

ENVIRONMENTAL DETERMINANTS OF CIRCADIAN ACTIVITY OF FREE-RANGING IBERIAN LYNXES

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From February 1983 to May 1985, 12 Iberian lynxes (*Lynx pardinus*) (six adults and six juveniles) were radiotracked at hourly intervals for 114 24-h periods at Doñana National Park, southwestern Spain. Nine environmental factors were related, by season and age class, to 12 indices of daily activity of lynxes derived from movement rates and pulses of the motion sensor in the transmitters. Coefficients of determination were higher in winter and summer than in spring. Juvenile lynxes appeared more sensitive to environmental factors than adults. Photoperiod had a major influence ($R^2 = 29\%$) on circadian activity pattern throughout the year. Environmental factors significantly related to activity of lynxes during winter were maximum temperature, pressure changes, evaporation, and moonphase. In summer, important variables were maximum temperature, moonphase, hours with moonlight, and high pressures. In spring, only rainfall and temperature (minimum and maximum) showed a slight but significant influence on activity of lynxes. Although some climatological factors may have a direct effect on the circadian activity of Iberian lynx, others (e.g., moonlight) may act indirectly by influencing the activity of the Mediterranean rabbit, the lynx's main prey.

Key words: circadian activity, Iberian lynx, *Lynx pardinus*, Mediterranean rabbit, *Oryctolagus cuniculus*, weather

Activity patterns are part of the adaptations of species to their environment (Daan and Aschoff, 1982; Enright, 1970); changes in activity patterns may occur in response to changes in environmental conditions (Tester, 1987). Environmental influences on the activity of vertebrates are well documented for amphibians (Banks and Beebe, 1986), birds (Blem and Shelor, 1986), and small mammals (Lockard and Owings, 1974a, 1974b; Marten, 1973; Veiga, 1986; Vickery and Bider, 1981). Studies have focused largely on prey species (Alkon and Saltz, 1988). In carnivores, similar studies are difficult to accomplish (Emmons et al., 1989), and radiotracking becomes necessary to cope with the common low densities, large ranges, and nocturnal habits of carnivores. Environmental influences are mostly considered for extreme climatic conditions, such as severe winter (Bailey, 1974, 1981; Nellis and Keith, 1968). Ables's

(1969) study on red foxes (*Vulpes fulva*) is pioneering in this respect. Influence of environmental factors on activity of carnivores is reported by Garshelis and Pelton (1980) on black bears (*Ursus americanus*), Zielinski et al. (1983) on pine martens (*Martes americana*), Ferguson et al. (1988) on black-backed jackals (*Canis mesomelas*), and Fowler and Racey (1988) on European badgers (*Meles meles*).

The Iberian lynx (*Lynx pardinus*) is an endangered species (Beltrán and Delibes, 1993; International Union for Conservation of Nature, 1986) currently restricted to southwestern Spain and Portugal (Rodríguez and Delibes, 1992). Its staple prey is the Mediterranean rabbit, *Oryctolagus cuniculus* (Beltrán, 1987; Beltrán and Delibes, 1991; Delibes, 1980); in fact, the sharp decrease observed in Mediterranean rabbits due to a disease in the late 1950s had a major impact on the decline in numbers of

the Iberian lynx (Delibes, 1979). Iberian lynxes, although basically crepuscular and nocturnal, present considerable variability in activity pattern depending on individual, age, season, and habitat (Beltrán, 1988). Juvenile lynxes are mostly crepuscular and diurnal, with increasing nocturnal activity after their 1st year; adult lynxes with home ranges in the same habitat synchronize their activity patterns. During winter, lynxes may be active throughout the 24-h period, which contrasts with their almost strictly nocturnal summer habits (Beltrán, 1988).

As part of a long-term study on the population biology of the Iberian lynx (Beltrán et al., 1992), we determined variation in activity patterns of lynxes according to endogenous factors (Tester, 1987) such as sex, age, and individual (Beltrán, 1988), and exogenous factors such as season, weather, and rabbit behavior. This paper examines the variation in activity patterns of lynxes by age class in relation to environmental determinants. We tested the hypotheses that climatological variables would have no direct effect on activity of lynxes and environmental factors might be related to activity of lynxes indirectly, by influencing the activity of rabbits.

