



Seasonal effects on locomotor and feeding rhythms in indoor cats



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ABSTRACT

Different synchronizers can modify daily rhythms during an annual cycle. Nevertheless, the fluctuation of these external factors is often ignored in studies on cat locomotor activity and feeding rhythms, thereby focusing on one single season. To fill this gap, the activity and feeding rhythms of six cats living in a research cattery, receiving natural daylight, were monitored during 3 weeks for each season. Although under minimal influence of seasonal fluctuations in ambient temperature and humidity, the cats showed maxima in daily covered distance during spring and autumn, and minima during winter. The activity and feeding rhythms followed 24-hour periodicity during all seasons and bimodality was detected, with decreased covered distance and food intake around midnight and midday. These daily rhythm troughs were robust and stable across seasons, whereas the inter-seasonal differences in activity level resided in the timing of daily peaks. However, the daily eating pattern was less affected by seasonal variations. Human interactions systematically enhanced locomotor activity and food consumption at the same time for each season, whereas spontaneous peaks of feeding and activity rose during the twilight times according to the season, confirming the crepuscular nature of the species. Human presence and attention seem responsible for more diurnal patterns in the studied cats. This study demonstrates that natural seasonal daylight fluctuations modulate the locomotor and feeding rhythms of indoor cats.

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Introduction

Understanding how cats daily and seasonally manage their locomotor activity and feeding behavior under natural daylight would provide a strong basis for better management of their needs in different environments. As day lengths and timing of twilights (i.e., sunrise and sunset) vary across seasons, one could expect animal behavior to fluctuate in a similar way. Yet, most studies on activity and feeding rhythms, especially in cats, focus on single seasons, preventing an overall assessment of their general behavior. Indeed, twilight onsets vary across seasons and regular peaks of activity in the cat near natural of artificial dawn and dusk have

been described in many studies (Kavanau, 1971; Dards, 1979; Jones & Coman, 1982; Izawa, 1983; Kuwabara et al., 1986; Podberscek et al., 1991; Haspel & Calhoun, 1993; Kappen et al., 2013; Parker et al., 2019), showing a tendency towards being crepuscular.

Several authors reported cats being more active during warm seasons than during cold ones (Dards 1979; Romanowski, 1988; Haspel & Calhoun, 1993; Weber & Dailly, 1998), leading to considerations that these differences in activity are probably due to differences in day length. In fact, Goszczyński et al. (2009) demonstrated that the density index of the cats in rural areas correlated positively with day length. Nevertheless, the home ranges of adult feral males were larger in summer but also in winter in the study of Langham & Porter (1991), and Horn et al. (2011) observed greatest activities in “unowned” cats from October to February, probably due to higher energetic demands or more time needed to capture prey at those times. The authors presume “seasonal variation in home range size likely reflects changes in prey availability, habitat use, environmental (e.g., thermal) stress, and mating strategies”.

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Regarding daily activity pattern, peaks of activity constantly occurred at dusk throughout the year in the results of Izawa on feral cats (1983), but house cats in rural areas presented a two-peaked activity pattern in spring and summer in the study of Goszczyński et al. (2009). These findings are in accordance with the observations of Jones & Coman (1982) where peaks occurred near dawn and dusk and lows occurred near midday during the warm season of the year. The cats studied by Izawa (1983), however, showed a more stable activity pattern throughout the day during the cold seasons.

The behavioral flexibility of the cat, able to adjust to food availability to maintain its energy balance, is well suited to its lifestyle as an opportunistic feeder. Its changeable activity rhythm is in accordance with the adaptability this predator must show regarding the variety of rhythms of its prey (Konecny, 1987): rodents are usually nocturnal while most song birds are diurnal. For most authors, the feeding pattern of the cat is entirely random, some pointing out the large variability between individuals (Mugford, 1977; Mugford & Thorne, 1980; Kane et al., 1981; Thorne, 1982; Johnson et al., 1983; Randall et al., 1985). In fact, Thorne (1982) suggested that the cat has a behavioral repertoire containing different patterns of feeding, each being used when appropriate. The cat could therefore adapt its feeding behavior according to the fluctuating seasonal conditions.

Photoperiod is known to cause physiological changes in seasonal mammals, including changes in body weight (Ebling, 2014) and could thus constitute a *zeitgeber* (i.e., external rhythm synchroniser). Sensitivity to photoperiod has been demonstrated in the domestic cat through the circulating melatonin concentration and oestrous cycle (Dawson, 1941; Leyva et al., 1989; Michel, 1993). A recent study even demonstrated that cats born during times of increasing photoperiod had significantly more chance to develop obesity at 9 years (Cave et al., 2018). However, studies on feeding habits in cats according to the seasons are scarce. During short-day conditions, neutered group-housed male cats fed twice a day required lower energy intake to maintain body weight (Kappen, 2012). Accordingly, energy requirements based on energy expenditure were higher in young cats in summer compared with winter (Kappen et al., 2013), possibly reflecting an increased growth rate of hair in the cat (Hendriks et al., 1998). On the contrary, a longer study on a larger and more varied population with *ad libitum* access to food (Serisier et al., 2014) found food intake was lowest during summer months and highest during late autumn and winter, suggesting that feeding behavior occurred in response to changes in energy for thermoregulation.

Effects of the natural light-dark cycle across seasons on the timing and pattern of feeding and daily activity rhythms in cats have not yet been studied in detail. The main reason is that, until recently, reliable automated recording devices did not exist and most of the recordings of the activities of cats had to be carried out by direct observation or in laboratories. By improving our understanding of the effect of photoperiod on the feeding and activity rhythm in domestic cats, season-specific feeding and housing recommendations could be developed. The aims of this study are thus to clarify whether seasonal differences of daily rhythms of food intake and locomotor activity exist in cats maintained under indoor conditions and, if so, to determine the influence of daylight length and onsets.

Material and methods

Animals and conditions

One group of 6 cats, 7 months of age at the beginning of the experiment, was studied. This group constituted of 5 spayed fe-

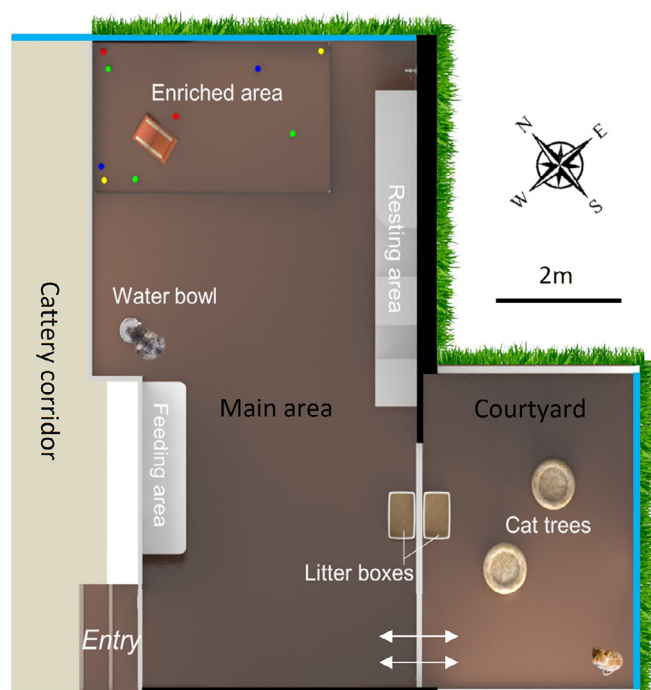


Figure 1. Map of the study room. The main area, accessed from the cattery corridor by the “entry” (stairs leading to the main area front door), contains an enriched area (represented in the rectangle and containing several cat toys), a resting area (large 5-level wall shelf containing several hiding places and cushions), a water bowl renewed daily, a feeding area (large 2-level collar-operated feeding station) and a litter box renewed daily. The courtyard was accessed to with hermetic cat flaps (orientation illustrated by the horizontal white arrows) and contained two cat trees (containing cushions) and another litter tray. Cats were exposed to a natural daylight through large bay windows (position indicated by blue lines). “(For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)”

males and 1 castrated male of different breeds (exotic shorthair, American shorthair, Selkirk rex and Selkirk straight shorthair).

