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Behavioural response of a trophic specialist, the Iberian lynx, to supplementary food: Patterns of food use and implications for conservation

José V. López-Bao*, Alejandro Rodríguez, Francisco Palomares

Department of Conservation Biology, Estación Biológica de Doñana, CSIC Avda. María, Luisa s/n, 41013 Seville, Spain

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ABSTRACT

Prey scarcity compromises population survival, especially for specialist predators. Supplementary feeding is a management tool that can be applied to reverse the decline of food-limited populations. We analyse how a population of Iberian lynx, a threatened food specialist, initially reacted to, and subsequently used, supplementary food. Twenty-seven feeding stations (FS) with domestic rabbits were placed in the Doñana Biological Reserve, SW Spain, between 2002 and 2005. We recorded lynx tracks inside and around stations to analyse spatio-temporal patterns of use, as well as the performance of several station designs. Iberian lynx used 62% of the FS installed, and consumed most of the supplied food. All station designs were used and food provision apparently covered the energetic needs of the lynx inhabiting the reserve. There was spatial aggregation in the use of the FS. Fourteen weeks were needed on average for lynx to become familiar with feeding stations and making a regular use of the supplementary food. Seasonal variations in consumption frequency appeared to be modulated by fluctuations of wild rabbit numbers throughout its annual cycle as well as by variation in energy demand of breeding females. The Iberian lynx responded positively to our supplementary feeding programme. We show that this technique allows the persistence of lynx populations during long periods in areas where wild rabbits are extremely scarce. Supplementary food may be used to sustain lynx whenever rabbit populations need recovery, as well as in the context of lynx restocking or reintroduction programmes.

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1. Introduction

In a conservation context, supplementary feeding (SF) is a management tool that consists of the artificial supply of food to reverse the decline of populations which are thought to be food-limited. Supplementary feeding may improve body condition, growth rates, survival or reproductive success (Elliot et al., 2001; Draycott et al., 2002; Jonsson et al., 2002). A better condition or higher productivity may be reflected in density,

survival rates and other population parameters (Hoodless et al., 1999; Magris and Gurnell, 2002).

To be efficient, a supplementary feeding programme should fulfill the following conditions: (1) food should be presented in such a way that most of it will be consumed by the target species, reducing its use by competitors; (2) food should be readily accessible: spatial dispersion of structures designed to reduce consumption by competing species should not hamper the access to food by the target species; (3) the total

* Corresponding author: Tel./fax: +34 954 621125.

E-mail address: jvlb@ebd.csic.es (J.V. López-Bao).

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amount of supplied food and its distribution over time, alone or as a complement of available wild prey, should satisfy the energetic needs of the managed population; and (4) since SF is meant as a transitory measure, SF should minimize non desired behavioural changes that alter spatial organisation or the ability of individuals to efficiently exploit wild prey. Finally, given that these conditions hold, a regular use of SF should result in positive changes in the population parameters (increase in survival, reproductive success, growth rates, and decrease in mortality and emigration).

Most studies on the effects of SF compare attributes of individuals or populations between areas or experimental settings where SF was or was not implemented (e.g., Draycott et al., 2002), paying less attention to the details of how supplied food was used by the target species. Neglected aspects include how much food is consumed, whether the way of presenting food influences the frequency at which feeding stations are visited, or whether the use of supplied food is constant over space and time. Quantitative factors of this kind conceivably modulate the response of the target population and should be taken into consideration. Furthermore, the inference drawn from how species use supplementary food is relevant for the design and duration of the programmes as well as for assessing their costs and benefits regarding explicit conservation goals.

SF has been widely applied to generalist species, where a positive response seems to be easier to obtain since they exploit a broader range of trophic resources and, therefore, would exhibit a greater adaptability to exploit new resources (Boutin, 1990). However, few experiences with trophic specialists have been undertaken so far (Angerbjörn et al., 1991; Tannerfeldt et al., 1994). Carnivore populations may be naturally food-limited (Gittleman et al., 2001). As a result, food limitation might be exacerbated, becoming a threat for population survival, especially for specialist predators. This is the case for the Iberian lynx (*Lynx pardinus*), a solitary felid that feeds almost exclusively upon rabbits (*Oryctolagus cuniculus*; Delibes et al., 2000). Consequently, thresholds in rabbit density determine lynx breeding (Palomares et al., 2001), local variation in habitat use (Palomares, 2001) and regional variation in lynx presence and density (Rodríguez and Delibes, 2002). Rabbit populations crashed in the late 1950s by introduced myxomatosis, a viral disease, and have been kept depressed since. Rabbit scarcity is considered a major factor of decline in the Iberian lynx (Delibes et al., 2000), and still poses the most important threat for the two isolated populations that remain today in southern Spain. One of these populations, whose estimated size is about 40 individuals (Román et al., 2006), lives in and around the Doñana National Park. A supplementary feeding programme has been recently implemented as an emergency measure to prevent further decline of this lynx population.

In this study we analyse how lynx initially reacted to, and subsequently used, supplementary food. Firstly, we compare the degree to which the diverse structures we designed to provide extra food were accessible for lynx and efficiently excluded other mammalian predators. Secondly, we measured how much food was taken by lynx to assess whether the total amount supplied was enough, and whether the frequency of provisioning was suitable, to sustain the lynx population.

