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Original Investigation

The influence of daylight regime on diurnal locomotor activity patterns of the European hare (*Lepus europaeus*) during summer

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ABSTRACT

Knowledge on diurnal locomotor activity pattern in wild nocturnal medium-sized mammals, such as the European hare (*Lepus europaeus*) is scarce. In this study, we tracked nine European hares during the vegetation period using GPS-transmitters. In particular, we focused on the question how the timing of sunset and sunrise influences the activity peaks in this species. The horal distances between two consecutive hare positions were used as a measure of locomotor activity. European hares showed two distinct peaks in their daily activity. If sunset or sunrise were earlier, the maximum activity peaks of individual European hares occurred after sunset or sunrise, whereas activity peaks were shifted before sunset or sunrise when sunset or sunrise were later. During summer, when the nights are probably too short to allow the hares to cover their energetic requirements, the study animals regularly showed activity peaks in full daylight. In conclusion, our results imply that, although daylight regime normally regulates the diurnal locomotor activity pattern in mammals, other additional factors may play a role in modifying this regulation in European hares during summer.

Introduction

In mammals, circadian rhythms are predominantly regulated by light (Goldman 1999; Cermakian and Sassone-Corsi 2002; van der Merwe et al. 2011). Numerous studies have shown that the impact of light as zeitgeber might be affected by various other intrinsic and extrinsic factors, such as food availability, weather, temperature, sex, season, reproductive status, and age (Getz 1961; Garshelis and Pelton 1980; Zielinski et al. 1983; Ferguson et al. 1988; Larivière et al. 1994; Kolbe and Squires 2007; Wronski et al. 2006; Rödel et al. 2012). However, sunrise and sunset have been suggested to trigger the onset and cessation of activity in a wide range of species (Daan and Aschoff 1975; Benstaali et al. 2001).

Hares (genus *Lepus*) have been described as mostly nocturnal mammals (Chapman and Flux 2008), although this seems to be true only during winter (Homolka 1986; Pépin and Cargnelutti 1994; Holley 2001). In summer, activity of hares appears to be less consistent and partly diurnal (Mech et al. 1966; Cederlund and Lemnell 1980; Figala et al. 1984). Irrespective of this, also in hares sunset and sunrise appear to play a major role concerning the onset and cessation of activity, respectively (Mech et al. 1966; Figala et al. 1984; Pépin and Cargnelutti 1994; Holley 2001).

In winter, hares start their daily activity shortly after sunset and end it shortly before sunrise (Cederlund and Lemnell 1980; Pépin and Cargnelutti 1994). However, studies on different hare species report contradictory results regarding the influence of sunrise and sunset as zeitgebers during late spring or summer. Snowshoe hare's (*Lepus americanus*) cessation of activity has been reported to be on average 1 h before sunrise (Mech et al. 1966; Figala et al. 1984), however, with notable variation. For some individuals the onset of activity was 1 h after sunset (Mech et al. 1966), whereas another one was observed to start its activity more than 2 h before sunset (Figala et al. 1984). European hares began to leave their forms before sunset and to enter them after sunrise as the nights shortened in the early part of the year (Holley 2001). That means, in all studies during late spring or summer sunrise and sunset somehow trigger onset and cessation of hares' activity, but the impact of these zeitgebers is various.

It has been argued that the impact of sunrise and sunset in summer was altered by the number of daily night hours (Holley 2001). In this European hare study the duration of the activity period did not remain constant but decreased from 15 h in January to 12 h at the end of March, mirroring the number of daily night hours. At this point, the activity period was not further contracted but the hares suddenly started to increase their activity period by including daylight activity. This sudden transition from a totally nocturnal to a partially diurnal regime was explained by an aversion to daylight activity. Consequently, we suppose that the number of daily night

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hours alter the impact of the predominant zeitgebers sunrise and sunset. Hence, the hares' activity pattern should display a sudden start of daylight activity at the beginning and an abrupt withdrawal from daylight activity at the end of summer.

In addition, a high ambient temperature might influence the activity pattern of mammals. For example, in black bears (*Ursus americanus*) it was shown that temperatures above 25 °C substantially reduced the level of activity (Garshelis and Pelton 1980). Furthermore, the meadow vole (*Microtus pennsylvanicus*) was found to abandon diurnal activity in favour of nocturnal and/or crepuscular activity when the temperature rose above 20 °C (Getz 1961). We hence assumed that the impact of the zeitgebers sunrise and sunset might be altered by a high ambient temperature in which case the hares' activity would be restricted to the dark period.

