

Activity patterns of brown bears (*Ursus arctos*) in Slovenia and Croatia

P. Kaczensky¹, D. Huber², F. Knauer³, H. Roth⁴, A. Wagner⁵ & J. Kusak²

1 Institute of Wildlife Biology and Game Management at the Agricultural University of Vienna, Vienna, Austria

2 Biology Department, Veterinary Faculty of the University of Zagreb, Zagreb, Croatia

3 Department of Wildlife Ecology and Management, Institute of Forest Zoology, University of Freiburg, Freiburg, Germany

4 Centro Studi Ecologici Appenninici, Parco Nazionale d'Abruzzo, Italy

5 Institute of Evolutionary Biology and Ecology, University of Bonn, An der Immenburg, Bonn, Germany

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Correspondence

Petra Kaczensky. Current address: Department of Wildlife Ecology and Management, Institute of Forest Zoology, University of Freiburg, Tennenbacher Strasse 4, D-79085 Freiburg, Germany. Email: petra.kaczensky@wildlife.uni-freiburg.de

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Abstract

In most of Europe, true wilderness areas do not exist and brown bears *Ursus arctos* generally have to cope with human disturbance and infrastructure. The few studies in Europe that have investigated brown bear activity have demonstrated a predominantly nocturnal and 'shy' behaviour in bears. There is still quite a debate on whether the shy, nocturnal bears of Europe are the result of centuries of persecution by men (genetically fixed trait) or whether hunting and the high disturbance potential in the multi-use landscapes are the driving force (individually learnt trait). We analysed the activity pattern of 16 individual bears monitored for 3372 h between May and October 1982–1998 in the Dinaric Mountains of Slovenia and Croatia. The data were collected via time sampling and basically analysed using two approaches: a general linear model with seasonal component to delineate the most important variables influencing the activity pattern and level and cluster analysis to group bears according to their 24-h activity pattern. Time of day and age were the most important variables predicting activity. Although individual variation in the activity pattern was high among individual bears, in general, yearlings were more diurnal and had a less distinct difference between day- and night-time activity levels than adult bears. Subadults were somewhat intermediate to adults and yearlings. We believe that nocturnal behaviour is most likely driven through negative experiences with humans, giving space for much individual variation. More research is needed to prove the causal relationship of nocturnal behaviour and the degree of disturbance that an individual bear is exposed to.

Introduction

The activity pattern of animals is determined by internal and external factors. Most vertebrates are active either during the day (diurnal) or during the night (nocturnal), often with peaks of high activity around dawn or dusk (Ashby, 1972 cited in Halle & Stenseth, 1994; Enright, 1970). Light and temperature act as an external synchronizer for a certain activity pattern (Nielsen, 1983), whereas the availability of resources, competition, predation (Geffen & Macdonald, 1993) or disturbance (Liddle, 1997) may alter the genetically fixed and physiologically regulated circadian rhythm.

Few studies in Europe have addressed activity patterns in brown bears *Ursus arctos* because of the difficulties of observing and following a far-ranging, forest-dwelling species (Swenson *et al.*, 2000). The few studies in Europe that investigated brown bear activity demonstrated a predominantly nocturnal activity pattern (Roth, 1980; Roth & Huber, 1986; Clevenger, Purroy & Pelton, 1990; Wabakken

& Maartmann, 1994; Rauer & Gutleb, 1997). In addition, bears are known to avoid people and are considered 'shy' (avoid people, e.g. by running upon first sight of humans) and unaggressive animals (Metz, 1990; Swenson *et al.*, 1996, 1999; Swenson, 1999; Zedrosser *et al.*, 2001).

In North America, on the other hand, brown bears seem largely diurnal (Klinka & Reimchen, 2002) and more aggressive than their European counterparts (Swenson *et al.*, 1996, 1999). However, contrary to North America, brown bears in Europe coexist with humans in densely settled, multi-use landscapes (Mattson, 1990; Swenson *et al.*, 2000; Linnell *et al.*, 2002). Bear habitat in Europe is almost exclusively restricted to forested area (Knauer, 2000; Knauer, Kaczensky & Rauer, 2000), but these forests are heavily managed by foresters and hunters and are used by the general public for camping, hiking, mountain biking, and berry and mushroom picking. Because almost all human activities are confined to daytime hours, bears can largely avoid encounters with humans by being nocturnal.

In North America, diurnal activity levels of brown bears may also vary with the intensity of human presence. In areas with low intensity of human utilization, bears are largely diurnal, whereas in areas with high intensity of human utilization or during periods of frequent human access, bears shift to nocturnal behaviour (Gunther, 1990; MacHutchon *et al.*, 1998; Olson, Squibb & Gilbert, 1998; Klinka & Reimchen, 2002). There are also situations when, in the absence of aggressive human behaviour (hunting) and with access to abundant forage, bears may become habituated to humans and shift back to a diurnal activity pattern (Smith, Herrero & DeBruyn, 2005).

In Europe the pressure on bears to behave inconspicuously and to avoid humans is high. Bears that do not avoid people run a high risk of being shot in hunted populations, and to become food-conditioned and subsequently removed as 'problem bears' in protected populations (Rauer, Kaczensky & Knauer, 2003). In addition, diurnal bears have a higher risk for surprise encounters with humans, which occasionally have resulted in human injury or death (Adamič, 1996; Swenson *et al.*, 1996, 1999) and subsequently in the killing of the bears involved. Public acceptance of brown bears is greatly challenged by such accidents and may hinder or even stop bear conservation efforts (Kaczensky, 2000a,b; Kaczensky, Blazic & Gossow, 2004). Therefore, shy and nocturnal behaviour in European brown bears is preferable and deserves more intensive studies.