Some felids exhibit a marked reluctance to approach artificial structures (Beier, 1995). Lynx might need some time to learn that they can safely exploit a valuable resource supplied in artificial structures. Therefore, we examined whether there was a period of habituation, and analysed how its length varied with time from the onset of food provisioning. As adult Iberian lynx are territorial against individuals of the same sex (Ferrerías et al., 1997), and food seems to be the primary resource defended by territorial females (Palomares et al., 2001), the dispersion of predictable food supplied in stations could disrupt lynx spatial organisation. Fourthly, we tested this hypothesis, which predicted a random use of feeding stations, whereas the alternative hypothesis of maintenance of social organisation predicted a spatial aggregation of used stations. Fifthly, we tested the hypothesis that intake of SF by lynx was inversely related with seasonal variations in the availability of wild rabbits, and positively related with seasonal variations in lynx energy demands, especially during the breeding season (spring and summer). We conclude by discussing whether SF helped to retain lynx in a context of extremely low rabbit density.

2. Materials and methods

2.1. Study area

Between August 2002 and October 2005, we conducted our study in the Doñana Biological Reserve, SW Spain (37°10' N, 6°23' W), an area of 6784 ha with sandy soils (Fig. 1). In the 1980s, the eastern half of this area used to hold a dense sub-population of Iberian lynx (Palomares et al., 1991) that exhibited a positive demographic balance within the Doñana metapopulation (Gaona et al., 1998). Following the rabbit haemorrhagic disease outbreak in 1989 (Villafuerte et al., 1994), carrying capacity decreased to 50% of the former lynx density. At the onset of the SF programme, the average rabbit density throughout the study area, was 100 times lower (authors, unpublished data) than the threshold value that allows lynx reproduction (Palomares et al., 2001). The western half of the Doñana Biological Reserve features lower rabbit densities than the eastern half, and has not been used by resident lynx during the past 25 years.

2.2. Feeding stations

From August 2002 to April 2003, we used live domestic hens to provision feeding stations (FS). During the next months we gradually substituted hens by domestic rabbits, so that lynx were exclusively fed with live domestic rabbits since June 2003. Domestic rabbits came from a single farm subjected to sanitary control. Within FS, rabbits were fed with dry alfalfa and water.

Twenty-seven FS were activated sequentially: four in 2002, five in 2003, and 18 during 2005 (Table 1). FS were set in areas suitable for the establishment of lynx breeding territories and to explore whether SF alone could help transient individuals to settle down. The spatial distribution of FS was fairly even and overall density was 0.44 stations/km² (Fig. 1). Following the mean home range of breeding females described in

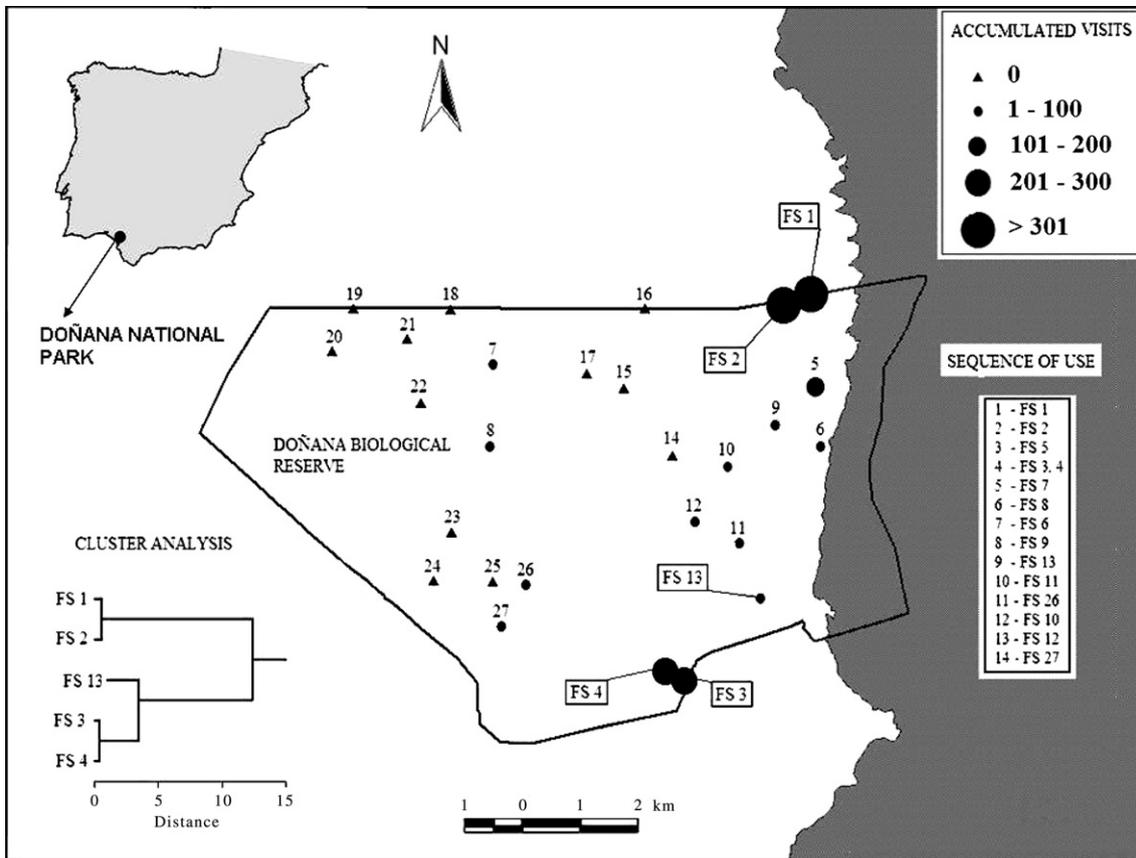


Fig. 1 – Distribution of feeding stations (FS) in the Doñana Biological Reserve. Numbers: identity of FS. Box on the right: FS ordered according to the date they were first visited by lynx. Circles: categorized number of accumulated visits by lynx. Bottom left diagram: The aggregation of the five FS that were regularly used by lynx in two spatial clusters can be noted. The panel shows a cluster analysis based on the Euclidean distance (km) between pairs of regularly used stations.