MATERIALS AND METHODS

The study area was the Doñana National Park, a 500-km² reserve on the Atlantic coast of southern Spain, at the mouth of the Guadalquivir River (37°N, 6°30'W). The climate is Mediterranean, with hot, dry summers (mean 23.5°C, range of monthly maximum temperatures for 1983–1985 of 28.8°C in July to 33.8°C in August) and mild winters (9.3°C, range of monthly minimum temperatures for 1983–1985 of 2.7°C in January to 4.7°C in March—Beltrán, 1988). Annual rainfall averages 529 mm with peaks in October–November and March–April (Beltrán and Delibes, 1991). The major habitats are marshlands, shrublands, and sand dunes. Detailed descriptions of the area are in Valverde (1958) and Rogers and Myers (1980).

Free-ranging Iberian lynxes were trapped, anesthetized, and fitted with radiocollars (Delibes and Beltrán, 1986), which incorporated a

motion sensor (Biotrack, Wareham, UK, and Wildlife Materials Inc., Carbondale, IL) triggering either a slow (45–60 beats/min) or a fast (72–104 beats/min) pulsing transmission depending on the collar position. Signals from transmitters were received with a LA-12 receiver and a three-element hand-held Yagi antenna (AVM Instrument Co., Livermore, CA). From blind tests and transmitters placed at known positions, we estimated our location error at <6° for 90% of the radiolocations; average distance from transmitter to receiver was ≤1 km. During 24-h cycles, the position and activity (active versus inactive) of radioinstrumented lynxes were recorded. Signals from a transmitter were monitored for 2 min to determine if the animal was active or inactive. Animals were considered as resting between hourly radiotriangulations when estimated distance traveled was ≤100 m (Beltrán, 1988).

Twelve activity variables were determined, including eight movement rates (i.e., distance traveled/h), and the absolute distance traveled in 24 h. Four periods were considered in the circadian cycle; dawn, day, dusk, and night. Length of dawn and dusk were considered constant at 2 h throughout the year. Nightlength and daylength were estimated as follows: a) from November to February, 9 h/day, 11 h/night; b) March, April, September, and October, 11 h/day, 9 h/night; c) from May to August, 13 h/day and 7 h/night. For resting periods (i.e., as measured by 1-h intervals) and for percent of activity variables, only two intervals (day and night) were considered; these followed the same seasonal pattern previously described, with the addition of 2 h each (one from dawn and another from dusk). In addition, three resting variables were determined; hours resting during day, night, and the 24-h cycle. Using this grouping, we also included three variables measuring percentage of activity (percentage of locations with active animals), as estimated from changes on the activity switch of the radiotransmitter. Three seasons were defined (Aldama et al., 1991; Beltrán, 1988): spring (March–June); summer (July–October); winter (November–February). Two age classes were considered: juveniles (≤2 years old) and adults (>2 years old). Capture date, body measurements, and tooth wear were criteria used for age determination (Beltrán and Delibes, 1993).

Nine environmental variables, mostly recorded

at the study area, were associated with each circadian period; photoperiod (length of daylight), minimum and maximum temperatures, rainfall, evaporation (method of Piché—Smith, 1975), moonphase (estimated for each day, scale from 0 = new moon to 1 = full moon), hours with moonlight between sunset and sunrise (Instituto Nacional de Meteorología, 1983, 1984, 1985), barometric pressure (as measured at 1800 GMT, Observatorio Meteorológico of Huelva, ca. 45 km west of the study area), and changes in barometric pressure (estimated as the difference between the values of pressure at 0700 GMT for each circadian period of radiomonitoring).

For analysis of data, we used the BMDP statistical package (Dixon et al., 1983). Programs P1R (multiple linear regression) and P2R (stepwise regression) were used. Regressions were performed with log-transformation (\log_{10} [distance in meters + 1]) of the activity variables. Standardized partial-regression coefficients (r) were used throughout as a measure of the effect of each environmental variable on the total variation accounted by the coefficient of determination, R^2 , as percent (Zar, 1984). Those environmental factors with nonsignificant contribution to the regression analysis were eliminated, and the regression recalculated (Ables, 1969).

