Intraspecific interference influences the use of prey hotspots

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Resource clumping (prey hotspots) and intraspecific competition may interact to influence predator foraging behaviour. Optimal foraging theory suggests that predators should concentrate most of their foraging activity on prey hotspots, but this prediction has received limited empirical support. On the other hand, if prey concentration at hotspots is high enough to allow its use by several individuals, increased competition may impose constraints on foraging decisions of conspecifics, resulting in a temporal segregation in the use of shared resources. We investigated how artificial prey hotspots influence foraging behaviour in the Iberian lynx *Lynx pardinus*, and examined variations in the use of prey hotspots by individuals with different competitive abilities. All lynx, irrespective of their position in the competitive hierarchy, focused their activity on prey hotspots. Supplemented lynx concentrated higher proportions of active time on 100 m circular areas around hotspots than non-supplemented lynx did on any area of the same size. However, we found evidence for a dynamic temporal segregation, where inferior competitors may actively avoid the use of prey hotspots when dominants were present. Dynamic temporal segregation may operate in solitary and territorial predators as a mechanism to facilitate coexistence of conspecifics in the absence of opportunities for spatial segregation when they use extremely clumped resources.

Foraging is a fundamental behaviour strongly modulated by spatio-temporal variations in food availability (Stephens et al. 2007). Recently, a growing interest has emerged about the response of foraging predators to the spatio-temporal clumping of their prey (Rohner and Krebs 1998, Roth and Lima 2007, Stephens et al. 2007). Prey hotspots can be defined as predictable patches of highly concentrated prey in space, time, or both. When food is patchy, optimal foraging theory (Krebs 1978) predicts that predators should spend a substantial fraction of their foraging activities in prey hotspots rather than uniformly or randomly across their home ranges (Stephens and Krebs 1986, Stephens et al. 2007). However, few empirical studies have tested the prediction of disproportionate hotspot use by predators and obtained contradictory results (Rohner and Krebs 1998, Roth and Lima 2007).

Competitive interactions also affect foraging behaviour in space and time (Kotler et al. 2005, Stephens et al. 2007). When food can be shared by animals differing in competitive ability, ideal free distribution models (Fretwell and Lucas 1970) predict a truncated distribution of individuals (Parker and Sutherland 1986, Tregenza et al. 1996). Superior competitors may impose constraints on foraging decisions made by inferior competitors (Richards 2002, Rode et al. 2006, Bonanni et al. 2007). In particular, inferior competitors may not concentrate their activity at prey hotspots heavily used by superior competitors in order to avoid increased chances of interference (Cosner et al. 1999, Anderson 2010).

Some degree of spatial or temporal segregation between conspecifics may occur when (1) food is clumped, predictable

and accessible for all individuals (Ruckstuhl and Neuhaus 2002, López-Bao et al. 2009), and (2) individuals exhibit unequal competitive abilities (Donazar et al. 1999, López-Bao et al. 2009). As a result, individuals of different sex or age may exhibit divergent behaviours (Marcelli et al. 2003, Rode et al. 2006), where superior competitors monopolize the most profitable places and times (Frye 1983). When the extremely clumped distribution of food does not allow spatial segregation, temporal segregation or shifts in activity may enable food sharing by unequal competitors while avoiding direct confrontation (Schoener 1974, Kronfeld-Schor and Dayan 2003).

In this study, we investigate whether the experimental addition of prey hotspots alter the foraging behaviour of the Iberian lynx *Lynx pardinus*, and test whether interference prompts activity shifts and temporal segregation at hotspots. The Iberian lynx is a sexually dimorphic (males are larger, Beltrán and Delibes 1993), solitary (Ferreras et al. 1997), and specialist predator that feeds almost exclusively upon European rabbits *Oryctolagus cuniculus* (Ferreras et al. 2010). Individuals with different competitive ability share the same breeding territory: one adult male, one adult female, and offspring <2 year old (Ferreras et al. 1997, 2004, López-Bao et al. 2009). Lynx are active mostly during twilights and the night, with a well-defined activity peak at dusk and a trough around midday (Beltrán and Delibes 1994).