Ferreras et al. (1997), we estimate that each resident female had access to five FS. Lynx often move along sandy roads and firebreaks. We placed FS close to these roads to help lynx to detect them quickly, and to ease food supply and monitoring.

The basic structure of a FS consisted of a square 16 m² enclosure in which the floor and walls were made of a metallic rigid net (Fig. 2). Walls were 1.3 m high and were covered by a layer of dry heath. A mound of sand, shaped as a ramp, was placed at some distance from one of the walls to help lynx to detect rabbits and to hamper the access of carnivore species with lower jumping skills. We essayed five FS designs by modifying or adding elements to the basic structure and three different types of refuge for domestic rabbits inside in order to stimulate lynx hunting skills. FS designs, numbered 1–5, differed in the height and separation of the ramp, as well as in the presence or absence of logs, pyramids, environmental enrichment and additional fencing (Table 2). Logs on top of enclosure’s walls were placed to allow lynx to sit and wait from there. Pyramids were mounds of sand in the centre of the enclosure that served the same function as that of logs. We wanted to keep and to elicit natural hunting behaviour through environmental enrichment which consisted in increasing structural complexity inside the enclosure through the addition of woody plants, trunks and wooden elements

that could favour both lynx stalking and the chances of rabbits to escape lynx attacks. Finally, in design five we placed the feeding station in a corner inside a 1-ha enclosure with taller (2 m), partially buried fences and wooden structures that favoured lynx access. The large wrapping enclosure contained wild rabbits, and offered the maximum level of exclusion for other carnivores (Table 2).

Refuge type one was a wooden structure resembling a flat box (80 × 80 × 8 cm) with a single entrance for rabbits. Refuge type two was a squared assemblage of four structures of type one, so that at least two entrances had to be surveilled by lynx waiting for hidden rabbits to come out. Refuge type three (Fig. 2) consisted of two blocks, made of three assembled modules of type one, that were connected through a wooden tunnel of rectangular section (230 × 25 × 20 cm). The tunnel had a small door to introduce the rabbits. Refuge type three had several entrances well apart inside the enclosure, and further reduced the predictability about the place where rabbits came out for feeding.

2.3. Supplementation protocol and monitoring

Our purpose was to provide enough supplied food to cover the daily energetic requirements (1 rabbit/day per non-breeding individual, and 2–3 rabbits/day per breeding female; Aldama

Table 1 – Timing and frequency of use by Iberian lynx of feeding stations (FS) in Doñana Biological Reserve from August 2002 to October 2005

FS	FS design	Date of			Monitoring days ^c	Time to first entrance (d) ^d	Total events (d)					
		Month of installation	First operation	Last operation			Visit	Entrance	Consumption	Monthly visit frequency	N. visits/year	N _{months}
1	5	Jul-02	07-31-2002	10-31-2005	447 (170)	110	313 (78)	309 (66)	264 (49)	0.66 ^a	94 ^b	29
2	3/4 ^e	Jul-02	08-13-2002	10-31-2005	444 (147)	91	373 (48)	372 (41)	352 (40)	0.84 ^a	117 ^b	28
3	3/4 ^e	Jul-02	08-17-2002	10-31-2005	422 (140)	354	283	280	257	0.67 ^a	96 ^b	27
4	2	Jul-02	08-17-2002	10-31-2005	445 (140)	396	215	206	165	0.52 ^a	68 ^b	29
5	2	Jul-03	07-17-2003	10-31-2005	414	16	148	143	126	0.37	40	28
6	2	Jul-03	07-29-2003	10-01-2005	358	92	53	47	33	0.16	18	25
7	2	Aug-03	08-21-2003	10-31-2005	318	48	17	17	12	0.05	8	24
8	2	Aug-03	08-26-2003	10-31-2005	263	59	11	11	8	0.03	5	22
9	2	Nov-03	12-12-2003	10-30-2005	287	0	91	85	67	0.29	34	21
10	1b	Nov-04	01-28-2005	10-30-2005	108	41	1	1	1	0.02	2	7
11	1b	Nov-04	02-06-2005	10-30-2005	150	6	30	28	24	0.38	24	8
12	1b	Nov-04	02-04-2005	10-30-2005	106	27	9	7	6	0.12	12	5
13	1b	Nov-04	02-03-2005	10-31-2005	190	0	52	48	42	0.58 ^a	50	8
14	1a	Nov-04	01-28-2005	10-30-2005	94	–	–	–	–	–	–	–
15	1a	Nov-04	01-28-2005	03-23-2005	26	–	–	–	–	–	–	–
16	1a	Nov-04	01-28-2005	04-28-2005	22	–	–	–	–	–	–	–
18	1a	Nov-04	04-10-2005	10-18-2005	86	–	–	–	–	–	–	–
19	1b	Nov-04	04-08-2005	10-30-2005	64	–	–	–	–	–	–	–
21	1b	Nov-04	04-15-2005	10-30-2005	74	–	–	–	–	–	–	–
22	1a	Nov-04	04-15-2005	10-30-2005	78	–	–	–	–	–	–	–
23	1a	Nov-04	08-25-2005	09-17-2005	66	–	–	–	–	–	–	–
24	1a	Nov-04	10-02-2005	10-30-2005	40	–	–	–	–	–	–	–
26	1b	Nov-04	02-06-2005	10-30-2005	114	19	4	4	3	0.12	7	7
27	1b	Nov-04	02-06-2005	10-23-2005	90	239	2	1	1	0.04	2	5

FS that were operative less than one month are not included (17, 20 and 25). Results for stations fed with hens between August 2002 and June 2003 are shown in brackets. For each FS we also show the mean monthly visit frequency and the number of visits/year. FS that show mean monthly visiting frequency above 0.5 are considered used regularly. FS not used by lynx were checked with less frequency than FS used by lynx.

a FS that showed a regular use.

b FS that were used to evaluate the habituation process in the first phase of the study.

c Days in which the station was baited and monitored.

d Since the date of first operation.

e FS of the design four are the same FS that in design three modified, respectively in November 2004 and April 2005.