RESULTS

We completed 114 24-h cycles of radiotracking on 12 Iberian lynxes; four adult males, two adult females, and six juveniles (three males and three females). Number of 24-h cycles monitored for an individual averaged 9.66 (range of 1–41); all individuals were pooled for analyses.

Photoperiod had a significant, inverse relationship with percent activity throughout the year, during both day ($r = -0.406$, $P < 0.001$, $R^2 = 29.2$, $P < 0.001$, $df = 1, 112$) and night ($r = -0.180$, $P < 0.001$, $R^2 = 22.5$, $P = 0.06$) and in the 24-h cycle ($r = -0.381$, $P < 0.001$, $R^2 = 19.7$, $P = 0.004$). Lynxes were more active during day and night as photoperiod decreased, revealing a major influence of season on activity of lynxes. Further analyses were performed within seasons.

The maximum average influence of environmental factors on activity was in win-

ter ($R^2 = 35.7\%$, $P \leq 0.01$, for the percentage of locations active; $R^2 = 40\%$, $P \leq 0.05$, for the rate of movement during day, Table 1). The relation of environmental factors to activity of lynxes in winter depended on the interval considered. Barometric pressure changes and evaporation were related negatively ($r = -0.385$, and $r = -0.367$, respectively) and significantly ($P = 0.02$, both) to the activity in a 24-h period (Table 1). Barometric pressure and evaporation also were related to the time spent resting during day, i.e., lynxes rested less during winter when barometric pressure or evaporation was high (Table 1).

Movement rates at night increased significantly, thus decreasing hours resting, when maximum temperatures increased ($r = 0.687$, $P \leq 0.05$, and $r = -0.766$, $P \leq 0.05$, respectively). Conversely, lynxes spent more time resting at night and during a 24-h period ($r = 0.674$, $P \leq 0.01$) as winter minimum temperatures increased. In this season, moonphase related significantly to the rate of displacements of lynxes at dusk ($r = 0.424$, $P \leq 0.05$); number of hours with moonlight also was positively related to movement rates of lynxes at dawn ($r = 0.546$, $P \leq 0.01$, Table 1).

During summer, only two activity variables had significant coefficients of determination: percentage of diurnal locations showing activity ($R^2 = 23.3\%$, $P \leq 0.01$) and distances traveled in 24 h ($R^2 = 19.0\%$, $P \leq 0.04$, Table 2). Maximum temperature was the environmental factor with the highest relation to activity of lynxes during summer. Diurnal activity levels were significantly and negatively related to maximum temperature ($r = -0.513$, $P = 0.01$). Moonlight hours were inversely related to percentage of total active locations ($r = -0.501$, $P = 0.06$) and absolute distance traveled during night ($r = -0.346$, $P = 0.09$, not tabulated); moonphase, however, corresponded positively to percentage of total active locations ($r = 0.433$, $P = 0.07$, Table 2). High summer barometric pressures were associated with significant de-

TABLE 1.—Winter (November–February) standardized partial regression coefficients (r), coefficient of multiple determination (R^2) of selected environmental variables to activity (percentage of fixes active and movement rates) of radiomonitored ($n = 24$ -h) Iberian lynxes (six adults and five juveniles).

Variable	Temperature		Rainfall	Pressure			Moon		R^2	P
	Maximum	Minimum		Current	Changes	Evaporation	Hours	Phase		
Activity (%)										
Day			0.205		-0.341	-0.265			19.9	0.10
Night					-0.256	-0.384*		0.277	32.0	0.02
Total (24 h)					-0.385*	-0.367*		0.147	35.7	0.01
Movement (per hour)										
Day	-0.256	0.111	0.389*		-0.294	-0.286		-0.361	40.0	0.05
Night	0.687*	-0.490		-0.383					20.7	0.10
Dusk				-0.296		-0.200		-0.424*	26.2	0.05
Dawn	0.111			-0.219		-0.282	-0.546**		33.0	0.04
Dusk + dawn	0.179			-0.327		-0.264		0.557	39.5	0.01
Total (24 h)	0.431	-0.337		-0.275		-0.264			20.5	0.20
Resting (hours)										
Day	0.264		-0.276	-0.398*	0.251	0.338		0.232	39.0	0.06
Night	-0.766*	0.573		0.251			0.376	-0.433	24.3	0.23
Total (24 h)	-0.648**	0.674**							22.8	0.03

* $P \leq 0.05$.