Only two Iberian lynx populations are left today, and one of them occurs in Doñana (southwestern Spain, Ferreras et al. 2010). In 1989 rabbit populations crashed in most of the Doñana area, and rabbit abundance has remained

extremely low since (Moreno et al. 2007). As a result, a food supplementation programme has been implemented recently (López-Bao et al. 2008, 2010a). Supplemental food was provided in the form of penned domestic rabbits in permanent feeding stations (FS) which were presumably easy to capture compared with wild rabbits, continuously supplied, clumped, predictable and, for some lynx territories, the main source of food, acting hence as prey hotspots (López-Bao et al. 2008). All lynx exposed to food supplementation consumed supplemented rabbits regularly (López-Bao et al. 2009), and all individuals sharing a breeding territory used the same FS, showing no evidence of spatial segregation in the use of the artificial resource (López-Bao et al. 2008, 2009). However, competitive asymmetries in the frequency of access to supplemental food suggested a clear hierarchy based on body size and reproductive status (adult males > adult females and subadults > juveniles, López-Bao et al. 2009).

We examined the following predictions derived from optimal foraging theory: 1) all lynx should detect FS (prey hotspots) and spend a high proportion of their foraging time around them; and 2) this focalization on prey hotspots should occur regardless of variations in wild rabbit abundance within lynx home ranges. If all lynx focus their activity on prey hotspots, ideal free distribution models predict that 3) temporal segregation in the use of FS should occur and should reflect competitive asymmetries. We considered two possible forms of temporal segregation: fixed and dynamic. Under fixed temporal segregation, subordinates would shift their foraging activity to times of day when the probability of encountering dominants at FS would be low, that is, subordinates would not visit FS around dusk. Conversely, under dynamic temporal segregation subordinates would actively avoid dominants regardless of the time of day.

Material and methods

Study site

Fieldwork was carried out in Doñana National Park, south-western Spain (37°10'N, 6°23'W). The climate is Mediterranean sub-humid with two well differentiated seasons: mild and wet winters, and hot and dry summers. During the study period, the average annual rainfall was around 600 mm and the average minimum and maximum temperatures were 11.4°C and 23.6°C, respectively.

We studied lynx foraging behaviour in two lynx nuclei called Vera (VE) and Coto del Rey (CR), two lynx subpopulations intensively studied over the last three decades (Ferrerías et al. 1997, Palomares et al. 2001, López-Bao et al. 2010a). VE and CR differ remarkably in rabbit abundance. During the last decade, the average rabbit density in VE during the annual trough (autumn) was lower (0.012 rabbits ha⁻¹) than reference values reported in areas of high lynx density (1 rabbit ha⁻¹, Palomares et al. 2001), while in CR average rabbit density was close to the reference value (around 0.6 rabbits ha⁻¹).

The experimental feeding programme

From 2002 to 2007, we provided supplemental food to lynx in the form of live domestic rabbits in permanent 4 × 4 m

FS placed evenly across both areas (López-Bao et al. 2008) but randomly within lynx home ranges. The supplementation schedule was designed to provide a temporally (FS were checked in the morning every other day, and new rabbits added if necessary) and spatially (extra food was provided ad libitum) predictable source of food, covering the daily energy requirements of all resident lynx (López-Bao et al. 2008, 2009). Only 38% of supplied rabbits were consumed by lynx, and a negligible proportion was taken by other predators (López-Bao et al. 2008). Further details about the supplementation procedure are given in López-Bao et al. (2008).

Data collection

We used radio-tracking and automatic photographic cameras to study the use of FS by lynx. We used a database with radio-tracking positions from 42 lynx captured with box-traps and fitted with radio-collars between 1989 and 2007 in VE and CR. Seventeen lynx (nine females and eight males) had access to FS within their home ranges; whereas 25 individuals (11 females and 14 males) had not. Lynx were located between two and four random times per week as well as during weekly intensive 24 h radio-tracking sessions where we recorded the position and activity on an hourly basis. Lynx activity was determined by means of activity sensors incorporated to radio-collars. Radio-tracking procedures were exactly the same for both non-supplemented and supplemented animals (Ferrerías et al. 1997, Palomares et al. 2001, López-Bao et al. 2010a). Methods of capture and handling of lynx were specifically approved by the competent administration (Regional Government of Andalusia and the Doñana National Park).

