ETHOLOGY AND BIOLOGICAL RHYTHMS OF THE CAT

Marine Parker

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Marine PARKER

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ETHOLOGIE ET RYTHMES BIOLOGIQUES DU CHAT

THÈSE dirigée par :

Dr Etienne CHALLET	INCI, Université de Strasbourg

RAPPORTEURS :

Pr Heiko RÖDEL	LEEC, Université Paris 13, Villetaneuse
Pr Caroline GILBERT	Ecole Nationale Vétérinaire d'Alfort, Maison-Alfort

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AUTRES MEMBRES DU JURY :

Pr Bertrand DEPUTTE	Ecole Nationale Vétérinaire d'Alfort (co-encadrant), Maison-Alfort
Dr Jessica SERRA	Mars Petcare Research centre (co-encadrante), Aimargues
Dr Valérie SIMONNEAUX	INCI, Université de Strasbourg (examinatrice interne)

A Bonne-maman

« Le chat est un animal fascinant.

Il pose des défis à tous les concepts. »

Pr Bertrand Deputte

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Une thèse de doctorat est un long et tortueux chemin où les intempéries se succèdent mais ne se ressemblent pas. Heureusement, soutiens et coups de main apparaissent, de manière attendue ou inattendue. Sans eux, ce manuscrit n'aurait sans aucun doute jamais vu le jour. C'est pourquoi j'aimerais remercier tous ceux qui ont apporté leur étincelle !

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Les rythmes biologiques sont cruciaux pour les organismes vivants, leur permettant de programmer certains processus dans la fenêtre temporelle la plus appropriée. Entre autres, les rythmes circadiens, phylogénétiquement anciens et universels, ont une période proche de celle de la rotation terrestre (24 h). Chez les Mammifères, ils dépendent d’oscillations endogènes contrôlées par une horloge interne principale située dans le noyau suprachiasmatique de l’hypothalamus. Pour rester en phase avec l'environnement, la rythmicité circadienne doit être quotidiennement entraînée par des facteurs externes périodiques appelés *zeitgebers*, le cycle jour/nuit ayant été établi comme le plus puissant.

En tant que carnivore stricte, le chat domestique (*Felis catus)* est dépendant du rythme journalier de ses proies. Or, certaines de ses proies sont nocturnes, comme la plupart des rongeurs, alors que d’autres sont diurnes, comme de nombreux oiseaux. Cette variabilité a probablement conduit à une flexibilité dans le comportement alimentaire du chat qui rend difficile la caractérisation du rythme journalier associé, la plupart des scientifiques le qualifiant d’aléatoire. Concernant son rythme locomoteur, le chat a souvent été décrit comme nocturne dans la littérature scientifique, comme une majorité de petits mammifères. Pourtant, certaines études ont indiqué une activité diurne supérieure à l’activité nocturne de l’animal, et ont suggéré que l’activité accrue en journée des humains en était responsable.

A vrai dire, une dichotomie diurne-nocturne ne s’applique pas à toutes les espèces et cette ambiguïté chez le chat pourrait simplement résulter de la faculté de l’animal à adopter différents patterns d’activité dans différentes conditions D’ailleurs, une grande variabilité interindividuelle de chronotypes a été observée chez le chat dans plusieurs études. Cependant, un rythme d’activité crépusculaire (i.e. pics majeurs à l’aube et au crépuscule) et bimodal, retrouvé aussi chez l’ancêtre du chat domestique, est très souvent retrouvé chez les individus étudiés. Ces deux caractéristiques semblent donc le mieux définir le rythme journalier de l’espèce.

La plasticité comportementale du chat se remarque aussi dans les variations de son rythme journalier selon la saison ou selon l’habitat des individus. Bien qu’une augmentation de l’activité ait pu être observée durant les saisons chaudes comparées aux saisons froides, peu d’études se sont penchées sur l’effet des saisons sur les habitudes locomotrices ainsi qu’alimentaires du chat. Ces données pourraient pourtant nous renseigner sur l’influence de la durée du jour (photopériode) sur le comportement journalier des animaux. De plus, leur mode de vie diffère selon leur milieu de vie, de nombreux facteurs (notamment : espace disponible, conditions alimentaires, conditions météorologiques, opportunités d'activité, taille de la population) pouvant impacter leurs comportements.

Une façon d'élargir nos connaissances sur le comportement général des chats serait de les étudier à différentes saisons et dans les différentes conditions environnementales dans lesquelles ils peuvent être trouvés. Pour cette raison, les études de cette thèse ont été menées durant les quatre saisons et sur deux populations d'individus. L'une a vécu en intérieur dans la chatterie de Royal Canin (Gard), l'autre en extérieur dans un enclos du refuge Aide aux Vieux Animaux (Normandie). Cette thèse visait à caractériser et comparer les rythmes d'activité locomotrice et d'alimentation chez les chats d'intérieur et d'extérieur, et à évaluer l'impact des saisons sur ces variables grâce à des techniques télémétriques avancées (technologie UWB, identification par radiofréquence individuelle et pesage automatique des aliments).

RESULTATS PRINCIPAUX

1^er^ article : Rythmes journaliers de la prise alimentaire et de l'activité locomotrice chez des chats domestiques vivant en colonie

Le protocole d'étude de cet article a été conçu afin de valider notre technique d'enregistrement du comportement félin à des vues d'analyses chronobiologiques, la technologie ayant été validée pour l'étude du comportement locomoteur des chats dans l'article paru en 2017 (Parker et al.).

Deux groupes de huit et six chats, stérilisés (sept femelles et sept mâles) et de pure race (Chartreux et British shorthair) nés en 2010 ont été suivis en continu pendant sept jours. Les groupes ont été hébergés chacun leur tour dans un panel de 29 m² sous conditions ambiantes contrôlées à la chatterie de Royal Canin située dans le sud de la France (Aimargues) et exposés à la lumière naturelle via des baies vitrées. Les chats ont eu un accès *ad libitum* aux croquettes (Fit32, Royal Canin) et à l'eau. Deux dispositifs électroniques (tags) étaient attachés au collier de chaque individu, l'un pour le suivi de leur activité locomotrice (technologie UWB) nous fournissant en continu la distance parcourue de chaque chat toutes les 10 minutes, le second pour le suivi de leurs habitudes alimentaires (RFID passive et balances électroniques) nous fournissant en continu le moment et la quantité des croquettes consommées.

La distance parcourue et la consommation alimentaire par jour ont été analysées et comparées, ainsi que cinq paramètres rythmiques pour chaque variable (alimentaire et locomotrice) : la période du rythme (durée d'un cycle entier), son amplitude (une mesure de la robustesse de la rythmicité), sa stabilité inter-jours (IS, quantifie l'invariabilité entre les jours successifs), les cinq heures les moins actives de la journée (L5, les cinq heures continues durant lesquelles l'activité locomotrice ou la consommation de nourriture est la plus faible) et le mode du rythme (un rythme bimodal étant défini à l'aide du périodogramme par une amplitude du pic à 12 heures supérieure ou égale à la moitié du pic à 24 heures).

Tous les chats avaient un rythme locomoteur de 24 h, tandis que 11 individus sur 14 avaient un rythme alimentaire de 24 h, les trois restants étant arythmiques. Douze chats pour le rythme locomoteur, et sept pour le rythme alimentaire ont montré un rythme bimodal.

Les chats ont présenté deux pics principaux d'activité et de prise alimentaire : le matin, surtout durant les heures précédant le lever du soleil et le renouvellement de nourriture, et le soir, principalement après le départ du personnel animalier et précédant le coucher du soleil. On retrouve une baisse significative d'activité et de prise alimentaire au milieu de la journée et de la nuit.

Les mâles, plus lourds que les femelles, ont eu tendance à parcourir plus de distance que les femelles et mangeaient davantage. Leur rythme locomoteur était plus robuste que celui des femelles, et les individus arythmiques dans leur comportement alimentaire étaient tous des femelles.

Nous avons catégorisé les chats en fonction de leur chronotype dominant, nocturne ou diurne, en se basant sur les caractéristiques des actogrammes, les valeurs de L5 et les taux d'activité/consommation nocturnes et diurnes. Les pics d'activité et de consommation des individus catégorisés comme nocturnes étaient significativement plus élevés que ceux des individus catégorisés comme diurnes, mais les creux journaliers ne différaient pas significativement selon le chronotype.

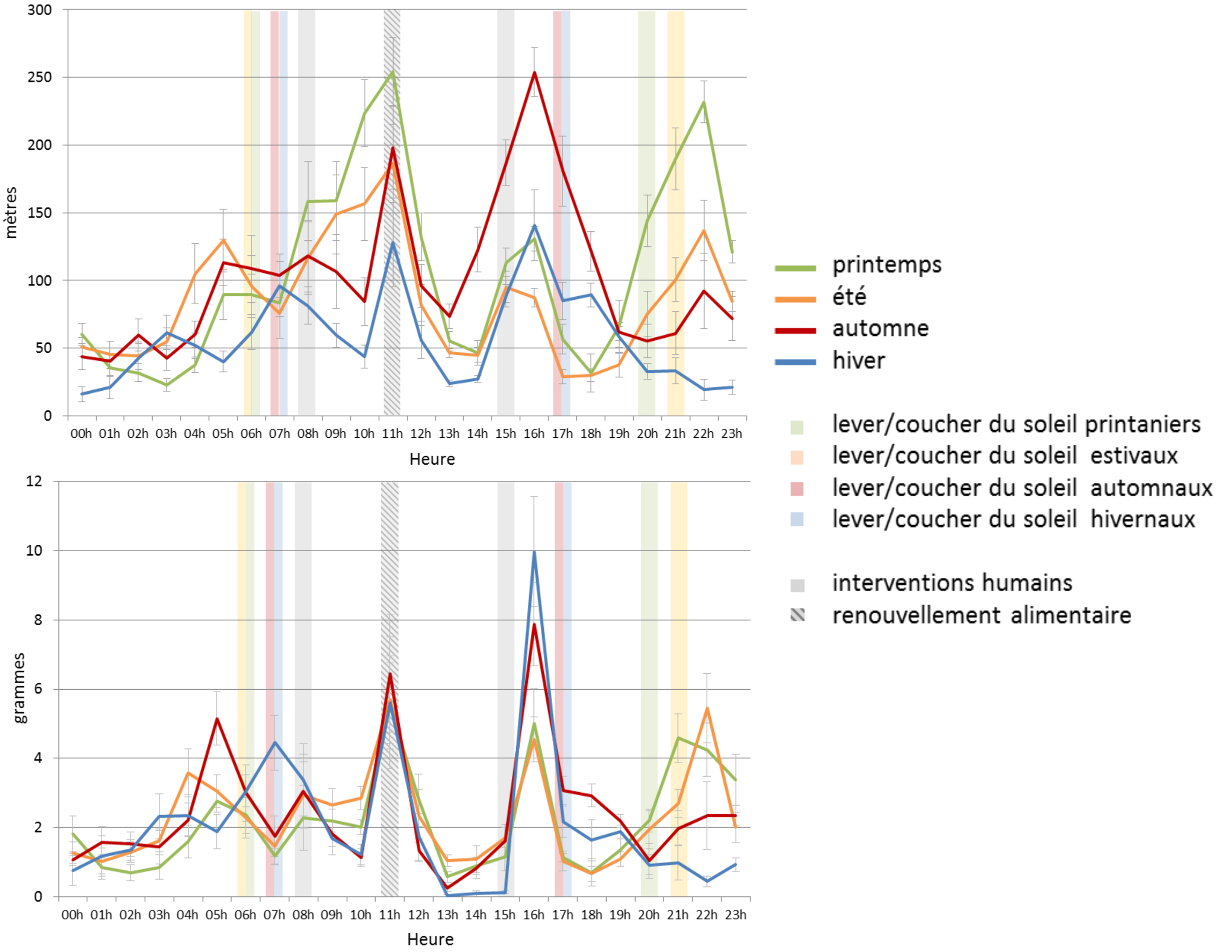
Nous en avons conclu que la bimodalité, plus que le chronotype des individus, définit leurs rythmes locomoteur et alimentaire, caractérisés par des pics crépusculaires. L'impact du lever et coucher du soleil apparaît donc décisif dans le comportement journalier des chats.

Afin d'étudier cet effet ainsi que le rythme journalier du chat sur une base annuelle, nous avons poursuivi par une deuxième étude sur une seconde population de chats d'intérieur vivant dans la même chatterie au cours des quatre saisons.

2nd article : Impact saisonnier sur les rythmes locomoteur et alimentaire de chats d'intérieur

Cette fois, un groupe de six chats, stérilisés (un mâle et cinq femelles) et de pures races variées (Exotic shorthair, American shorthair, Selkirk rex et Selkirk straight shorthair) nés en 2015, a été suivi en continu et simultanément chaque saison pendant 21 jours. Les mêmes conditions alimentaire et d'hébergement que lors de l'étude précédente ont été appliquées. La nourriture a été renouvelée tous les jours à 9h et le personnel animalier entrait de manière standardisée trois fois par jour pour nettoyer la salle, s'assurer du bon état des lieux, du matériel et des animaux et interagir avec eux. Les chats étaient exposés à la lumière naturelle à travers de grandes baies vitrées. La durée moyenne du jour était de 14h21 au printemps, 14h56 en été, 09h51 en automne et 09h56 en hiver.

Tous les individus ont consommé et se sont déplacés avec une cyclicité de 24 heures à chaque saison. L'arythmie observée dans notre étude précédente était probablement due à la plus courte période d'enregistrement comparée à celle-ci. Quotidiennement, ce groupe de chats a été le moins actif en hiver (1.38 ± 0.17 km), le plus au printemps (2.56± 0.17 km) et a consommé le moins de croquettes en hiver (50.2 ± 4.1 g).



Distance parcourue (m, haut) et consommation alimentaire (g, bas) moyennes à chaque heure selon la saison.

Quelle que soit la saison, les chats bougeaient et consommaient davantage lorsque les humains étaient présents dans le panel, surtout lorsque les humains interagissaient avec eux. On a retrouvé des pics d'activité en anticipation du lever du soleil ainsi que suivant son coucher, malgré le décalage de ces moments selon la saison. Ces résultats démontrent un impact des variations lumineuses saisonnières sur le comportement des individus. Leur comportement alimentaire était cependant moins impacté par ces variations lumineuses que leur comportement locomoteur. Comme retrouvé lors de l'étude précédente, les chats étaient le moins actifs et consommaient le moins au milieu de la nuit et au milieu de la journée. Nous avons donc retrouvé un rythme bimodal chez cette nouvelle population, indépendamment des variations saisonnières.

En comparant les taux d'activité locomotrice et de consommation alimentaire selon la période lumineuse (jour vs nuit), on s'aperçoit que ces chats étaient très majoritairement plus actifs le jour que la nuit, possiblement à cause des pics associés dus aux interventions humaines diurnes.

Le rythme alimentaire des chats étudiés est devenu de plus en plus robuste avec le temps, suggérant le développement d'une routine alimentaire chez ces individus d'un jeune âge au début de l'étude. Leur comportement locomoteur était le plus rythmique au printemps, le moins en automne. Nous estimons que la plus courte durée d'enregistrement de ce comportement en automne, due à des soucis techniques, en est responsable. Le rythme locomoteur des chats était significativement plus stable et robuste que leur rythme alimentaire, quelle que soit la saison.

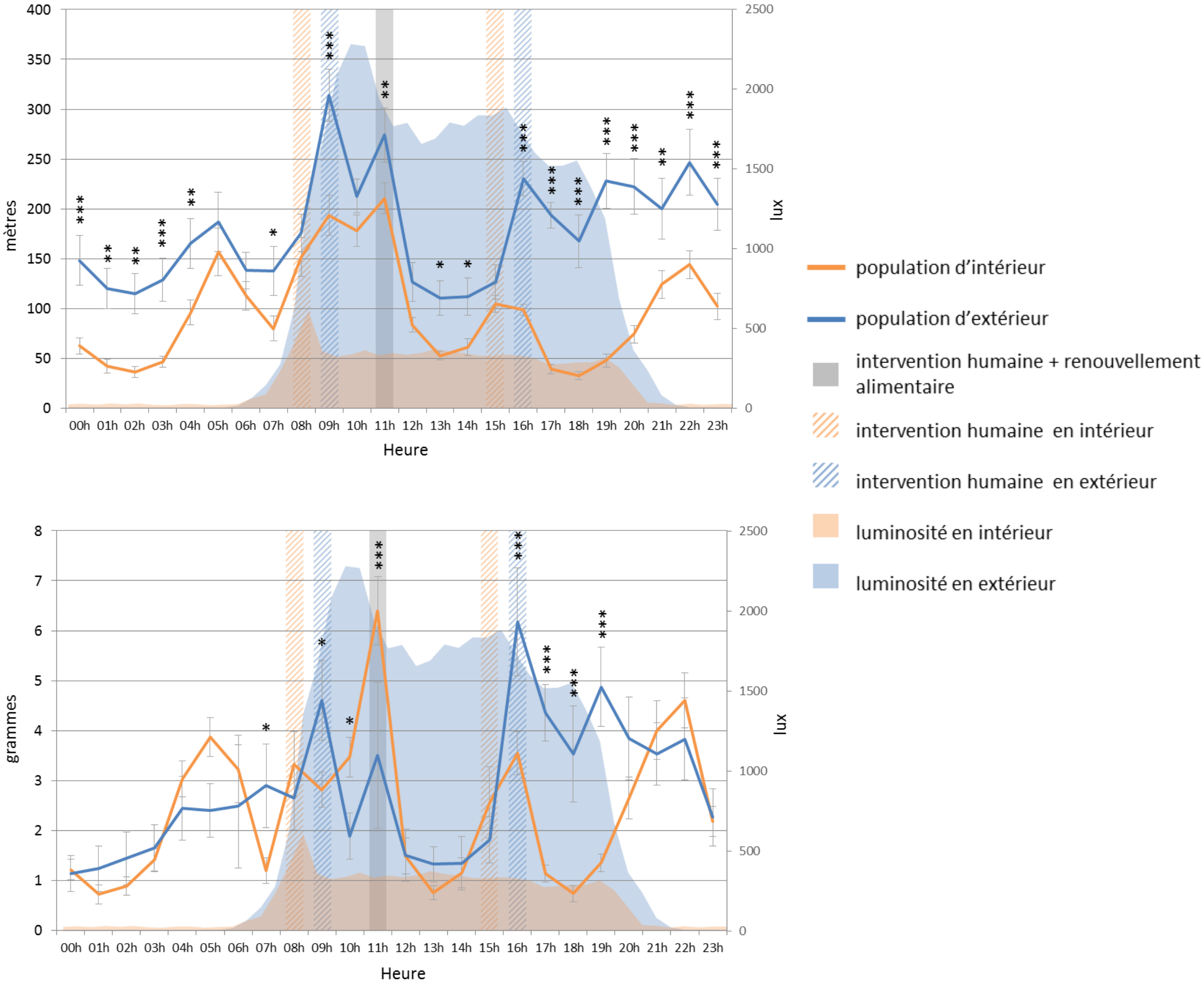
Cette étude a démontré une nouvelle fois que la lumière du jour est un *zeitgeber* majeur chez les chats en soulignant son impact dans des conditions de température et d'humidité constantes au fil des saisons.