There is still quite a debate on whether the shy, nocturnal bears of Europe are the result of centuries of persecution by men (genetically fixed trait) or whether hunting and the high disturbance potential in the multi-use landscapes are the driving force (individually learnt trait; see also Swenson *et al.*, 1996; Swenson, 1999). This question can be tested by comparing the activity patterns and behaviours of brown bears in wilderness environments versus those in multi-use landscapes. Whereas these comparisons are possible in North America and data suggest the importance of individual learning, in densely settled Europe large wilderness areas do not exist anymore (EUROPARC & IUCN, 2000) and human population densities are high, even in the remaining bear areas (Mattson, 1990; Swenson *et al.*, 2000). In addition, almost all protected areas are smaller than an individual bear's home range (Huber & Roth, 1993; Linnell *et al.*, 2002), hunting is an integral part of game and bear management in most areas (Swenson *et al.*, 2000), and human access to forested areas is facilitated by a dense network of forest roads (Kaczensky, 2000b). Unfortunately, data on brown bears from wilderness areas in Asia are largely anecdotal (Swenson, 1999).

Thus the question of whether nocturnal behaviour in European brown bears is genetically fixed or learnt can only be approached indirectly. If the nocturnal behaviour is genetically fixed, we would expect the same nocturnal activity pattern for all bears with a low degree of individual variation. Although the activity pattern might vary among age classes because of maturity effects, there should be little individual variation within the same age class.

If, on the other hand, nocturnal activity is a result of individual learning and experience, we would expect a high level of individual variation. Because age is a surrogate for other, more germane effects, more difficult to measure – in particular, the cumulative effects of learning and life experience, as well as somatic changes that include increasing size – we would expect age to be a key variable that determines the activity pattern in bears.

In order to study this question, we analysed the activity pattern of 16 individual bears from the continuous brown bear population in the Dinaric Mountain range of Slovenia and Croatia. Our expectation was that nocturnal activity is a result of individual learning and experience and we expected to see the following:

- (1) age is a key variable explaining differences in the activity pattern of individual bears;
- (2) young, inexperienced bears are less nocturnal than adult, experienced bears; and
- (3) individual variation is high among and between different age classes.

Study area

All three study areas were located in the Dinaric Mountain range in Slovenia (Menisija) and Croatia (Gorski Kotar and Plitvice Lakes) (Fig. 1). They are within the range of the contiguous Dinara-Pindus bear population stretching from Slovenia in the north into Albania and Greece in the south. The total number is estimated at about 2800 bears, of which 300–500 are believed to live in Slovenia and about 600–1000 in Croatia (Servheen, Herrero & Peyton, 1998; Swenson *et al.*, 2000; Zedrosser *et al.*, 2001; Dečak *et al.*, 2004). In both countries bears are hunted between 1 October and 30 April after a quota system (Huber & Frković, 1993; Simonič, 1994).

The relief shows typical karst phenomena, water sink holes (dolines), steep canyons, caves and shallow soils. Surface water is rare as water run-off is largely underground. Periodical lakes (poljes) and rivers that submerge after short distances are typical landscape features. Elevations range from 300 to 1200 m in the Menisija region, from 600 to 1500 m in Gorski Kotar and from 500 to 1200 m in the Plitvice Lakes area. Bear habitat consists of mixed, uneven aged forest stands. The most common forest community in our study areas (*Abieti-Fagetum dinaricum*) is dominated by beech *Fagus sylvatica* and fir *Abies alba*, intermingled with varying amounts of spruce *Picea abies*, maple *Acer pseudoplatanus* and elm (*Ulmus spec.*). Only selective cutting is allowed, resulting in a dense network of forest roads (1.5–2.0 km roads km⁻²; Kusak & Huber, 1998; Kaczensky, 2000b), most of them opened for public use. Overall forest cover is high and varies between 66% in Gorski Kotar and 74 and 75% in the Menisija and Plitvice Lakes area, respectively.

Human population density is low to moderate by European standards and ranges from 13 inhabitants km⁻² in the Plitvice Lakes area to 27 and 42 inhabitants km⁻² in the Gorski Kotar and Menisija area, respectively. Concerning

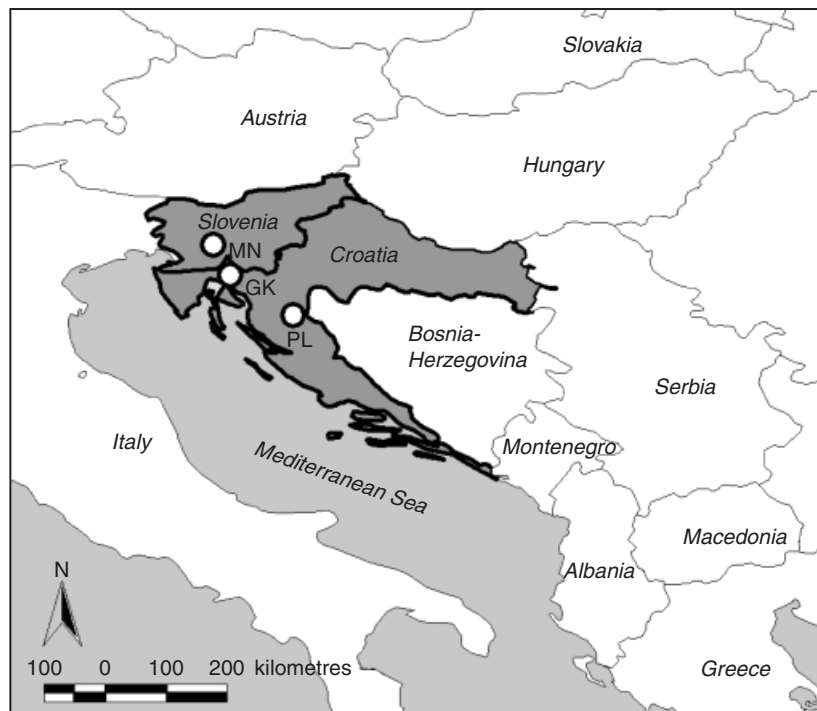


Figure 1 Location of the three study areas in Slovenia and Croatia (MN, Menisija; GK, Gorski Kotar; PL, Plitvice Lakes).

the intensity of human use, the Plitvice Lakes area is famous for the Plitvice Lakes National Park (200 km²), which is a major tourist attraction. The Menisija area (1500 km²) is located only 30 km from Ljubljana, the capital of Slovenia, and is heavily used for recreation. The Gorski Kotar area (1500 km²) is known for the Risnjak National Park (30 km²). Even though there is no bear hunting within the Risnjak and Plitvice Lakes National Parks, movements of all monitored bears covered ranges larger than the parks (Huber & Roth, 1993) and it can be assumed that bears in all three areas are exposed to hunting pressure at least in part of their range. Additional disturbance arises from forestry operations, collections of plant parts and various recreational uses (camping, hiking, mountain-biking, etc.).