Between 2002 and 2007, we placed automatic cameras in 22 FS (seven in CR and 15 in VE) to record lynx entrances to FS. We used 13 Trailmaster active infra-red systems with automatic 32-mm cameras, seven Cuddeback digital cameras and two Stealth Cam digital cameras. For accurate lynx identification two cameras were first set up per FS until we had pictures of both flanks for all animals; subsequently, we used a single camera. Cameras were set at a height of 35 cm, were programmed to run continuously and to trigger as soon as the infrared beam was broken with a delay of one minute between events, and were checked once a week (López-Bao et al. 2009). Date and time were automatically recorded in each picture. To avoid overestimates in the usage of FS, we considered consecutive entrances of the same individual to the same FS as independent if at least 30 minutes elapsed between them (López-Bao et al. 2009). Since age was known for all individuals in VE and CR (López-Bao et al. 2009), lynx were categorized as young (<2 year, all individuals in the predispersal phase, Ferrerías et al. 2004) or adults (>2 year).

We estimated the relative abundance of wild rabbits within each breeding territory subjected to supplementation by counting faecal pellets in 1 m-diameter plots (Palomares 2001a). Each year pellets were counted in 50–106 random sampling plots per territory (mean = 60 plots, n = 11). Due to large temporal fluctuations in rabbit abundance and pellet numbers (Palomares 2001a) all counts were carried out during autumn to make results comparable.

Analyses

We used a total sample of 14758 radio-tracking positions (9516 for non-supplemented and 5242 for supplemented lynx; average number of positions $\pm$ SE per individual = 351 ± 49 , range: 30–1372). Lynx activity was treated as a binary attribute of each position: active or inactive. Our sampling effort of 51 542 camera-nights over six years (42 575 and 8967 camera-nights in VE and CR, respectively) resulted in a total of 5282 pictures and 22 individuals identified (López-Bao et al. 2009). Only 45.2% of pictures recorded independent visits. We excluded 745 pictures for which time and date could not be recorded.

Predictions from optimal foraging theory were tested using radio-tracking information. We used the extension Home Range for ArcView GIS 3.2 (Rodgers and Carr 1998) to calculate the size of 90% fixed kernel estimates of annual home ranges. Home ranges were calculated using at least 30 independent positions per year, and the time interval between consecutive positions to assume independence was >6 h (Ferrerías et al. 1997). Then, for each supplemented lynx, we generated circular buffers around FS located inside its home range. We used 100 m radius buffers because estimates of the telemetry error using test transmitters in our study area was < 100 m. Next, for each lynx we calculated the proportion of total activity positions that fell within buffers ($n = 2388$ positions for all lynx combined; mean $\pm$ SE per individual = 133 ± 33 , range: 6–620). We then randomized the positions of FS and calculated the proportion of activity positions that overlapped 100 m buffers around these locations (Roth and Lima 2007). This procedure was repeated 1000 times. We tested whether lynx used buffers more than expected from random. For the 1000 simulations we calculated the mean proportion of active positions and a 95% confidence interval. If the observed proportion of activity around feeders was above the upper limit of the 95% confidence interval, we considered that the lynx focused its activity around FS. In addition, for each lynx we compared the observed proportion of activity around FS with the distribution of simulated proportions of activity using a Bonferroni corrected type I error ($\alpha = 0.002$). Across supplemented lynx, the influence of FS on foraging behaviour was assessed comparing the observed and the mean number of randomized activity positions that overlapped buffer areas using a Wilcoxon signed-rank test.

To ascertain whether the experimental addition of prey hotspots had an effect on lynx foraging behaviour, we need to discard that non-supplemented lynx also concentrated their activity in small areas. We used two different approaches to tackle this question. First, as the average number of FS per range was three (Table 1), we simulated the positions of three FS within the home range of each non-supplemented lynx and generated 100 m radius buffers around them. We calculated the proportion of total active positions that fell within circular areas ($n = 4488$ positions for all lynx combined; mean $\pm$ SE per individual = 180 ± 34 , range: 33–619). Next, we bootstrapped the positions of simulated FS 1000 times and calculated the mean proportion of active positions within buffers. We then compared the observed activity positions in supplemented lynx and the mean randomized activity positions in non-supplemented lynx that overlapped

on buffer areas using a Mann-Whitney U-test with a Bonferroni corrected type I error ($\alpha = 0.0007$).