The cats were housed at the cattery of Royal Canin located in the South of France (Aimargues). The group lived in an indoor heated main area under controlled conditions for temperature (21–23°C) and relative humidity (40%) of 22.50 m² (6.40 m (l) x 3.51 m (w) x 2.60 m (h)) as well as in an inner courtyard of 7 m² (2.90 m (l) x 2.40 m (w) x 2.60 m (h)), a small confined room opened on fresh external air through narrow gaps underneath and on the top of windows, separated from the main area with hermetic cat flaps (Figure 1). In the main room, the cats had free access to a large 5-level wall shelf containing several hiding places and cushions (resting area) and to an area containing several cat toys (enriched area), a wall scratching post, a collar-operated feeding station (feeding area, see details in section “Feeding and human intervention”), a water bowl and a litter tray. In the courtyard, the cats had access to two cat trees containing cushions and another litter tray.

During the entire year the present study was conducted, the cats were exposed to a natural light/dark cycle through large windows (blue lines in Figure 1). During the recording periods, the cycle averaged 14h21 of daily light in spring (sunrise at 06:28; sunset at 20:49), 14h56 in summer (sunrise at 06:19; sunset at 21:16), 09h51 in autumn (sunrise at 07:30; sunset at 17:21) and 09h56 in winter (sunrise at 07:57; sunset at 17:54). The times used in this study followed daylight saving times accordingly.

The health and well-being of each individual were regularly verified (daily and weekly) by the animal caretakers and veterinarians. In the cattery, whenever alarming signs in body weight and food

intake would occur in a cat, the animal would be removed from the study panel. This eventuality did not present itself during the present study.

Recording periods

The cats were observed continuously and simultaneously during 21 subsequent days each season in order to maximise cat availability and the number of protocols at the cattery, where variable studies are conducted. Their locomotor activity and feeding behavior were recorded between April 25th 2016 and May 15th 2016 for the spring season, between July 11th and 31st 2016 for the summer season, between October 30th 2016 and November 20th 2016 for the autumn season and between January 23rd 2017 and February 12th 2017 for the winter season. Each period of 21 subsequent days of recording took place after a week of habituation. This was necessary to give the cats time to acclimate themselves to the present study conditions (feeding, human interventions, recording tags) which differed from those of previous studies conducted in the room. In autumn, however, the locomotor activity recordings were restricted to a period between the 8th and 19th of November 2016 because of technical difficulties.

Feeding and human intervention

The cats were fed *ad libitum* with the same food throughout the four seasons (extruded dry diet -Fit32, 3859 kcal/kg-, Royal Canin, Aimargues, France). Food in excess and water were renewed every day at 11:40. As a free-feeding situation, this provided no external constraints on food availability and allowed the animals to choose freely the timing and size of their meals.

The cats fed from a two-level feeding station, each floor leading to 5 trap doors and each trap door giving access to two feeding bowls. Each individual had free access to its own feeding bowls, as each collar enabled the opening of one specific trap door of the feeding station.

The animal caregivers entered the panel every day between 08:20 and 08:50 to clean the facility, between 11:15 and 11:45 and between 15:45 and 16:00 to interact with the cats and check the room. The animals were already familiar with the caregivers at the beginning of the study.

Tracking technologies

Two small tags were attached to a collar on each cat, one to track their locomotor activity (UWB technology, see Parker et al., 2017), the second to track their feeding habits (passive RFID and electronic scales). The tags continuously provided us with distance covered by each cat every 10 minutes and the time and weight of consumption (see Parker et al., 2019 for more details). These tags had no adverse effect on the physical condition of the animals and were accepted without behavioral disturbance. This protocol was approved by the ethical committee of Royal Canin.

Rhythm analyses

The same rhythm parameters as in our previous study (Parker et al. 2019) were calculated and compared for each behavior, feeding and locomotor. Briefly, the period (duration of a full cycle) and amplitude (a measure of how much of the activity or food intake that does occur is actually rhythmic) were measured using the periodogram of the rhythm, calculated by the Clocklab software (v. 2.72, extension of Matlab v. R2013a). The interdaily stability, intradaily variability and onset of the least active 5 hours were calculated by the ActiWatch software (v. 7.31). The interdaily stability

Table 1

Energy requirements of growing cats (sampled, according to the age of the cats of our study, from Case et al., 2011).

Age	Energy needs (kcal/kg body weight)
7-8½ months	100
9-11 months	80
12 months	60

quantifies the variability among successive days, its values (arbitrary units) decreasing with higher day-to-day variation of the activity or feeding patterns, thus ranging from 0 for Gaussian noise to 1 for maximal interdaily stability. The intradaily variability evaluates the fragmentation of the rhythm, its values (arbitrary units) ranging from 0 for a perfect sine wave, to about 2 for Gaussian noise. The least active 5 hours onset is a parameter established to give an indication about the moment daily troughs happen in the pattern of daily rhythms (Witting et al., 1990). A strong and robust rhythm will be characterised by high amplitude and interdaily stability, and low intradaily variability. In order to establish if the cats tend to consume/be active more during night or day hours, we assessed their activity/consumption by hour and by day according to the light condition (night hours versus day hours), using the sunrise and sunsets hours (provided by national almanac) as phase references. An individual was considered to show a tendency towards bimodality (period of 12 hours) when the magnitude of the 12 hours peak was equal or superior to half of the 24 hours peak (highest one) on its periodogram.

Food intake and energy intake measurements

Being 7 months old at the beginning of our recording periods, the cats in our study were still growing. We therefore also looked at cat energy intake divided by the corresponding energy needs across seasons (Table 1).

Statistical analyses

Every statistical comparison was made with Sigmaplot (v. 13.0, Systat Inc., San Jose, California, USA). The individuals being the same in each season, tests with repeated measures were conducted. One-way analyses of variance (ANOVAs) with repeated measures were performed to compare the daily covered distance, food and energy intake, the rhythm parameters, the body weight and the nocturnal and diurnal hourly covered distance and food consumption according to the season. The same test was performed to compare the total and hourly covered distance and food consumption according to the lighting phase, as well as to compare the covered distance by hour in spring and in summer. However, the hourly covered distance in autumn and winter, as well as the hourly food consumption at all seasons, did not follow statistical normality (Shapiro-Wilk test for normality) or homogenous variances (Brown-Forsythe test for equal variance). Friedman ANOVAs with repeated measures were thus conducted for these data. Finally, two-way ANOVAs with repeated measures were completed to compare the covered distance and food consumption according to the season and to the hour of the day, the total and hourly covered distance and food consumption according to the lighting phase and to the season, the rhythm parameters according to the variable (activity versus feeding behavior) and the data every 20 minutes when looking at the 16:00 activity and feeding peak. Holm-Sidak post-hoc tests were performed with the ANOVAs and Tukey post-hoc tests with the Friedman ANOVAs. Results are given as mean \pm standard error, with a significance threshold of $P < 0.05$ (* when $0.01 \leq P < 0.05$, ** when $0.001 \leq P < 0.01$, *** when $P < 0.001$).

< 0.001 on graphs). On some graphs, the data of two bars with different letters are significantly different, while there is no significant difference between the data of two bars containing similar letters. Lower case letters are not to be compared to upper case ones and vice versa.

Results

Body weight

The indoor cats significantly gained body weight throughout the seasons (One-way RM ANOVA: $F_{3, 15} = 62.99, 23, P < 0.001$). They were heavier in summer (2.85 ± 0.15 kg) compared to spring (2.53 ± 0.11 kg; Holm-Sidak post-hoc test, $P < 0.01$) and further heavier in autumn (3.32 ± 0.21 kg) and winter (3.39 ± 0.17 kg) compared to summer and spring (Holm-Sidak post-hoc test, $P < 0.001$).

Locomotor activity and behavior

Locomotor rhythm

The locomotor activity rhythm of all the individuals has a 24 hour periodicity during the four seasons.

The activity rhythm amplitude, with an average of 618 ± 53 (Figure 2A), as well as the intradaily variability of the activity rhythm, with an average of 1.42 ± 0.06 (Figure 2B), were impacted by the season (One-way RM ANOVA: $F_{3, 15} = 18.79, 23, P < 0.001$ and $F_{3, 15} = 3.63, 23, P < 0.05$, respectively). The amplitude was highest and lowest in spring and autumn, respectively (Holm-Sidak post-hoc test, $P < 0.01$), and intermediate in summer and winter (Holm-Sidak post-hoc test, $P < 0.01$). The intradaily variability values in winter were higher than in autumn (Holm-Sidak post-hoc test, $P < 0.05$).

The interdaily stability of the activity rhythm of the cats was of 0.45 ± 0.02 in spring, 0.39 ± 0.05 in summer, 0.45 ± 0.05 in autumn and 0.33 ± 0.05 in winter and was not impacted by the season (One-way RM ANOVA: $F_{3, 15} = 2.55, 23, P = 0.094$).