A more detailed description of the study areas can be found in Huber & Roth (1993), Roth & Huber (1986), Kusak & Huber (1998) and Kaczensky (2000b).

Materials and methods

Capture and radio-marking

We captured bears with Aldrich foot snares at bait sites and chemically immobilized them with either Tiletamin and Zolazepam or a mixture of Ketamin and Xylazine. Traps were checked each morning in the Croatian study area, and continuously monitored with trap transmitters in the Slovenian study area. Trapping, chemical restraint and radio-marking procedures followed methods described by Huber, Kusak & Radisić (1996) and Kaczensky *et al.* (2002). A rudimentary first premolar tooth was extracted for age estimation (Stoneberg & Jonkel, 1966).

Bears were fitted with different types of radio-collars [Croatia: Advanced Telemetry Systems (ATS), Isanti, MN, USA, AVM Instruments Company, Colfax, CA, USA and Telonics, Mesa, AZ, USA; Slovenia: MOD-600, MOD-400, Telonics] or ear tag transmitters [EL-2(42), Holohil, Ontario, Canada]. Each collar was fitted with a drop-off system made of corroding wires or cotton spacers to prevent the lifelong wearing of the device.

Activity monitoring

Bear activity was monitored via time sampling (Tyler, 1979). Only clearly audible signals were used to determine the activity status of monitored bears. We used analogue receivers with a meter for signal strength that could be adjusted to reception strength (Croatia: AVM Instruments Company; Slovenia: YAESU, Wagener, Germany).

In Croatia, bear activity was recorded at sampling intervals of 15 min. Observers listened to at least 30 signal pulses ('beeps') and classified the bear 'active' if at least four out of 30 signal pulses clearly differed in signal strength, else 'inactive' (for details refer to Roth, 1980; Roth & Huber, 1986). Visual observations during wake-up and random observations during fieldwork showed that typically an active animal showed more than four fluctuations of signal volume over 30 beeps (D. Huber, unpubl. data). In this way, we realized a maximum of four activity samples per bear and hour during each monitoring session.

In Slovenia, bear activity was recorded slightly differently. Activity was checked at sampling intervals of 10 min and observers listened for a 1-min sampling period. As in Croatia, we considered the bear active if the strength in the

Table 1 Dataset used for individual analysis of brown bear *Ursus arctos* activity in Menisija (MN), Slovenia, and Plitvice Lakes (PL) and Gorski Kotar (GK), Croatia

Bear	Age (years)	Sex	Activity monitoring		Activity readings	Total hours ^a	Study area ^b
			Start	End			
Adults							
FRANJO	5	Male	21.06.1982	09.10.1982	268	285	PL
	6	Male	14.05.1983	04.10.1983	254		PL
	7	Male	20.05.1984	09.09.1984	713		PL
	8	Male	26.05.1985	07.09.1985	6		
HAL	6	Male	16.05.1983	19.09.1983	260	49	PL
HANS	5	Male	18.05.1985	28.10.1985	422	135	PL
	7	Male	10.05.1987	05.09.1987	209		
DADO	4	Male	16.05.1986	06.10.1986	197	45	PL
GABI	5	Female	14.06.1986	12.10.1986	512	135	GK
	6	Female	21.05.1987	19.09.1987	136		
MAJA	9	Female	01.05.1997	19.06.1997	600	103	MN
ANCKA	Adult	Female	14.05.1998	09.10.1998	1982	338	MN
POLONA	5	Female	15.05.1998	24.10.1998	2259	385	MN
Subadults							
LILI83	2	Female	09.05.1983	30.07.1983	500	108	PL
INGA	3	Female	27.05.1987	10.09.1987	220	43	GK
LUCIA	2	Female	04.05.1997	08.10.1997	3334	564	MN
SRECKO	3	Male	04.05.1997	09.10.1997	2634	448	MN
Yearlings							
LILI82 ^p	1	Female	01.05.1982	17.10.1982	798	144	PL
PEPI	1	Male	10.07.1987	19.09.1987	414	91	GK
VANJA	1	Female	01.05.1997	11.08.1997	1615	277	MN
VERA	1	Female	07.05.1997	28.05.1997	590	97	MN
DUSAN	1	Male	10.05.1997	09.07.1997	718	125	MN
			Total		18 641	3372	

^aMonitoring hours with ≥ 3 activity samples.

^bWas used to compare with data from *LILI83*, but not in multi-bear comparisons.

signal pulse was clearly different in ≥ 4 beeps. This activity criterion was previously determined from the Zoo experiment, where we had simultaneously radio-monitored and observed a radio-collared bear (Kaczensky, Wagner & Walzer, 2004). In Slovenia, we realized a maximum of six activity samples per bear and hour during each monitoring session. Previous tests with different sampling intervals have shown only minor differences for sampling intervals of 10 versus 15 min (I. Reinhardt, unpubl. data).

Each activity sample resulted in information on the activity status, coded as a dichotomous variable and the time of the day [middle European standard time (MEZ)]. To compare different bears we only used data collected between 1 May and 31 October, the time when all bears were active outside their winter dens. We grouped bears according to three age classes: yearlings (1 year), subadults (2–3 years) and adults (≥ 4 years). All yearlings monitored had already separated from the mother. All adult females monitored were without offspring.