Second, for each lynx, we identified the 100 m radius circular area that concentrated the maximum number of activity positions using the Spatial Analyst Tools for ArcGIS 9. For supplemented lynx we also determined whether these small areas matched the location of FS. We built a generalized linear mixed model (GLMM) with binomial error and logit link to test for differences in the proportion of activity positions within 100 m radius buffers between non-supplemented and supplemented lynx. The binomial denominator was the overall number of activity positions, and the numerator the number of activity positions recorded in circular buffers with maximum activity. The presence of food supplementation was a fixed factor and we included the identity of individuals, the area (CR or VE) and the year as random factors.

We averaged and log-transformed the number of rabbit pellets m^{-2} per breeding territory. Every year, we assigned the same value of relative rabbit abundance for all individuals that shared the same breeding territory. Then, we regressed the proportion of lynx activity positions within buffers against wild rabbit abundance to evaluate whether prey abundance influenced the intensity of use of prey hotspots.

We addressed the occurrence of temporal segregation using information from photographs. Since individuals were identified by their unique combination of coat spots (López-Bao et al. 2009), we were able to determine at what time each lynx entered a FS, and therefore the temporal pattern of resource use. We defined four time blocks corresponding to well-defined differences in lynx circadian activity called dawn, midday, dusk, and midnight (Beltrán and Delibes 1994). Dawn and dusk started 1 h before, and ended 1 h after, sunrise and sunset, respectively. Likewise, midday was a 2-h period centered at noon, and midnight was the 2-h period resulting of summing up 12 h to the midday block. This way to define time blocks accounted for fluctuations in the length of photoperiod throughout the year, which affects the behaviour of rabbits and lynx (Beltrán and Delibes 1994). Within each time interval, we calculated the proportion of entrances to FS, and the number of entrances per hour, for each of the following lynx classes in decreasing order of competitive ability (López-Bao et al. 2009): adult males, adult females, young males and young females.

We categorized all independent photographs as a binary variable: occurrence/absence in each time interval. Then, we built GLMMs with binomial error and logit link to test for differences between lynx groups (sex, age and interaction term) in the frequency of entrance during each time block. Individual identity, year, and area were treated as random effects. We also included in the models six additional factors that could affect temporal variation in consumption of supplemental food, in order to statistically control their potential effect. First, in analogous supplementation experiments, exposure time has been found to affect the circadian pattern of foraging activity (Beckmann and Berger 2003). Therefore, we calculated 'exposure time' as the time elapsed (in months) between the date on which each lynx began to consume supplemental food and the date when each photograph was taken. Second, lynx foraging behaviour is indirectly influenced by moon phase

Table 1. Percentage of lynx activity positions within circular buffers with a radius of 100 m around FS, and the mean percentage of activity positions inside the same number of buffers randomly placed within lynx home ranges (replicated 1000 times). We grouped individuals in six breeding territories (I–VI). VE: Vera; CR: Coto del Rey. Numeric identity codes denote age and sex of individuals; A: adult, Y: juvenile, F: female, M: male.

	Lynx area			Percentage (%) of activity positions			
	Year	Territory	Number of FS	Observed	Mean randomized	95% CI	p
VE							
AM136	2005	I	9	21.7	0.21	0.18–0.25	0.001
AF137	2005	I	3	23.7	0.66	0.59–0.73	0.001
AM138	2005	II	4	23.3	0.29	0.24–0.35	0.001
AF93	2005	II	3	27.2	0.37	0.31–0.43	0.001
AM138	2006	I	5	24.1	0.15	0.11–0.20	0.001
AF137	2006	I	2	13.9	0.92	0.82–1.01	0.001
AF137	2007	I	5	15.4	0.74	0.67–0.82	0.001
YM160	2007	I	4	17.3	0.38	0.32–0.45	0.001
YF159	2007	I	7	30.3	0.26	0.16–0.36	0.001
YM154	2007	III	3	8.8	0.39	0.33–0.45	0.002
AF155	2007	III	3	9.1	0.73	0.64–0.81	0.003
mean $\pm$ SD				19.5 $\pm$ 7.1	0.5 $\pm$ 0.2		
CR							
AM139	2006	IV	1	14.7	0.69	0.59–0.78	0.005
AF120	2006	IV	1	20.3	0.91	0.80–1.03	0.002
AM136	2006	V	2	16.1	1.06	0.96–1.16	0.001
AF140	2006	V	2	17.4	1.03	0.93–1.14	0.001
AM141	2006	VI	3	8.2	0.70	0.62–0.78	0.005
AF127	2006	VI	2	5.9	0.98	0.88–1.08	0.001
AF120	2007	IV	1	10.6	0.50	0.41–0.58	0.003
AM136	2007	V	2	16.0	0.64	0.52–0.76	0.001
AF140	2007	V	1	17.4	0.67	0.53–0.80	0.001
YM144	2007	V	2	25.0	1.11	0.93–1.30	0.005
YM143	2007	V	2	9.1	1.14	1.02–1.26	0.008
AM141	2007	VI	3	12.5	0.71	0.55–0.86	0.006
AF127	2007	VI	3	3.6	0.99	0.87–1.11	0.039
YF156	2007	VI	3	10.9	0.76	0.62–0.89	0.002
YF157	2007	VI	3	8.1	1.2	1.10–1.30	0.019
mean $\pm$ SD				13.1 $\pm$ 5.8	0.9 $\pm$ 0.2		