Many cats showed tendencies towards bimodality in their activity rhythm: 13 times out of 24, the peak of their activity periodogram at 12 hours was higher than half of their 24-hour peak.

Daily covered distance

The cats covered 2.11 ± 0.13 km per day, on average (Figure 3). This distance is impacted by season (One-way RM ANOVA: $F_{3, 15} = 32.82, 23, P < 0.001$), with cats covering the greatest and shortest distance in spring and winter, respectively (Holm-Sidak post-hoc test, $P < 0.001$). Covered distance decreased in summer (Holm-Sidak post-hoc test, $P < 0.01$), but returned to the spring level in autumn.

Nocturnal versus diurnal activity rate

Daily, the cats covered significantly more distance during daytime than at night (Two-way RM ANOVA: $F_{1, 15} = 19.89, 47, P < 0.01$). There was an interaction between the lighting phase (day versus night) and the season (Two-way RM ANOVA: $F_{3, 15} = 8.71, 47, P < 0.01$). The cats covered significantly more distance during daytime than at night in spring (Holm-Sidak post-hoc test, $P < 0.001$) and summer (Holm-Sidak post-hoc test, $P < 0.01$), while distances covered during daytime and nighttime were very close in autumn or winter (Holm-Sidak post-hoc test, $P > 0.1$, Figure 4A).

During daytime, the cats covered the largest distance in spring (Holm-Sidak post-hoc test, $P < 0.01$), with intermediate values in summer and autumn (Holm-Sidak post-hoc test, $P < 0.01$), and the lowest distance in winter (Holm-Sidak post-hoc test, $P < 0.01$, Figure 4A). At night, they covered more distance in autumn than in

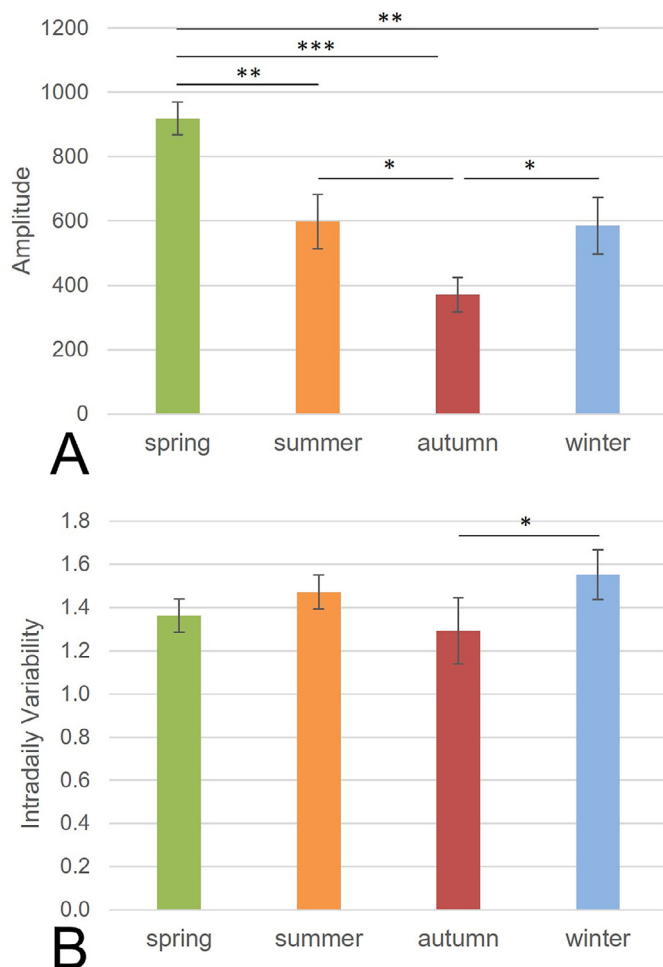


Figure 2. Mean amplitude (A) and Intradaily Variability (B) of the activity rhythm of the cats ($N=6$) according to the season. Error bars represent standard errors, (*) indicates $P < 0.05$, (**) indicates $P < 0.01$, (***) indicates $P < 0.001$. "(For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)"

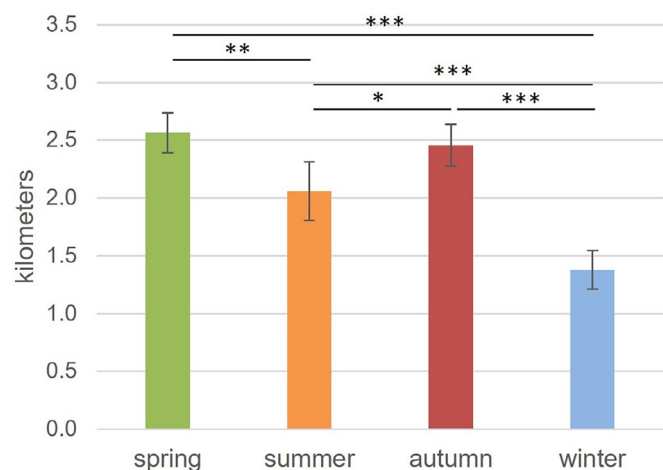


Figure 3. Mean daily distance (km) covered by the cats ($N=6$) according to the season. Error bars represent standard errors, (*) indicates $p < 0.05$, (**) indicates $P < 0.01$, (***) indicates $P < 0.001$. "(For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)"

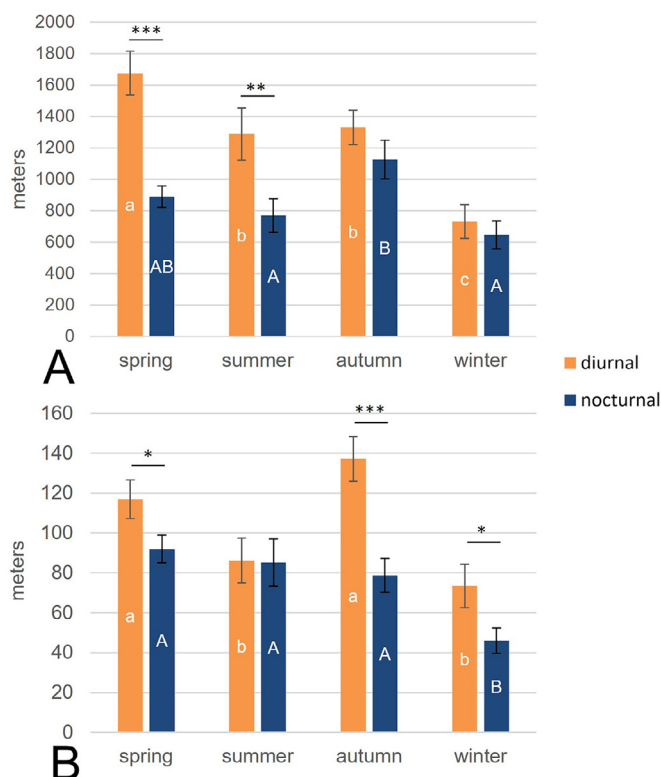


Figure 4. Mean daily (A) and hourly (B) nocturnal and diurnal distance (m) covered by the cats (N=6) according to the season. Error bars represent standard errors. Asterisks represent differences between day periods (diurnal versus nocturnal) within one season: (*) indicates $P < 0.05$, (**) indicates $P < 0.01$, (***) indicates $P < 0.001$. Letters represent differences between seasons within one day period: low-case letters for the diurnal phase, upper-case letters for the nocturnal one. Different letters represent a significant difference, similar letters a non-significant one. Low-case is not to be compared to upper-case letters and vice versa. ("For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.")

winter (Holm-Sidak post-hoc test, $P < 0.001$), in summer (Holm-Sidak post-hoc test, $P < 0.05$), and in spring, although this effect did not reach statistical significance for the latter (Holm-Sidak post-hoc test, $P = 0.075$, Figure 4A).

Hourly, the cats also covered significantly more distance during daytime than at night (Two-way RM ANOVA: $F_{1,15} = 13.79$, 47, $P < 0.05$). There was an interaction between the lighting phase (day versus night) and the season (Two-way RM ANOVA: $F_{3,15} = 7.45$, 47, $P < 0.01$): they cover significantly more distance hourly at day than at night in spring (Holm-Sidak post-hoc test, $P < 0.05$), autumn (Holm-Sidak post-hoc test, $P < 0.001$) and winter (Holm-Sidak post-hoc test, $P < 0.05$, Figure 4B).