Fig. 2 – Pictures of a feeding station (FS) showing its basic structural elements.

et al., 1993) of all lynx inhabiting the area. We planned to keep one rabbit (mode = 1, range 1–7) permanently available per FS, except for particular stations used by more than one individual and by adult females during the breeding season. The mean (\pm SE) weight of a random sample of supplied rabbits (1129 ± 24 g, range 640–1560 g, $n = 145$) was similar (t -test, $p > 0.05$) to the mean weight of adult wild rabbits in the study area (1088 ± 15 g, range 890–1355, $n = 60$ for females; 1127 ± 20 g, range 920–1385, $n = 35$ for males; Calzada, 2000).

We monitored FS in order to check the number of available rabbits and how many were caught by lynx since our last visit. Artificial feeding was maintained at a nearly constant rate during the period in which rabbits were supplied (915 days). Supplementary food was available during 82% of the study period. We monitored FS on 492 days. Out of 4090 monitoring events, 52% took place one day after last checking, while 21% took place two days after the previous checking.

After introducing rabbits in a FS, we smoothed the sand in the ramp, inside the enclosure, and in a 1.5 m strip around it. Each time we checked a FS, we considered the occurrence of three events: (a) Visit, presence of carnivore tracks in the sand strip surrounding the enclosure; (b) Entrance, fresh tracks also appeared inside the enclosure; and (c) Capture, we found tracks inside the enclosure and at least one rabbit had disappeared. Tracks allowed us to identify the structural elements used by lynx to enter and leave the enclosure. From the size and age of lynx tracks, we could tell between single visits and multiple visits.

2.4. Data analyses

We only used data obtained during a monitoring interval of up to two days. Using longer intervals made difficult to estimate the exact date of events as well as their associated circumstances. Unless stated otherwise, we restricted our analyses to stations supplied with domestic rabbits. FS that were operative less than one month were excluded.

We defined visit frequency as the number of visit events (days with lynx visit) divided by the number of monitoring events. Entrance frequency was the ratio between the number of entrance events and the number of visit events. Capture

frequency was the number of capture events divided by the number of entrance events. We also calculated the proportion of rabbits supplied that were caught by lynx. We used generalized linear mixed models (GLMM) with binomial errors and logit link to analyse the effect of FS design, rabbit refuge type, and the amount of food supplied on visit, entrance and capture events. GLMMs with normal errors and identity link were used to analyse the effects of the same predictors on the arcsin-transformed proportion of rabbits caught. The number of lynx that visited the FS on the same day could influence the intensity of use; therefore, it was included as a covariate. For each FS, time since first operation (i.e. exposure time) was also included as a covariate. The identity of the enclosures was introduced as a random effect.

We estimated the number of domestic rabbits caught by lynx and compared it with the estimated energetic needs of the lynx population. We used GLMMs to assess whether the amount of rabbits we supplied affected enclosure use, capture frequency, and the number of rabbits consumed. If a given level of food supply was not enough for the energetic demands, we would expect a positive relationship between the number of available domestic rabbits and rabbit consumption.

We called habituation phase to the period of lynx's familiarization with SF and the artificial structures, from the first operation of a given FS until it was regularly used. We considered that the use of a FS was regular when the monthly visit frequency was sustained above 0.5. For each FS, we defined detection time as the time (days) between station activation and the first visit, entrance time as the time between the first visit and the first entrance, and capture time as the number of days between the first entrance and the first capture. To characterize the habituation phase we computed these measurements at two temporal resolutions: ten-day periods during the first 100 days, and monthly during the first ten months. We restricted this analysis to FS that remained operative at least 25 months and that received at least 50 visits ($n = 4$; Table 1). We expected the duration of the habituation phase to decrease in successive years.

From unpublished radio-tracking and track survey data we could establish that only two breeding territories, about 2–3 km apart, were occupied in the study area. With this

Table 2 – Summary of the structural elements present in the different designs of feeding stations (FS), and overall use by the lynx population

Design	N _{used}	N _{Tot}	Ramp		Logs ^b	Pyramid ^c	Environmental enrichment ^d	Additional fencing ^e	Monitoring FS-days	Visit frequency	Entrance frequency	Capture frequency
			Separation ^a (m)	Height (m)								
1a	0	7(10)	2.5–3.0	1.5	No	No	No	No	760	0.07	0.93	0.90
1b	6	8	2.5–3.0	1.5	Yes	No	No	No	1681	0.23	0.96	0.80
2	6	6	1.5	1.5	Yes	No	No	No	487	0.72	0.98	0.91
3	2	2	1.5	1.5	Yes	No	No	No	169	0.83	0.99	0.80
4	2	2	1.5	1.5	Yes	No	Yes	No	351	0.64	0.98	0.90
5	1	1	0.0	0.7	No	No	No	Yes				

Three FS excluded in the analyses belong to the design 1a. The overall number of monitoring days, visit frequency, entrance frequency and capture frequency are shown.

a From one of the enclosure's walls.
b Placed on the wall top.
c Pyramidal mound of sand (base side = 2.5 m; height = 1.0 m) in the centre of the enclosure.
d Woody vegetation, tree trunks and other wooden structures that facilitated lynx stalking, and increased escape chances for domestic rabbits.
e Large enclosure (1 ha) made of wire mesh (0.5 m buried plus 2.0 m high) where wild rabbits were restocked in two artificial burrows. Lynx could enter this enclosure either jumping two wooden steps 1.2 and 2.0 m high, placed at 0.5 m from the fence, or climbing a vertical trunk (diameter = 0.7 m; height = 2.0 m) adjacent to the fence.

separation of territories, if a regular use of FS was caused by recurrent visits of resident lynx, we would expect that regularly used enclosures were spatially aggregated. We tested this prediction by means of a cluster analysis on the spatial position of FS that were regularly used and the number of visits received. To analyse whether there was any spatial contagion in the probability that a FS was visited, we recorded for each station whether the closest enclosure had or had not been previously used by lynx. We entered this binary factor as a predictor in binomial GLMM models to analyse whether FS were or were not visited by lynx. The identity of enclosures was introduced as a random effect.