and weather through their effect on rabbit availability (Beltrán and Delibes 1994). For each photograph we recorded moon phase (three levels: full, new, quarter), daily rainfall (daily mean rainfall in mm), and minimum and maximum daily temperature (°C). Third, the use of supplementary food may be conditioned by seasonal variations in lynx energy demand and rabbit abundance (López-Bao et al. 2008). We defined three seasons according to lynx behaviour and relative rabbit abundance: 1) December–March (mating season and medium rabbit abundance), 2) April–July (rearing of cubs and high rabbit abundance) and, 3) August–November (females accompanied by juveniles, dispersal phase, and low rabbit abundance).

In order to test for temporal avoidance between individuals (dynamic temporal segregation) we defined consecutive entrances for pairs of lynx sharing the same breeding territory when two entrances occurred in the same circadian activity cycle (24 h, starting at midday). We assigned each pair of consecutive entrances to one of the following categories: adult males and adult females (AM–AF); adult males and young lynx (AM–Y) and adult females and young lynx (AF–Y). Since active avoidance of superior competitors by subordinates could occur regardless the order in which animals acceded to FS, we did not distinguish whether the dominant or the subordinate lynx entered FS first. Differences in the time elapsed between consecutive lynx entrances

across lynx dyads were examined using a GLMM with gamma error and log link, treating dyad identity, year, and area as random effects. All GLMMs were fitted with SAS 9.2 (procedure GLIMMIX, Littell et al. 2006).

Results

Use of prey hotspots

Supplemented lynx spent between 6% and 30% of their active time within 100 m of FS (mean proportion of activity $\pm$ SD = 0.15 $\pm$ 0.07, n = 26, Table 1, Fig. 1). Although these figures may not seem particularly high in absolute terms, such amount of activity was concentrated in areas ranging between 0.03 km² and 0.28 km², depending on the number of available FS (Table 1), that is, between 0.2% and 6.6% of the annual mean home range size of adult females or breeding territories (4.67 to 15.2 km², Ferreras et al. 1997, López-Bao et al. 2010a). During their activity period, the proportion of lynx positions around FS was between 5 and 160 times higher than in areas of the same size around random points. These differences were significant (Wilcoxon signed-rank test: Z = 4.46, p < 0.0001, n = 26), and consistent across years and territories (Table 1). The number of FS did not significantly influenced the

Figure 1. A representative example of the use of space by non-supplemented (A) and supplemented (B) Iberian lynx. We show the outline of 90% fixed kernel estimates of annual home ranges, circular buffers of 100 m radius around feeding stations (grey circles) and the distribution of activity positions (dots).

proportion of activity around FS (Spearman correlation analysis: $r_s = 0.214$, $p = 0.294$, $n = 26$).

Non-supplemented lynx only spent between 0.02% and 2.85% of their active time within 100 m of simulated FS points (Fig. 1). The mean percentage of activity ($\pm$ SD) for non-supplemented lynx was 0.01 ± 0.008 , ($n = 42$), 14 times lower than the corresponding mean for supplemented lynx. These differences were significant (Mann-Whitney U-test: $Z = 6.89$, $p < 0.0001$, $n = 68$). Within the home ranges of supplemented lynx, the 100 m radius circular area containing the maximum proportion of activity positions matched the location of FS in 90% of cases ($n = 25$, Fig. 1). On average, supplemented lynx significantly spent more time active in buffers of highest density of activity positions (mean proportion of activity positions $\pm$ SD = 0.13 ± 0.06 , $n = 25$) than non-supplemented animals (mean proportion of activity positions $\pm$ SD = 0.06 ± 0.02 , $n = 41$, $\chi^2 = 59.41$, $DF = 1$, $p < 0.001$).