Pour notre étude suivante, nous nous sommes penchés sur l'impact des signaux environnementaux sur l'activité locomotrice et la consommation alimentaire des chats, en conduisant la même étude simultanément en été chez des groupes de chats vivant en intérieur ou en extérieur.

3ème article : Comparaison des rythmes d'alimentation et locomoteur entre chats d'intérieur et chats d'extérieurs vivant en captivité

Nous avons comparé le comportement de 15 chats d'intérieur (neuf femelles et six mâles), vivant dans les mêmes conditions que précédemment, avec huit chats vivant en extérieur dans un groupe de 27 individus. Comme dans les conditions d'étude des chats d'intérieur, les individus d'extérieur ont été suivis en continu pendant 21 jours et recevaient croquettes et eau *ad libitum*. Nous sommes entrés dans l'enclos de manière standardisée trois fois par jour pour renouveler la nourriture et l'eau, nous assurer du bien-être des chats, de l'état de l'enclos et des technologies de suivi. Les chats d'extérieur provenaient cette fois d'origines variées (venant de la rue, trouvés ou placés par des propriétaires), âgés entre 2 et 11 ans, hébergés dans un enclos à ciel ouvert d'environ 1145 m² au refuge AVA (Cuy-Saint-Fiacre, France) et donc exposés aux variations journalières de luminosité, température et humidité ambiantes.

Quotidiennement, les chats du refuge parcouraient plus de distance et consommaient davantage de croquettes que ceux vivant en chatterie (4.29 ± 0.27 km et 67.4 ± 2.6 g versus 2.33 ± 0.17 km et 57.7 ± 2.9 g, respectivement). Nous avons observé que les chats d'extérieur étaient plus actifs que ceux d'intérieur surtout le soir et la nuit. Cela pourrait représenter une préservation du comportement d'exploration nocturne lorsque les chats vivent dans un environnement extérieur. D'ailleurs, l’augmentation de leur consommation alimentaire survenait surtout durant le jour (en particulier, en fin d’après-midi).



Distance parcourue (m, haut), consommation alimentaire (g, bas) et luminosité (lux) moyennes à chaque heure selon l’habitat. * : p < .05, ** : p < .01, *** : p < .001 (différences significatives entre les deux sites à une heure donnée)

Que ce soit en extérieur ou en intérieur, tous les chats présentaient une périodicité de 24 h dans leur rythme locomoteur. Par contre, les chats d’intérieur étaient plus rythmiques que les chats d’extérieur : l’amplitude et la stabilité de leurs rythmes locomoteur et alimentaire étaient supérieures. De plus, parmi les chats d’extérieur, trois individus sur huit avaient un comportement alimentaire arythmique.

Une nouvelle fois, plusieurs chats ont montré une bimodalité dans leurs rythmes et leur comportement locomoteur était systématiquement plus rythmé que leur comportement alimentaire. Les chats présentaient encore des pics d’activité et de consommation lorsque les humains interagissaient avec eux, surtout en intérieur, ainsi que pendant les périodes précédant le lever du soleil et suivant son coucher. Dans les deux populations, nous avons retrouvé des creux d’activité au milieu de la journée et de la nuit.

Cette dernière étude a démontré des différences de comportement selon l'habitat des individus. L'activité locomotrice (surtout la nuit) et la consommation alimentaire des chats étaient plus importantes et leurs rythmes respectifs étaient moins soutenus en extérieur, milieu dans lequel l'espace disponible et les perturbateurs de rythme étaient supérieurs. Nous avons cependant aussi trouvé des similarités entre les deux populations, comme l'impact humain et l'influence des lever et coucher du soleil sur leur comportement. Ces derniers résultats suggèrent que les variations quotidiennes lumineuses, davantage que les variations d'humidité ou de température ambiantes, jouent un rôle majeur dans les comportements rythmiques du chat domestique.

CONCLUSIONS

Au cours de cette thèse, nous avons cherché à caractériser les rythmes locomoteur et alimentaire quotidiens du chat dans différentes conditions (à chaque saison, en extérieur et en intérieur), afin de clarifier les résultats hétérogènes sur son comportement dans la littérature scientifique.

Nos principales constatations démontrent clairement que les chats suivent une périodicité de 24 heures, indiquant que la photopériode est un facteur déterminant dans leur comportement. Ceci a été confirmé par des changements saisonniers dans l'activité locomotrice et la prise alimentaire, ainsi que dans les variations quotidiennes correspondantes, chez les chats d'intérieur recevant les fluctuations saisonnières uniquement de la lumière du jour. Cela ne signifie pas pour autant qu'ils adoptent des schémas nocturnes ou diurnes clairement distincts. D'ailleurs, cette thèse a mis en évidence l'absence d'un chronotype binaire pour le chat. Néanmoins, les interventions humaines ont eu un impact sur le rythme journalier des individus. En particulier, leurs horaires diurnes semblent responsables de l'augmentation de l'activité et de la consommation alimentaire des chats le jour plutôt que la nuit dans nos études.

Comme attendu, les chats ont montré une certaine multimodalité dans leurs habitudes quotidiennes : nous avons démontré que la meilleure façon de caractériser les rythmes d'activité et alimentaire de l'espèce repose sur des modèles bimodaux et crépusculaires. En effet, que ce soit à l'extérieur ou à l'intérieur, des pics majeurs de prise alimentaire et d'activité locomotrice sont systématiquement présents à l'aube et au crépuscule, en dehors de toute influence humaine. De plus, des creux ont été détectés deux fois dans la journée, au milieu de la nuit et du jour, ce qui corrobore la littérature scientifique à ce sujet. Ce comportement a été exprimé chez des individus nourris *ad libitum* alors que la nature crépusculaire du chat domestique est présumée résulter d'une adaptation aux rythmes de vie de ses proies diurnes et nocturnes à l'état sauvage. Cette rythmicité, qui s'est déplacée en fonction de l'heure du crépuscule à chaque saison, semble donc intrinsèque à l'espèce et s'être maintenue en dépit de la domestication.

Par ailleurs, le rythme alimentaire des chats est plus variable que leur rythme locomoteur, rappelant le caractère opportuniste de ce chasseur. Aussi, la plasticité comportementale de l'espèce a été confirmée. Par exemple, les chats se sont adaptés différemment à leurs conditions d’hébergement. En extérieur, les facteurs environnementaux ont entraîné des rythmes quotidiens plus faibles en amplitude et un comportement exploratoire nocturne, comparativement aux conditions d’intérieur dans lesquelles les chats étaient plus sujets à la routine.

En conclusion, les chats domestiques expriment une grande souplesse dans leur comportement journalier. Malgré la domestication, ils restent adaptés à la vie en plein air avec la préservation de leurs traits ancestraux de prédateurs, comme en témoignent les pics d'activité crépusculaires qui apparaissent dans des conditions intérieures contrôlées. Ils s'adaptent aussi à la vie en intérieur, en faisant preuve de tolérance et d’adaptabilité aux différentes conditions d’hébergement et en intégrant la proximité humaine dans leur vie de tous les jours. Ceci peut expliquer la multiplicité et la durabilité des populations de ces félins sur Terre, allant des chats de compagnie vivant en appartement aux chats sauvages errant sur des hectares de nature.

INTRODUCTION

BIOLOGICAL RHYTHMS

Rhythms are crucial for living organisms. Among others, the circadian rhythm, based on the day/night cycle, is ancient and universal.

From the short cellular events to long seasonal changes, biological rhythms are crucial for living organisms as they help them to schedule certain processes within the temporal window that is most suitable. In order to adapt to their cyclic environment and effectively react to the competing demands of life, species need their activities (e.g. feeding, sleeping and moving) to be temporally adjusted in order to occur at optimal times of the day or the year (Sharma, 2003).

Day–night cycles caused by the rotation of the Earth around its axis highly influence living organisms. As the simple response to the daily light/dark cycle is not enough to time metabolic processes anew each day, many organisms have evolved endogenous biological clocks. This is why rhythms displaying oscillations of a period of about 24 hours are observed in numerous behaviour and physiological functions. They are phylogenetically very ancient, as supposed by their detection in cyanobacteria where a circadian clock helps in their photosynthesis (Johnson et al., 1996; Johnson & Golden, 1999). Some fossil evidence suggests that daily rhythms were already present 400 million years ago (Kahn & Pompea, 1978; Wells, 1963), while the gene analyses in cyanobacteria indicate endogenous circadian clocks have existed since 3500 to 3800 million years ago (Dvornyk et al., 2003). This rhythmicity is universal, described in a great variety of other organisms such as fungi (Loros & Dunlap, 2001; Merrow et al., 2001), insects (Williams & Sehgal, 2001), mammals (Reppert & Weaver, 2001) and also plants (Alabadi et al., 2001). These rhythms were called circadian rhythms (Halberg, 1960) to emphasise their period duration (from latin *circa* meaning "around" and *dies* meaning "day"). They are based upon endogenous self-sustained oscillations controlled by an internal master clock located in the hypothalamic suprachiasmatic nucleus (SCN) in mammals (see Golombek & Rosenstein, 2010). This has been proven by the unambiguous detection of free-running circadian periods in animals kept in constant environmental conditions, i.e. in periods of constant darkness or constant light (**fig. 1**). However, in order to keep synchrony with the environment, circadian rhythmicity needs to be daily entrained by periodic external factors called *zeitgebers* (i.e. time givers; **fig. 2**). The light/dark cycle has been established as the most dominant one, as light signals perceived by the retina are sent to the SCN clock via direct retino-hypothalamic projections. Daily scheduled feeding can also play the role of a *zeitgeber* in some animals, through food-anticipatory activity (Mistlberger, 1994).

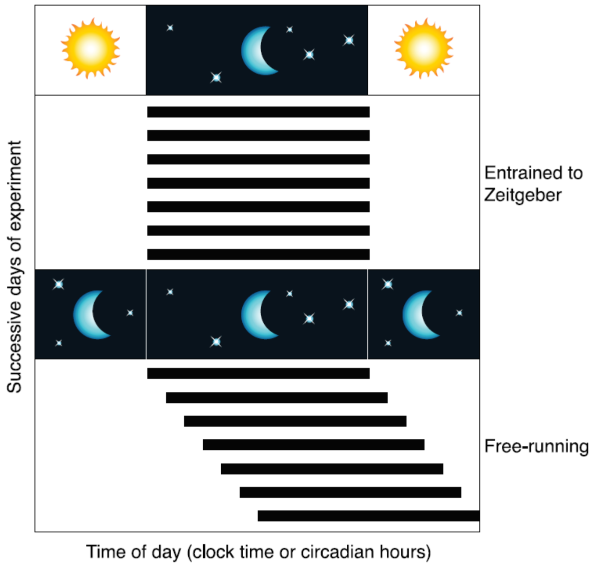


Figure 1: Entrainment of a circadian rhythm to light. The actogram represents daily rhythm of locomotor activity initially entrained to a 24-h light-dark cycle. Upon transfer to constant dark conditions (represented by the black bar in the center of the actogram), circadian rhythms resume with their endogenous period (from Golombek & Rosenstein, 2010).

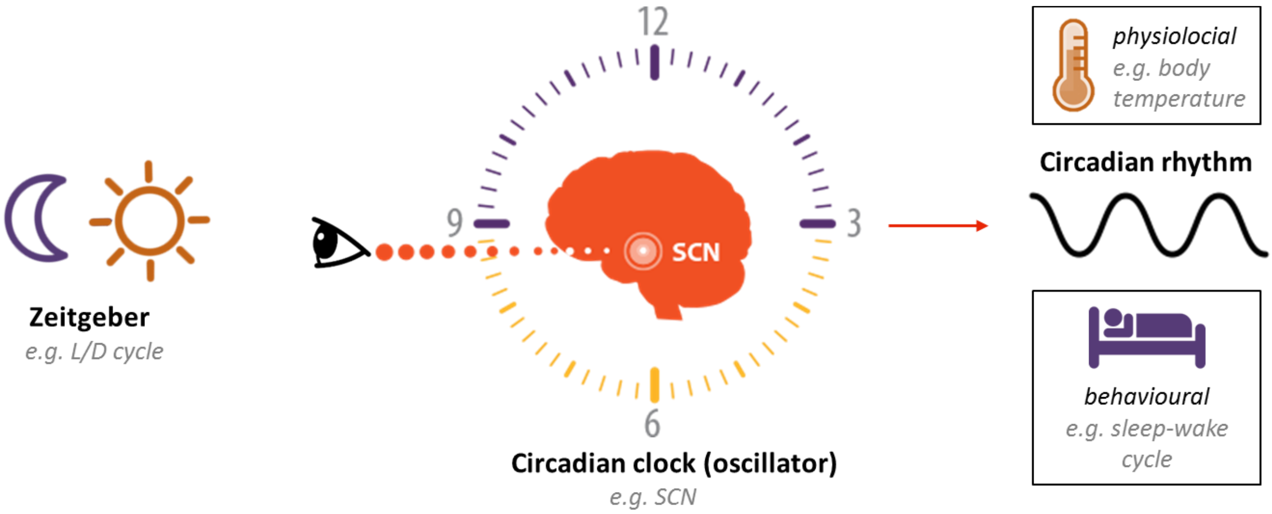


Figure 2: Simplified scheme of the circadian system, a linear model which includes the environmental entrainment agent (zeitgeber), an endogenous oscillator (SCN), and the output that governs physiological or behavioural rhythms.

In animals, rhythms make it possible to adapt to their cyclic environment.

Animals need rhythmicity in order to adapt to their changing environment. For instance, the behaviour of littoral species subjected to periodicity of tides and the migration or reproduction periods in species subjected to seasonal variations need to occur at specific times. Rhythms can also be related to energetic economy, as phases of rest during the day enable animals to digest and recover from phases of activity during which they have hunted or foraged.

Some depend on circannual rhythms, usually synchronised by the seasonal changes in photoperiod, such that an optimal adjustment to the annual environmental cycle is guaranteed. Where photoperiod fluctuations are less contrasted, such as in equatorial environments, birds use seasonal changes in daytime light intensity as a *zeitgeber* to adjust their migration (Gwinner, 2003). Endogenous circannual rhythmicity can also generate reproductive activity and moulting in ungulates (Lincoln, 2003) and target a hibernation-specific protein in chipmunks (*Tamias sibiricus*, Kondo et al. 2006).

Circadian rhythmicity is of importance in the synchronisation of daily behaviours and it is not surprising that it has been observed in perhaps all animal species, enabling them to “show oscillations which approximately match the natural frequency of Earth rotation” (Aschoff, 1966). In mammals, physiological aspects such as sleep (Mistlberger 2005) and body temperature (Refinetti & Menaker 1992) are regulated by the SCN clock. However, this regulation also affects behavioural aspects such as general activity (Carpenter, 1985).

Preys and predators are flexible towards the daily rhythms of each other.

This cyclicity can for instance allow individuals to model their activities on those of their preys or predators, in order to better survive (Kavanau, 1971). Indeed, while it is considered that cyclic environmental stimuli such as daylight, ambient temperature and humidity were the first to give rise to circadian clocks, the rhythmic activity of preys and predators also participate in this selection. For instance, preys have been reported to adjust their sleeping behaviour to lower the risk of predation (Acerbi & Nunn, 2011) and nocturnal Norway rats (*Rattus norvegicus*) with minimal daily disturbers at a midden at the University Farm, Wytham (UK) timed their activity diurnally to avoid predation from red foxes (*Vulpes vulpes;* Fenn & MacDonald, 1995). Predators are expected to also adapt their behavioural rhythms to the rhythms of their preys.

DAILY RHYTHM AND FEEDING BEHAVIOUR OF THE CAT

The cat feeds on several types of prey/makes several meals a day.

The domestic cat (*Felis catus*) spends 1 to 3% (15-45 min per day) of its active time feeding (Eckstein & Hart, 2000; Panaman, 1981). In the wild, it is an opportunistic solitary hunter, like many of its fellow felids (Kleiman & Eisenberg, 1973; Rochlitz, 1999; Crowell-Davis et al., 2004). This selective carnivore, as shown by its large canines to sever the neck of their preys and carnassials to shear flesh from bone (Van Valkenburgh, 1989), is able to accommodate the trophic changes it meets and to favour a prey according to its abundance (Weber & Dailly, 1998). Being an obligate carnivore (contrary to dogs), in the wild, the cat is particularly dependent on the availability of its preys (Bradshaw et al., 1996). Its choice in food is constrained by the loss of certain key metabolic enzymes in the common ancestor of the cat family species (Bradshaw, 2006). In the wild, its resulting narrowed nutritional requirements are filled by a diet largely consisting of vertebrate prey such as rodents, rabbits, amphibians, birds, reptiles and fish.

To sustain its needs and due to its small size, the cat has to catch numerous small preys per day, this pattern of small meals not being due to any physical limitations of gut content volume (Bradshaw, 2006; Thorne, 1982). In accordance with this feature, even when fed a free-feeding regime by humans, cats adopt a so-called “nibbling” pattern of food consumption, spontaneously eating several small meals per day (Houpt, 2011; Mugford & Thorne, 1980). They usually maintain an overall energy balance: their feeding pattern will consist in many small meals under *ad libitum* diets, but can change to infrequent large meals when food availability is more limited than in the wild (scarcer through time; Thorne, 1982). Studies on the feeding behaviour of cats do not agree on the characterisation of a given meal. It is alternatively defined as a period of eating with a minimum inter-meal interval of 3 min (Kane et al., 1987), 5 min (Mugford & Thorne, 1980), 10 min (Kanarek, 1975), more than three consecutive readings recording a decrease in food weight finished by 10 consecutive readings without any weight loss (Peachey & Harper, 2002) or even visits of the feeding stations with eating recordings (Wichert et al., 2012). According to this literature, cats eat 7 to 19 small meals per day (Kanarek, 1975; Kanarek, 1975; Kane et al., 1981, 1987; Mugford & Thorne, 1980; Peachy & Harper, 2002; Wichert et al., 2012) throughout the 24h period (Bradshaw & Thorne, 1992; Kane et al., 1981; Mugford, 1977; Mugford & Thorne, 1980; Peachey & Harper, 2002; Thorne, 1982; **fig. 3**), likely reflecting a daily pattern of multiple small prey kills in their ancestor, the solitary territorial predator.