During daytime, the cats covered significantly more distance per hour in autumn and spring (Holm-Sidak post-hoc test, $P < 0.05$), and less in summer and winter (Holm-Sidak post-hoc test, $P < 0.01$, Figure 4B). At night, they covered more or less the same distance from spring to autumn, and decreased their activity in winter (Holm-Sidak post-hoc test, $P < 0.01$, Figure 4B).

In spring and autumn, the least active 5 hours of the cats were all nocturnal (onset between 20:00 and 01:00). In summer, it occurred at night for 4 cats (onset between 23:00 and 00:00) and during daytime for the 2 others (onset between 20:00 and 01:00). In winter, these least active hours occurred at night for 5 cats (onset between 20:00 and 22:00), and during daytime for the other cat (onset at 10:00).

Mean activity rhythm during the day

Hour of day had an impact on the covered distance of the cats (One-way RM ANOVA: $F_{23,115} = 21.02$, 143, $P < 0.001$ in spring; One-way RM ANOVA: $F_{23,115} = 9.74$, 143, $P < 0.001$ in summer; Friedman: $\chi^2_{23} = 83.34$, 23, $P < 0.001$ in autumn; Friedman: $\chi^2_{23} = 104.03$, 23, $P < 0.001$ in winter).

For all seasons, we found three systematic peaks in the locomotor activity of the cats: one before or during sunrise, another at 11:00 during the food renewal and second human intervention (first one with interspecific interactions), and another after or during the sunset according to the season (Figure 5). In spring, autumn and winter, significant peaks were detected at 16:00, after the end of human presence in the cattery.

The cats were significantly less active in the middle of the night during all seasons: between 01:00 and 05:00 in spring, between 00:00 and 04:00 in summer, between 00:00 and 04:00 in autumn, between 22:00 and 02:00 in winter. The cats were significantly less active in the middle of the day in summer and winter (between 13:00 and 15:00).

During the most active seasons (spring and autumn), the difference in the daily covered distance mainly resides in higher peaks rather than in a global higher hourly activity (Figure 6): in spring, the evening peak is significantly higher than during the other seasons (Holm-Sidak post-hoc test, $P < 0.001$), in autumn, the peak at the end of human presence in the cattery (right before sunset in this season) is significantly higher than during the other seasons (Holm-Sidak post-hoc test, $P < 0.001$). In winter, the least active season, the peaks are less pronounced.

Examination around the 16-hour activity peak

The last human intervention of the day happening between 15:45 and 16:00, we examined the activity of the cats around 16:00 with smaller time-lapse (20 min) between 15:00 and 17:00 (Figure 7). The cats covered significantly more distance at 15:40 and at 16:00 compared to the preceding or following 40 minutes (Holm-Sidak post-hoc test, $P < 0.001$).

Feeding rhythm and behavior

Feeding rhythm

Every cat ate with a 24h-cyclicity throughout the four seasons.

The amplitude of the feeding rhythm, with an of average 178 ± 24 (Figure 8A), was impacted by the season (One-way RM ANOVA: $F_{3,15} = 5.81$, 23, $P < 0.01$), being higher in winter than in spring (Holm-Sidak post-hoc test, $P < 0.05$) and in summer (Holm-Sidak post-hoc test, $P < 0.05$).

The interdaily stability of the feeding rhythm of the cats averaged 0.34 ± 0.04 (Figure 8B). It was impacted by the season (One-way RM ANOVA: $F_{3,15} = 7.08$, 23, $P < 0.01$), with higher values in autumn than in summer (Holm-Sidak post-hoc test, $P < 0.01$), spring (Holm-Sidak post-hoc test, $P < 0.01$) and winter, although this effect did not reach statistical significance for the latter (Holm-Sidak post-hoc test, $P = 0.088$). The intradaily variability of the feeding rhythm averaged 1.92 ± 0.09 (Figure 8C). It was also impacted by the season (One-way RM ANOVA: $F_{3,15} = 6.53$, 23, $P < 0.01$), being the lowest in autumn (Holm-Sidak post-hoc test, $0.01 < P < 0.05$).

Many cats show tendencies towards bimodality in their daily feeding rhythm: 13 times out of 24, the peak of their feeding periodogram at 12 hours is higher than half of their 24-hour peak.

Daily food consumption

The cats ate on average 53.88 ± 2.1 g per day without significant changes across the seasons (One-way RM ANOVA: $F_{3,15} = 3.37$,

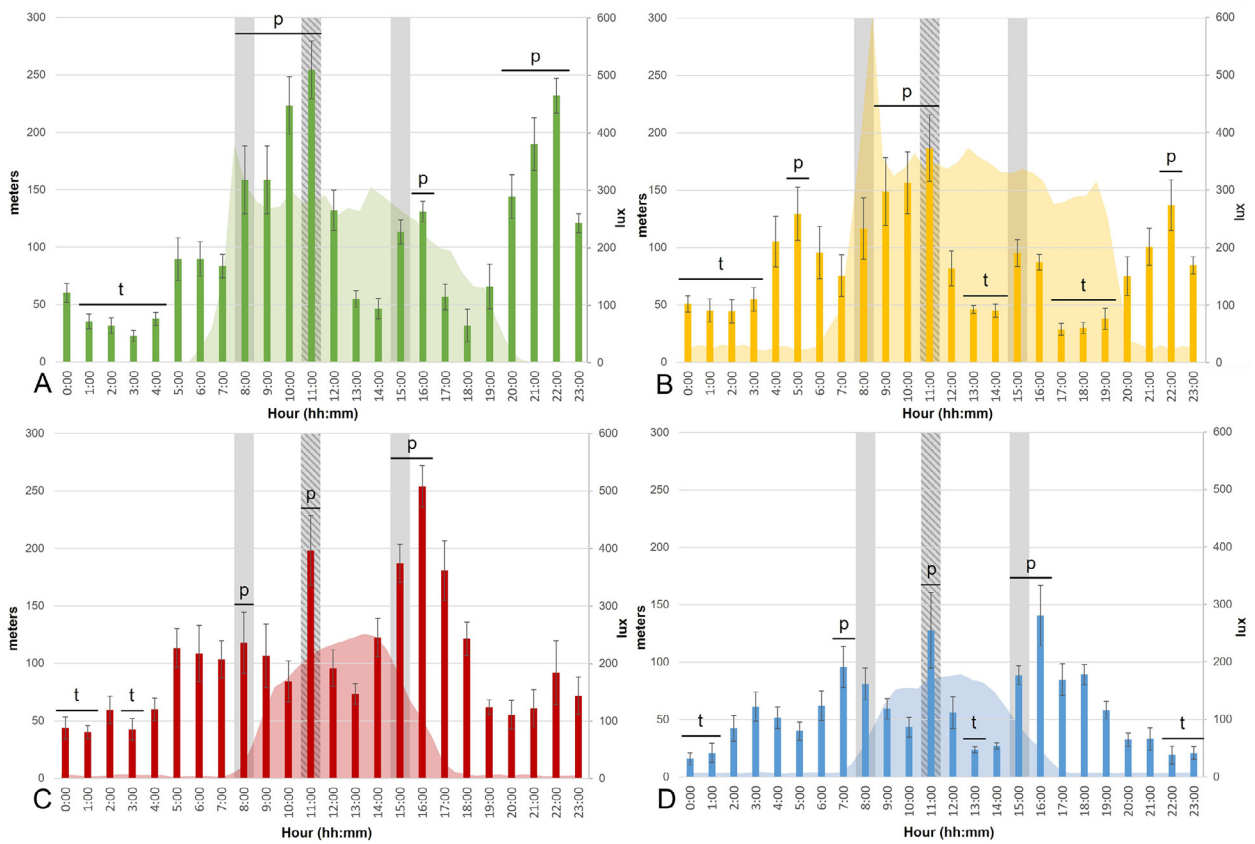


Figure 5. Mean distance (m, bars) covered by the cats (N=6) and luminosity (lux, area) every hour (hh:mm) in spring (green, A), summer (yellow, B), autumn (red, C) and winter (blue, D). Error bars represent standard errors, (p) indicates a significant peak, (t) indicates a significant trough (for more details, see Parker et al., 2019). “(For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)”

23, $P > 0.05$ among seasons). However, season had an effect on the energy intake divided by the energy needs of the cats ($F_{3, 15} = 9.959, 23, P < 0.001$, Figure 9). This effect was significantly greater in autumn than in spring (Holm-Sidak post-hoc test, $p < 0.001$) or winter (Holm-Sidak post-hoc test, $P < 0.05$).