In the low rabbit abundance area (VE), concentration of activity around FS was more marked than in CR, where wild rabbit density was higher (Table 1, Fig. 2). In VE, only two lynx with access to rabbit abundance levels comparable to those in CR spent $< 10\%$ of their active time around FS (Fig. 2).

Temporal segregation

Lynx visited FS mainly at dusk, when we recorded 21% of total lynx entrances to FS, and 65% of lynx entrances within

the four fixed time blocks. We also recorded visits with some frequency around midnight (Fig. 3). This pattern held for all sex and age classes. We did not find indication of temporal segregation in the use of FS between unequal competitors during fixed time blocks (Fig. 3). The effect of sex and age on the frequency of lynx entrance to FS was not significant in any model ($p > 0.070$) with the only exception of the interaction term at dawn ($p = 0.038$, Fig. 3).

However, we found evidence for a dynamic temporal avoidance between individuals with different competitive abilities. The mean time between two consecutive entrances of different individuals to a shared FS increased with the distance in the competitive hierarchy between the two lynx involved (Fig. 4). Adult females and young lynx spaced out their entrances on average 2.4 and 3.2 h, respectively, regarding either a previous or a later visit by adult males (Fig. 4). However, the mean interval between successive visits by adult females and young was lower (2.1 h, Fig. 4). The time elapsed between consecutive lynx entrances differed among lynx dyads ($AM-Y > AM-AF > AF-Y$, Fig. 4). Overall these differences were significant ($F_{2,266} = 3.13$, $p = 0.045$), although post hoc analyses revealed significant differences only between AM-Y and AF-Y dyads (Tukey's HSD-test: $p = 0.040$). Despite several FS were available in each breeding territory (Table 1), most consecutive lynx entrances (90%, $n = 291$) took place in the same FS, giving additional support to the lack of spatial segregation in the use of prey hotspots.

Figure 2. Regression between the proportion of lynx activity positions within circular buffers with a radius of 100 m around feeding stations and an index of rabbit abundance within lynx breeding territories ($r^2 = 0.411$). Black circles: lynx from VE, grey circles: lynx from CR.

Discussion

Lynx adjusted their foraging strategies to spatial changes in food availability (prey hotspots) in agreement with optimal foraging theory (Stephens and Krebs 1986, Stephens et al.

Figure 3. Proportion of lynx entrances to feeding stations (upper panel), and number of entrances h^{-1} (lower panel) recorded at dawn, midday, dusk, and midnight time blocks in different combinations of sex and age classes.

Figure 4. Mean time elapsed ($\pm$ SE) between consecutive lynx entrances to feeding stations for three lynx dyads whose members differed in the distance that separate them through a competitive hierarchy: AM-Y (adult males – young lynx, $n = 7$); AM-AF (adult males – adult females, $n = 6$) and AF-Y (adult females – young lynx, $n = 6$).

2007). Lynx were active close to FS with higher frequency than around randomly located points, as predicted by optimal foraging theory (Rohner and Krebs 1998, Sih 2005, Stephens et al. 2007). This pattern held across individuals with different competitive ability, and was independent of the number of FS available. This confirms that inferior competitors had free access to FS and the absence of competitive spatial exclusion at prey hotspots.

The negative relationship between the concentration of activity around FS and the abundance of wild rabbits again suggests flexibility in foraging behaviour and agrees with the higher proportion of domestic rabbits found in the lynx diet when wild rabbits occurred at very low density (López-Bao et al. 2010b). As other studies have pointed out, such flexibility in foraging behaviour may be adaptive to cope with environmental changes (Eide et al. 2004). The increased activity away from FS when more wild rabbits were available also suggests that there might be some cost in concentrating a large proportion of activity in a single or a few points, for example, travel costs if adults should tradeoff feeding and patrolling their territories.