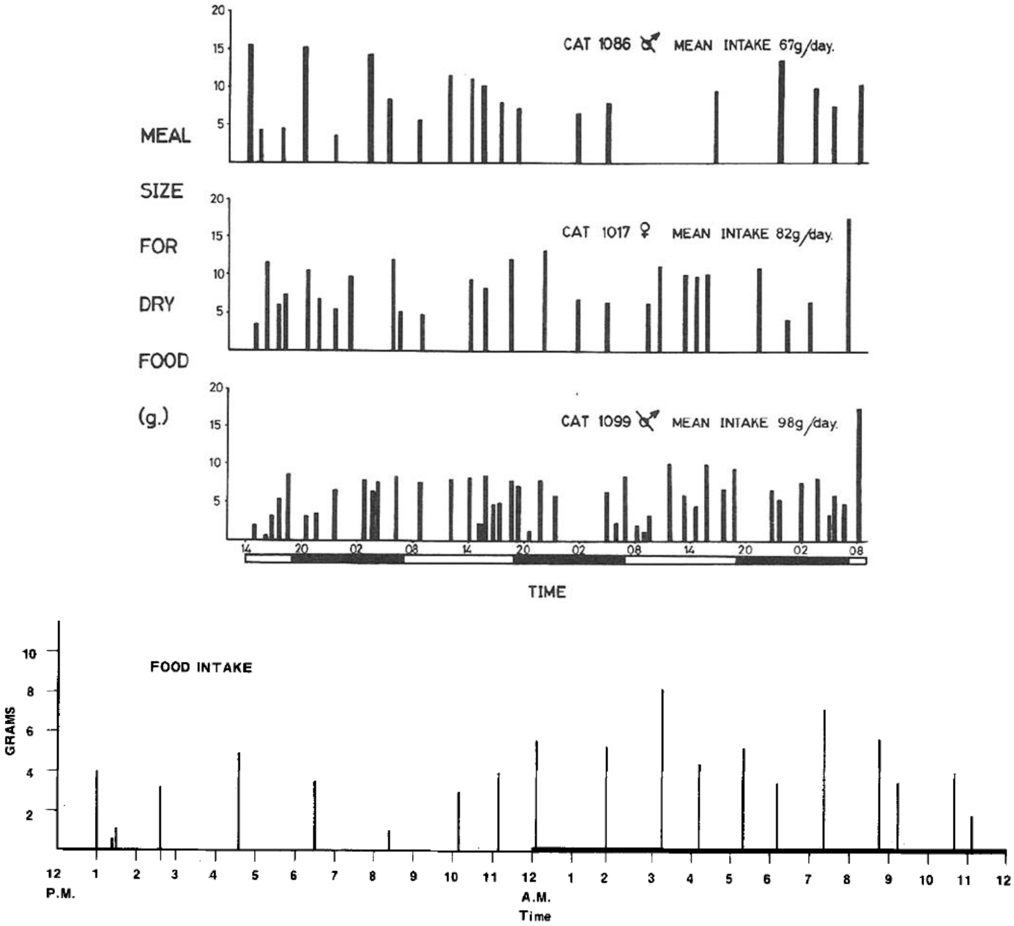


Figure 3: Feeding patterns of three cats (from Mugford & Thorne, 1980, top) and one cat (from Kane et al., 1981, bottom) on a dry diet

The feeding behaviour of cats is unique in regard to circadian rhythm, cats being stochastic feeders (Becques et al., 2014). For most authors cited above, the feeding pattern of the cat is entirely random. Other findings diverge on the subject. For instance, some observed a predominantly nocturnal feeding pattern in two isolated laboratory cats (Kanarek, 1975) or frequent meals between 8:00 and 9:00 in group housed cats in addition to a period of general high activity (Podberscek et al., 1991). Others noticed that some young individually housed cats almost stopped eating between 15:00 and 17:00, perhaps due to a decrease in activity, not measured in this study, but observed at that time of the day by Peachey & Harper (2002). On her part, Izawa (1983) found peaks of feeding coincided with the locomotor activity peaks of the cats, i.e. at dusk. However, this may be a result of the food condition of the feral cats which mainly fed on fishery waste casted at dusk. In laboratory conditions, total darkness, an unnatural environment for cats, was reported to reduce food intake (Randall et al., 1985).

Most authors point out a large variability between individuals in their feeding behaviour (Johnson et al., 1983; Kane et al., 1981; Mugford, 1977; Mugford & Thorne, 1980; Randall et al., 1985; Thorne, 1982). This may come from the flexibility of the feeding habits this opportunistic hunter must display in the wild to adapt to the various daily living rhythms of its preys, as suggested by Konecny (1987). The cat can thus adjust its feeding pattern with respect to prey/food availability. In fact, Thorne (1982) surmises that the cat has a behavioural repertoire containing different patterns of feeding, each being used when appropriate. This hypothesis is supported by a shift from diurnal towards nocturnal distributions when artificial starlight was introduced in laboratory conditions (Randall et al., 1985). Also, some cats increased meal size and duration while maintaining their body weight when constraints were placed on food availability (Kanarek, 1975).

It seems that, based on available literature, no clear cyclicity has yet been discerned regarding feeding habits in cats so far. The adaptability in their behaviour is ideally suited to the life style of the species as an opportunistic feeder, enabling the animal to use food availability to the best advantage in terms of energy balance. Many of these factors may be ascribed to genetic influences, but there are idiosyncrasies of feeding behaviour whose origins remain unknown and complex, requiring further study.

Some try to categorise the cat as nocturnal or diurnal. Yet, as an opportunistic animal, its daily activity pattern is variable.

Recognised as the most potent cue for circadian entrainment in most organisms, the L/D cycle can lead to chronotype i.e. nocturnal or diurnal categorisation in individuals, light suppressing locomotor activity in some mammals (nocturnal species) but promoting it in others (diurnal species; Redlin, 2001). In most small mammals, including small felids, the wake period is nocturnal (Vickery & Bider 1981, Madison 1985, Getz 2009). From this perspective, the cat is often considered to be a nocturnal animal.

In fact, its activity pattern has been described with a tendency towards nocturnality in many studies and its visual system seems to indicate an adaptation to night-active life. Indeed, Walls (1942) described the *tapetum lucidum* in the anatomy of the eyes of the cat, a "mirror" behind the retina which reflects light back through the retina and thereby increases sensitivity in dim light. Besides this physiological evidence, most records indicated a tendency towards nocturnalism in laboratory cats isolated in circadian chambers for periods ranging from 3 to 10 months (Johnson et al., 1983). In another laboratory study, individually housed cats slept more during the light period (7:00 to 19:00) compared with the night period (Kuwabara et al., 1986). As for non-laboratory findings, some feral and farm (i.e. semi-dependent) cats were generally more active at night (**fig. 4,** Alterio & Moller, 1997; Jones & Coman, 1982; Macdonald & Apps, 1978) and night-time movements from shelters involved significantly greater distances than diurnal ones in Canberra (South-East of Australia, Barratt, 1997).

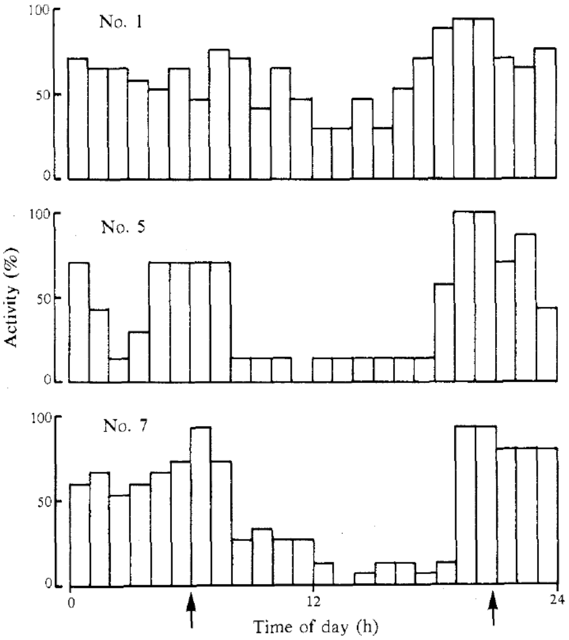


Figure 4: Daily activity patterns of three cats during the 1980-81 summer in the Hattah-Kulkyne study area, averaged over 15, 7 and 17 days respectively. Arrows indicate the times of sunrise (left) and sunset (right; reproduced from Jones et al. (1982) with permission from CSIRO Publishing)

Similarly, free-roaming cats intensified the use of open areas at night in villages situated in a Warsaw suburban zone (Romanowski, 1988). Also, nocturnal home ranges were significantly larger than diurnal ones in feral cats monitored on New Zealand farmland (Langham & Porter, 1991), the surroundings of rural and suburban areas in Korea (Moon et al., 2013) as well as in the previously mentioned suburban and farm cats in South-East of Australia (Barratt, 1997). A pilot study of Haspel & Calhoon (1993) revealed four times more activity between 22:00 and 07:00 than during midday hours in free-ranging cats in Brooklyn (USA). Finally, "unowned" cats (i. e. free-roaming and without human contact) on the outskirts of Champaign-Urbana (USA) were more nocturnal than "owned" cats (i.e. pets), possibly reflecting activity patterns of their usual preys (**fig. 5,** Horn et al., 2011).

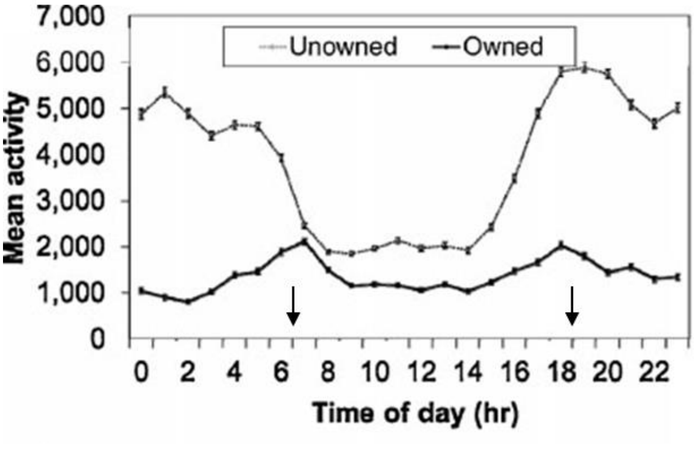


Figure 5: Diel patterns of activity by free-roaming "owned" and "unowned" cats in Illinois, USA, 2007–2008. Activity is represented as mean number ± SE of positional shifts recorded by activity sensors per 3-min interval per cat, by hour of the day. Arrows indicate the times of sunrise (left) and sunset (right; adapted from Horn et al., 2011)

Yet, Szymanski (as cited in Randall et al., 1985) defined an "almost unbroken rest period during the night hours". In the same lines, the total activity duration of a laboratory cat at daytime was about 1.4 times that of the activity at nighttime during a 12h light-dark cycle in a study (Hawking et al., 1971). Lower levels of activity at night than at day were also noted in dockyard cats in Portsmouth, UK (Dards, 1979). Be that as it may, human interventions or daily feeding conditions were often presumed to be responsible for this more diurnal behaviour (Dards, 1979; Hawking et al., 1971; Kappen et al., 2013; Kavanau, 1971), while Horn et al. (2011) consider the activity of cats living partly with their owners might reflect times when the latter are rising for or returning from work. Another group of cats, living in stronger symbiosis with owners, was most active during the photophase (daytime) than individuals having outdoor access more often and which exhibited the highest level of activity during the scotophase (nighttime, Piccione et al., 2013).

Besides, a simple diurnal-nocturnal dichotomy is not applicable to some species, as highlighted by Refinetti et al. (2007). Several mammals like the degu (*Octodon degus*), the golden spiny mouse (*Acomys russatus*), or the tayra (*Eira barbara*) and grison (*Galictis vittatus*) can spontaneously shift from diurnal to nocturnal activity patterns under particular environmental conditions (Kas & Edgar, 1999; Kavanau, 1971; Shkolnik, 1971; **fig. 6**). In fact, Aschoff (1962, as cited in Randall et al., 1987) rejected nocturnal versus diurnal labels because a same individual may exhibit different patterns on different occasions. In the cat, this ambiguity may therefore simply be due to the faculty of an individual to show various activity patterns at various times (Randall, et al., 1987). It could also result from the adaptability the species, a predator, must show regarding the variety of the living rhythms of its preys (Konecny, 1987): rodents are usually nocturnal while most song birds are diurnal. Some studies indeed observed either variability among the chronotypes of the different individuals (Horn et al., 2011; Panaman, 1981; Piccione et al., 2013; Randall et al., 1985) or shifts according to the season (Izawa, 1983). Also, Hawking et al. (1971) observed no clear cycle of body temperature in the cat. This feature distinguishes the species from pure nocturnal or diurnal ones for which the body temperature reaches its acrophase respectively during the night or during the day (Refinetti, 1996). This notion of chronotype ambiguity was also more recently confirmed by Refinetti et al. (2016) who studied the activity rhythm of 3 individually housed male cats exposed to 12 h: 12h L/D cycles for 10 days at the University of Messina (Italy). The authors emphasised the idea that the diurnal-nocturnal dichotomy should not apply to domestic cats, as their chronotype spread (measuring the variability of chronotypes among individuals) was the highest compared to 15 other species (ranging from Indian field mouse (*Mus booduga*) to cows (*Bos taurus*)), meaning some individuals are mostly active at day while others are mostly active at night. These reasons as well as the undecided literature let us wonder whether the nocturnal/diurnal distinction is applicable to cats, due to their behavioural plasticity.

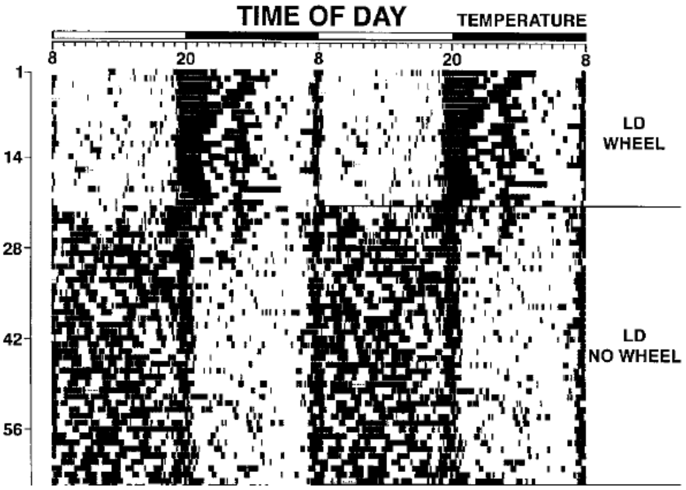


Figure 6: The inversion of phase preference as a function of running wheel availability in *Octodon degus*. The timing of mean and above mean body temperature is indicated by vertical tick marks. In this representative animal, wheel-running activity inverted the phase preference in LD 12:12 (adapted from Kas & Edgar, 1999)

Yet, some studies reported circadian activity rhythm in the cat.

Most of chronobiological studies are conducted on laboratory animals to enable proper assessment of circadian rhythmicity through the detection of free-running behaviours. In such laboratory conditions, the locomotor activity of the cat has sometimes been described as arrhythmic. First in 1971, many short bursts of activity, distributed irregularly throughout the 24h period, were described with no evidence of a daily cycle (Hawking et al., 1971). The authors mainly supported this by a lack of alteration in the activity of the cat by continuous darkness or continuous light. On the same year, Kavanau agreed in classifying the activity of the cat as arrhythmic. However, the very small sample size in both studies (n = 1) and short recording period (8 days in Hawking et al., 1971, 7 in Kavanau, 1971) make this conclusion doubtful. Later and during more convincing conditions, daily fluctuations in total sleep time (slow wave sleep + rapid eye movement sleep) and in brain temperature were detected (Kuwabara et al., 1986). A general periodicity in the occurrence of waking and sleeping patterns were also observed (Sterman et al., 1965). While the sleep-waking rhythm in cats seems ultradian (i.e. a rhythm with a period much shorter than 24h), the authors found that daily influences affect this rhythm such that longer waking periods occur during the night and longer sleep periods during the day. Other laboratory individuals showed free-running circadian rhythms in constant conditions, and entrained nocturnal patterns in most of the light-dark cycles (Johnson et al., 1983). Furthermore, in isolation from humans and human noises, some cats exhibited random patterns of activity in constant light, but free-running circadian rhythms in constant darkness as measured by infrared photobeams (Randall et al., 1985).

As evoked earlier, laboratory conditions are necessary to determine if a rhythm is truly circadian, as the environment can be tightly controlled. These conditions allow genetically determined patterns to be expressed in absence of ecological factors. Be that as it may, such unnatural conditions, including confinement in cages, can erase the influence of external factors determining natural patterns in animals. Besides, Randall et al. (1985) admitted discovering the problem of what the adequate *zeitgeber* is for this species in different light/dark (L/D) cycles. Nonetheless, genetic and ecological factors appear to be in conflict in some cases, and the activity pattern must result from these independent forces. From an ecological perspective, the cat, as a "highly adaptable and opportunistic species" (Kavanau, 1971), might be predicted to respond in ultradian cycles in a complex environment and exhibit less rigid relation to L/D transitions.

Being predators, cats must take the rhythm of their preys into account, which in addition can be diurnal or nocturnal. This leads to crepuscularity and bimodality in the daily rhythm of the cat.

Authors reported peaks of activity near times of sunrise and sunset in cats roaming freely in rural areas of central Poland (Goszczynski et al., 2009), on the outskirts of Champaign-Urbana (Illinois, USA, Horn et al., 2011), in The Hattah-Kulkyne National Park (South-eastern Australia, Jones & Coman, 1982, **fig. 4**), in the Galapagos Islands (Konecny, 1987), in Portsmouth Naval Dockyard (UK, Dards, 1979), or in Ainoshima Island (Japan, Izawa, 1983, **fig.7**).