We grouped months into seasons following three ecological criteria: (a) fluctuations in wild rabbit density throughout the annual cycle. Following Palomares et al. (2001), we defined seasons of high (May–July), medium (December–April, August), and low density of wild rabbits (September–November); (b) vulnerability to predation of wild rabbits due to the incidence of viral zoonoses. According to Villafuerte et al. (2000) the season of high vulnerability to predation of infected wild rabbits has been reported between May and September; we assigned low vulnerability to the rest of the year; (c) energy demands of breeding lynx females. We defined seasons with high demand (June–September; females provide food to their offspring), medium demand (March–May; lactation and strong dependence), and low demand (October–February; young become independent). For FS used by lynx, we examined the effect of season on the visit and capture frequencies by means of GLMMs with binomial errors and logit link, including year and FS as a random factor.

3. Results

3.1. Accessibility

Lynx used 15 FS (62%) at least once (Fig. 1). On 92% of monitoring days at least one lynx visited one FS, and up to eight FS were visited on the same day. The daily mean (\pm SD) number of stations visited by lynx was 2.80 ± 1.53 , and the mode was 1 FS/day. Overall, we recorded 1162 lynx visit events. Lynx entered the FS on 98% of visits events, and captured at least one food item on 87% of entrance events. A single lynx visited FS in 84% of 1122 occasions where tracks allowed us to distinguish whether single or multiple lynx visits occurred.

Ramps were used to enter and exit with a frequency significantly lower than the ground (20%, $\chi^2 = 22.08$, $df = 1$, $p < 0.001$) and were used more often to enter than to leave the enclosure (13%, Z -test = 2.04, $p = 0.04$, $n = 240$). The frequency with which lynx used ramps placed 1.5 m apart (20% of entrance events) was significantly higher than the frequency of use of ramps at 2.5–3.0 m (2%, Z -test = 2.99, $p = 0.003$). For the subsample of observations in FS with logs ($n = 797$), sand in the log surface indicated that lynx walked or sat on the logs in 33% of occasions. For design five, lynx used wooden steps in almost all entrance events (94%, $n = 195$).

Capture frequency was at least 0.80 in all designs tested (Table 2). The design of feeding stations and rabbit refuges

had not significant effects on visit, entrance and capture frequencies, or on the proportion of rabbits captured (Table 3). The time that FS had been operative had significant effects on visit and entrance frequencies showing a greater use of FS operated earlier (Table 3). The number of lynx that visited the FS had significant positive effects on capture frequency and proportion of rabbits caught (Table 3).

3.2. Exclusivity

We recorded 2129 visit events of carnivores, of which 966 were visits by species other than lynx, 908 by red fox (*Vulpes vulpes*), 34 by Egyptian mongoose (*Herpestes ichneumon*), 11 by Eurasian badger (*Meles meles*), 7 by European wildcat (*Felis silvestris*), and 6 by common genet (*Genetta genetta*). Non-target species entered (588 occasions, 60% of visit events; 99% by red fox) and captured prey (372 occasions, 63% of entrance events; 99% by red fox) with a much lower frequency than lynx (entrance: Z-test = 19.36, $p < 0.001$; capture: Z-test = 10.88, $p < 0.001$). The probability that a domestic rabbit was consumed by lynx was 0.50, three times higher than the probability that it was caught by other carnivores (0.17). Furthermore, out of 966 visits by non-target carnivores, 93% have been recorded in FS that were not used regularly by lynx. Restricting our analyses to FS regularly used by lynx, the frequency at which rabbits were taken by non-target carnivores decreased to 0.013.

3.3. Food supply vs. needs of the lynx population

We supplied 4749 domestic rabbits which yielded an average availability of 5.2 rabbits/day during the study period, and an average daily availability of 0.22 rabbits/FS per day ($n = 915$ days). The estimated availability of extra food per territory was 1 rabbit/day. Availability differed across stations depending upon their use by lynx. While used by lynx, FS had an average daily availability of 0.33 rabbits/FS, equivalent to 1.5 rabbits lynx territory⁻¹ · day⁻¹.

Lynx caught 38% of the rabbits supplied ($n = 4749$). In 42% of the monitoring events recorded in FS used by lynx, at least one live rabbit was found; when a station was not used by lynx, this percentage was reduced to 25%. The mean (\pm SD) number of rabbits left per day was 3.4 ± 3.8 . Lynx never visited all FS available during the same day. Actually, if a particular FS was visited by lynx one day, the probability that any of the four nearest neighbours were visited on the same day

was 0.61, and the probability that all four nearest neighbours were visited was only 0.04. The overall capture rate was 1.2 rabbits/entrance. This gives an estimated consumption of 0.40 rabbits lynx territory⁻¹ · day⁻¹ (40% of the available prey per territory and day). The proportion of rabbits consumed significantly decreased with the number of rabbits supplied (Table 3).