** $P \leq 0.01$.

*** $P \leq 0.001$.

TABLE 2.—Summer (July–October) standardized partial-regression coefficients (r), coefficient of multiple determination (R^2) of selected environmental variables to activity (percentage of fixes active and movement rates) of radiomonitored ($n = 24$ -h) Iberian lynxes (three adults and three juveniles).

Variable	Temperature		Pressure		Evaporation	Moon		R^2	P
	Maximum	Minimum	Current	Changes		Hours	Phase		
Activity (%)									
Day	-0.513**	0.261						23.3	0.01
Night	0.118		-0.199		-0.240	-0.211		6.4	0.70
Total (24 h)	0.261		-0.188			-0.501	0.433	23.1	0.10
Movement (per hour)									
Day		-0.214	-0.380**	0.214		-0.309		22.6	0.01
Night				-0.236		-0.161	-0.134	12.7	0.20
Dusk		0.307					-0.168	11.4	0.16
Dawn	-0.246				0.255		-0.299	16.0	0.16
Dusk + dawn	-0.226	0.247			0.253		-0.263	16.2	0.27
Total (24 h)						-0.167	-0.293	19.0	0.04
Resting (hours)									
Day		0.234	0.277		0.269		0.268	21.1	0.14
Night		-0.162	-0.174				0.185	7.8	0.49
Total (24 h)					0.196		0.303	11.5	0.15

* $P \leq 0.05$.

** $P \leq 0.01$.

*** $P \leq 0.001$.

TABLE 3.—Spring (March–June) standardized partial-regression coefficients (r), coefficient of multiple determination (R^2) of selected environmental variables to the activity (percentage of fixes active and movement rates) of radiomonitored ($n = 24$ -h) Iberian lynxes (four adults and five juveniles).

Variable	Temperature		Rainfall	Pressure			Moon		R^2	P
	Maximum	Minimum		Current	Changes	Evaporation	Hours	Phase		
Activity (%)										
Day		0.179	0.280			0.198			9.8	0.17
Night	0.270*		0.190	0.190				0.165	14.4	0.10
Total (24 h)		0.320*	0.310*	0.263			0.250		17.7	0.05
Movement per hour										
Day			0.139			0.194	−0.139		5.1	0.46
Night	0.187	−0.337*	−0.140						11.0	0.10
Dusk	0.267*					−0.139		0.251	10.6	0.14
Dawn		0.090	0.124	0.188					3.5	0.60
Dusk + Dawn	0.135		0.143	0.226	0.093				6.6	0.50
Total (24 h)	0.091				0.116	0.123		0.122	4.8	0.66
Resting (hours)										
Day	0.355**	−0.264	−0.396**			−0.417**	0.223	−0.212	27.7	0.01
Night	−0.242	−0.253		−0.201			−0.236		22.8	0.01
Total (24 h)			−0.255			−0.328		−0.218	17.7	0.02

* $P \leq 0.05$.

** $P \leq 0.01$.

*** $P \leq 0.001$.

TABLE 4.—Winter standardized partial-regression coefficients (r), coefficient of multiple determination (R^2) of selected environmental variables to the percentage of fixes active, and resting time of six adult Iberian lynxes ($n = 24$ 24-h cycles).