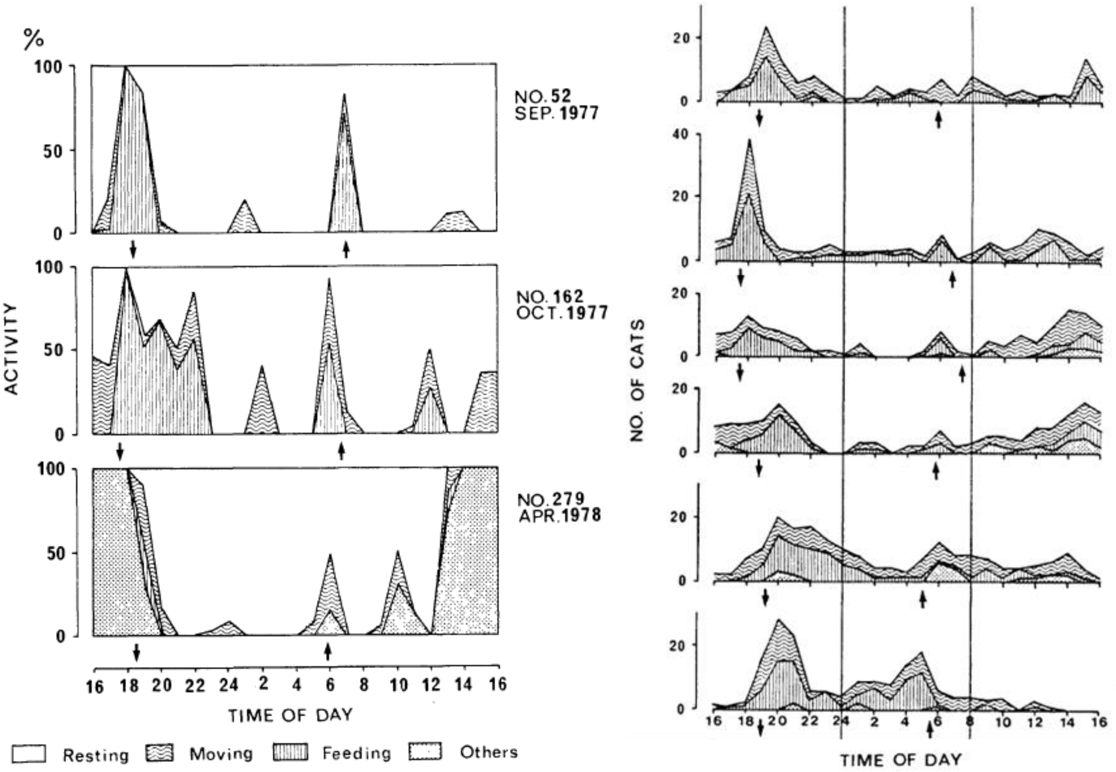


Figure 7: Activity pattern obtained from the focal-animal follows (left) and daily activity pattern obtained from censuses (right). Activity is expressed by percentage of time spent in behaviour of each category in an hour (left) or by the observed frequency of behaviours of each category (right). The arrows, up and down show the time of sunrise and sunset, respectively (adapted from Izawa, 1983)

The scientists sometimes characterised these specific moments as key periods in biological and ecological processes such as prey activity, feeding condition, body temperature, or colonic motility.

When twilight was artificial, enhanced activity was also observed near moments light was switched on or off (Kappen et al., 2013; Kavanau, 1971; Kuwabara et al., 1986; **fig. 8**). A similar activity can be found in the European wildcat (*Felis silvestris,* Guggisberg, 1975), suggesting these fundamental characteristics were inherited from the ancestors of the domestic cat and remained through domestication. Randall et al. (1987) acknowledged "if crepuscular fishes, birds or rodents provided a major dietary component in the evolutionary history of the cat, two peaks in the general physiology and behaviour might arise and be maintained as a temporal adaptation to the availability of prey". The role of the *tapetum lucidum* described by Walls (1942) may therefore be of use when luminosity is reduced at dawn and dusk and not necessarily result from pure nocturnalism.

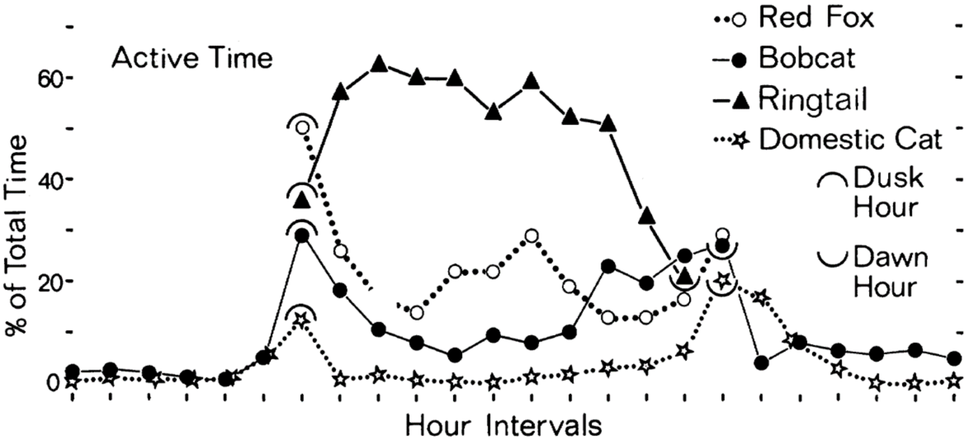


Figure 8: Plots of locomotor indices as a function of time of day for a red fox (*Vulpes vulpes*), a bobcat (*Felis rufus*), a ringtail (*Bassariscus astutus*) and a domestic cat (*Felis catus*) (adapted from Kavanau, 1971)

For a more general view of the daily pattern of the cat, studies have discussed the number of more global activity peaks in the day. Although some species show single or three and more peaks of activity in their daily pattern, a two-peaked activity is the most commonly observed rhythm (Aschoff, 1957, as cited in Aschoff, 1966) and has been detected in the cat (Refinetti et al., 2016). An activity pattern with two peaks in laboratory cats and a double-peaked density pattern in free-roaming individuals have also been evoked (Randall et al., 1987; Goszczyński et al., 2009). Others indicate the time of the daily diurnal activity trough: least activity and lowest observability near midday were recorded in free-roaming cats tracked only during day-hours (Konecny, 1987; Kunz & Todd, 1978; respectively). In another study, stretching behaviour, indicating the end of a resting period, occurred the most often between 15:00 and 16:00 in group housed cats (Podberscek et al., 1991). The authors put these findings in parallel with the occurring of a large amount of sleep from 09:00 to 15:00 in laboratory cats (Kuwabara et al., 1986).

As could be expected, dawn and dusk are designated as the main environmental factor playing a role in the two peaks of activity in the cat, whereas troughs were believed to respond to a decrease in ambient humidity or increase in ambient temperature (Aschoff, 1966; Konecny, 1987). Yet, these rhythm features were also observed in conditions where humidity and temperature were kept constant during the day (Podberscek et al., 1991; Randall et al., 1987). Aschoff (1966) concluded the environmental conditions do not produce the basic pattern anew each day but can still suppress or accentuate parts of it. Randall et al. (1987) consider bimodal activity pattern "may be the one factor that is common to the idiosyncratic patterns of entrainment in this species" and, to recall our previous suppositions, may have been selected to match the similar rhythms in crepuscular preys constituting major dietary component of the life history of the species.

VARIOUS POPULATIONS OF DOMESTIC CATS

The cat has been domesticated. Yet, today, populations range from feral to pet cats and from solitary life to group living.

The phylogeny and speciation of species in the *Felis* genus is still disputed today. In a recent study, one branch groups five taxa: the Chinese desert cat (*F. bieti*), the Central Asian wildcat (*F. ornata*), the southern African wildcat (*F. cafra*), the European wildcat (*F. silvestris*) and the North African/Near Eastern wildcat (*F. libyca*; O'Brien et al., 2008). The latter, *F. libyca*, is the closest taxon to the domestic cat of today, *F. catus*. In another phylogenetic study based on 1504 characters (karyologic, morphological, molecular), the « domestic cat » clade groups six species, *F. nigripes* (the black-footed cat), *F. chaus* (the jungle cat), then a new branch with *F. margarita* (the sand cat) and *F. silvestris* and finally the latest branching with *F. catus* and *F. libyca* (Mattern & McLennan, 2000). It seems that *F. libyca* is generally considered as the closest relative to the domestic cat today. The oldest remains, found in excavations of the Jericho Tell (West Bank) of tamed or semi-domesticated *F. libyca*, are presumed to date from 7000 and 8000 years BCE (Clutton-Brock, 1969, 1981).

Studies strongly suggest the cat domesticated itself rather than got domesticated by humans. This started with cats hunting rodents from accumulated grain and scavenging garbage in villages (Baldwin, 1975; Todd, 1978) and the cult the Egyptians devoted to the species is considered to have played a major role in the process (Baldwin, 1975). One could wonder if the cat is tamed rather than truly domesticated, as the animal does not provide a production or work for humans, unless to protect crops from rodents (Coli et al., 2016). Without the necessity to highly collaborate with humans or any restriction in their movements and propagation, cats thus experienced far less selective breeding than dogs, as indicated by the preservation of ecological traits of their wild ancestor and the few morphological differences between the domestic cat and *F. libyca* (**fig. 9**). Some behavioural traits however occurred through domestication, such as the emergence of higher pitched meows, presumably designed to exploit the auditory sensitivities of human receivers (Nicastro, 2004). Today, cats keep company to more and more humans every year. In France in 2016, their population rose from 10 to 13.5 million in ten years, exceeding dog population which decreased from 8.1 to 7.3 million (FACCO/KANTAR-TNS, 2016).

Figure 9: Picture of *Felis libyca* (from panthermedia.net)

The mild impact of domestication on the cat is illustrated by the ability of the domestic individuals to easily survive away from humans, as ancestral traits related to a wild life subsist. For instance, one could wonder why hunting behaviour has persisted in the cat at a time when refrigeration availability has spread and the feeding requirements of the cat have been elucidated by nutritionists and applied by pet food manufacturers. Bradshaw et al. (1999) suggest hunting has been selected in individuals to obtain key nutrients at a time when food provided by humans did not meet all their nutritional needs.

Consequently, the world population of domestic cats divides up among different housing conditions. Feral cats usually roam freely in rural or urban areas, relying on preys and food left by humans (e.g. fishing remains, garbage). Some pet cats live entirely in captivity in apartments, houses, breeding centres or rescuing shelters, while others have partial or full access to outdoors. Thereby, the way of life of cats differs according to their living environment, as many factors (e.g. space, feeding conditions, weather, activity opportunities, population) can have an impact on their behaviours (Horn et al., 2011; Piccione et al., 2013).

In relation to the ability of the cats to adapt to different life styles, the difficulty authors meet, when trying to characterise them, mainly resides in important interindividual variability in their behaviour, as previously pointed out. For instance, home range sizes of free-roaming cats can be highly variable (7 to 28 ha in Barrat, 1997; 70 to 990 ha in Jones & Coman, 1982; 3 to 35 ha in Moon et al., 2013; 0.1 to 29.7 ha in Weber & Dailly, 1998) as well as home ranges overlap, ranging from 0.7 to 15 ha in free-ranging female farm cats in Cornwall, England (Panaman, 1981). Sitting, vocalisation, play or contact attention behaviours were also noted to highly vary among the individuals, indicating temperament differences (Podberscek et al., 1991) and the amount of total sleep time is also heterogeneous among animals (Kuwabara et al., 1986).

As for the daily rhythms of the cat, individual variations were also met in the feeding (Johnson et al., 1983; Thorne, 1982) and physical activity (Randall et al., 1985) behaviours, extending from nocturnal to diurnal patterns, sometimes even leading the authors to consider this large variability as the most important finding of a study on the feeding behaviour of cats (Thorne, 1982). This characteristic seems particularly high in the domestic cat: the intersubject variability in activity onset, greater than the intrasubject variability, was the highest in the cats compared to 15 other species in a recent study (Refinetti et al., 2016).

Aside from this high interindividual behavioural variability, behavioural plasticity may also be responsible for the findings plurality about rhythms in the cat. Indeed, cats demonstrate undoubtful ease in adapting to various conditions, possibly resulting from their intrinsic opportunistic and thus flexible nature. It proves to be another key characteristic of the species, enabling the individuals to adapt to various conditions, as met in other mammals such as the degu, the golden spiny mouse or the tayra and grison and their spontaneous shift from diurnal to nocturnal activity patterns under particular environmental conditions, as evoked earlier (Kas & Edgar, 1999; Kavanau, 1971; Shkolnik, 1971). The facility, for the domestic cat, to prosper in the diverse new habitats where it has been introduced, in present or historic times, may be the most obvious demonstration of this adaptability. A first example of this plasticity is that, although the species is fundamentally characterised as a solitary one, when environmental resources are available and abundant, the density of the individuals can increase and it is not rare to observe gatherings of individuals (Dards, 1983; Natoli, 1985; Panaman, 1981). For instance, Natoli (1985) observed the grouping of 39 urban stray cats in the historic centre or Rome (Italy) and Devillard et al. (2003) a population of 70 feral cats in a hospital park in the centre of Lyon (France). Besides, there is evidence that different factors such as human disturbance, weather fluctuations, space and resource availability or housing conditions interact with the variable (such as photoperiod) of which we attempt to study the impact on the behaviours of the cat (Randall et al., 1987; Izawa, 1983). In fact, for Konecny (1987), “the feral cat provides an ideal model for an examination of the behavioural and ecological adaptations of a species introduced into a new environment”.

When living outdoors in polar and temperate climates, animals continually have to adapt to seasonal demands of survival. While the activity rhythm of the cat seems difficult to assess on a 24h-period basis, one could wonder how the environmental factors of seasons affect its behaviour, knowing its activity patterns are influenced by weather conditions; rainfall, mainly, appears to decrease their level of activity (Dards, 1979; Goszczyński et al., 2009; Harper, 2007; Izawa, 1983). Furthermore, the circulating melatonin concentration and oestrous cycle in the cat demonstrate it is sensitive to photoperiod (Dawson, 1941; Leyva et al., 1989; Michel, 1993).

Populations living outdoors may have to adapt to the seasons.

Locomotor activity according to the season

Seasonal differences in activity levels of feral populations of the Iriomote cat (*Prionailurus Iriomotensis*) were discerned with increased activity in spring and summer associated with increased prey availability (Schmidt et al., 2009). As for the domestic cat, free-roaming individuals were also subject to seasonal changes in several studies. Higher locomotor activity in summer and spring and lower locomotor activity in winter were reported in cats roaming in villages in a Warsaw suburban zone (**fig. 10,** Romanowski, 1988).

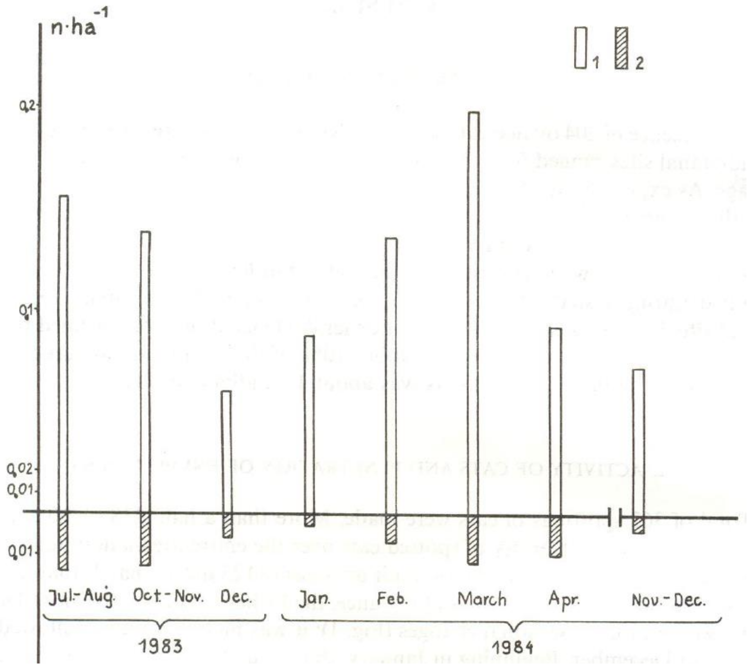


Figure 10: Abundance (n/ha) of cats on built up (1) and open (2) areas (from Romanowski, 1988)

These findings were later confirmed by a decline of the activity levels throughout autumn and an increase in spring in free-ranging individuals in Brooklyn (USA, Haspel & Calhoon, 1993), a decrease of the home ranges of farm cats in winter compared to other seasons in a Swiss mountainous area (Weber & Dailly, 1998), or even the detection of the fewest cats from November to March and the most in June and August in rural areas of central Poland (**fig. 11,** Goszczyński et al., 2009).

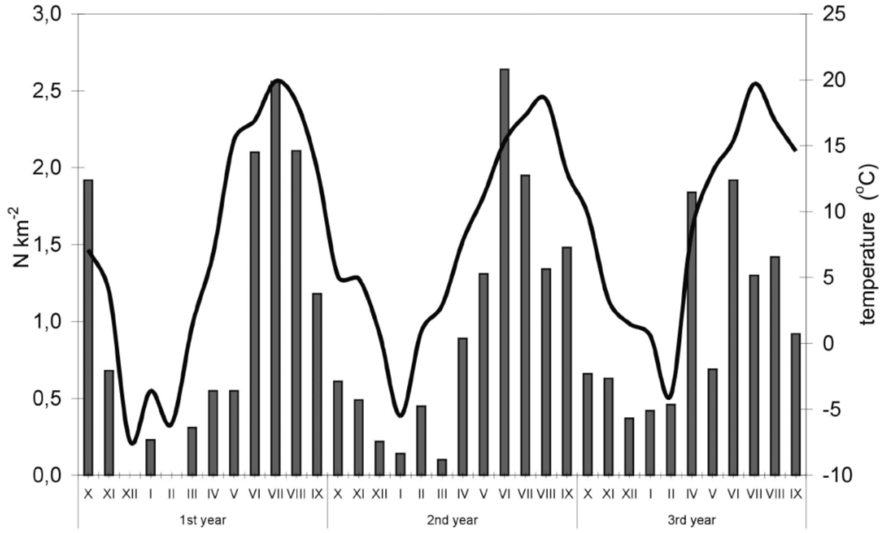


Figure 11: Annual display of monthly changes of cat density indexes in relation to mean temperature (from Goszczyński et al., 2009)

Witnessing frequencies of locomotor and alert behaviour of Portsmouth (UK) dockyard cats in the summer being double those in December, Dards (1979) considers these differences are probably due to variations in day length. In fact, the density index correlated positively with average monthly temperature and day-length in the rural cats of central Poland (Goszczyński et al., 2009). However, this pattern was also observed in laboratory conditions where temperature remained constant: during long-day conditions (8 hours of darkness, 16 hours of light), neutered group housed male cats showed higher total voluntary activity than cats under short-day conditions (16 hours of darkness, 8 hours of light), primarily due to an increase in dark period activity (**fig. 12,** Kappen et al., 2013).