Nocturnal versus diurnal consumption

The lighting phase (night versus day) had no effect on the daily nor on the hourly mean feed consumption of the cats (Two-way RM ANOVA: $F_{1, 15} = 2.59, 47, P = 0.169$ and Two-way RM ANOVA: $F_{1, 15} = 1.03, 47, P = 0.357$, respectively).

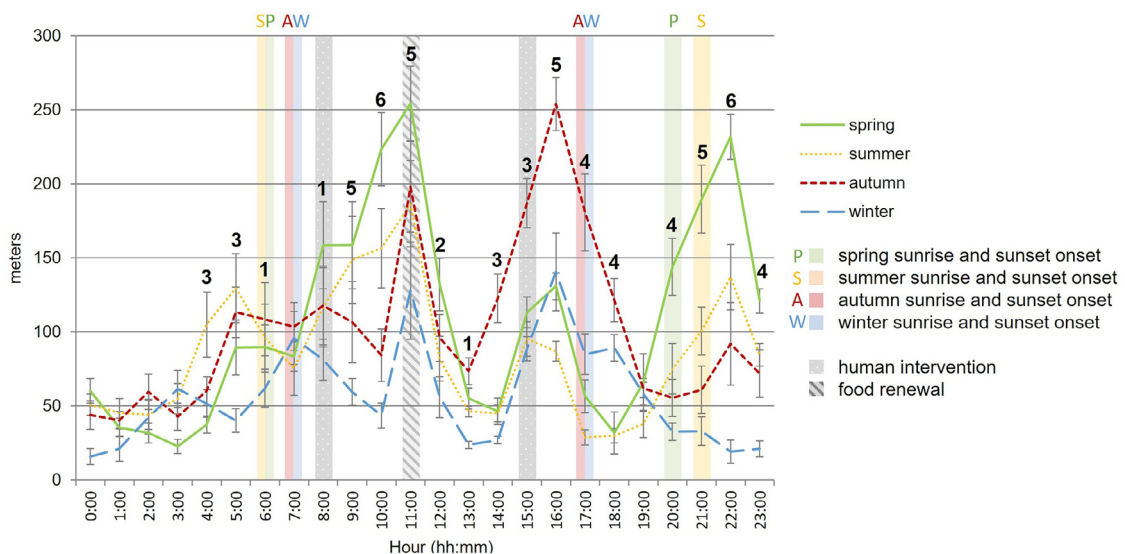


Figure 6. Mean distance (m) covered by the cats (N=6) every hour throughout the day according to the season. Error bars represent standard errors. 1/2/3/4/5/6 represents one/two/three/four/five/six significant difference(s) among the seasons within a given hour. “(For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)”

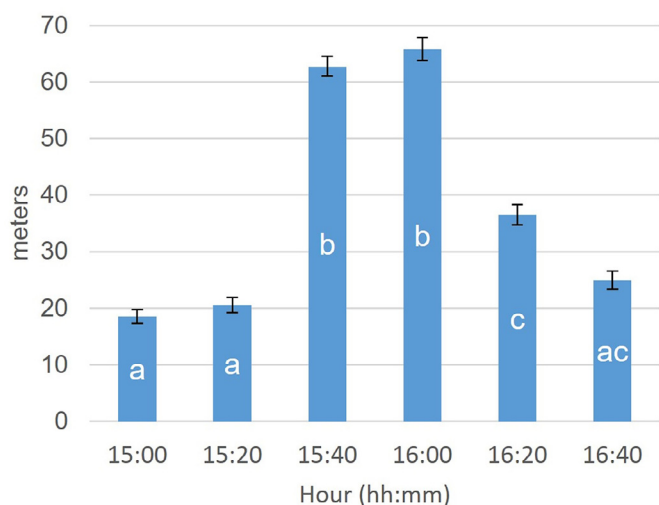


Figure 7. Mean distance (m) covered by the cats (N=6) every 20 min between 15:00 and 17:00. Error bars represent standard errors. Different letters represent a significant difference between data, similar letters represent a non-significant difference between data. “(For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)”

In spring and winter, the 5 hours during which the cats ate the least were nocturnal for 5 cats out of 6 (onset between 18:00 and 01:00), diurnal for the other (onset at 11:00 or at 14:00). In summer and autumn, it occurred at night for half of the cats (onset between 19:00 and 00:00), at day for the other half (onset between 05:00 and 17:00).

Mean feeding rhythm during the day

The hour of the day had an effect on the food intake of the cats (Friedman: $\chi^2_{23}=81.67$, 23, $P < 0.001$ in spring; Friedman: $\chi^2_{23}=81.95$, 23, $P < 0.001$ in summer; Friedman: $\chi^2_{23}=64.89$, 23, $P < 0.001$ in autumn; Friedman: $\chi^2_{23}=83.51$, 23, $P < 0.001$ in winter).

For all seasons, three peaks of consumption were systematically found: between 11:00 and 12:00 during food renewal and human interactions, between 16:00 and 17:00 after the end of human presence in the cattery, and around sunset (which can happen at the same moment as the 16:00 peak in autumn and winter; Figure 10). In autumn and winter, the cats also ate more before or during sunrise. In spring, autumn and winter, the cats eat less food between 13:00 and 15:00.

There are fewer differences in the hourly consumption between seasons, especially at 11:00 when no significant difference stands out (Figure 11). Nevertheless, the third peak of the day is higher in autumn and winter, when the sunset happens earlier than in spring and summer. The consumption during autumn and winter is lower around 21:00 and 22:00 than during spring and summer, when the sunset happens at those times.

For all seasons, cats ate the least in the middle of the night and in the middle of the day. It is interesting to see that there was no consumption during the midday trough even in winter.

Examination around the 16-hour activity peak

Cats ate significantly more active at 16:00 compared to the preceding 60 minutes or following 40 minutes (Holm-Sidak post-hoc test, $P < 0.001$, Figure 12).

Feeding versus locomotor activity rhythm

The amplitude of the locomotor activity rhythm was significantly higher than that of the feeding rhythm (618 ± 53 ver-