During the study period no more than four resident lynx lived in the area (authors, unpublished data). Following the daily energetic needs of lynx described in Aldama et al. (1993) and assuming that resident individuals occupied permanently the study area, the lynx population would have needed 3660 rabbits. This is only 77% of the rabbits we supplied, and twice the number of domestic rabbits consumed by lynx during the study period. If the daily energetic needs remained constant through time, supplementary food may have covered half of the energy needed by the lynx population.

3.4. Regularity and spatial autocorrelation in FS use

The lynx population made a regular use of five FS (Table 1). Actually, FS with a regular use were more common among stations that were operative for longer periods (>2 years; Mann-Withney U Test, $z = 2.27$, $p = 0.002$) than among stations activated recently (Table 1). Enclosures that were regularly used aggregated in two well defined spatial clusters in the eastern half of the study area (Fig. 1). When the closest FS had been previously visited by lynx, the probability that a FS was also used by lynx was significantly higher than when the closest FS had not been visited ($F = 8.50$, $df = 1$, $p = 0.004$), which suggests spatial contagion in the use of stations at two different scales: the study area, and sets of neighbouring FS.

3.5. Habituation to supplementary food

The time elapsed between activation of the first FS and the first lynx visit was 30 days. Time between the first visit recorded and the first entrance to any FS was 78 days, and one day later lynx caught the first supplied prey. The mean (\pm SE) detection time was 76 ± 115 days, the mean (\pm SE) entrance time was 17 ± 31 days, and the mean (\pm SE) capture time was 12 ± 18 days (Table 1).

For regularly used FS, visit frequency and entrance frequency quickly increased and stabilized above 0.5 about 50

Table 3 – F values in GLMMs of visit, entrance and capture frequencies, and the proportion of domestic rabbits caught by lynx at FS

Predictors	Visit frequency		Entrance frequency		Capture frequency		Proportion of rabbits caught	
	F	p	F	p	F	p	F	p
Exposure time (3 levels)	4.36	0.037	5.03	0.025	0.22	0.658	0.07	0.797
FS design (5 levels)	0.38	0.765	0.25	0.856	0.17	0.914	0.77	0.511
Refuge design (3 levels)	0.57	0.568	1.32	0.267	0.02	0.982	0.55	0.577
Number of rabbits	0.78	0.378	1.55	0.214	4.22	0.040	40.20	<0.0001
Number of lynx					0.02	0.885	8.22	0.004

Frequencies and proportions were computed for each FS on a daily basis ($n = 792$). Data for these analyses were taken between November 2004 and October 2005.

days after the first lynx contact with the enclosure (Fig. 3). The temporal pattern of capture frequency during the habituation phase was similar to that of entrance frequency. Detec-

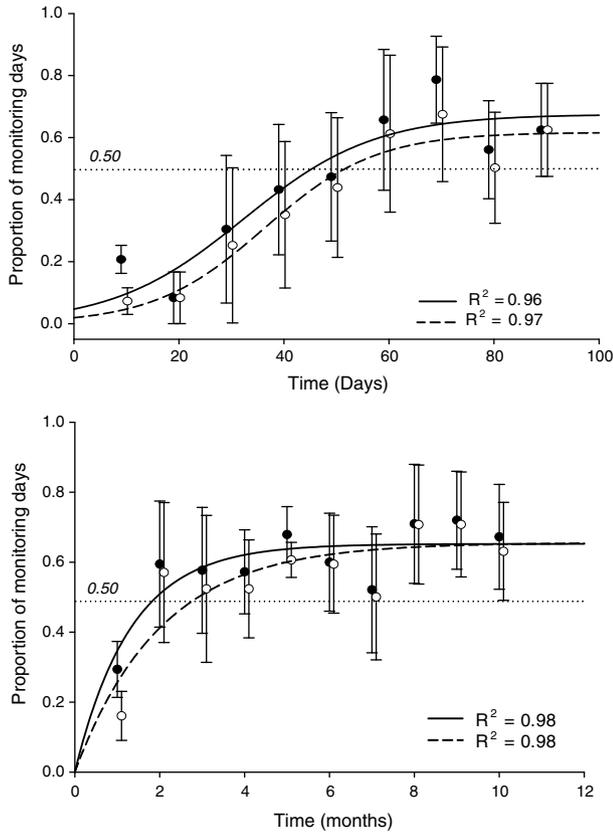


Fig. 3 – Mean (\pm SE) visit (black symbols, solid line) and entrance (open symbols, broken line) frequencies of lynx to regularly used FS. During the first 100 days of operation, frequencies were calculated over successive 10-day periods and sigmoidal curves were fitted (upper panel). During the first 10 months of operation, means of monthly frequencies and fitted exponential curves are shown (lower panel).

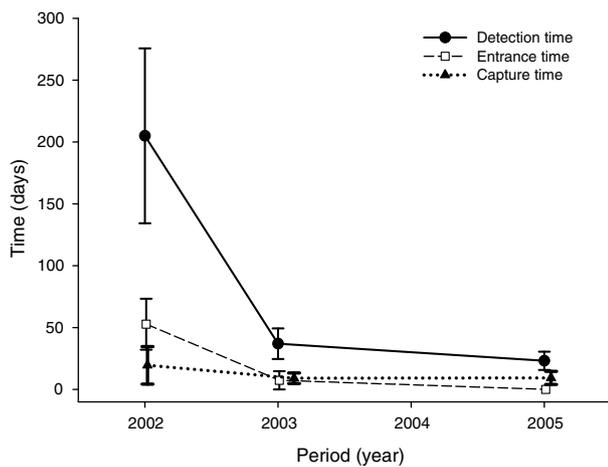


Fig. 4 – Variation in mean detection time (\pm SD), mean entrance time (\pm SD), and mean capture time (\pm SD) in FS used by lynx as a function of the time since first exposure of FS to the lynx population.

tion time and entrance time significantly decreased through time elapsed since the onset of the food supplementation in the area (detection time: $r_s = -0.55$, $p < 0.05$, $n = 15$; entrance time: $r_s = -0.61$, $p < 0.05$, $n = 15$; Fig. 4). Capture time also decreased with time, but this relationship was not significant (capture time: $r_s = -0.20$, $p = 0.5$, $n = 15$; Fig. 4).