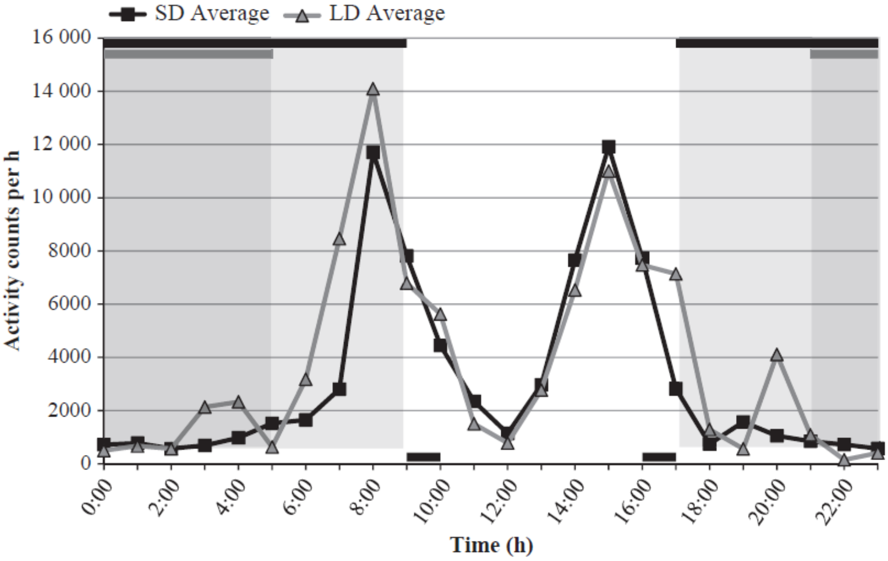


Figure 12: Daily activity profile of short-day (SD)-and long-day (LD)-housed cats at week 12 (n = 11). Dark periods for SD and LD treatments are represented by solid lines located at the top of the graph. Feeding times are highlighted by the dark bars located at the bottom of the graph (from Kappen et al., 2013)

Others found different seasonal variations in the amounts of locomotor activity of the cat. In Australia, summer maxima and winter minima were indeed reported, but also spring minima, assumably caused by emigration of the feral cats (Jones & Coman, 1982). Others noticed the home ranges of adult feral males in New-Zealand were larger in summer, but also in winter (Langham & Porter, 1991). These last findings recall those of Horn et al. (2011) who observed greatest activities in free-roaming cats in Illinois (USA) from October to February, probably due to higher energetic demands or more time needed to capture preys 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”. For their part, the pet cats of the study had slightly depressed activity in January-February but also in August-September.

In some mammals, the activity rhythm can also be markedly altered with season. For instance, the timing of the two peaks of activity in spider monkeys (*Ateles geoffroyi*) exposed to natural light, temperature and humidity cycles, correlated with day-length (Muñoz-Delgado et al., 2004). Free-roaming Arabian oryx (*Oryx leucoryx*) exhibited diurnal activity during winter, distinct nocturnal and crepuscular activity during summer, and intermittent patterns during autumn and spring (Davimes et al., 2017), while free-ranging cabrera and water voles (*Microtus cabrerae* and *Arvicola sapidus*) showed bimodal crepuscular activity during the dry season and more diurnal activity during the wet season (Pita et al., 2011). Wolves (*Canis lupus*, Merrill & Mech, 2003) and migratory birds (Cochran, 1987; Rattenborg et al., 2004) have been observed to switch from being nocturnal and diurnal to the opposite phasing, respectively, during dispersion and migrations. Also, bat-eared foxes (*Otocyon Megalotis*) switched between nocturnal phasing in summer to diurnal phasing in winter, in relation to prevailing temperatures and prey availability (Lourens & Nel, 1990).

In the cat, peaks of activity constantly occurred at dusk through the year in feral individuals in Japan (Izawa, 1983) and house individuals presented a two-peaked activity pattern in spring and summer in rural areas of Poland (Goszczyński et al., 2009). This reminds observations of peaks near dawn and dusk and lows near midday during the warm season of the year, but a more stable activity pattern throughout the day during the cold seasons in the feral cats in Australia (Jones & Coman, 1982). The feral cats in Japan shifted their active time seasonally from a nocturnal habit in summer to a more diurnal habit in winter (**fig. 7**, Izawa, 1983).

Feeding behaviour according to the season

Annual changes in feeding behaviour are observed in predators. For instance, honey badgers (*Mellivora capensis*) could increase the diversity of their diet while their foraging yield declined in winter (Begg et al., 2003). Food intake reduced in winter in artic foxes (*Vulpes lagopus*) and increased in spring in the honey badgers, reflecting food availability (Fuglei & Oritsland, 1999; Prestrud & Nilssen, 1992). Besides, a positive energy balance can be necessary for other behaviours in mammals, such as the mating behaviour which fluctuates annually.

The study of feeding habits in the cat according to the seasons has rarely been conducted so far. In 25 neutered cats housed in individual pens, fed *ab libitum* and exposed to natural light and seasonal ambient temperatures, food intake was lower in winter, compared to summer (Bermingham et al., 2012). The authors suppose this difference in energy requirements reflects increased and decreased growth rate of hair in summer and winter, respectively (Hendriks et al., 1998). Similar results were obtained in 11 group-housed male cats which showed lower food intake in short- than long-day conditions, while ambient temperature and humidity were this time controlled (Kappen et al., 2013).

However, these studies regulated the diets of the cats in order to maintain body weight, preventing the assessment of photoperiod impact on voluntary food intake throughout the day. Plus, they did not examine possible seasonal effects throughout the year. In an indoor environment, where the feeding behaviour was compared at all seasons during four years, voluntary food intake in 38 *ad libitum* fed cats was the greatest in late autumn to winter and least in summer (**fig. 13**, Serisier et al., 2014). Homogenous body weight led the authors to consider these differences occurred in response to changes in energy needs such as thermoregulation or activity. Annual peaks and troughs in both temperature and daylight length occurred at times similar to those in food intake. A combination of the two environmental factors is suspected to play a role in these seasonal differences, daylight length presumably being a triggering stimulus to prepare the cats for increased thermogenesis during colder months (Serisier et al., 2014). Limitations of this study yet reside in the variation in diets and the indoor exclusive housing condition of 8 cats while the 30 other had unlimited outdoor access. The authors however point out no effect of the diet or housing condition was detected.

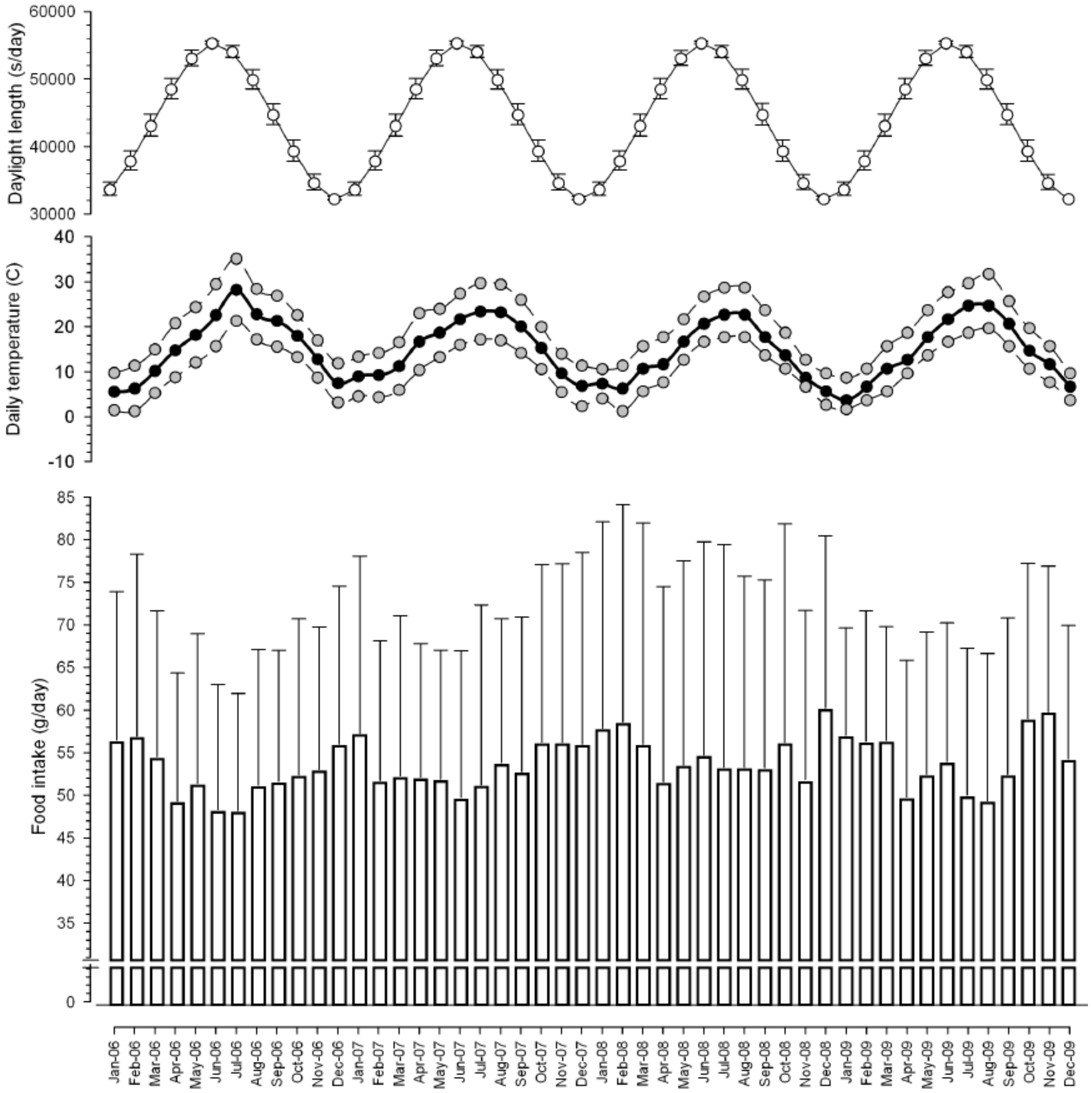


Figure 13: Environmental and food intake from the study cats parameters during the course of the study. Daylight length is expressed as mean and standard error for each month; daily temperature is expressed as mean and minimum and maximum; and food intake is expressed as mean and standard deviation intake (adapted from Serisier et al., 2014)

Both Bermingham et al. (2012) and Serisier et al. (2014) consider differences in activity levels may constitute a determining factor in the feeding behaviour of the cats. On one hand, Bermingham et al. (2012) suspect larger summer food intake reflects higher energy requirements due to higher levels of activity during this season. In fact, increased voluntary physical activity during the long-day conditions was considered to be responsible for increased energy intake to maintain body-weight in Kappen et al. (2013). On the other hand, Serisier et al. (2014) consider larger winter food intake may come from increased physical activity in colder seasons to help produce heat production. Nevertheless, activity behaviour was not measured in either of these studies, preventing confirming or invalidating these hypotheses.

The populations also adapt to their housing condition.

Another example of decisive factors modulating the activity of the cats is the housing conditions they live in. Differences in home range size, habitat use and activity patterns between "owned" individuals -i.e. fed and cared by humans and partly living in human dwellings- and "unowned" individuals -i.e. not observed being fed or cared for by humans- were observed on the outskirts of Champaign-Urbana (Illinois, USA, Horn et al., 2011). "Unowned" cats were more active than "owned" cats throughout the year and were more nocturnal in their diel activity, possibly reflecting activity patterns of their preys (**fig. 5**). Daily activity of "owned" cats was more consistent throughout the day, leading the authors to speculate supplemental feeding and the availability of reliable shelter lessened their need to correspond activity with prey activity patterns. The increased activity in early mornings and during evenings is considered to come from availability of the preys in "unowned" cats but from activity of the owners in "owned" cats. In another study, the activity patterns of one group (B), living in large houses, having free access to large gardens (2000-2500 m²) and kept outside at night was compared to another group (A) which had access to a smaller garden (20-40 m²) only during one hour in early morning (Piccione et al., 2013). Group B was also mainly nocturnal and displaying an active lifestyle, along presenting a more robust daily rhythmicity than group A which was mainly diurnal and also more active when their owners were home compared to when they were away. The authors consider restricted activity and exercise area, human care and cleaning, can be cause of shifts in diurnal/nocturnal active phase and generate weaker rhythms in the cats.

HUMAN IMPACT ON THE BEHAVIOUR OF THE CAT

The proximity of cats to humans constitutes an additional factor impacting their behaviour, as we started to review in the above section. As a “friendly symbiont”, cats maintained a certain independence from humans but still sometimes rely on them as their main food source. In the literature, this can result in difficulty to distinguish environmental from human factors on the behaviour of domestic cats. First of all, the frequent sterilisation of domestic cats prevents them to show behaviours related to sex hormones. This means the behavioural deductions we make from observations of pet cats usually do not reflect the original way of life of the species.

Then, there is the effect of captivity, restricting the available space the cats can roam in, which has been discussed earlier. Besides, confinement is sometimes also associated with multiple cats sharing the same space. We already evoked cats can increase their interindividual tolerance when environmental resources are gathered (Dards, 1983; Natoli, 1985; Panaman, 1981). Still, one must not forget cats are characterised as a solitary species which, in the wild, use dispersion or avoidance to reduce aggression risk with congeners (Leyhausen, 1979). Thus, in confined conditions, they may develop stress from proximity with conspecifics, especially when they are not related (Casey & Bradshaw, 2000). This is why it is preconized to distribute feed, rest and elimination areas in different sites, to prevent monopolisation of certain areas when several cats share the same space (van den Bos & de Cock Buning, 1994). Overall, enrichment of the environment of pet cats is crucial for their welfare, involving social, physical, occupational sensory, and nutritional approaches (Rochlitz, 1999, 2005).

Outside conditions where individuals live in captivity, the activity of the cats reported in field studies was often also related to human impact. On one hand, dusk activity peaks coincided with times of food provision by fishery waste of human residents in the feral cats in Ainoshima Island (Japan, Izawa, 1983). Similarly, the diurnal activity of dockyard feral cats in Portsmouth (UK) was suspected to depend on peaks in human activity (Dards, 1979), as food provided in excess from humans, rather than the natural prey of the cats, was utilised as main source of food. In farm cats in Cornwall (UK), authors speculate the dawn activity peak of the individuals was deferred because of early morning milk dole (Panaman, 1981). On the other hand, rather than an activity-enhancing influence of humans, other authors reported avoidance behaviour, such as in the free-ranging cats in Brooklyn (USA) which did not exhibit sunset peak when humans were present (**fig. 14**, Haspel & Calhoon, 1993).

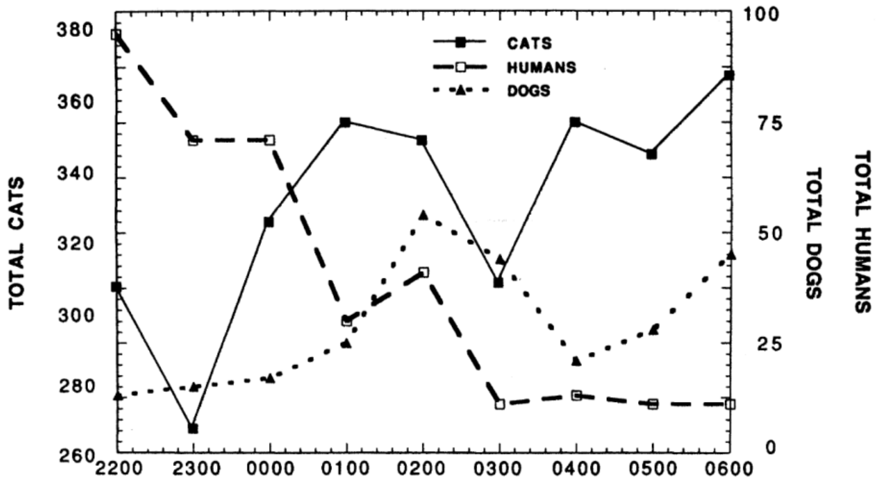


Figure 14: Number of sightings by hour for total cats, humans, and dogs from 2200 to 0600 h in Brooklyn, New York, autumn 1982 (from Haspel & Calhoon, 1993)

Human impact is therefore not only a matter of food provision. In laboratory conditions, human care was also assumed to be a potent stimulus in modulating the pattern of locomotor activity and food consumption. Some noted the daytime activity or disruption of a basic nocturnal pattern of laboratory cats was probably attributable to human activity or noises (Johnson et al., 1983; Kavanau, 1971). In another study, the presence of humans increased the food intake and physical activity of laboratory cats (Randall et al., 1985, 1987) to an extent that the authors consider the presence of humans as a more powerful factor than light/dark cycles or the degree of illumination of the dark phases. The effect of routine care and cleaning must therefore be taken into consideration in studies of the activity and feeding rhythms of cats. Evidently, the behaviour of cats living with their owners is not spared from human-induced rhythm disruptions, as already mentioned in the studies of Piccione et al. (2013) and Horn et al. (2011).

RHYTHM MEASUREMENT FOR THE CAT

As the locomotor activity and feeding rhythms of the cats have been reported to be variable or irregular, traditional rhythm analysis tools are not always adapted. Still and firstly, actograms (for activity rhythms) or feedograms (for feeding rhythms), representing data for two days per line with successive days appearing on successive lines and essential for chronobiological studies, permit to visualise the rhythm of a cat (**fig. 15**).