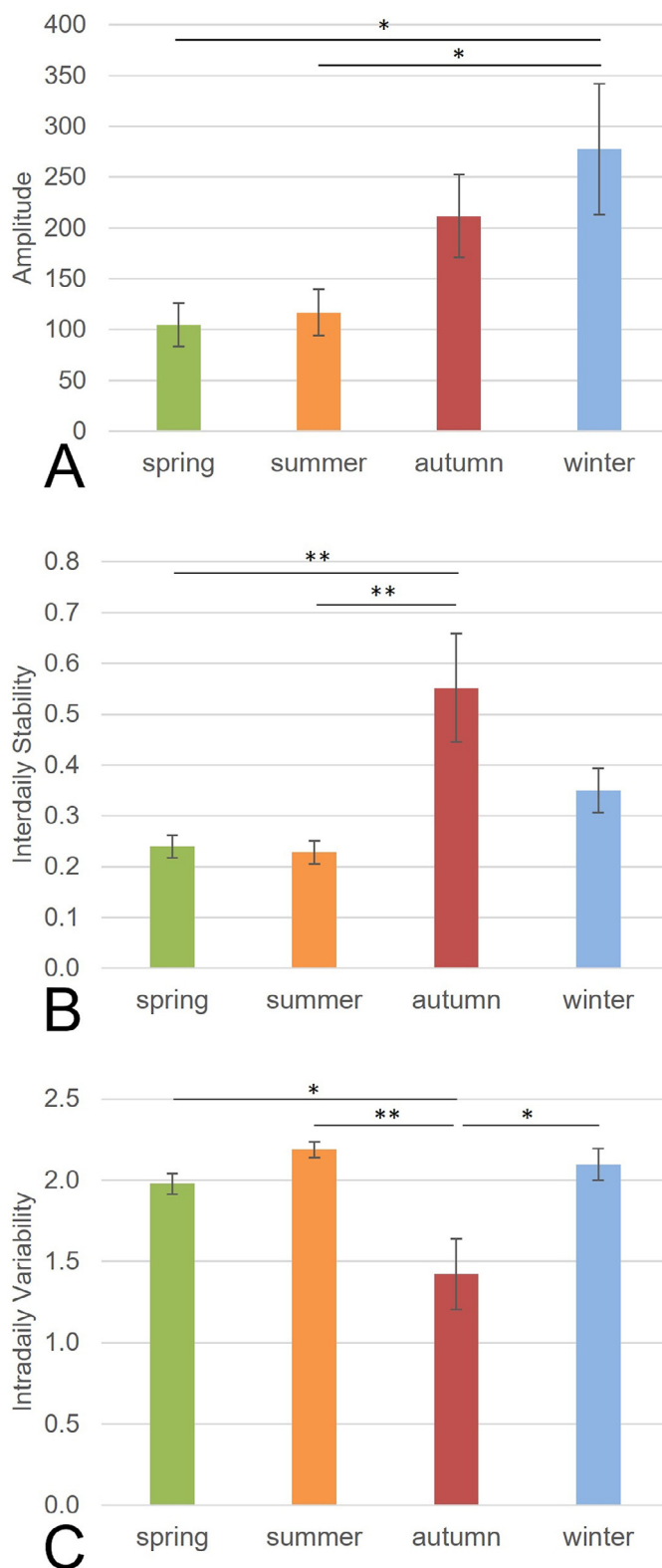


Figure 8. Mean amplitude (A), Interdaily Stability (B) and Intradaily Variability (C) of the feeding rhythm of the cats (N=6) according to the season. Error bars represent standard errors, (*) indicates $P < 0.05$, (**) indicates $P < 0.01$. “(For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)”

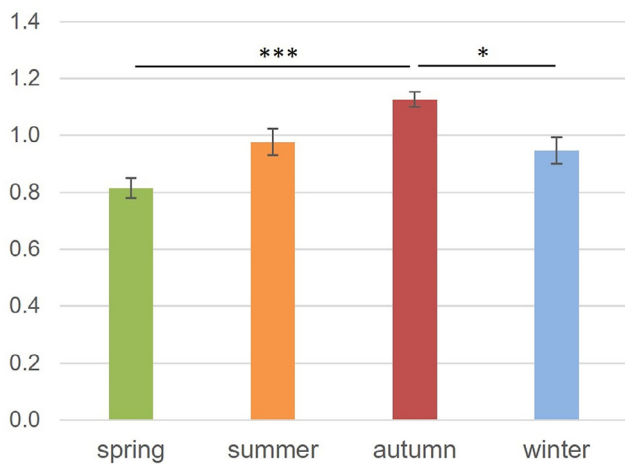


Figure 9. Mean daily energy intake divided by energy needs (kcal) of the cats (N=6) according to the season. Error bars represent standard errors, (*) indicates $P < 0.05$, (***) indicates $P < 0.001$. “(For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)”

178 ± 24, respectively, Two-way RM ANOVA: $F_{1, 15} = 38.77, 47, P < 0.01$) and the intradaily variability of the locomotor activity rhythm was significantly lower than that of the feeding rhythm (1.42 ± 0.06 versus 1.92 ± 0.09 , respectively, Two-way RM ANOVA: $F_{1, 15} = 58.47, 47, P < 0.001$). There was an interaction between the rhythm type (feeding versus activity) and the season (Two-way RM

ANOVA: $F_{3, 15} = 19.63, 47, P < 0.001$ for the amplitude; Two-way RM ANOVA: $F_{3, 15} = 3.76, 47, P < 0.05$ for the intradaily variability, Table 2): the amplitude was higher and the intradaily variability lower in the locomotor activity rhythm than in the feeding rhythm of the cats in spring (Holm-Sidak post-hoc test, $P < 0.001$), summer (Holm-Sidak post-hoc test, $P < 0.001$), winter (Holm-Sidak post-hoc test, $P < 0.01, P < 0.001$, respectively), but not in autumn (Holm-Sidak post-hoc test, $P = 0.103, P = 0.335$, respectively).

No significant difference was found between the feeding and the locomotor activity rhythms regarding their interdaily stability (Two-way RM ANOVA: $F_{1, 15} = 1.80, 47, P = 0.237$). However, there also was an interaction between the rhythm type and the season (Two-way RM ANOVA: $F_{3, 15} = 6.05, 47, P < 0.01$) so that the interdaily stability was higher in the locomotor activity rhythm than in the feeding rhythm of the cats in spring and summer (Holm-Sidak post-hoc test, $P < 0.01, P < 0.05$, respectively), but not in autumn or winter (Holm-Sidak post-hoc test, $P = 0.156, P = 0.777$, respectively).

Discussion

This study enabled us to assess the locomotor activity and feeding rhythms of six indoor cats, during continuous 24 hours recording throughout four consecutive seasons. The animals were exposed to natural seasonal luminosity fluctuations such as day length but also sunrise and sunset timings, sun position in the sky and light intensity. Furthermore, annual exposition of the cats to natural luminosity ensured that they fully integrated the long-term effects of seasonal light conditions in their behaviors.

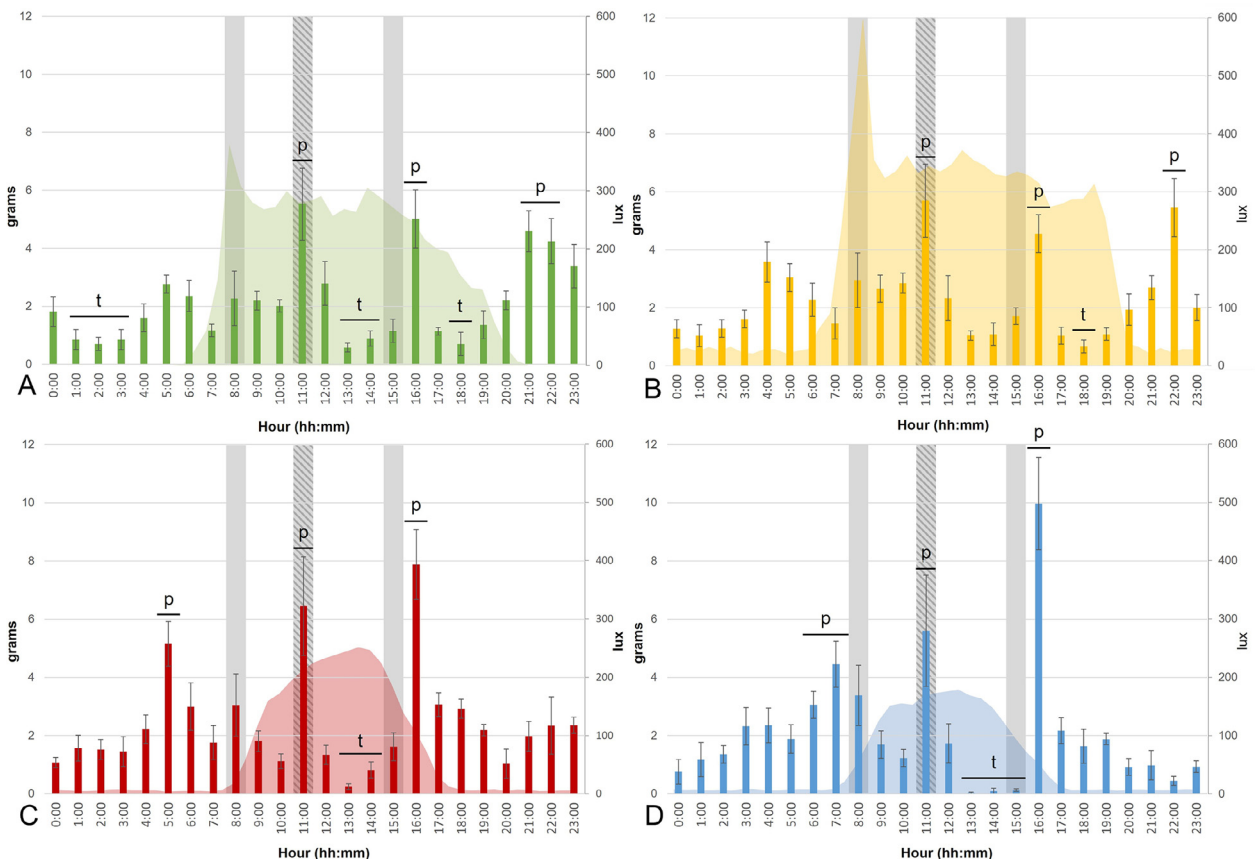


Figure 10. Mean food consumption (g, bars) of the cats (N=6) and luminosity (lux, area) every hour (hh:mm) in spring (green, A), summer (yellow, B), autumn (red, C) and winter (blue, D). Error bars represent standard errors, (p) indicates a significant peak, (t) indicates a significant trough (for more details, see Parker et al., 2019). “(For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)”

