
|---------|----|---------------|----------------|-----------------|
| Delibes 1980 | 1573 | 1973–1976     | Doñana-Aljarfe | 0.060           |
| Beltrán & Delibes 1991 | 209 | 1983–1984     | Doñana-Aljarfe | 0.279           |
| Palomares 2001 | 1171 | 1993–1996     | Doñana-Aljarfe | 0.005           |
| Gil-Sánchez et al. 2006 | 360 | 2001–2002     | Andújar-Cardeña | 0.035           |

Table 2. Frequency of occurrence (FO) of prey categories in scat samples of Iberian Lynx (n=46) collected in the study area between January 2015 and May 2018.

| Prey category | FO in spring–summer | FO in autumn–winter | Total FO |
|---------------|----------------------|----------------------|----------|
| Small mammals | 50%                  | 40%                  | 54%      |
| Lagomorphs    | 26.31%               | 53.33%               | 29%      |
| Birds         | 21.05%               | 0%                   | 17%      |
| Ungulates     | 2.63%                | 6.67%                | 4%       |

Figure 2. Bar graph showing the frequency of occurrence (FO) of each prey category within analysed scat samples collected in the two seasons.
et al. 2001; Ferrer & Negro 2004; Gil-Sánchez et al. 2006). There are such strong links between these two species that the collapse of Rabbit populations can even inhibit the reproductive capability of the Iberian Lynx which has been interpreted as its ‘inability’ to switch its main prey (Ferreras et al. 2011). In this research, we compared niche breadth and overlap between a potential population in the central Iberian peninsula and prior knowledge obtained from southern populations. Our results show differences in comparison with those obtained from the four studies used as a comparative reference (Fig. 3). Therefore, our study is the first record in which lagomorphs are not the main prey, showing a 30% lower FO than in the lowest record so far (70%, Beltrán & Delibes 1991). On the contrary, the FO of small mammals is clearly over-represented (47.5% higher) in comparison with prior studies.

A similar pattern than the one observed here was already recorded in Delibes et al. (1975). In this study carried out in the provinces of Cáceres and Salamanca (closer to our study area than to southern populations), the recorded FO for Rabbits was 56.5% while the small mammals and birds occur in the 27% and 12% of samples, respectively. These results, although still different to ours, show a pattern of Iberian Lynxes farther inland feeding on alternative prey other than Rabbits more frequently.

Rabbit distribution within our study area shows clear differences between main landscape regions. The population in the north is naturally fragmented, most likely because of the patchy distribution of suitable habitat (Virgós et al. 2003). In the south, Rabbits are widespread (Blanco & Villafuerte 1993) due to the existence of a high density of boundaries between croplands and scrublands (Calvete et al. 2004) where they find a suitable combination of trophic resources and shelter (Tapia et al. 2014). As far as we know there is no more actualized information about new population trends, but the described spatial arrangement coincides with our field observations throughout the sampling period.

The observed pattern in our study area could be a response to: (i) Iberian Lynx adaptation that shows a different trophic behaviour in different environments. Note that 65% of the Iberian Lynx scat samples analysed were collected in the landscape region of the Guadarrama Mountains, where Rabbit distribution is patchy. This could lead to the exploration of different trophic niches in areas where Rabbit abundance is lower. A similar pattern was obtained by Sáez-Gómez et al. (2018) and Nájera et al. (2019), who recorded Iberian Lynxes preying on Red-necked Nightjar Caprimulgus ruficollis eggs and Domestic Cats, respectively, as a response to the decline of Rabbit abundance; (ii) an uncertain proportion of our Iberian Lynx scat samples could come from juvenile individuals, whose habitat requirements are less restrictive than those of resident individuals (Gastón et al. 2016). Therefore, trophic plasticity could be wider too, which would add some noise to our results; and (iii) overestimations of the FO of small species might have been obtained (Torres et al. 2015). These have more hair and other indigestible matter per unit of body mass, which can cause their occurrence in a higher number of scat samples per unit of consumed mass (Floyd et al. 1978). Despite this, earlier studies on the trophic ecology of the Iberian Lynx did not suggest evidence of overrepresentation of small prey (Delibes 1980; Aymerich 1982; Beltrán et al. 1985; Beltrán & Delibes 1991; Calzada & Palomares 1996; Palomares et al. 2001; Ferrer & Negro 2004; Gil-Sánchez et al. 2006). Therefore results are still comparable.

The observed seasonal variation in the diet of the Iberian Lynx in our study area corroborates results of previous studies on the species (Delibes 1977; Beltrán & Delibes 1991; Gil-Sánchez et al. 2006) as well as on the Eurasian Lynx (Krofel et al. 2011). Lagomorph predation resulted in a 27% lower value during the spring–summer period, while small mammals consumed showed a 10% increase in comparison with the autumn–winter period. Bird predation was only recorded in spring–summer (FO = 21%). $B_{stand}$ also shows differences between both
seasons, being higher in spring–summer (0.58) than in autumn–winter (0.41). Therefore, during the cold season of the year, the Iberian Lynx consumes a lower variety of trophic resources, whilst this pattern changes in the warm season.

This could be motivated by two facts that are likely to produce a synergic effect: (i) during autumn–winter, when high precipitation and low temperature occur, the daily activity of prey is reduced, being less available for Iberian Lynxes (Beltrán & Delibes 1994). On the other hand, during the spring–summer season, climatic conditions are less adverse, which allows for an increase in daily activity and, therefore, higher availability of different prey species; (ii) the Rabbit reproduction period begins in October–November and can last until June–July, depending on environmental conditions. This produces a maximum peak of abundance just before summer. Then Rabbits become the most abundant prey and, as a consequence, predators apply the highest pressure to a single trophic resource. Moreover, Rabbits do not reproduce during summer (Soriguer & Palacios 1994). Therefore, a quick and deep decrease of Rabbits occurs, forcing Iberian Lynxes to prey on alternative trophic resources (Delibes 1980) for the rest of the summer.

Our results reinforce the key role that lagomorphs play in the diet of the Iberian Lynx. This category is the most frequent prey when diversity of available prey is lower. Here, however, we provide evidence for a lower trophic dependence of the Iberian Lynx on lagomorphs than in the areas of Doñana-Aljaraf and Andújar-Cardena. In our study area, the Iberian Lynx shows its adaptive capacity, adopting a relatively generalist strategy when trophic diversity is high, and a more specialist strategy when diversity is low. Despite this, the low number of samples collected in autumn–winter season (n=15) must be taken into account and, therefore, the pattern showed here may change with a larger dataset.

Knowledge of predator-prey relationships is fundamental for the adequate design and implementation of species conservation plans (Popp et al. 2018). Therefore, the results of our research provides base line information for designing conservation actions for the Iberian Lynx in central Spain. We show that the Iberian Lynx is capable to adapt to a wider prey spectrum than previously assumed by Ferrer & Negro (2004) and Ferreras et al. (2011). Based on the described pattern, we think that Iberian Lynxes can profit from an increase in prey diversity provided in enrichment programmes carried out at captive breeding centres (Rivas et al. 2016).

Familiarising them with a broader prey diversity may enhance the ability of reintroduced individuals to colonise and survive in new territories.

Future research efforts on the trophic ecology of the Iberian Lynx should focus on increasing the number of scat samples for analysis of diet composition, but also on prey availability and the estimation of ‘real’ proportion each prey species contributes to the diet by means of correction factors, as suggested by Wachter et al. (2012) and Klare et al. (2011). This will provide more reliable information about the trophic needs of the Iberian Lynx.

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