For analysis we only used bears that were monitored for at least 48 h evenly distributed over all hours (equally covering day- and night-time hours), which means a minimum of 192 activity samples for the Croatian dataset and 288 activity samples for the Slovenian dataset. In the Croatian study

areas, several bears were monitored over several years. The data were pooled if the bear did not change its age class status (three adult bears), or otherwise subdivided according to age class (one bear). For all multi-individual analyses, each bear was used in only one age class and the one bear that changed the age class was assigned to the age class with the smaller sample size.

For analysis we used only hours with ≥ 3 activity measures and calculated the average activity for each hour a bear was monitored on a given day. In total, we had 3372 h of 16 individual bears available for analysis (Table 1). For age class-specific comparison of activity patterns, we additionally used 170 h from 13 individual bears (each with less than 200 activity samples) pooled by age class (Table 2).

Triangulation of monitored bears

In the Slovenian study area, we continuously followed bear movements during 24-h monitoring sessions by car or on foot. Because of a dense network of forest roads, the distance between observer and bear was generally less than 1000 m. After each activity sample, we checked whether the bear had changed its position. If so, we determined the new position by triangulation, taking successive bearings by a

Table 2 Dataset of bears with less than 200 activity samples, used for analysis pooled by age class

Bear	Age (years)	Sex	Activity monitoring		Activity readings	Surveyed hours ^b	Area ^a
			Start	End			
Adults					309	51	
<i>VIOLETA</i>	10	Female	10.07.1987	05.09.1987	87	18	GK
<i>NIVA</i>	13	Female	02.05.1990	13.10.1990	71	11	GK
<i>BOB</i>	5	Male	16.05.1986	29.08.1986	6	1	PL
<i>VLADO</i>	5	Male	16.05.1986	17.05.1986	5	1	PL
<i>NENO</i>	12	Male	30.07.1986	19.10.1986	140	20	GK
Subadults					380	60	
<i>JURICA</i>	2	Female	03.05.1985	31.05.1985	160	24	PL
<i>JURA</i>	3	Male	18.05.1983	30.07.1983	28	6	PL
<i>GORAN</i>	3	Male	06.07.1986	17.09.1986	49	6	GK
<i>FRKO</i>	3	Male	27.05.1987	03.08.1987	143	24	GK
Yearlings					446	59	
<i>LINDA</i>	1	Female	07.07.1990	12.12.1990	69	9	GK
<i>DARKO</i>	1	Male	03.05.1985	11.09.1985	152	24	PL
<i>MIKI</i>	1	Male	11.06.1990	12.10.1990	84	7	GK
<i>NEJC</i>	1	Male	12.06.1998	14.07.1998	141	19	MN
			Total		1135	170	

^aMN, Menisija (SLO); GK, Gorski Kotar (HR); PL, Plitvice Lakes (HR).

^bHours monitored with ≥ 3 activity samples.

single observer. The accuracy of the position was estimated by the observers from the angle between the different bearings, the signal strength and the topography, and was classified as:

- (1) location error ≤ 50 m: bear circled on close range and/or radio-signal close to maximal;
- (2) location error ≤ 250 m: bear only partly circled or circled at a longer distance and/or topography limits the maximum distance between bear and observer;
- (3) location error ≤ 500 m: bear not circled, or circled on long distance (> 1 km), and/or azimuth between most distant bearings less than 120° apart.

Accuracy of locations was opportunistically confirmed when searching for daybeds, feeding signs or scats the following day (D. Huber & P. Kaczensky, unpubl. data). We classified bears as travelling (travelling activity) when the distance between two locations was more than the expected location error, and as active on the same area (stationary activity) if the change was within the expected location error; this information was only available for the Slovenian dataset.

Standardization of the variable time

We compared activity among bears based on average activity per hour. However, the data were collected between May and October, and thus sunset and sunrise as well as their centre, local noon and local midnight change over the season. To compare hours with the same light regime, we standardized the variable time to the average day of the observation period. On average, sunrise was at 4:53 h and sunset at 19:10 h. On days with later (earlier) sunset and earlier (later) sunrise than on the average day, the time between sunrise and sunset was relatively stretched (shor-

tened, respectively). We separately conducted a linear transformation for each day to fit the time intervals to an average day:

$$t_{st} = MP_{st} - \frac{|MP_r - t_r| |MP_{st} - S_{st}|}{|MP_r - S_r|}$$

where t_{st} is the transformed time, t_r the measured time (Central European time), MP_{st} the standardized midpoint: local noon (12:00 h) or midnight (0:00 h after midnight or 24:00 h before midnight), MP_r the real midpoint, S_{st} the standardized sunrise/sunset and S_r the real sunrise/sunset.

Noon was used as the midpoint (reference) for the time between sunrise and sunset, else midnight. Sunrise was used for the time between midnight and noon, else sunset. This resulted in four different formulas (combinations of different midpoints and sunrise/sunset). Local noon and midnight change over the year because of the ellipsoid trajectory of the earth around the sun. By using this transformation, long and short days can be directly compared. Although the real time available during night- and daytime is slightly changed, this does not seem to be problematical, because season had no significant influence on bear activity (see Table 3).

General linear model (GLM)

In order to test for the influence of different variables on activity, we used a GLM with age, sex, season and study area as factor variables. From a first visual analysis of activity patterns, it seemed that most bears roughly followed a monophasic or 24-h activity rhythm and to a lesser extent a biphasic or 12-h rhythm. Because of this periodic behaviour and the circular structure of the time, we fitted sine curves with 24- and 12-h rhythms (seasonal component) into

Table 3 Effects of different variables on the activity pattern of bears using a general linear model with seasonal component (12- and 24-h rhythm)

Parameter	Sum of squares	d.f.	Mean square	<i>F</i>	<i>P</i> -value
Corrected model	188.19	18	10.46	116.26	<0.01
Constant	51.08	1	51.08	568.04	<0.01
Age	1.35	2	0.67	7.48	<0.01
Sex	0.05	1	0.05	0.58	0.45
Act_1	82.18	1	82.18	913.81	<0.01
24-h rhythm	5.17	2		57.46	<0.01
12-h rhythm	5.63	2		62.63	<0.01
Age × 24-h rhythm	4.77	4		26.51	<0.01
Age × 12-h rhythm	0.75	4		4.18	<0.05
Sex × 24-h rhythm	2.34	2		25.97	<0.01
Error	227.79	2533	0.09		
Corrected total	415.99	2551			

variation
 $R^2 = 0.452$

The activity of the hour before (Act_1) has the most effect on activity (according to the sum of squares) followed by the periodic activity rhythms (12- and 24-h rhythm) and interactions of them with age and to a lesser degree with sex. Age alone has only a slight effect and sex alone has no significant effect. Note that age and sex affect the pattern of the daily activity more than the level.

the model (Zar, 1999). As time-series data are usually autocorrelated, we used time-lagged variables of the dependent variable as explanatory variables. The periodic structure of the data results in the absence of a linear trend and thus we did not have to de-trend the data, as is usually done in time-series analysis.