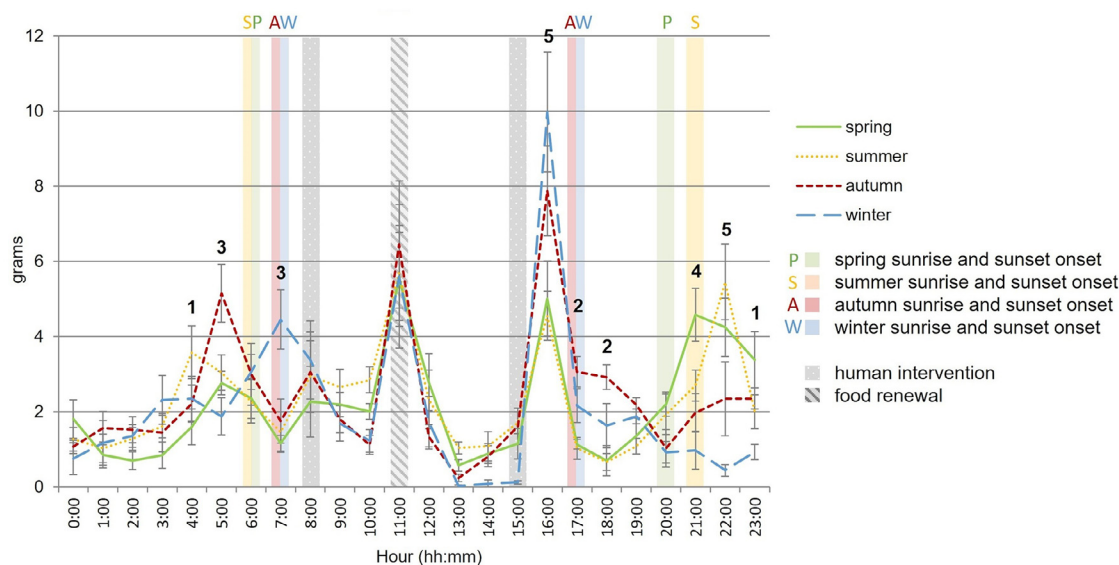


Figure 11. Mean food consumption (g) of the cats (N=6) every hour throughout the day according to the season. Error bars represent standard errors. 1/2/3/4/5 represents one/two/three/four/five significant difference(s) among the seasons within a given hour. “(For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)”

Table 2
Mean ± SE of Amplitude, interdaily stability (IS) and intradaily variability (IV) according to the rhythm (locomotor or feeding) of the cats (N=6) and the season (spring, summer, autumn, winter).

Variable	Rhythm	Amplitude		IS		IV	
		locomotor	feeding	locomotor	feeding	locomotor	feeding
Season	Spring	919 ± 51	105 ± 21	0.45 ± 0.02	0.24 ± 0.02	1.36 ± 0.08	1.98 ± 0.06
	Summer	599 ± 85	117 ± 23	0.39 ± 0.02	0.23 ± 0.02	1.47 ± 0.08	2.19 ± 0.05
	Autumn	371 ± 53	212 ± 41	0.45 ± 0.11	0.55 ± 0.11	1.29 ± 0.15	1.42 ± 0.22
	Winter	585 ± 87	278 ± 64	0.33 ± 0.04	0.35 ± 0.04	1.55 ± 0.11	2.10 ± 0.10

In contradiction with previous statements about behavioral arrhythmicity in the cat (Hawking et al., 1971; Kavanau, 1971) or random patterns of eating (Mugford & Thorne, 1980; Kane et al., 1981; Thorne, 1982; Johnson et al., 1983; Randall et al., 1985), the

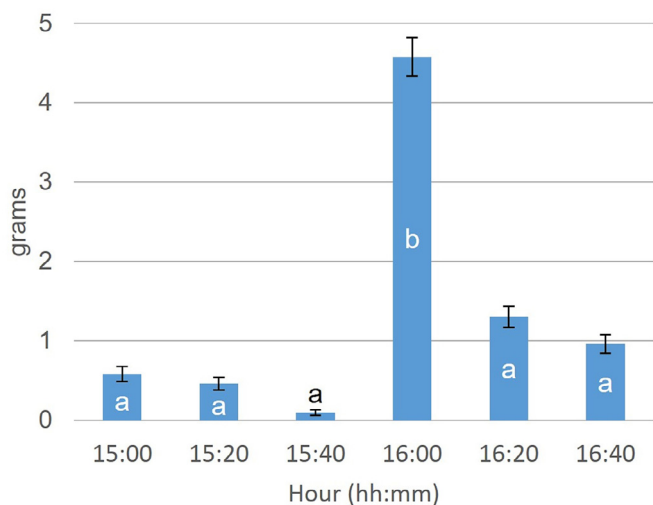


Figure 12. Mean food intake (g) of the cats (N=6) every 20 min between 15:00 and 17:00. Error bars represent standard errors. Different letters represent a significant difference between data, similar letters represent a non-significant difference between data. “(For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)”

present study, using precise automatic tracking technology during 21-day long protocols, showed that cats moved and ate with 24-hour cyclicality at every season. Some cats in similar study conditions (Parker et al., 2019) did not show this daily rhythmicity in their feeding behavior. The recording period duration may be responsible for this difference. To support this assumption, when we calculated rhythmicity of the cats of the present study over a seven-day or even 14-day period, 24-hour rhythmicity was not always detected. This strongly suggests the importance of recording the behavior of the cats over long periods in order to detect its rhythmicity.

Under wild conditions, mammals react to a combination of seasonally fluctuating environmental cues. In laboratory conditions, however, they often respond to photoperiod alone (Heldmaier et al., 1982), which therefore constitutes the driving factor for numerous seasonal physiological changes in these animals. For example, few reports have highlighted physiological changes in the domestic cat according to photoperiod (Hendriks et al., 1997; Blottner & Jewgenow, 2007; Alexandre-Pires et al., 2012). With negligible effect of seasonal variations in ambient temperature and humidity, daily covered distance by the cats of the present study still showed seasonal fluctuations with autumn and spring maxima and winter minima. We could therefore consider that natural luminosity fluctuations constitute a powerful external rhythm-synchronizer, that is *zeitgeber*, in the domestic cat.

While spring maxima and winter minima were also detected in free-roaming cats (Dards, 1979; Romanowski, 1988; Haspel & Calhoun, 1993; Weber & Dailly, 1998; Goszczyński et al., 2009), autumn maxima have not yet been reported in literature. This

finding might be due to our study conditions: compared to the other 3 seasons, autumn is the only season during which the higher activity peak (i.e., lasting longer and being more massive) takes place in the afternoon. This timing is particular during early-sunset seasons, as it constitutes a combination of two positive influential factors on the activity of the cats: effect of last human intervention and upcoming of sunset. This sequence might have heightened the level of locomotor activity of the cats to the point of making autumn one of the most active seasons. In fact, the enhanced activity during the most active seasons seems primarily due to a rise in the peaks of covered distance: the spontaneous sunset peak is higher in spring than during the other seasons.

The season had no effect on the mean daily amount of food ingested by the cats. However, age was confounded with season in this study because we were monitoring growing individuals with different energy needs according to the season in our study. Cats commonly reach adult body size between 9 and 12 months of age (Case et al., 2011). In order to better apprehend the energy intake of the cats and take into account the effect of growth, we compared the energy intake of the cats divided by their appropriate energy needs across seasons (Case et al., 2011). In that case, the cats ate the most in autumn. These findings diverge from those showing lesser energy intake in short-day conditions or winter compared to long-day conditions or summer (Kappen et al., 2012, 2013) or less dietary energy intake during winter than in summer (Bermingham et al., 2012). However, these studies regulated the diets of the cats in order to maintain body weight or did not examine possible seasonal effects throughout the year. In contrast, findings in Serisier et al. (2014) show food intake was greatest during late autumn to winter and suppose ambient temperature, daylight length, or a combination of the two, are responsible for these differences. Most of the cats in the study by Serisier et al. (2014; 30 out of 38) had free access to an outdoor area (14 m²) larger than their indoor area (13 m²), while the individuals of the current study only received little fresh air through narrow gaps underneath and at the top of windows in a 7 m² inner courtyard, smaller than the temperature-controlled main area (22.5 m²). It therefore seems daylight length played a more important role than ambient temperature in the feeding behavior of the cats in the present study. Greater energy intake in autumn in our study may indicate the remnants of a seasonal anticipation of the winter period.