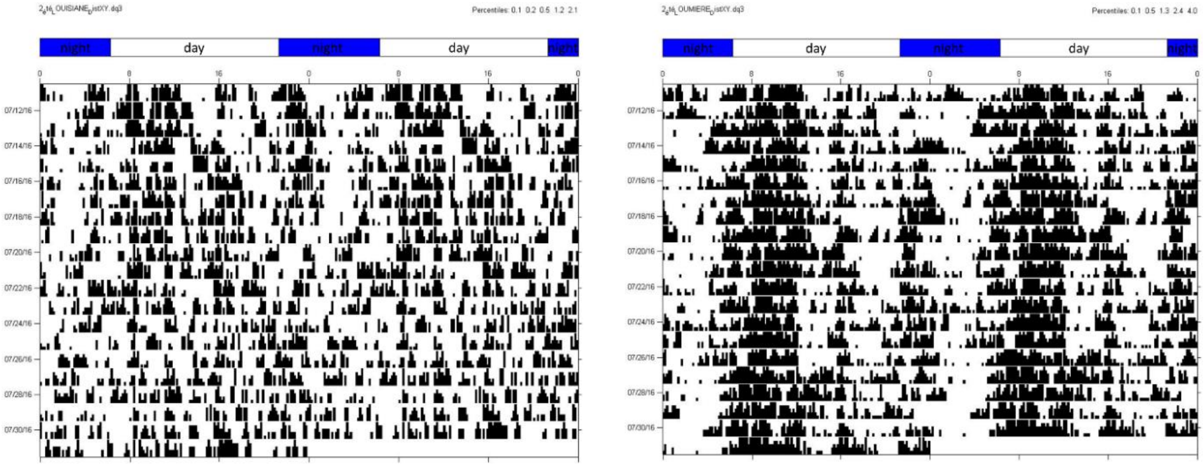


Figure 15: Actograms of an arrhythmic individual (left), showing IS of 0,146 and IV of 1,647 and a rhythmic individual (right), showing IS of 0,541 and IV of 0,99 (Parker, unpublished data)

Secondly, the rest–activity rhythm is commonly studied using actigraphy, a non-invasive measure of circadian activity. The parameters that describe rhythm characteristics include amplitude (A), period (P) and phase. Finally, other measures, such as interdaily stability (IS), intradaily variability (IV) and the least active 5 hours (L5), have first been developed by Witting et al. (1990) in order to study the effect of age and Alzheimer's disease on rest–activity rhythm (see examples of an arrhythmic cat and a rhythmic cat in **fig. 15**). These variables, called nonparametric as they are not associated with parameters of a known function, were later used by Van Someren et al. (1996, 1999) who described them as a more appropriate way to investigate and discriminate circadian rhythms which are disturbed and/or sensitive to change even in small samples (Van Someren et al., 1999). These analyses therefore seem more fitted for our studies. Besides, Piccione et al. (2013) already used them to study the influence of different housing conditions on daily activity rhythm in cats.

PHD OBJECTIVES AND PREDICTIONS

One could argue that the best way to expand our knowledge on the general behaviour of pet cats would be to study them in different environmental conditions they live in. For this reason, this PhD focused on two populations of captive cats: one living in an indoor environment at the cattery of Royal Canin (Aimargues, France), the other living in an outdoor environment in the shelter Aide aux Vieux Animaux (AVA, Cuy-Saint-Fiacre, France; **fig. 16, see respective feeding devices in Appendix 1**). We mainly focused on sterilised domestic individuals to best match the domestic cat of today.

Figure 16 – Pictures of an indoor study room (top) and the outdoor enclosure (bottom)

A new and promising ethological tool, Ultra-Wide-Bands technology (UWB), has been complementing the methods of Royal Canin research team since 2013 in order to track the locomotor behaviour of cats. As a result, a large bulk of behavioural data has been analysed from this technology in 2014 and 2015 on cats living in group in the indoor cattery of Royal Canin (Parker et al., 2017; see Appendix 1).

As rhythms are known to play an important role in the behaviour of individuals, we decided to go further in the study of cat behaviour by adding a chronobiological aspect in the research of this PhD. By studying its rhythms, we do not solely allow ourselves to better comprehend its behaviour, but also qualify us to elaborate nutrition and housing strategies to better fit to the behavioural needs of the domestic cat. Furthermore, until now, with the exception of classic sleep studies, circadian rhythms and their connection with nutrition have rarely been studied in this species.

Using UWB technology, as well as other advanced telemetric technics, i.e. individual radio-frequency identification (RFID), and automated food intake weighing, these PhD studies therefore aim to:

- characterise daily activity and feeding rhythms in indoor cats
- assess the impact of seasons on these rhythms
- identify and compare the daily activity and feeding rhythms of outdoor and indoor cats

As detailed earlier, the literature indicated that the locomotor activity and feeding rhythms of the cat are complex. Also, with domestication, the rhythm of life of this predator of diurnal and nocturnal species integrated human influence. One could therefore wonder if ancestral traits of the cats disappeared, if new patterns emerged, or if a combination of old and new patterns constitute the daily rhythms of the individuals of today. We expect to observe rhythm multimodality and changes according to the external synchronisers cats are exposed to, such as in various seasons and housing conditions. Also, we intend to assess which of these stimuli are the most determining in the daily behaviour of the cats.

CONDUCTED STUDIES

ARTICLE 1

AIM: CHARACTERISE THE DAILY RHYTHMS OF INDOOR CATS

DAILY RHYTHMS IN FOOD INTAKE AND LOCOMOTOR ACTIVITY IN A COLONY OF DOMESTIC CATS

Marine Parker*[a], Sarah Lamoureux[b], Etienne Challet[a],
Bertrand Deputte[c], Vincent Biourge[b], Jessica Serra[b]

SUBMITTED

[a] Institut des Neurosciences Cellulaires et Intégratives (INCI), CNRS, Université de Strasbourg, 8 allée du général Rouvillois, 67000 Strasbourg, France

[b] Royal Canin research center, 650 avenue de la petite Camargue, 30470 Aimargues, France

[c] Ecole Nationale Vétérinaire d'Alfort (ENVA), 7 Avenue du Général de Gaulle, 94700 Maisons-Alfort, France

*corresponding author: Marine PARKER, +33(0)3 88 45 66 68, marineparker@gmail.com, INCI, as above.

ABSTRACT

Daily rhythms have been widely investigated in various mammals but, surprisingly, literature is scarce and conflicting regarding the domestic cat, *Felis catus*. Two groups of indoor cats (14 in total) living in a cattery panel, were followed on a 24 hour/7 day basis, using advanced telemetry technologies, i.e. passive RFID, automated weighing of electronic scales and UWB technology with accuracy ensuring a good reliability of the results. While covering on average 1.74 ± 0.4 km and eating 46.4 ± 3.6 g (≈ 179 kcal) of dry food per day, findings indicate 24 hours periodicity in the locomotor and feeding rhythms of the cats. In their daily patterns, the indoor individuals showed two main troughs of activity and food intake - in the middle of the day and in the middle of the night - and two main peaks: one in the morning (especially before sunrise and food renewal), the other in the evening (following the end of the work day of the animal staff and before sunset), supporting previous work demonstrating peaks at dusk and dawn and confirming the crepuscular nature of the species. No general pattern emerged according to a more nocturnal versus diurnal organisation. Bimodality, more than chronotypes, seems therefore to best characterise the activity and feeding rhythms of the cats as it was demonstrated in the individuals among the different categorisations. Systematically, the locomotor behaviour of the cats was more rhythmic than their eating behaviour ($p < 0.01$), possibly reflecting the flexibility of the eating patterns of the cat initially enabling it to adapt to daily rhythms of its preys.

Key words: *Cat, circadian rhythms, feeding pattern, locomotor activity, chronobiology*

1. INTRODUCTION

From the short cellular events to long seasonal changes, biological rhythms are systematic for living organisms. They are of importance in the synchronization of daily behaviours. In order to adapt to their environment and effectively react to the competing demands of life, species adjust their activities (e.g. feeding, sleeping, moving) to occur at optimal times (Sharma, 2003). A circadian rhythm displays oscillations of a period of about 24 h. This endogenous cyclicity can for example allow individuals to model their activities on those of their preys or predators, in order to better survive (Kavanau, 1971). The circadian rhythms and their consequences can be investigated in various species through different parameters. In mammals, sleep (Mistlberger 2005), body temperature (Refinetti & Menaker 1992) and also general activity (Carpenter, 1985) are regulated by an internal master clock located into the suprachiasmatic nucleus of the hypothalamus, which is mainly adjusted by the environmental light/dark cycles the individual encounters (Golombek & Rosenstein, 2010). In addition, light can directly trigger or inhibit behaviours depending on the species (Redlin, 2001).

Literature is scarce and contradictory regarding the rhythmicity of domestic cat, *Felis catus*. Hawking et al. (1971) reported that cats do not have circadian activity rhythms. Yet, Kuwabara et al. (1986) showed circadian fluctuation in total sleep time (slow wave sleep+ rapid eye movement sleep) and in brain temperature. They also demonstrated the existence of a bimodal pattern of wakefulness displaying dawn and dusk peaks under artificial light:dark cycle. Randall et al. (1985) found a free-running circadian organization of activity in cats kept in constant darkness as measured by infrared photobeams. These cats, isolated from humans and human noises, showed, in addition, random patterns of activity when kept in constant light. Defining cat’s lifestyle is indeed difficult: some recorded diurnality in its behaviour (Dards, 1979; Hawking et al., 1971), others consider it as nocturnal (e.g. MacDonald & Apps, 1978; Kanarek, 1975; Walls, 1942) or crepuscular (Kavanau, 1971). Yet, this ambiguity may simply be due to the faculty of an individual to show various activity patterns at various times (Randall, et al., 1987) or even result from the adaptability the cat, a predator, must show regarding the variety of its preys’ rhythms in the wild (Konecny, 1987): rodents are usually nocturnal while song birds are diurnal. Besides, a simple diurnal-nocturnal dichotomy is not applicable to all mammals: some species like the degu (*Octodon degus*), the golden spiny mouse (*Acomys russatus*), or the tayra (*Eira barbara*) and grison (*Galictis*) can shift from diurnal to nocturnal activity patterns under particular environmental conditions (Kas and Edgar, 1999; Kavanau, 1971; Shkolnik, 1971). In fact, Horn et al. (2011), as well as Piccione et al. (2013), observed different chronotypes according to the housing conditions of the cats.

In the wild, the cat is an opportunistic solitary hunter, like many of its fellow felids. It catches numerous small preys per day to sustain its needs as a carnivorous. In accordance with this feature, even when fed by humans, the cat spontaneously eats several small meals per day (Lewis, et al., 1987; Houpt, 2011; Mugford and Thorne, 1980). Kane et al. (1981) reported cats ate approximately 16 (usually 12-20) small meals throughout the 24 h period. Yet, no cyclicity has been reported regarding eating habits in cats so far.

In this context, the aim of this study is to investigate locomotor activity and feeding rhythms in domestic cats living in a cattery. In order to record individual cat's activities in the most accurate way, we used the latest animal tracking method used in ethology, namely Ultra-WideBands (UWB) technology (Parker et al., 2017).

2. MATERIALS & METHODS

2.1. Animals and conditions

The tracking technology being installed in a single room (fig. 1), two groups of domestic cats (*Felis catus*) of respectively eight and six individuals were observed one after the other in order to maximise our sample size while providing enough living space for each individual to roam in. Each group was studied continuously for one week during spring 2015.

The five females and three males of the first group (A) as well as the two females and the four males of the second one (B) were all neutered and five years-old. They belonged to two different breeds: Chartreux (12) and British Shorthair (2). The individuals of both groups had been living together since 2010. Nevertheless, in group A, two individuals (who have been living together since 2010) were introduced at the time of this protocol.

The cats were housed at the cattery of Royal Canin located in the South of France (Aimargues). They lived in a main room of 22.5 m² (6.4 m (l) x 3.51 m (w) x 2.60 m (h)) under controlled conditions (20-23°C, 44% RH). All cats had also free access to an inner courtyard of 7 m² (2.9 m (l) x 2.4 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. The cats had at their disposal a wall shelf containing several hiding places and cushions, an "enriched" area containing several cat toys, a wall scratching post, a feeding area, a water bowl, two litter trays, two cat trees with cushions and a plastic seat. Both groups were exposed to the natural light:dark cycle, with an average of 13h39 of light for group A and 15h50 of light for group B.

Figure 1 – Map of the study room (light blue lines represent the location of the bay windows)

Two tags were attached to the collar of each cat, one for the UWB technology, the second for the electronic scales (see below). These tags had no adverse effect on the physical condition of the animals. This protocol was approved by the ethical committee of Royal Canin.

2.2. Feeding and human intervention

All the cats had an *ad libitum* access to dry food (Fit32 (5.5% moisture, 32% protein, 15% crude fat, 4.6% crude fibre, 3% minerals and vitamins, 3859 kcal/kg), Royal Canin) and water. The food was renewed every day at 10:00 h. Humans were present within the panel around 06:00 h for cleaning, and then occasionally between 08:30 h and 12:00 h and/or between 14:00 h and 16:00 h to interact with the cats and check the panel.

2.3. Locomotor activity and recording

Each cat wore an Ultra-Wide Band tag (Ubisense, Paris, France) on its collar, continuously emitting radio waves to antennas placed on strategic spots in the room. More precise than GPS systems and with less spatial constraints than passive Radio-Frequency Identification, this technology automatically records, in real time and three dimensions, the position of a tag-wearing individual all day long with a sampling interval of 0.9 s and an accuracy of 15 cm (Parker et al., 2017). From these location data, a specific software calculates some behavioural data such as the covered distance of each cat by period of time (periods of 10 min were used to calculate the rhythm parameters).

The mean travelled distance per day refers to the distance travelled by an individual over the collection period, divided by the number of collection days. To infer daily activity patterns, we also calculated the mean travelled distance per cat and per 20min on a 24-hour time period.

The tags and sensors use extremely low power radio transmitters and met all applicable EU requirements, including those for human exposure to electromagnetic radiation. Staff entering the room was also equipped with a transmitter attached to a collar to assess the effect of human presence on animal behaviour.

2.4. Eating behaviour and recording

Each cat had free access to its own dedicated feeder, thanks to the passive-RFID (M Tronic device, Montévrain, France) tag on its collar which gives access to the food by opening a specific tilting door, access to the other feeders being made impossible. The electronic scales (Metal Process, Montévrain, France) recorded the time and weight of consumptions with a sensitivity of one gram, and a specific software (M Tronic device, Montévrain, France) was continuously recording the daily consumption for each animal.

Files from electronic scales were exported with Excel (Microsoft Office). The raw consumption, i.e. the weight of kibbles ingested (in grams), and number of meals by period were calculated. The mean daily consumption per day refers to the total consumption of the individual over the collection period, divided by the number of collection days. After examination of several ingestion kinetics, we considered meals consisted of one or more eating bouts of at least 2 g separated by an interprandial pause of at least 20 minutes.

2.5. Rhythm parameters and measurements

To visualise the rhythm of an individual, we used actograms (activity rhythm) or feedograms (feeding rhythm) representing data for two days per line with successive days appearing on successive lines (Clocklab software, v. 2.72, Actimetrics, Wilmette, IL, USA, associated to Matlab, v. R2013a, MathWorks, Meudon, France).

The rest–activity rhythm is commonly studied using actigraphy, a non-invasive measure of circadian activity. The parameters that described rhythm characteristics included amplitude (A), period (P) and phase. Other analyses, such as interdaily stability (IS), intradaily variability (IV) and the least active 5 hours (L5), had first been developed by Witting et al. (1990) in order to study the effect of age and Alzheimer's disease on rest–activity rhythm. These variables, called nonparametric as they are not associated with parameters of a known function, were later used by Van Someren et al. (1996, 1999) who described them as a more appropriate way to investigate and discriminate disturbed circadian rhythms, as well as sensitive to change even in small samples (Van Someren et al., 1999). The rhythms of the cat having previously been described as variable or irregular, these analyses seemed more fitted for our study. Besides, Piccione et al. (2013) already used them to study the influence of different housing conditions on daily activity rhythm in cats.

Also, in order to establish whether the cats tended to consume/be active more during night or day hours, we assessed a rate of activity/consumption by hour according to the light condition (night hours vs day hours), using local timing of sunrise and sunsets as phase references.

2.5.1. Period and amplitude of the rhythms

To measure the period, mode and amplitude, we used the periodograms given by the Clocklab software (v. 2.72, Actimetrics, Wilmette, IL, USA) associated to Matlab (v. R2013a, MathWorks, Meudon, France) which is using the method of Sokolove and Bushell (1978). Periodograms are constructed by the calculation of values for various periods ranging from 5 to of 30 h. Unless the time series contains more than one rhythmic component, the highest peak shown in the periodogram corresponds to the estimated period of the time series.

The period (P) of a rhythm is the duration of a full cycle (that is, the reciprocal of its frequency), corresponding to the time interval measured between two episodes that will recur identically during the variation. The highest peak shown in the periodogram graphs yields the period for which the rhythm of the individual repeats its pattern. Typically, the period of a circadian rhythm lasts about 24 hours.

Secondary peaks can sometimes exist. In most cats, this peak corresponded to 12-hour periods, showing a tendency to bimodality in the rhythms. We decided to consider an individual displayed a tendency to bimodality when the size of the 12-h peak was superior or equal to half of the 24-h peak.

The amplitude (A) of a rhythm is a relative measure of how much of the activity or food intake is actually rhythmic. The higher amplitude, the more robust the rhythm.

2.5.2. Interdaily Stability, Intradaily Variability and Least active 5 hours onset

Interdaily stability, Intradaily variability and the least active 5 hours period were all determined with the ActiWatch software (v. 7.31, Cambridge NeuroTechnology, Cambridgeshire, UK).

The Interdaily Stability (IS) quantifies the variability among successive days, that is, the strength of coupling of the rhythm to stable external zeitgebers (Van Someren et al., 1996, 1999; Witting et al., 1990). The IS values (arbitrary units), ranging from zero for Gaussian noise to 1 for maximal IS, decrease with higher day-to-day variation of the activity/eating patterns.

The Intradaily Variability (IV) evaluates the fragmentation of the rhythm, that is, the frequency and extent of transitions between rest and activity (Van Someren et al., 1996, 1999; Witting et al., 1990). The IV values (arbitrary units) vary from near zero for a perfect sine wave to about 2 for Gaussian noise.

The least active 5 hours (L5) are computed by averaging the 5 lowest hourly means of the 24h pattern (Van Someren et al., 1996, 1999; Witting et al., 1990). This gives us an indication about the moment daily troughs happen in the pattern of the cats. We can then compare interindividual differences.

2.6. Chronotypes

We based a nocturnal versus diurnal categorisation of the individuals on the position of the least active 5 hours (nocturnal or diurnal), inspection of the actograms (more nocturnal or diurnal activity/consumption peaks) and comparison of the nocturnal/diurnal activity/consumption rates.