For the GLM we used the following independent variables:

Act_n: activity of *n* hours before – covariate;

Age: age class (1 = yearling, 2 = subadult, 3 = adult) – factor;

Sex: sex (1 = male, 2 = female) – factor;

Season: month (1 = May, 2 = June, ..., 6 = October) – factor;

Area: study area (1 = MN, 2 = GK, 3 = PL) – factor;

24-h rhythm – covariate;

12-h rhythm – covariate; and

interactions of these variables.

We selected variables stepwise in a backwards fashion, removing those that failed to be significant at the 0.05 significance level. For the final model, we tested the residuals for normal distribution (which was roughly the case) and confirmed that they were not autocorrelated.

Comparing diel activity patterns of individual bears

To describe similarities in the diel activity pattern, we ran a cluster analysis using squared Euclidean distances between all bears based on average activity level of each hour. Bears

were attributed to clusters using the between-group linkage – this method uses the average distance between all samples in a cluster to determine the distance to a new cluster, thus considering all samples of a cluster.

Data from bears with small datasets of activity samples

We pooled activity samples of an additional 13 bears that did not have the minimum number of activity measures required for individual analysis, first by bear and monitored hours and then by age class (Table 2). We visually compared activity patterns and mean activity levels with the results from the individual analysis.

All statistical analysis was done in SPSS 12.0.1 (SPSS Inc., Chicago, IL, USA).

Results

Main variables influencing activity

The outputs of the GLM showed that the activity in the hour before, the underlying 12- and 24-h activity rhythm, and the 24-h activity rhythm modified by age class were the most important factors predicting activity or non-activity of a given hour (Table 3). Less important were age class alone and the 24-h activity rhythm modified by sex. Sex by itself was not a significant variable, nor was season or study area. The model explains 45% of the variation (Table 3) in activity and shows differences between age classes in the activity rhythm as well as the overall activity level (Table 3). Differences in overall activity levels were significantly different between adults (52%) and yearlings (62%), with subadults ranging somewhat in between (57%; *post hoc t*-test, $P < 0.01$). Yearlings have a distinct break in activity from 23:00 to 3:00 h, which is comparable to their mid-day break (12-h or biphasic pattern). Adults, on the other hand, have a more distinct and extended break during the day, but are basically active all night (monophasic or 24-h rhythm). Subadults were somewhat intermediate (*post hoc t*-test, $P < 0.01$ for 24-h rhythm and $P < 0.01$ for 12-h rhythm).

Bivariate comparisons among age classes showed a significant difference between yearlings and adults only for daytime activity levels (adults 39%, subadults 52%, yearlings 64%; ANOVA $P = 0.02$, $P_{\text{adult-yearling}} < 0.01$; $P_{\text{adult-subadult}} = 0.50$; $P_{\text{yearling-subadult}} = 0.48$), but not for night-time activity levels, mainly due to higher individual variation (adults 72%, subadults 68%, yearlings 60%; ANOVA $P = 0.32$; Fig. 2).

One bear (*LILI*) changed the age class during the monitoring period and showed a reduction in the daytime activity level with increasing age. As a yearling (*LILI82*) she was active 66% during the day and 78% during the night, whereas as a subadult (*LILI83*) she was active 46% during the day and 77% during night (*t*-test $P_{\text{day(yearling-subadult)}} < 0.01$, $P_{\text{night(yearling-subadult)}} = 0.85$; Fig. 3).

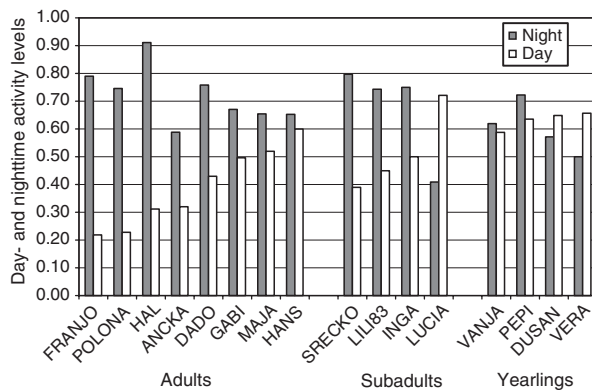


Figure 2 Activity level during day- (white) and night-time (grey) hours for adult, subadult and yearling bears.

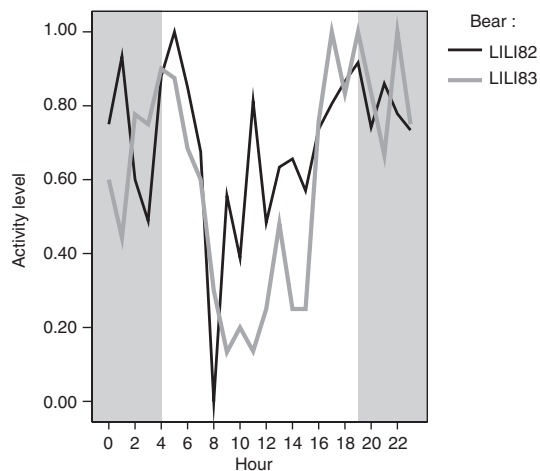


Figure 3 Activity patterns of one bear monitored during different seasons and changed from the yearling to the subadult age class.