The abundance of wild rabbits greatly varies across lynx home ranges (Palomares 2001b, Fernández 2005), and non-supplemented lynx might also spend significant proportions of their foraging time on high-density patches of wild rabbits. However, all supplemented lynx allocated disproportionately higher proportions of activity around prey hotspots than did non-supplemented animals in areas of similar size. Moreover, the maximum density of activity positions in the home ranges of supplemented lynx usually occurred around prey hotspots, and similarly high densities were never recorded in the ranges of non-supplemented lynx, reflecting again that FS increased the spatial predictability of lynx activity (see Roth and Vetter 2008 for similar results). This suggests that natural and artificial rabbit patches were of different nature. First, as supplemented rabbits cannot move freely the game between predator/prey predictability reported in natural patches of wild prey (Roth and Lima 2007) does not hold

in artificial prey hotspots (FS). Second, whereas the position of wild rabbit patches changed frequently (Fernández 2005), FS had a fixed location so that the spatial predictability of artificial food patches was highest. Third, the frequent artificial supply of FS probably raised rabbit density within FS (1–7 exposed rabbits in enclosures of 16 m², López-Bao et al. 2008) above the maximum local density elsewhere within lynx home ranges (Fernández 2005, Moreno et al. 2007). Finally, supplemented rabbits were readily available for any lynx irrespective of their sex or age (López-Bao et al. 2009). Overall, lynx consumed large amounts of extra food especially where wild rabbits were scarce (López-Bao et al. 2008, 2010b), and the vulnerability of domestic rabbits to foraging lynx was probably higher than that of wild rabbits (López-Bao et al. 2008).

Foraging theory postulates that interference is a foraging cost affecting patch exploitation and activity budgets (Kotler et al. 2005, Stephens et al. 2007, Anderson 2010). Although all lynx sharing the same breeding territory focused their activity on prey hotspots and made a regular but asymmetrical use of supplemental food (López-Bao et al. 2009, Fig. 3), our results did not support a temporal segregation between competitors in fixed time blocks. In the competitive hierarchy, low ranking lynx did not shift their temporal pattern of resource use to times of the day when superior competitors visited FS with low frequency (see Bonanni et al. 2007 for similar results). Indeed, most lynx entered FS at dusk irrespective of their position in the competitive hierarchy.

Yet, the remarkable correlation between time elapsed between consecutive entrances and the difference in competitive rank between the two lynx involved suggests that interference could produce a dynamic temporal segregation or active avoidance between individuals at prey hotspots irrespective of the time of day. Active temporal avoidance could enable subordinates to exploit the same predictable food patches than dominants use, while decreasing the probability of agonistic interactions. Signs of interference avoidance occurred not only between adult males and younger lynx of the same sex, which may be related to competition for territories (Ferrerías et al. 2004), but also between adult males and females, as found in other species (Feinsinger 1976). Young lynx and adult females, especially when accompanied by their juvenile offspring < 1 year old, could actively avoid social encounters and the associated risk of agonistic interaction with dominant adult males that frequently used FS (López-Bao et al. 2009). An analogous dynamic temporal segregation at prey hotspots has been documented, and attributed to interference, in social carnivores consuming large prey (temporal prey hotspots, Schaller 1972, Peterson and Ciucci 2003).

The relatively long intervals between the entrances of adult females or young lynx and the entrances of adult males could also partly reflect the solitary habits of the Iberian lynx, where contacts between adult males and other individuals of the same breeding territory rarely occur (Ferrerías et al. 1997). That inferior competitors actively avoid the surroundings of FS when adult males are present implies some sort of continuous spatial tracking of adult male behaviour by adult females and young. This avoidance may facilitate coexistence not only in food patches, but also elsewhere in the shared home range. The higher temporal correlation

between consecutive visits of AF–Y dyads may be explained by the fact that adult females and their offspring often forage together (Ferrerías et al. 1997).

On the other hand, the high concentration of activity positions around FS may not be exclusively related to foraging. The presence of prey hotspots may intensify social interactions (Skalski and Gilliam 2001). In particular, dominant adult males may invest more time patrolling and actively defending FS inside their territories, while some subordinates, particularly unskilled juveniles, may starve with higher frequency and then check FS frequently for the occurrence of rabbits and the presence of dominants (López-Bao et al. 2008, 2009).

Our study documents how prey hotspots can be exploited by conspecifics with marked differences in competitive ability by means of dynamic temporal segregation among individuals. In contrast with the findings of recent studies (Roth and Lima 2007), our results suggest that prey clumping in predictable and profitable hotspots elicit a parallel concentration of activity that could be explained by a balance between foraging behaviour, resource defence, and avoidance of potentially aggressive encounters.

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