2.7. Statistical analyses

Every statistical comparison was made with Sigmaplot (v. 13.0, Systat Inc., San Jose, California, USA). We used unpaired t-tests or Mann-Whitney Rank Sum tests (when the data passed Shapiro-Wilk test for normality or Brown-Forsythe test for equal variance) to determine the effects of sex (male versus female), group (group A versus group B) or chronotype (nocturnal versus diurnal) on the daily covered distance or food consumption, weight and amplitude, interdaily stability and intradaily variability of the rhythms. Because the data did not follow statistical normality (Shapiro-Wilk test for normality) and could not be normalized with standard transformations, Friedman analyses of variances (ANOVAs) with repeated measures were conducted to compare the covered distance or food consumption according to the hour of the day. Two-way ANOVAs with repeated measures were performed to assess the effects of sex or chronotype on the covered distance and food consumption according to the hour of the day. Tukey post-hoc tests with Friedman ANOVAs and Holm-Sidak post-hoc tests with Two-way ANOVAs were performed. Finally, paired t-tests or Wilcoxon signed rank tests (when the data significantly deviate from normality according to Shapiro-Wilk test) were conducted to evaluate the effect of the variable type (feeding versus locomotor activity) on the chronobiological parameters (i.e. amplitude, interdaily stability and intradaily variability). Our results are given as mean ± 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 $p < 0.001$ on graphs).

3. <u>RESULTS</u>

3.1. Rhythm of locomotor behaviour

The cats covered on average 1.74±0.4 km daily. This distance highly varies according to the individual (min: 0.54 km; max: 4.13 km) and the group: group A covered significantly more daily distance than group B (3.05±0.38 versus 0.77±0.06 km, respectively; Mann-Whitney, $U = 0.0$, $p < .001$).

Every cat showed a locomotor rhythm of 24±0.01 h, with a mean amplitude of 433±48 (min: 147; max: 749). The interdaily stability of the locomotor rhythm of the cats was of 0.40±0.03 (min: 0.16; max: 0.55) and its intradaily variability of 1.63±0.09 (min: 1.18; max: 2.37).

Twelve out of the 14 cats showed a tendency towards bimodality in their activity rhythm, the last 2 being only unimodal. Examples of bimodal and unimodal rhythms are shown in figure 2.

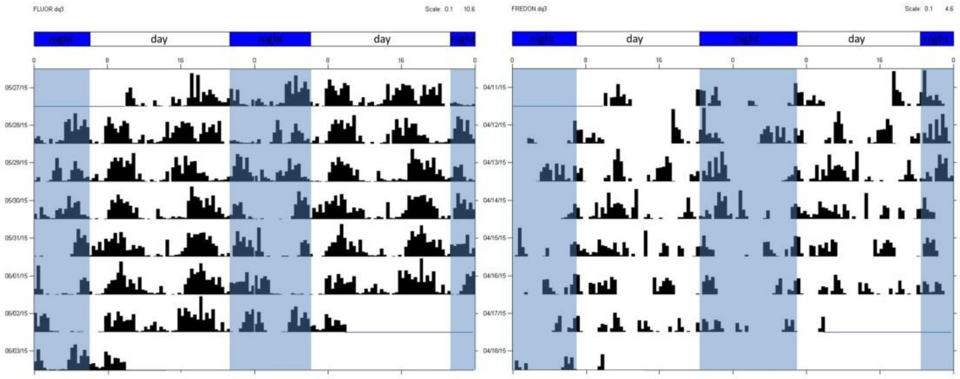


Figure 2 – Actograms of 2 males: a bimodal one (left) and a unimodal one (right).
Actograms show data for two days per line, with successive days appearing on successive lines (cf Refinetti et al., 2014).
Blue areas represent night time, white areas day time.

The least active 5 hours (L5) in the locomotor behaviour of the cats began between 22:00 h and 01:00 h for eight cats, between 10:00 h and 11:00 h for the six others.

The mean hourly distance covered by the cats, shown in figure 3, differed significantly according to the hour (Friedman, $\chi^2_{23} = 146.77$, $p < .001$). There were two main peaks of activity during the day: cats were more active in the morning, more precisely between 05:00 h and 06:00 h (preceding the sunrise) and between 09:00 h and 11:00 h (preceding and during the food renewal), and in the evening, more precisely between 16:00 h and 18:00 h (following the end of the working period of the caretakers and preceding sunset). The cats were the least active during two main troughs: between 01:00 h and 03:00 h, and between 12:00 h and 15:00 h. For details, see appendix 1.

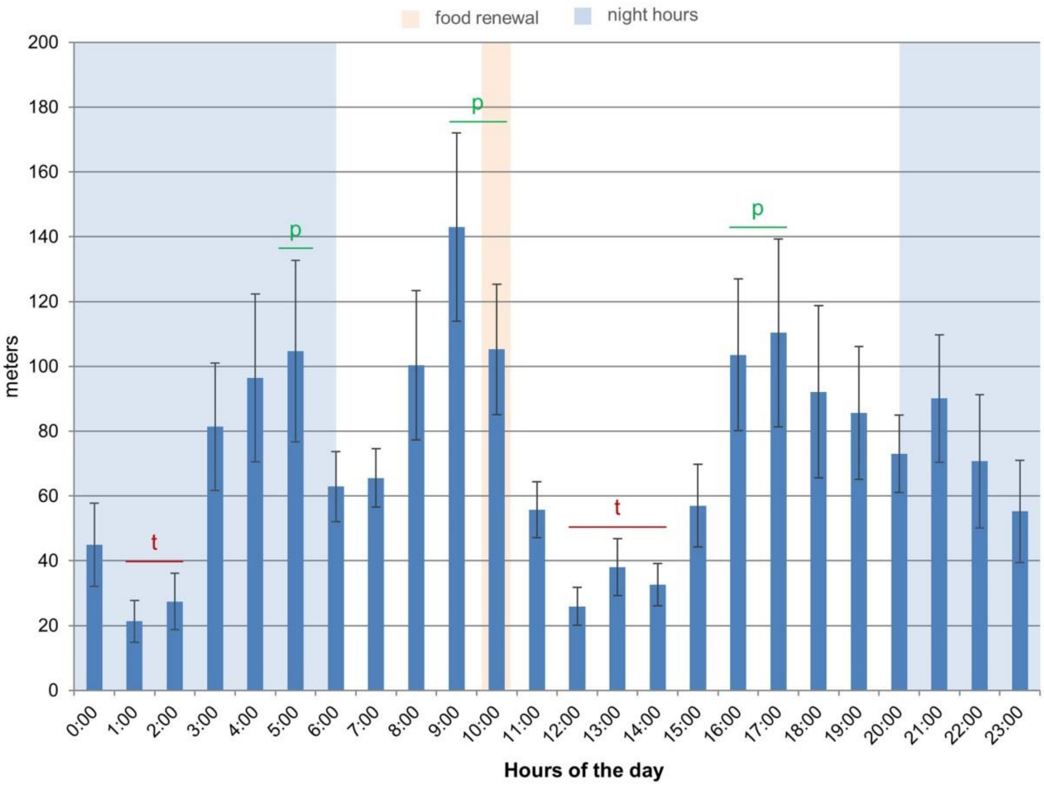


Figure 3 – Mean distance (meters) covered by the cats (n = 14) every hour.
Error bars represent standard errors, (p) indicates a significant peak, (t) indicates a significant trough.

3.2. Rhythm of eating behaviour

The cats ate approximately eight meals of 5.9±0.7 g a day, i.e. an average of 46.4±3.6 g of dry food per day (min: 27.2 g; max: 72.4 g). No group effect was detected (50.7±4.8 g for group A, 43.1±5.1 g for group B; $t_{12} = 1.045$, $p = 0.316$).

Eleven out of the 14 individuals showed a feeding rhythm of 24±0.04 h, the three others being arrhythmic. The interdaily stability of the feeding rhythm of the cats was of 0.30±0.02 (min: 0.24; max: 0.40) and its intradaily variability of 2.05±0.06 (min: 1.59; max: 2.27). The feeding rhythm mean amplitude of rhythmic individuals was of 253±23 (min: 161; max: 390).

Seven cats showed a tendency towards bimodality, four others being unimodal and the three others amodal (i.e. arrhythmic).

The least active 5 hours (L5) in the eating behaviour of the cats began between 21:00 h and 00:00 h for five cats, between 11:00 h and 13:00 h for the nine others.

The mean hourly food intake of the cats, shown in figure 4, differed significantly according to the hour (Friedman, $\chi^2_{23} = 112.18$; $p < .001$). There were two mains peaks of consumption during the day. They ate more between 04:00 h and 10:00 h (mostly preceding the sunrise and food renewal), and between

17:00 h and 21:00 h (following the end of the caretakers' work and preceding the sunset). The cats ate less during two main troughs: between 01:00 h and 02:00 h and between 12:00 h and 15:00 h. For details, see appendix 2.

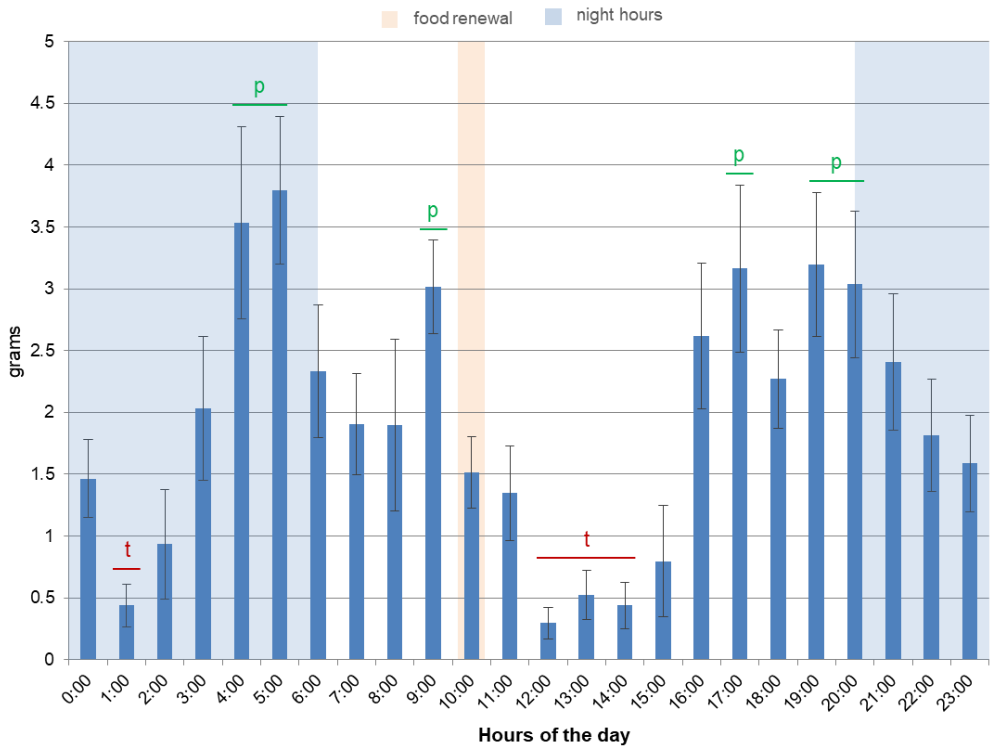


Figure 4 – Mean daily food consumption (grams) of the cats (n = 14) every hour.
Error bars represent standard errors, (p) indicates a significant peak, (t) indicates a significant trough.

3.3. Influence of sex

The males were significantly heavier than the females (6.41±0.26 kg versus 4.36±0.22 kg, respectively; t-test, $t_{12} = -6.071$, $p < .001$).

3.3.1. On locomotor behaviour

Males tended to cover more distance daily than the females (2.40±0.57 versus 1.09±0.26 km, respectively; Mann-Whitney, U = 10.0, p = .073). When looking at the division in 20-minute increments, the males covered significantly more distance than the females at several occasions during the day, as shown in figure 5.

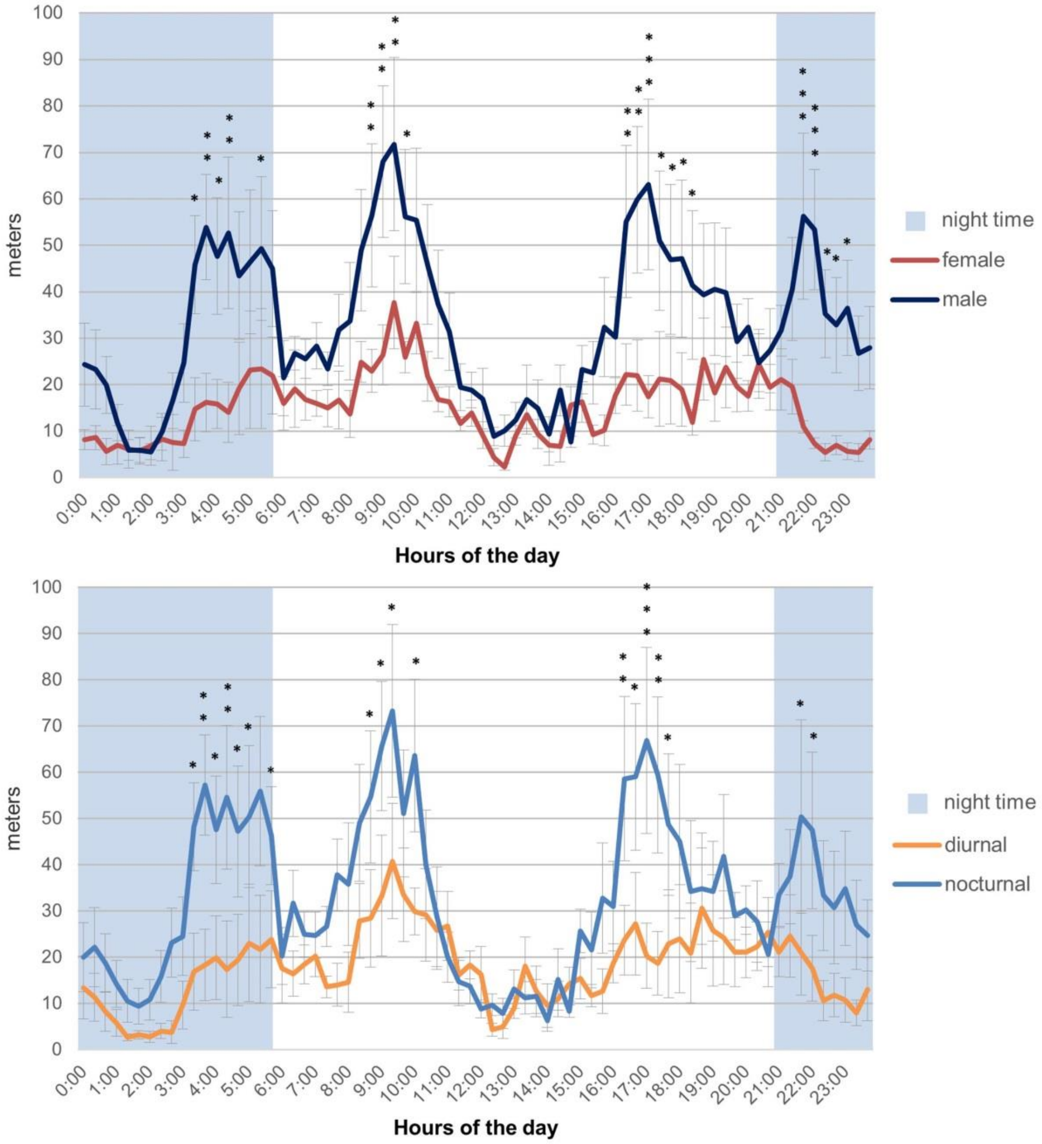


Figure 5 – Mean daily distance (meters) covered every 20min according to the sex (female (n = 7) vs male (n = 7), top) and according to the chronotype (diurnal (n = 8) vs nocturnal (n = 6), bottom). Error bars represent standard errors, (*) indicates p < .05, (**) indicates p < .01, (***) indicates p < .001.

The amplitude of the activity rhythm (AR) of the males tended to be higher than those of the females (533±70 versus 332±39, respectively; Mann-Whitney, U = 10.0, p = .073). The AR tended to be more interdaily stable in males than in females (0.45±0.03 versus 0.35±0.04, respectively; t-test, t_{12} = -1.971, p = .072). However, there was no significant difference concerning the intradaily variability (IV) of their AR (1.60±0.15 versus 1.66±0.10 for the males and females, respectively; t-test, t_{12} = 0.325, p = .751).

3.3.2. On eating behaviour

On a daily basis, the males ate significantly more food than the females (52.6±3.5 versus 40.2±5.6 g, respectively; Mann-Whitney, U = 7.0, p < .05). The amplitude of the feeding rhythm (FR) of the rhythmic cats, interdaily stability and intradaily variability of every cat did not significantly differ between the females and the males (Amplitude: 230±40 versus 267±28, respectively, t-test, t_9 = -0.758, p = .468; IS: 0.27±0.03 versus 0.33±0.02, respectively, t-test, t_{12} = -1.546, p = .148; IV: 2.14±0.13 versus 1.97±0.08, t-test, t_{12} = 1.444, p = .174). Nevertheless, it is worth noting that all the three arrhythmic cats in their eating behaviour (not taken into account when comparing the FR amplitude) were females.

The males ate significantly more food than the females in late night and late afternoon (fig. 6; Two-way RM ANOVA, interaction: $F_{71,\,852}$ = 1.590, p < .01). The females ate significantly more food than the males only at 20:20 (Holm-Sidak post-hoc test, p < .01).