Activity	Environmental factor	Regression coefficient	P	R^2 total (%)	P
Activity (%)					
Day	Rainfall	0.240	0.20	42.0	0.01
	Pressure change	-0.530	0.01		
	Evaporation	-0.370	0.05		
Night	Pressure change	-0.350	0.08	24.9	0.04
	Evaporation	-0.290	0.14		
Total (24 h)	Maximum temperature	-0.130	0.50	44.2	0.02
	Pressure change	-0.510	0.01		
	Evaporation	-0.330	0.09		
	Moonphase	0.120	0.48		
Resting (hours)					
Day	Rainfall	-0.480	0.02	35.1	0.03
	Pressure change	0.360	0.08		
	Evaporation	0.370	0.06		
Night	Maximum temperature	-0.500	0.10	14.6	0.18
	Minimum temperature	0.500	0.89		
Total (24 h)	Maximum temperature	-0.580	0.04	23.3	0.06
	Minimum temperature	0.660	0.02		

TABLE 5.—Summer standardized partial regression coefficients (r), coefficient of multiple determination (R^2) of selected environmental variables to the percentage of fixes active, and resting time of three adult (A, $n = 23$ 24-h cycles) and three juvenile (J, $n = 10$ 24-h cycles) Iberian lynxes.

Activity	Age	Environmental factor	Regression coefficient	P	R^2 total (%)	P
Activity (%)						
Day	J	Maximum temperature	-0.420	0.22	18.0	0.22
	A	Maximum temperature	-0.550	0.01	29.8	0.01
Night	J	Moonlight (hours)	-0.690	0.03	48.0	0.02
	A	Moonlight (hours)	0.440	0.05	19.5	0.05
Total (24 h)	J	Moonlight (hours)	-0.670	0.03	45.5	0.03
	A	Maximum temperature	-0.310	0.17	21.0	0.13
		Moonphase	0.340	0.14		
Resting (hours)						
Day	J	Maximum temperature	0.880	0.40	16.8	0.70
		Minimum temperature	0.220	0.60		
		Evaporation	-0.430	0.60		
	A	Maximum temperature	0.320	0.40	7.5	0.70
		Minimum temperature	0.050	0.80		
		Evaporation	-0.130	0.70		
Night	J	Moonphase	0.500	0.14	25.0	0.13
Total (24 h)	J	Moonphase	0.740	0.01	54.9	0.01
		Evaporation	-0.700	0.03		
	A	Minimum temperature	0.330	0.05	19.0	0.04
		Evaporation	-0.300	0.08		

TABLE 6.—Spring standardized partial regression coefficients (r), coefficient of multiple determination (R^2) of selected environmental variables to percent of fixes active, and resting time of four adult (A, $n = 33$ 24-h cycles) and five juvenile (J, $n = 19$ 24-h cycles) Iberian lynxes.

Activity	Age	Environmental factor	Regression coefficient	P	R^2 total (%)	P			
Activity (%)									
Day	J	Minimum temperature	0.430	0.08	18.1	0.07			
	A	Evaporation	0.210	0.21	4.4	0.20			
Night	J	Maximum temperature	0.380	0.08	13.3	0.34			
		Pressure change	0.370	0.14					
	A	Rainfall	0.150	0.40	6.1	0.38			
		Moonphase	0.230	0.20					
Total (24 h)	J	Minimum temperature	0.450	0.06	20.3	0.06			
Resting (hours)									
Day	J	Minimum temperature	-0.440	0.13	55.0	0.02			
		Maximum temperature	0.670	0.03					
		Rainfall	-0.700	0.01					
		Evaporation	-0.390	0.15					
	A	Minimum temperature	-0.090	0.60	16.8	0.20			
		Maximum temperature	0.340	0.12					
		Rainfall	-0.300	0.11					
		Evaporation	-0.360	0.09					
		J	Moonphase	-0.430			0.07	18.7	0.07
			A	Moonphase			-0.240		
Total (24 h)	J	Minimum temperature	-0.500	0.11	27.7	0.08			
		Evaporation	-0.700	0.03					
	A	Maximum temperature	0.330	0.05	19.0	0.04			
		Evaporation	-0.300	0.08					

clines in the diurnal movement rate ($r = -0.380$, $P = 0.04$, Table 2).

During spring, activity of lynxes appeared little influenced by environmental factors (Table 3). Nevertheless, 28% ($P \leq 0.01$) of the variation in daytime resting hours and 23% ($P \leq 0.01$) of nighttime resting may be explained by environmental factors (Table 3).