While free-roaming cats are more frequently described as nocturnal in literature (Romanowski, 1988; Langham & Porter, 1991; Barratt, 1997; Horn et al., 2011; Moon et al., 2013), the individuals of our study were more diurnal than nocturnal in their locomotor rhythm. As suggested in the study of Horn et al. (2011), in which pet cats were found to be diurnal and feral cats nocturnal, our findings may be due to human influence, the interventions of the caretakers happening only during daytime. Such interventions have already been described in the literature as positive modulators of the cat activity (Randall et al., 1987; Piccione et al., 2013; Parker et al., 2019). Shorter day length prevented this difference to be significant in autumn and winter regarding the total daily activity. Hourly, however, the cats covered significantly more distance during daytime hours than during nighttime hours for all seasons except in summer. In fact, in summer, the diurnal locomotor activity was reduced, with significant activity troughs in the afternoon. The cats may associate long photoperiods with high ambient temperature and consequently adopt reduced locomotor activity, as activity troughs have been proposed as a response to a rise in ambient temperature (Aschoff, 1966; Konecny, 1987). This emphasises the difficulty to categorise the cat as purely nocturnal or diurnal, with its daily peaks and troughs seeming to be more suited to describe daily activity patterns. Actually, our results indicate that total activity is increased primarily by enhanced diurnal

activity: while the diurnal hourly covered distance is larger during the most active seasons (spring and autumn) than during the less active seasons, the nocturnal hourly covered distance is more similar between the seasons, except in winter where it is still the lowest. Contrary findings in Kappen et al. (2013), in which higher activity during the long day condition was due to an increase in the dark period activity, may be due to the diurnality of activity-enhancing human interventions in our conditions.

Based on its amplitude, the locomotor rhythm of the cats was the strongest in spring, the weakest in autumn. It is likely that the shorter locomotor activity recording period in autumn (12 days instead of 21 days) resulted in a weaker assessed locomotor rhythm, as discussed earlier. This could also explain the similar amplitude, stability and variability between the feeding and locomotor activity rhythms for this season, while they significantly differed during the other seasons. On one hand, the feeding rhythm of the cats was more stable and less variable in autumn compared to the other seasons. On the other hand, the feeding rhythm of the cats grew stronger along the seasons. As the cats acquired their adult age, they may have developed a feeding routine in relation to the study conditions which were standardised at each season. In keeping with this hypothesis, the amplitude of the feeding rhythm of the older cats in Parker et al. (2019) was higher than for the young cats of this study.

Except in autumn, the locomotor behavior of the cats was always more rhythmic than their eating behavior. This reminds us of the opportunistic nature of this solitary hunter. In the wild, the various daily rhythms of the different types of prey may result in flexibility in cat eating patterns, as suggested by Konecny (1987). Compared to their activity pattern, fewer seasonal differences were observed in the feeding pattern of the cats. In particular, no difference stood out between the seasons concerning their mean consumption between 08:00 and 16:00. Their 11:00 peak therefore did not differ according to the season. It thus seems the feeding behavior of the cats is more affected by human interactions and food renewal than by seasonal daylight fluctuations.

During all seasons, a positive modulator of activity and food consumption in fact relied on food renewal combined with the second human intervention (first human interactions) of the day. This enhancer was predictable, as the cats living in the cattery of Royal Canin tend to interact with the caretakers and as cats may be attracted by fresher food, given that, in the wild, they prefer to consume freshly killed carcasses rather than carrion (Bradshaw et al., 1996). As the caretakers entered the room for the last time between 15:45 and 16:00, the cats also started to be more active during this intervention and this continued for a while. Nevertheless, they started to eat more only after the end of this last intervention. It seems the cats moved to interact with the humans and then, when stimulation from the caretakers disappeared, they redirected their behavior towards eating. This suspected “appetite-trigger” should be further investigated using visual observation of the behavior of the cats.

Receiving natural daylight modulations, the cats of the present study showed increased locomotor activity and food intake around sunset independently of the season, similarly to the feral cats in the study of Izawa (1983). However, the sunset peak timings differed between the warm and cold seasons: peaks happened at the end of sunset in spring and summer, but at its beginning in autumn and winter. As previously discussed, the last human intervention happened right before sunset in the short-day seasons. The start of the sunset peak may therefore have coincided with the human-induced peak during those seasons. Furthermore, in autumn and winter, the consumption peak at 16:00 is significantly higher than during spring and summer, for which the sunset peaks are significantly higher. It would be interesting to study

these peaks with different human intervention schedules to investigate its effect on cat daily activity and feeding patterns. Nonetheless, these findings reflect the crepuscular activity of the species often characterised in literature (Kavanau, 1971; Dards, 1979; Jones & Coman, 1982; Izawa, 1983; Kuwabara et al., 1986; Podberscek et al., 1991; Haspel & Calhoun, 1993; Parker et al., 2019). While this crepuscular-related activity, inherited from its ancestor for which the availability of nocturnal and diurnal prey was increased at twilight, persisted throughout the domestication of the cat, it is interesting to see the individuals still express it in conditions where food is made available *ad libitum*.

The activity and food intake of the cats decreased in the middle of the night and in the middle of the day, while they almost stopped eating between 13:00 and 15:00 in winter. The absence of significance of these troughs in locomotor activity in spring and autumn might be due to the general enhanced activity during these more active seasons. The cats primarily show two peaks and two troughs of activity and food intake during the day, which is in agreement with the findings for 5 years-old cats in our previous study (Parker et al., 2019). These observations are consistent with earlier studies demonstrating similar bimodal activity patterns. The cats displayed lows near midday and peaks around dawn and dusk during the warm seasons of the year (Jones & Coman, 1982; Goszczyński et al., 2009) or in areas with warm, stable weather conditions year-round (Konecny, 1987). Bimodality therefore constitutes another key characteristic of the daily rhythm of the cats.

As already observed in the literature (Thorne, 1982; Johnson et al., 1983; Randall et al., 1985; Refinetti et al., 2016), we encountered considerable interindividual variability during our study. For example, some cats showed less reaction to human presence, others showed higher sunset or sunrise activity and feeding peaks. Nevertheless, the activity and feeding patterns of the cats are more homogenous in the daily troughs, differing mainly at peak hours.

Conclusions

Although the results observed in domestic cats do not appear to be as striking as those reported in other seasonal mammals, we demonstrated that activity and feeding patterns are different according to the season, despite the absence of large fluctuations of seasonal temperature or humidity. First, this study allowed us to confirm the previous results of Parker et al. (2019) and provided evidence of the role of twilights on the feeding and activity patterns of the cats. Next, the annual changes of day length predominantly affected the shift of active time: peaks of locomotor activity and food consumption happened around sunrise and sunset, confirming the crepuscular rhythm of the species and other *Felidae*. Cat activity patterns, however, could also be modified by study conditions, such as timing of food provision and other care activities: food renewal and human interactions moments, not fluctuating seasonally, constituted factors enhancing activity and especially food intake. We thus detected both preservation of the crepuscular behavior of the species as well as reactivity to human activity, by being more active during the day. This again highlights the behavioral flexibility of the domestic cat. These findings suggest feline housing and nutrition strategies may need to be adapted to a seasonal basis in the domestic cat, to ensure that space and availability meet differing demand throughout the year. For example, adapting the energy value of *ad libitum* food given to cats according to the season would be pertinent, because of apparent lesser energetic needs in winter than during the other seasons. Indoor cat owners could also use these results to accommodate feeding times around sunrise and sunset. Future studies on cats should focus on the seasonal fluctuations in the amount and timing of feed-

ing and locomotor behaviors. In particular, they should not expect similar activity at sunrise and sunset compared to the rest of the day. Finally, caution should be used when generalizing the results of the present study to the general cat population. For instance, the individuals under study consisted of one male and five females and were not yet adults at the beginning of the observations. This excluded the possibility of any effects of sex and should be the subject of future studies.

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Conflict of interest

We confirm that there are no known conflicts of interest associated with this publication.

Authorship statement

The project was conceived by Marine Parker, Jessica Serra, Bertrand Deputte and Etienne Challet. The experiments were designed by Marine Parker and Jessica Serra. Marine Parker and Brunilde Ract-Madoux performed the experiments. The data were analysed by Marine Parker and Marie Faustin and Marine Parker wrote the paper. This study has been funded by Royal Canin.

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