However, detailed quantitative and individual-based data on daily activity pattern in this genus are still scarce. In this study we investigated the European hare's (*Lepus europaeus*) diurnal locomotor activity patterns during summer. In particular, we did not only focus on the timing of onset and cessation of activity but also studied subtle changes of activity during 24 h. Our hypothesis was that sunrise and sunset, the predominant zeitgebers for the European hare's diurnal locomotor activity pattern, are slightly altered in their impact by the number of daily night hours (season) and the temperature. We tested this hypothesis by equipping nine individuals with GPS collars, allowing us to assess their diurnal locomotor activity patterns.

Material and methods

Study area

The study was conducted in Lower Austria near Zwerndorf (48°20′N, 16°50′E) and the study area consisted of 270 ha arable land with cereals as the main crop and an average field size of 3.1 (±0.3 SE) ha. Hare density in the study site was estimated in autumn 2009 by spotlight counts (Langbein et al. 1999) and accounted 35 European hares per 100 ha (SSB & KH, unpubl.).

Data collection

Nine adult European hares (4 males, 5 females) were caught in un-baited box traps from May until September 2009. All animals were sexed according to secondary sexual characteristics and equipped with a 70 g GPS collar (Telemetry Solutions, Quantum 4000 Enhanced). The collars were programmed to start working right after the animal's release and take 1 fix per hour. For additional information on the individual hares' GPS-data see the electronic appendix. The accuracy of the GPS collars was tested beforehand (see Harris et al. 1990) and yielded a mean precision of 3.5 m (±1.0 SE). Weather data and the time of sunrise and sunset were provided by the Austrian Central Institute for Meteorology and Geodynamics. Temperatures were recorded daily at 7 am and 7 pm CET.

Calculation of positional data

The positional data were digitised using the software ArcGIS 9.2 (ESRI). We only included locations with a solution in three-dimensional mode (based on ≥4 satellites) (Frair et al. 2010). The distances (in metres) between two consecutive hare positions (horal distance) were calculated. Although the horal distance does not reveal the effective distance the hare covered between these two fixes, it exposes a minimal distance the hare must have moved during this hour. In the following, the "horal distance" is used as a measure of hares' activity, and the term "activity" is always used in the sense of the hares' locomotor activity.

Statistical data analysis

We analysed the data using multivariate (generalized) linear mixed-effects models, allowing for the use of repeated measurements. Statistical analyses were done with the software R 2.12.0 (R Development Core Team 2011). Generalized linear mixed-effects models were fitted using the package lme4 (Bates 2005). P-values were extracted by likelihood ratio tests (Faraway 2006). When using linear models, we visually checked normality of the model residuals by normal probability plots. For all models, the homogeneity of variances and goodness of fit were examined by plotting residuals versus fitted values (Faraway 2006).

We initially included sex in all models tested. However, since there were never any significant effects of sex in our multivariate analyses ($p > 0.10$), this factor was omitted from the models before re-calculation.

Diurnal activity pattern

We tested the effect of time of the day (covariate, in hours) on the response variable horal distance by a linear mixed effects model. In addition, we tested similar models only including data subsets: one subset included all positional data with a shorter time interval to sunset than to sunrise, and the other one comprised the remainder. For all models, the response variable (horal distance) was log-transformed in order to obtain a normal distribution of the model residuals.

Since we expected a non-linear time course with at least one maximum peak, we used polynomials to model the data. For this, we gradually increased the complexity of the polynomials until the 9th order. All of these models were tested for significance, and, in addition, we directly compared the support of these models by using AICc (Burnham and Anderson 1998). The model with the lowest AICc score can be considered as the best approximating model of the model set. Note that different models can be considered to find equally good support by the data when the ΔAICc is smaller than 2.

All (mixed effects) models included hare identity as a random factor, in order to allow for the repeated measurements collected from the different hares, and also an individual-specific code for the day ("date") as a second random factor in order to account for the time series measured for each of the study animals during the different days of the study. As it could be expected, there was significant individual variation among the hares' locomotor activity (significant random factor "individual hare": $\chi^2 = 199.44$, $p < 0.001$) with a variance of 0.21 m/h (±0.55 SD).

Influence of different parameters on the activity peaks

A peak can be described mathematically by a parabola, i.e. by a 2nd-order polynomial. The first derivative is used to find the vertex of a parabola as the first derivative equals zero at the vertex. At the maximum point of the parabola the hare's activity is highest. Therefore, if the horal distance is a function of the time interval to and since sunrise or sunset, the independent variable of this function indicates the time interval of maximum locomotor activity.

Firstly, the time interval with the highest activity was determined. As the time of sunset and sunrise changes at about 1 min per day in summer, and as each of the nine hares provided a different number of horal distances, several maximum points for each animal were calculated. The horal distances of one day did not yield enough data to calculate a morning and an evening maximum point. For this reason, we pooled the horal distances of five days for every hare to calculate one evening and one morning maximum point. If