Rainfall and increased minimum temperatures corresponded to increased 24-h activity, as estimated by percent of active locations ($r = 0.310$, $P = 0.04$). Rainfall and evaporation also were inversely related to daytime resting ($r = -0.396$, and $r = -0.417$, respectively, $P \leq 0.01$, both), which was positively related with high maximum temperatures ($r = 0.355$, $P \leq 0.01$). Elevated maximum temperatures also corresponded with both increased movement rate at dusk ($r = 0.267$, $P \leq 0.05$)

and increased nocturnal activity ($r = 0.270$, $P \leq 0.05$; Table 3).

Due to small samples, only six variables based on day-night segregation were used to analyze the environmental determinants by age class within each season. During winter, removal of the five 24-h, radiomonitoring periods of juveniles resulted in increases in the determination coefficients of both active locations during 24 h (from 35.7%, $P \leq 0.01$, to 44.2%, $P \leq 0.02$) and diurnal active locations (from 19.8%, $P \leq 0.01$, to 42%, $P \leq 0.01$; Table 4).

During summer, moonlight hours were strongly related ($R^2 \geq 45\%$) to activity of juvenile lynxes (as measured by percent of active locations, during both night and 24-h periods, Table 5). Moonphase corresponded positively with resting time during night and 24-h periods, reaching $R^2 = 55\%$ ($P \leq 0.01$, Table 6). Activity of adults was main-

ly related to maximum temperatures during day (Table 5).

In spring, daytime resting of juveniles was strongly ($R^2 = 55\%$, $P = 0.02$) related to environmental factors; resting increased during higher maximum temperatures ($r = 0.670$, $P = 0.03$, Table 6) and decreased during rainfall ($r = -0.700$, $P \leq 0.01$). Minimum temperatures also were positively related to increased total activity of juveniles ($r = 0.450$, $P = 0.06$). Among adults, only total resting time was significantly related ($r = 0.330$, $P \leq 0.05$) to spring minimum temperatures (Table 6).

DISCUSSION

Our analyses of radiotracking data revealed some significant relationships between environmental factors and activity of Iberian lynxes. This may be a surprising result for a medium-sized carnivore in a temperate climate. Our results may be considered first in terms of direct effects on activity of lynxes (i.e., proximate factors). Photoperiod is considered to have a major influence on mammalian activity (Daan and Aschoff, 1975; Ferguson et al., 1988; Fowler and Racey, 1988). Precipitation resulted in decreased activity in red foxes, and decline in activity corresponded to amount of rainfall (Ables, 1969). Black bears were less active during rain, but more active than usual within 3 h after rain stopped (Garshelis and Pelton, 1980). Iberian lynxes increased their diurnal movement rate during rain; in adults, declines in minimum temperature in winter and spring corresponded to less resting time and greater movement rates. Ables (1969) reported that an adult red fox was more active when temperatures were low in autumn, and Kline (1965) noticed a similar relationship with roadside counts of cottontails. Juvenile lynxes tended to increase their resting time when minimum temperatures decreased in spring or when maximum temperatures increased. Zielinski et al. (1983) observed that activity of martens was positively related to temperature; Garshelis and Pelton (1980) also

observed increase in activity of black bears with temperature, up to a threshold of 20°C. Juvenile lynxes were largely day-active in their 1st year (Beltrán, 1988). From body mass, critical minimum temperature (McNab, 1970) for a 6-kg juvenile lynx (approximate body mass in March–June—Beltrán and Delibes, 1993) is 6°C; for adult lynxes, critical minimum temperatures are 1°C for females and -2.4°C for males. In this study, average minimum temperatures in the area ranged from 2.7°C (January) to 9.6°C (November) during the winter season and from 4.7°C (March) to 15.0°C (June) in spring. In juvenile lynxes, the diurnal activity pattern may be explained in part as a thermoregulatory response (see also Kavanau et al., 1972). Adult lynxes behave more independently of low temperatures but should be more sensitive to maximum temperatures in summer (Ables, 1969; Alvarez et al., 1983; Garshelis and Pelton, 1980), which are closer to the 39°C maximum critical temperature expected for this species according to body mass (MacNab, 1970).