Comparing diel activity patterns of individual bears

The results of the cluster analysis grouped bears into three distinct groups. Although the grouping did not sharply separate bears by age, adults tended to be in *group 1* (five adults, two subadults and one yearling) or *group 3* (two adults) and yearlings in *group 2* (one adult, one subadult and three yearlings; Fig. 4).

The main differences between groups are that bears in group 2 have a less distinct difference between day and night activity levels. They show a more biphasic activity pattern (12-h cycle) as compared with the largely monophasic activity pattern (24-h cycle) of bears in groups 1 and 3 (Fig. 5). However, both groups had peak activities in the early morning, a depression around noon, a second peak in the early evening and another depression around midnight. However, contrary to bears in groups 1 and 3, minimal activity levels of bears in group 2 are higher during the day

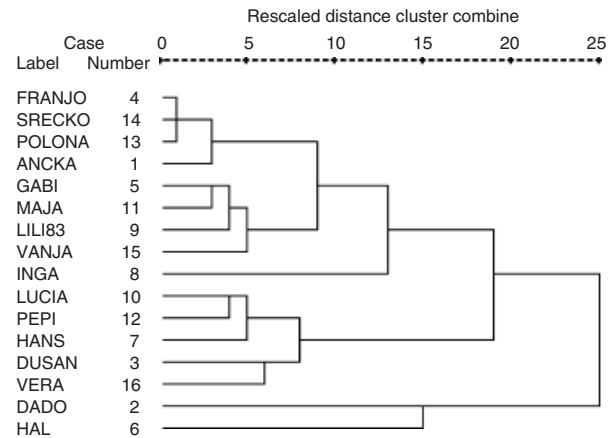


Figure 4 Dendrogram using average linkage (Euclidean distances between groups) of the cluster analysis comparing diel activity patterns between individual bears. Age composition of group 1: five adults, two subadults and one yearling; group 2: one adult, one subadult and three yearlings; and group 3: two adults.

than during the night (Fig. 5). One bear from group 2 (female *LUCIA*) did not follow the general pattern and showed a peak at noon (Fig. 5). The two adult males in group 3, like bears in group 1, had a distinct depression in their activity level during the day. However, contrary to bears in group 1, the activity gradually sloped down from peak activity levels in the morning to a low at 16:00 h and then steeply rose again to high activity levels during the night.

Stationary versus travelling activity

The difference in the activity patterns between adult and younger bears was even more distinct when comparing the 24-h distribution of travelling activity. Although three adult females hardly travelled at all between 8:00 and 17:00 h, three yearlings frequently travelled during the daytime (Fig. 6). One female yearling (*VERA*) even showed a peak of travelling activity around noon. Of the subadults, one male (*SRECKO*) showed a similar pattern to the adult females, whereas a female (*LUCIA*) almost exclusively travelled during the day, with a small depression around noon. This pattern of almost no activity during the day is much less distinct in adult bears, when looking at stationary activity (activity without displacement). The adult female *MAJA*, for reasons unknown, even showed a relatively high level of stationary activity during the day, similar to the pattern observed in the yearlings (Fig. 6).

Although mean travelling activity levels were lowest for adults during the day (adults 9%, subadults 20%, yearlings 22%) and highest during the night (adults 27%, subadults 25%, yearlings 18%), differences were not significant (ANOVA $P_{\text{day}} = 0.54$, $P_{\text{night}} = 0.12$), nor were differences in mean stationary activity levels (day: yearlings 41%, subadults 35%, adults 21%, ANOVA $P = 0.21$; night:

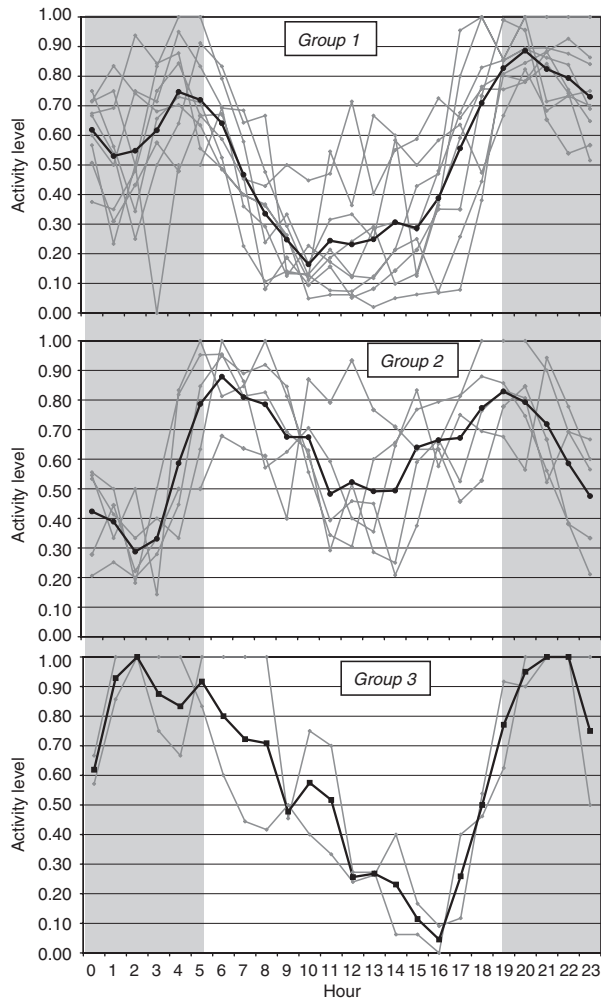


Figure 5 Activity per hour of all bears within the three groups identified by cluster analysis.

yearlings 37%, subadults 35%, adults 31%, ANOVA $P = 0.66$). However sample sizes in each age group were very small.

Data from bears with less than 200 activity samples

Twenty-four-hour activity patterns of an additional 13 bears pooled by age classes also produced the expected difference between the age classes, that is low activity levels for adults and peaks of high activity for yearlings throughout the day (Fig. 7). Again, subadults were somewhat in between adults and yearlings.