3.6. Seasonal patterns in FS use

The mean (\pm SD) monthly visit frequency was 0.40 ± 0.34 (range 0–1; $n_{FS} = 15$, $n_{months} = 272$), the monthly entrance frequency was 0.72 ± 0.44 , and the monthly capture frequency was 0.62 ± 0.43 . There were significant seasonal variations in the intensity of use of supplementary food when season was defined on the basis of wild rabbit availability or on the basis of energy demands of breeding females. Visit and capture frequencies increased when density of wild rabbits were lowest and during the lynx breeding season. There were not significant differences in the intensity of use when seasons were defined according to the vulnerability of wild rabbits associated with the incidence of viral zoonoses (Table 4).

4. Discussion

4.1. Evaluation of the supplementation protocol

Our supplementation protocol was extensive in space (the whole reserve was covered) and intensive in terms of frequency and amount of food provision. Our monitoring effort allowed a reliable knowledge of the amount of food consumed by the target species and how FS were used. The small size of enclosures and the sandy substrate favoured a quick checking. In addition, keeping enclosures small minimized construction and maintenance costs and maximized portability, helping to adjust their position to changes in distribution of lynx or in the abundance of wild rabbits.

Iberian lynx readily accepted live domestic rabbits as food. The high similarity in appearance and weight of the prey supplied with wild prey might have helped lynx to be attracted to FS. Lynx could easily find and enter all types of enclosures. Further, visit and capture frequencies were very high (>80%) irrespective of the design of FS. Therefore, we consider that food was accessible to the target species in FS.

Food consumption by non-target species may compromise the success of a SF programme (Landers and Muller, 1997). Although the Iberian lynx was the species that used FS with the highest frequency, other carnivores, mainly red fox, also visited them regularly, and exclusivity in the consumption by the target species was not complete. However, lower entrance and capture rates suggested that other carnivores were less efficient in exploiting food within FS, partly because the design of enclosures was not suitable for species of their size with poor jumping or climbing abilities. There was spatial segregation in FS used by lynx and those used by other carnivores. Since these competitors can be excluded by lynx through interference (Palomares et al., 1996), competitive exclusion might partly explain this spatial segregation. Avoidance of enclosures by carnivore competitors might help to explain why, considering only enclosures used by lynx, the proportion of domestic rabbits taken by other

Table 4 – GLMMs showing the effects of season on the visit and capture frequencies in FS used by lynx

Criterion	Season	Visit frequency					Capture frequency				
		Parameter estimate	SE	F	df	p	Parameter estimate	SE	F	df	p
1. Density of wild rabbits	Low	0.55	0.14	7.20	2	0.0007	0.94	0.14	19.97	2	<0.0001
	Medium	0.30	0.11				0.55	0.12			
	High	0					0				
2. Wild rabbit vulnerability	Low	0.02	0.12	0.03	1	0.890	-0.12	0.12	0.87	1	0.352
	High	0					0				
3. Lynx energy demands	Low	0.28	0.10	19.20	2	<0.0001	0.14	0.10	8.66	2	0.0002
	Medium	0.63	0.10				0.43	0.10			
	High	0					0				

Season was defined using three different ecological criteria.

carnivores was much lower than the proportion actually consumed by lynx. Therefore, provided that supplementary food was spatially accessible, it was primarily consumed by lynx, and the desirable trait of exclusive access to food by the target species was largely satisfied. However, consumption of supplementary food by other carnivores in FS not used by lynx could reduce the chances of transient lynx to find food within stations, and might interfere with their potential settlement.

The lynx population consumed less than half of the food provided. If lynx exclusively depended upon supplementary food, and if the number of rabbits we supplied was not enough to satisfy the needs of the lynx population, we would expect lynx to look for rabbits in other stations, resulting in an even spatial distribution of used FS that we did not observe. We would also expect a positive correlation between number of rabbits supplied and the proportion of rabbits caught by lynx. Conversely, this relationship was in fact negative, indicating that the number of rabbits consumed was fairly constant and that food provision was enough to cover the energetic needs of the lynx population. Furthermore, our results suggest that lynx kept on feeding on wild rabbits.

Lynx used all types of enclosure designs and refuge designs tested. Any FS design could be appropriate for supplying domestic rabbits, as long as the compromise between accessibility and stimulation of hunting behaviour is satisfied. Our results showed that use of FS was primarily influenced by time since first exposure and FS location. Enclosures operative for longer periods were those more frequently and more regularly used, which would suggest a kind of transmission of behavioural routines if several individuals were responsible for the observed pattern. Lynx probably identified FS as profitable and predictable food resource patches inside their territories and made an active defence of supplementary food as a valuable resource in an area where wild rabbits were scarce.

Offering live prey might be most appropriate to keep lynx hunting skills (Bashaw et al., 2003). Refuge type did not affect capture frequency, but complex refuges would stimulate the use of varied hunting behaviours. Environmental enrichment did not reduce capture frequency either, but structural complexity inside the enclosure might increase the chances of rabbits to escape and might somewhat counter the adverse effects of supplying food in a reduced space on the lynx' repertoire of

hunting behaviour (Shepherdson, 1994). Ramps were used mostly to enter the enclosure, and could favour checking for the presence of rabbits or observing their behaviour.