Environmental factors may act indirectly on behavior of Iberian lynxes. Moonlight, for example, may directly affect behavior of prey rather than that of lynxes. During moonlight, ocelots changed their use of habitat, and avoided trails (Emmons et al., 1989), in apparent response to the behavior of potential prey (Emmons et al., 1989). Ferguson et al. (1988) also found that the activity of prey might be the ultimate determinant of activity of jackals. They reported that black-backed jackals were most active during intermediate moonlight and decreased their activity during high, nocturnal illumination. Ferguson et al. (1988) suggested that prey could readily detect the jackals during full-moon periods, decreasing hunting efficiency of jackals and causing them to be inactive at such times; such decrease in activity in medium-size predators, however, might be to avoid encounters with other larger, sympatric predators (Emmons et al., 1989). The Iberian lynx's main prey year-round is the Mediterranean rabbit

(Beltrán and Delibes, 1991; Delibes, 1980), and preliminary studies indicate that activity patterns of Iberian lynxes closely follow those of rabbits, which are largely nocturnal (Beltrán, 1988). Temperature strongly influences activity of rabbits (Alvarez et al., 1983; Kolb, 1992; Villafuerte et al., 1993). Activity of rabbits was positively related to dawn and day-time temperature and negatively temperature-dependent at night (Villafuerte et al., 1993). This is an expected result since mass-based, estimated critical minimum temperature of the Mediterranean rabbit is 20°C (MacNab, 1970). Moonlight was the second most important influence on activity of rabbits (Villafuerte et al., 1993); in Doñana National Park, activity of rabbits is positively related to moonlight. This result contradicts the lunar phobia reported in rabbits (Kolb, 1992) and other prey species (Alkon and Saltz, 1988; Lockard and Owings, 1974a). However, other aspects such as habitat structure, availability of food, and type of predators made it difficult to examine the effect of night illumination on rabbits (Lockard and Owings, 1974b; Travers et al., 1988). In Doñana National Park, with mammals the only potential nocturnal predators of rabbits, lynxes seem to take advantage of moonlight nights. This behavior might be especially important during winter, when abundance of rabbits is low (Beltrán, 1991). The increase of movement rate of lynxes during dusk in winter may be a strategy to maximize predation on young or subadult rabbits that are forced to forage earlier by dominant adults (Soriguer, 1983). During summer, moonphase is significantly associated with decreased activity of juvenile lynxes and increased resting (at night and 24 h). In other carnivores, ambient light preferences of juveniles differ from those of adults (Kavanau et al., 1972); in general, juveniles of nocturnal species seem more active during day than are adults (Palomares and Delibes, 1988). Further studies on rabbit-lynx-moonlight interaction should address the following issues: 1) effects of moonlight on success of predation by lynx-

es; 2) use of habitat by rabbits; 3) seasonal differences in relation to moonlight (comparing summer, with high abundance of rabbits—Beltrán, 1991, low predation impact—Kufner, 1986, and elevated proportion of immature rabbits to winter, with low numbers of mostly adult rabbits and high predation pressure).

Our data support previous observations in other vertebrate species and indicate that activity of Iberian lynxes is higher when barometric pressure is decreasing. The influence of barometric pressure on the activity of vertebrates has been documented (Aschoff, 1981; Aschoff et al., 1982). In birds, courting displays and reproductive activity tended to peak during high and increasing barometric pressure (Castroviejo, 1975); in mammals, capture rates, an index of activity, are significantly related to changes in barometric pressure (Barick, 1952). Ables (1969) noted that the influence of barometric pressure is much easier to demonstrate than to explain and concluded that both positive and negative correlations between mammalian activity and barometric pressure exist, but that the causal mechanisms are not known. In his study on red foxes, Ables (1969) reported that the combined effect of weather factors was seasonally the greatest during winter; barometric pressure was the most important environmental factor and was negatively associated with activity of red foxes. Activity of free-ranging Iberian lynxes inhabiting a Mediterranean area may be in part explained by interactions with environmental factors; some of them are likely indirect effects influencing prey activity.

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