Whereas at night all age groups had significantly different activity levels, during the day only adults and yearlings differed significantly (day: adults 43%, subadults 48%, yearlings 60%, ANOVA $P < 0.01$, $P_{\text{adult-yearling}} = 0.05$, $P_{\text{adult-subadult}} = 0.85$, $P_{\text{subadult-yearling}} = 0.10$; night: adults 81%, subadults 60%, yearlings 38%, ANOVA $P = 0.02$, $P_{\text{adult-yearling}} < 0.01$, $P_{\text{adult-subadult}} = 0.08$, $P_{\text{subadult-yearling}} = 0.02$).

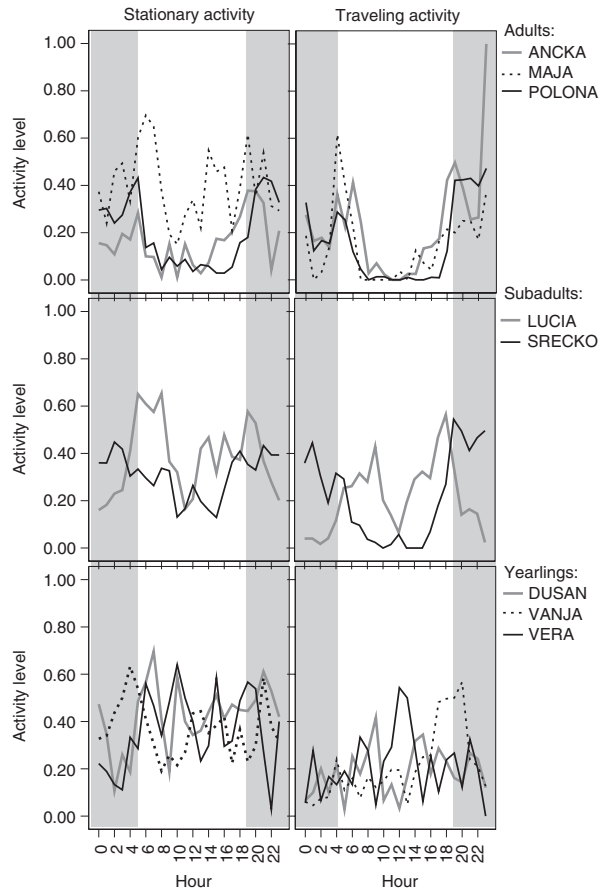


Figure 6 Travelling and stationary activity per hour for eight bears in three age groups. These data were only available for the Slovenian study area.

Discussion

Diurnal young bears and nocturnal adult bears

Our results showed a clear difference in the activity patterns of yearlings and adult bears, with subadults being somewhat in between. The general pattern was that adults are mainly nocturnal, whereas yearlings could be found active at any time. Individual variation was quite large and not all bears followed this general pattern. Our results support the assumption that the nocturnal activity pattern observed in European brown bears is more likely the result of individual learning than a genetically fixed trait.

The difference between adults and yearlings was even more pronounced when comparing travelling activity only. Adults hardly travelled at all during the daytime, whereas yearlings and also some subadults could be found travelling during the day. Consequently, their chances to encounter people were much higher. In the few cases (<20 occasions) where we saw bears, it was either a yearling or the subadult female LUCIA. However, contrary to the yearlings, LUCIA did not seem to be afraid of people and appeared to be

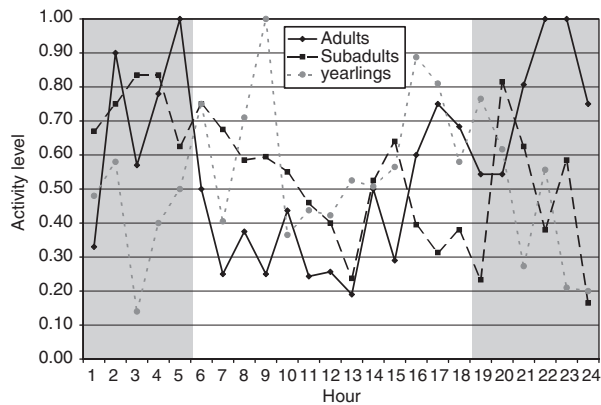


Figure 7 Activity per hour for an additional 13 bears pooled by age class.

habituated to human presence. These data correspond well with anecdotal observations by hunters and foresters in Slovenia and Croatia, who also claim to mainly see small bears (D. Huber & P. Kaczensky, unpubl. data).

For one adult female (*MAJA*) with a relatively high daytime activity level, this activity was largely confined to stationary activity, that is activity in or around the daybed area. As daybeds were mainly located in inaccessible areas (high cover or steep slopes; Kusak & Huber, 1998; Kaczensky, 2000b) the chances for bear–human encounters were minimal. However, as can be expected when dealing with individual learning and behaviour that is believed to be shaped by individual experience, not all bears strictly followed the same pattern. One adult bear (the male *HANS*) showed a high level of daytime activity. Unfortunately, we did not have data to distinguish between stationary and travelling activity, nor did we have any information about this experience with humans to better explain this behaviour.

The fact that subadult bears are more active during the day and expose themselves more frequently to humans compared with adult bears is also frequently described from North America (Ison, Gilbert & Squibb, 1997). It is often assumed that subadult bears are generally less affected by humans because of greater habituation (MacHutchon *et al.*, 1998). But other authors noted that subadults do not show the same tolerance as habituated adults (Braaten, 1988 cited in Olson *et al.*, 1998). The lower wariness is often explained by food competition or the avoidance of aggressive adult bears. In our study areas yearling bears did not actually shift from a nocturnal to a diurnal activity pattern, but rather showed equally high activity levels during day and night and thus did not really avoid the time most adult bears are active. Contrary to other regions (e.g. for Sweden, see Swenson *et al.*, 1997), we had no evidence of interspecific killings, possibly because young bears grow rapidly and yearling body masses in early spring often exceeded 55 kg (Kaczensky *et al.*, 2002).