4.2. Spatio-temporal patterns in the use of supplementary food by lynx

Lynx visited many stations but all of them were located in the eastern third of the study area, in agreement with the known distribution of resident lynx (Palomares et al., 1991, authors unpublished data). The inverse correlation between consumption in one FS and consumption in neighbouring FS during the same day is consistent with the inclusion of several FS within a lynx territory. The two clusters of FS used regularly had a size similar to that of female territories in the study area (Size of the minimum convex polygon (±SE): 12.6 ± 4.0 km²; Ferreras et al., 1997), which further suggests that continuous use could be attributed primarily to resident lynx. We lack complete information about the number of young lynx that came to the reserve during their natal dispersal period, or about the sectors visited, or the period they stayed. However, we detected at least 4 transient lynx through tracks or occasional sightings, mainly in the western half of the study area. In 2003, we had evidence that a few FS (numbers seven and eight) were used by a dispersing female during three months, but this individual left the area. We did not detect other instances of FS use close to the points where transient lynx were recorded, which suggests that dispersing individuals may not stay enough time to use an enclosure regularly.

Lynx required on average two and a half months to first visit an operative enclosure, two more weeks to enter it, and two additional weeks to kill the first rabbit. Fourteen weeks were needed on average for lynx to become familiar with SF. Since FS were placed on visible places, delayed detection was an unlikely explanation for such an extended period. Rather, lynx might be diffident in the first place with regard to new enclosures and their internal structures, and could also need some time to associate enclosures with available food. The length of the habituation period to new stations decreased in successive years, suggesting that lynx using enclosures installed late in the study period had previous contact with operative FS.

After the habituation phase, lynx used food at a high and quite constant rate, which is consistent with the persistent scarcity of wild rabbits. This steady consumption of domestic rabbits was predictable considering the potentially high energy costs of foraging for wild rabbits at very low densities (below 0.1 rabbits/ha), which definitely did not allow lynx reproduction (Palomares et al., 2001). We also doubt that low wild rabbit density, in absence of our SF programme, could even had allowed adult individuals to maintain their spatial organisation and occurrence in the area. Disruption of spatial organisation in the Iberian lynx like in other felids has been associated with severe prey scarcity (Rolley, 1985; Ferreras et al., 1997). According to their solitary habits (Ferreras et al., 1997), in most cases individual lynx visited FS alone.

Keeping the average use of domestic rabbits at high levels, seasonal variations in consumption frequency appeared to be modulated by fluctuations of wild rabbit numbers during its annual cycle. Use of SF decreased during the period of maximum rabbit abundance suggesting that lynx attempted to feed on wild rabbits when available. This result is promising concerning possible alterations of lynx foraging behaviour as a detrimental side effect of supplementation. Also, we find seasonal differences in consumption frequency when seasons were defined on the basis of energy demands of breeding females. Use of supplied food increased during the breeding season, which also coincides with the beginning of the season of wild rabbit scarcity.

4.3. Conclusions

The population of Iberian lynx under study successfully fed on supplemented domestic rabbits. Food was consumed regularly at high rates, suggesting that the structures used for food supply were suitable from the point of view of accessibility and exclusivity. Visit frequency was determined by the location of FS in relation to the distribution of resident lynx. Entrance frequency was mainly determined by time since station operation, due to the existence of a period of habituation. Consumption frequency was invariably high, associated with the bad situation of the wild rabbit population, and was little affected by the complexity of structures that enhance escape chances of domestic rabbits inside enclosures. The lynx population did not consume all rabbits supplied, food provision was apparently enough, and lynx kept on feeding on wild rabbits.

The techniques employed were useful to feed lynx and to retain them during long periods under conditions of extremely low prey abundance. Without artificial food supply, resident lynx might have abandoned the area. Keeping resident individuals in the Doñana Biological Reserve has a positive effect on the persistence of the Doñana population (Gaona et al., 1998). We found no evidence that supplementary food alone helped dispersing lynx to settle down in new territories, but we had poor information about the number of transient lynx visiting the reserve, and this topic deserves further investigation.

4.4. Conservation implications and recommendations

The SF protocol we evaluated may be useful to maintain populations of Iberian lynx in areas where wild rabbit density is not only well below the threshold value for lynx reproduc-

tion, but also possibly below the threshold for keeping resident individuals in their territories. It is unclear, however, whether SF is useful to help dispersing lynx to settle down in areas subjected to SF. Likewise, in the context of restocking or reintroduction programmes, SF may help to retain lynx subjected to soft release in target areas, especially if released individuals are familiar with enclosures and their content. Supplementary food has been employed for this purpose in other species (Phillips and Parker, 1988; Logan et al., 1993).

Any of the enclosure designs we compared could yield good results. We would recommend FS without ramp but with elements that allow for behavioural enrichment. Further investigation is needed to evaluate the possible effects of our supplementary protocol on the hunting behaviour. As a marginal lesson, our results show that, in the absence of more specific methods, the spatial pattern of food consumption in FS may reveal the distribution of resident lynx.

The length of the habituation phase might indicate the minimum time expected for a SF programme to be effective after implementation. Thus, our feeding protocol can hardly be efficient as a shock conservation measure to compensate for a sudden and strong drop in the availability of wild rabbits unless the target lynx population had been previously exposed during enough time to FS. To foresee such eventuality we recommend that all existing populations should be recurrently (e.g., every other year) exposed during periods of four months to operative feeding stations, in order to maximize the number of individuals that are acquainted with them. We also recommend a constant food supply during periods of wild rabbit scarcity and during the breeding season (summer and autumn). SF should be operated in the mid-term until the wild rabbit population will be fully recovered.

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