We speculate that young bears have a rather uniform activity pattern, with activity bouts throughout the day and

night, which through individual negative experience is changed into a predominately nocturnal pattern in adults. Anecdotal evidence from Austria and Croatia suggests that adult females are more diurnal in years with cubs than in years without cubs (Rauer & Gutleb, 1997; Rauer *et al.*, 2003; D. Huber, unpubl. data). Possibly, this is the result of nocturnal adult females having to cope with relatively high diurnal cub activity levels. Cubs of a wary, nocturnal mother probably have few encounters with humans and thus lack negative experience with people. After family break-up at 1½ years, young bears (yearlings) are no longer forced into a nocturnal activity pattern, but rather will be equally active during day and night.

Diurnal activity might allow young bears to access food bonanzas, like high-productivity berry patches or bait sites, which may be monopolized by large adults at night. This would be in accordance with the fact that it is mainly small bears that are observed at bait sites during daytime hours in Croatia and Slovenia (D. Huber & P. Kaczensky, unpubl. data). Klinka & Reimchen (2002) also speculate that the higher daytime foraging activity of females with cubs and subadult bears on spawning salmon on Knight Inlet, coastal British Columbia was mainly to avoid large nocturnal males.

Perhaps young bears first consider other bears more dangerous than humans. However, their high daytime activity will result in frequent encounters with humans and will, in combination with the fast gain in body mass (other bears are not a threat anymore), lead to a shift in the activity pattern in order to avoid people. That this is a process of individual learning is also suggested by the fact that bears can become habituated to humans when a negative stimulus is missing or even food conditioning when ‘not running from people’ is positively enforced by food (Rauer *et al.*, 2003).

Because we were not able to measure human activity or the degree of disturbance an individual bear was exposed to, we are unable to prove the causal relationship of nocturnal behaviour (used as a surrogate to avoiding humans) and age (used as a surrogate of experience). All bear populations in Europe are exposed to humans and, in addition, the observed behaviour might well be a result of past experiences that would be impossible to assess. Even a bear that lives in a remote area might have dispersed from an area of high human impact, as especially males are known to disperse long distances (Taberlet *et al.*, 1994; Knauer, 2000; Knauer *et al.*, 2000). However, all bears live in landscapes inhabited by people and in all areas hunting occurs; consequently, we assume that all bears were exposed to some negative experiences with humans.

We believe that hunting is one important negative stimulus to keep bears shy and nocturnal. Many game animals have adopted a nocturnal behaviour because of human persecution (Georgii & Schröder, 1983) and readily switch back to diurnal activity when protected (e.g. Kitchen, Gese & Schauster, 2000), also suggesting a high degree of individual learning. The first major selection against diurnal behaviour in bears of the Dinaric Mountains takes place during the fall hunting season (Frković *et al.*, 1987). By this

time most yearlings have masses around 70–100 kg (Kaczensky, 2000b) and are considered reasonable trophies. There is a quota system, but within a hunting unit there are often several hunters who are interested in shooting a bear. Often different hunters have to take turns at a bait site and thus seize the first opportunity to shoot a bear. The earlier a bear comes to a feeding site, the higher the chances of getting shot. The radio-collared female bear *LUCIA* was the only bear we monitored in Slovenia that was active during the day and did not show a fear of people. She was frequently seen by hunters at bait sites, but was spared because of her radio-collar.

However, removing diurnal bears does not have much to do with individual learning at least not for the bear shot dead. But bears are missed by bullets or get wounded: a collared bear shot in Croatia in 1997 had old fractures caused by bullets in the jaw and pelvis, and the skeletons of two other bears had old bullets imbedded in bones (D. Huber, unpubl. data). In addition, bears often come to established bait sites in groups: siblings, several males courting the same female in oestrous or females with cubs (D. Huber & P. Kaczensky, unpubl. data). Normally only one bear gets shot at any given bait site, thus providing a negative stimulus to the spared bears. Even if bears are not the target of a hunt and do not get physically harmed, they are often accidentally chased by hunters and their dogs during drive hunts for other game. In North America, it has been shown that black bears *Ursus americanus* become more nocturnal during the hound training season, possibly in an attempt to avoid people and their dogs (Bridges, Vaughan & Klenzendorf, 2004).

In Austria, where bears are strictly protected, several young bears started to be active during the day and did not show much fear of people. They were frequently observed by people with no negative consequences; on the contrary, some might have even been fed by people to allow for photographs and video sequences (Rauer & Gutleb, 1997; Rauer *et al.*, 2003). At least three of these bears were females and two had already raised cubs. Especially when accompanied by cubs, these females were often observed at close range and cubs never learnt to avoid people, predisposing them to get into trouble. Counteracting this process is a major concern of the Austrian bear conservation programme, and several attempts were made to aversively condition these bears (Zedrosser, Gerstl & Rauer, 1999; Rauer *et al.*, 2003). One of the prerequisites for aversive conditioning is that behaviour can be changed through a negative stimulus. Because in Europe shy behaviour is closely linked to a nocturnal activity pattern, aversive conditioning can only be successful if the activity pattern can be changed through individual learning. On the basis of the results of this study, this seems highly likely.

We believe that maintaining nocturnal behaviour in bears is one important prerequisite for the coexistence of brown bears and people in the multi-use landscapes of Europe. For this coexistence, it is essential to separate bears and people, either in space or in time. As it is almost impossible to restrict human access into bear habitat and because a viable

bear population needs a huge area, a separation in time reduces the probability of encounters between bears and humans. We are well aware that this will not solve all problems. Access to human-provided food and livestock needs to be minimized and people need to be educated not to feed bears intentionally or accidentally. Especially in small protected bear populations, this is a difficult task. People have lost the experience of living with bears and a bear that becomes visible will be perceived either as a threat to life and property or as a sensation and will attract lots of people. Unfortunately, the most likely outcome in both scenarios is a dead bear. How much and what negative feedback is necessary to maintain shy, nocturnal behaviour in protected populations is unknown and should be the focus of further studies.

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