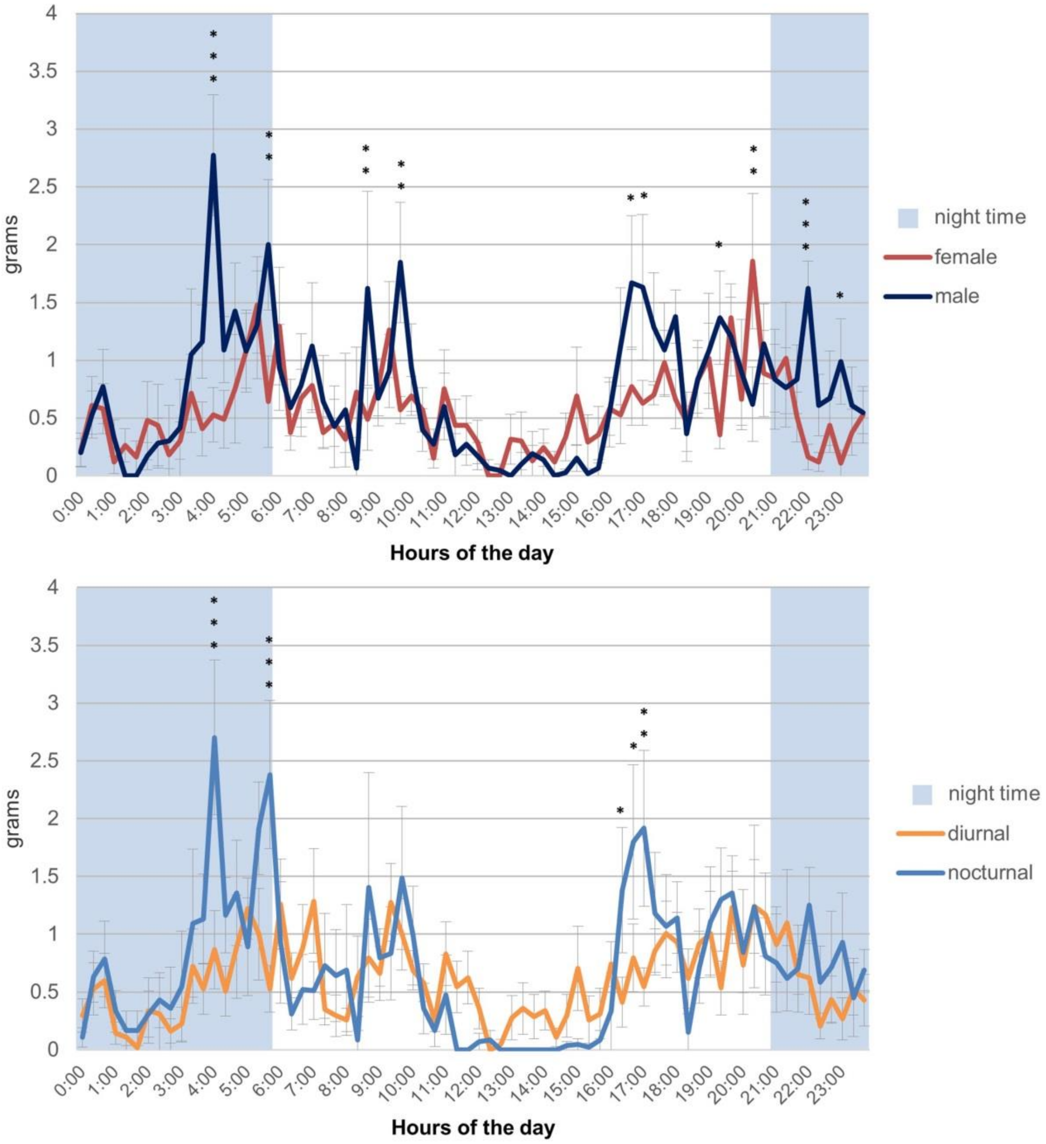


Figure 6 – Mean daily food consumption (grams) every 20min according to the sex (female (n = 7) vs male (n = 7), top) and according to the chronotype (diurnal (n = 8) vs nocturnal (n = 6), bottom). Error bars represent standard errors, (*) indicates p < .05, (**) indicates p < .01, (***) indicates p < .001.

3.4. Chronotype

Six females out of seven were categorised as globally diurnal, while five males out of seven were categorised as globally nocturnal. Feedograms of a nocturnal categorised male and of a diurnal categorised female are presented in the figure 7.

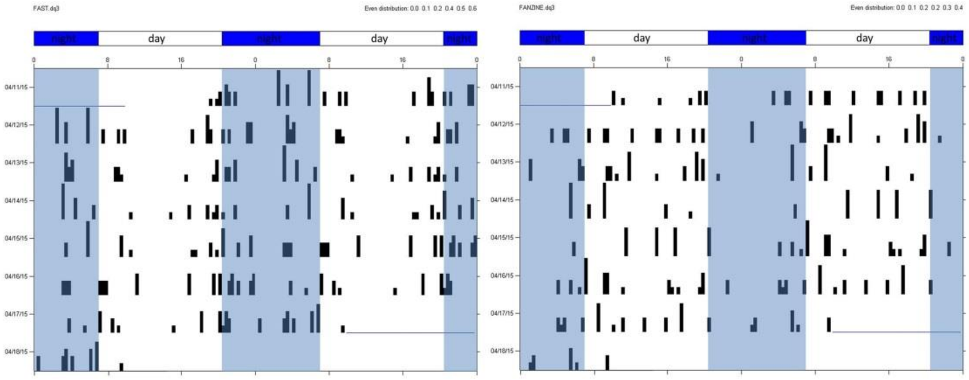


Figure 7 – Feedogram of a nocturnal categorised individual (left, male) and of a diurnal categorised individual (right, female)

3.4.1. *Locomotor behaviour according to the chronotype*

No statistical difference occurred between the chronotype concerning the daily covered distance (1.28±0.45 versus 2.37±0.49 km for the DIU and NOC, respectively; t-test, $t_{12} = 1.635$, $p = .128$). The amplitude of the activity rhythm (AR) of the nocturnal categorised individuals (NOC) was significantly higher than the amplitude of the diurnal categorised individuals (DIU) (t-test, $t_{12} = 3.448$, $p < .01$; fig. 8). The AR of the nocturnally categorised individuals was significantly more interdaily stable than the AR of the diurnally categorised ones (t-test, $t_{12} = 3.489$, $p < .01$; fig. 8), but no difference stood out concerning the intradaily variability (IV) of their AR (1.74±0.13 for the DIU; 1.48±0.09 for the NOC; t-test, $t_{12} = -1.553$, $p = .146$).

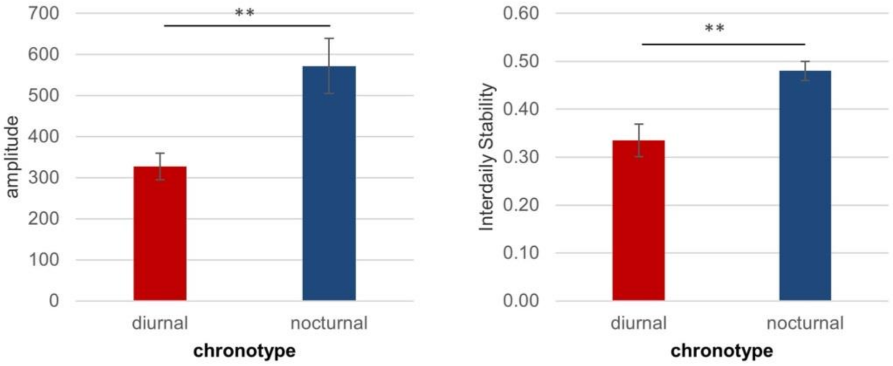


Figure 8 – Mean activity rhythm amplitude (left) and Interdaily Stability (right) according to the chronotype (diurnal (n = 8)/nocturnal (n = 6)). Error bars represent standard errors, (**) indicates p < .01.

The nocturnal individuals covered significantly more distance than the diurnal individuals most of the times (Two-way RM ANOVA, interaction: $F_{71,\ 852} = 2.274$, $p < .001$), except during daily troughs around midnight and midday (fig. 5).

3.4.2. Eating behaviour according to the chronotype

No statistical difference was detected between the daily consumption, amplitude, interdaily stability or intradaily variability of the feeding rhythm (FR) of the nocturnal individuals compared to the diurnal ones (consumption: 51±4 versus 43±6 g, respectively; t-test, $t_{12} = 1.064$, $p = .308$; amplitude: 276±19 versus 226±48, respectively; Mann-Whitney, $U = 7.00$, $p = .177$; IV: 1.99±0.06 versus 2.10±0.15, respectively; t-test, $t_{12} = -0.853$, $p = .410$). Albeit the nocturnal individuals tended to eat with a more interdaily stable rhythm than the diurnal ones (0.34±0.02 versus 0.27±0.02, respectively; t-test, $t_{12} = 2.088$, $p = .059$). Nevertheless, it is relevant to note that the only three arrhythmic cats in their eating behaviour (not taken into account when comparing the FR amplitude) were categorised as globally diurnal (diurnal rhythmic activity rhythm).

When looking at the consumption every 20 min, the nocturnal individuals ate significantly more food than the diurnal individuals (Two-way RM ANOVA, interaction: $F_{71,\ 852} = 1.458$, $p < .05$) at several times (fig. 6).

3.5. Locomotor versus feeding rhythms

The amplitude and interdaily stability (IS) of the locomotor rhythm (LR) were significantly higher than those of the feeding rhythm (FR) (Amplitude: 463±57 versus 253±23, respectively; paired t-test, $t_{10} = 3.872$, $p < .01$; IS: 0.40±0.03 versus 0.30±0.02, respectively, paired t-test, $t_{13} = 3.096$, $p < .01$). The intradaily variability (IV) of the locomotor rhythm was significantly lower than the IV of the feeding rhythm (1.63±0.09 versus 2.05±0.06, respectively; Wilcoxon, $Z = 2.542$, $p < .01$).

4. DISCUSSION

In this study, we investigated the locomotor activity and feeding rhythms in a colony of domestic cats living collectively and having *ad libitum* access to dry food and water. Using precise and elaborate animal tracking methods, i.e. UWB and passive RFID technologies, we mainly observed bimodality in the activity and feeding rhythms of these indoor cats with crepuscular peaks. Their bimodal patterns were not affected by sex or chronotypes.

Hawking et al. (1971) described many short bursts of activity distributed irregularly throughout the 24h period, with no evidence of a daily cycle in a laboratory isolated cat. On the same year, Kavanau (1971) agreed in classifying the activity of the cat as arrhythmic. Nevertheless, the very small sample size in both studies (n = 1) and short recording period (8 and 7 days in Hawking et al. (1971) and Kavanau (1971), respectively) make this conclusion doubtful. Recording the behaviour of more numerous individuals on a longer period, we have demonstrated 24 hour-periodicity of locomotor and eating behaviour in every cat or almost every cat (11 out of 14), respectively.

The least active 5 hours (L5), previously used only once on the activity rhythms in cats (Piccione et al., 2013), have proved to be a pertinent rhythmic parameter (i.e. phase-marker) to compare in our study. They indeed corresponded to the main daily trough: the hours of the day when the cats were significantly moving and eating less coincided with the locomotor activity and eating L5, occurring either in the middle of the night, or in the middle of the day. The nocturnal decrease of activity in eight out of the 14 cats reminds the results of Hawking et al. (1971) who noted the total duration of activity of a laboratory cat during light was about 1.4 times that of the activity during night during a 12h light-dark cycle.

Besides, the rhythmic behaviours of eating and locomotor activity of the cats were notably impacted by twilight, as already observed in the literature (Dards, 1979; Haspel & Calhoon, 1993; Izawa, 1983; Jones & Coman, 1982; Kavanau, 1971; Kuwabara et al., 1986; Podberscek et al., 1991). The many authors who reported peaks of activity at dawn and dusk sometimes characterised these specific moments as key periods in biological and ecological processes as prey activity, food condition, body temperature, or colonic motility (Goszczyński et al., 2009; Izawa, 1983; Jones & Coman, 1982; Konecny, 1987; Randall et al., 1987). In our colony, when looking at the daily activity and eating graphs according to the hour of the day, consumption and activity peaks were indeed noted mainly preceding sunrise (between 04:00 h and 06:00 h) and sunset (between 16:00 h and 21:00 h), especially in the most active group (B). Positive modulators of these peaks also relied on anticipation of food renewal in the morning and end of human presence in the late afternoon. Yet, if the cats showed ultradian rhythms with period of six hours or less rather than bimodal 24-h rhythms, peaks in the periodograms would then rise around six hours or at lower periods. This was not the case, i.e. based on periodograms, the cats showed only significant peaks at 24 hours and shorter ones at 12 hours. Therefore, we conclude of two main daily peaks of locomotor activity and food consumption, corresponding mostly on anticipation of twilights (i.e., sunrise and sunset).

A great interindividual variability was observed in the eating and activity behaviour of this population, as regularly found in the literature (e.g. Mugford and Thorne, 1980; Johnson et al., 1983; Randall et al., 1987; Refinetti et al., 2016). The sex of the cats was a factor that significantly impacted their behaviour. The males, heavier than the females, tended to be more active and were more rhythmic in their locomotor behaviour as shown by a trend for larger daily amplitude and lower interdaily stability. They ate significantly more than the females and none of them were arrhythmic in their eating behaviour, contrary to three females out of seven. When looking at the mean hourly covered distance and consumption, we noticed that the sex differences only happened at the peak hours, while both males and females diminished their activity and consumption simultaneously in the middle of the day and middle of the night.

Based on actogram characteristics, L5 values, and nocturnal and diurnal activity/consumption rates, we attempted to further investigate differences among individuals by categorising them according to typical dominant chronotypes: diurnal versus nocturnal. The main difference between diurnal categorised individuals and nocturnal categorised individuals resides in the more pronounced peaks of activity and consumption at twilights in the nocturnal categorised ones, while the activity and consumption troughs are similar between the two types of individuals. Therefore, the chronotype categorisation, which has been commonly used in other species, is difficult to highlight in the cats, which echoes the variable and contradictory categorisations in the literature (e.g. Kanarek, 1975; MacDonald & Apps, 1978; Walls, 1942). Refinetti et al. (2016) noticed the chronotype spread (i.e. a measure of the variability of chronotypes among individuals) was the greatest in cats (23 h) compared to 15 other species, concluding the diurnal-nocturnal dichotomy should not apply to cats, as some individuals are mostly active at day while others are mostly active at night. Furthermore, for Refinetti (1996), an absence of daily rhythm in the body temperature of the cat as found in the study of Hawking et al. (1971) indicates how the cat distinguishes itself from pure nocturnal species or diurnal species for which the body temperature reaches its acrophase respectively during the night or during the day.

No general pattern emerged according to the chronotype categorisation. Nevertheless, regular peaks in the feeding rhythm, and mostly in the activity rhythm of the cats, have decidedly been demonstrated in every cat, along a 24-hours periodicity. More precisely, most cats showed two main peaks and troughs in the day, different from typical circadian rhythms where only one main peak and one main trough are usually demonstrated. Bimodality, more than chronotypes, seems therefore the best way to categorise the activity and feeding rhythms of the cats. Accordingly, Randall et al. (1987) suggested that “two peaks may be the one factor that is common to the idiosyncratic patterns of entrainment in this species” and Refinetti et al. (2016) detected bimodality in the activity rhythm of cats while chronotypes varied greatly among individuals.

It is worth noting that some individuals - the nocturnal categorised ones - ate practically not at all in the middle of the day (between 11:20 and 15:00 h). This highly pronounced trough, studied on a seven days collection period, should constitute a pertinent feature for the eating behaviour of this species.

Systematically, the locomotor behaviour of the cats was more rhythmic than their eating behaviour: the activity rhythm of the cats was proved to have higher rhythm amplitude, interdaily stability, less intradaily variability, and every cat showed a 24 hours periodicity in their activity rhythm, while three cats were arrhythmic in their eating behaviour. This difference in rhythmicity may explain the less pronounced differences between categories in the feeding rhythm of the cats, than in the locomotor activity rhythm. Besides, this observation may be due to the opportunistic nature of this solitary hunter which, in the wild, feeds on several small preys per day with various rhythms (notably, diurnal birds and nocturnal rodents) and may therefore display flexibility in its eating patterns to adapt to the daily rhythms of its preys, as suggested by Konecny (1987).

One difficulty in the analyses of this study relied in group differences. The mean daily covered distance differed significantly between them, group B being more active. This may be explained by the fact that individuals of group B had been living together for five years, whereas two cats of group A were new to the group. Difference in activity rate might be due to avoidance, a common aspect in a solitary species in spite of large inter individual variation in tolerance: less tolerant individuals spending more time in avoiding other conspecifics.

Along with this difference in covered distance, a group effect affected sex and chronotype ratios: most cats of group B were males, most individuals of group A were females and males and females were mainly classified as nocturnal and diurnal, respectively. Therefore, we could not cross the sex and chronotype effects since it was not equally distributed, and could not distinguish the sex effect, the group effect and the chronotype effect from each other. Mainly, the males, nocturnal and from group B were more rhythmic and active than the females, diurnal and from group A. Nevertheless, this group difference is interesting as it underlines the plastic behavioural characteristic of this species, able to accommodate to group behaviours (Piccione et al., 2013). Furthermore, it would be interesting to establish whether intra-individual plasticity is stable or more variable with longer durations of data collection. It is noteworthy that cats of a same group showed very similar rhythms, while cats between the groups were more different. This social aspect of the species living collectively may confer an evolutionary advantage as it allows the individuals to adapt to various living conditions.

Variations in activity and food intake may be sensitive to exogenous factors, as temperature or photoperiod, and to human intervention. In our conditions, we could not standardise human activity due to time constraints imposed to technicians. This might have differentially affected the activity of the cats. A greater sample size and a standardisation of human activity might help in search of a daily rhythmicity in the cat's activity.

5. CONCLUSION

To conclude, we validated with this study the use of UWB and passive RFID tracking locomotor and eating tracking technologies in the analysis of the daily rhythms of the cat. This population of cats showed two main peaks of activity and consumption: in the morning, especially before sunrise and renewal of food, and in the evening, following the end of the work day of the animal staff of cattery and before sunset. The cats therefore displayed bimodality in their rhythms, along 24 hours periodicity, which is not affected by the sex of the cats. In order to better dissociate the influence twilights have on the cats' behaviour, a similar study on cats at different twilight times (e.g. according to seasons) could help clarify it. This would also enable to study the impact of day-length on the behaviour of cats.

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8. APPENDIX

Appendix 1 – Statistical significance of One-Way Repeated-Measures ANOVA comparing the distance covered by the cats every hour.

	01h00	02h00	03h00	04h00	05h00	06h00	07h00	08h00	09h00	10h00	11h00	12h00	13h00	14h00	15h00	16h00	17h00	18h00	19h00	20h00	21h00	22h00	23h00
00h00	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	**p<.01**	**p<.05**	*NS*	*NS*	*NS*	*NS*	*NS*	p<.1	p<.1	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
01h00		*NS*	**p<.05**	**p<.05**	**p<.05**	**p<.05**	**p<.05**	**p<.01**	**p<.01**	**p<.01**	**p<.05**	*NS*	*NS*	*NS*	*NS*	**p<.01**	**p<.01**	**p<.05**	**p<.05**	**p<.01**	**p<.01**	*NS*	*NS*
02h00			*NS*	*NS*	**p<.05**	*NS*	*NS*	**p<.05**	**p<.01**	**p<.01**	*NS*	*NS*	*NS*	*NS*	*NS*	**p<.01**	**p<.01**	p<.1	**p<.05**	**p<.05**	**p<.05**	*NS*	*NS*
03h00				*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
04h00					*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
05h00						*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	**p<.05**	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
06h00							*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
07h00								*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
08h00									*NS*	*NS*	*NS*	**p<.05**	p<.1	p<.1	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
09h00										*NS*	*NS*	**p<.01**	**p<.01**	**p<.01**	**p<.05**	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	**p<.05**	**p<.01**
10h00											*NS*	**p<.01**	**p<.05**	**p<.05**	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	p<.1
11h00												*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
12h00													*NS*	*NS*	*NS*	**p<.01**	**p<.01**	p<.1	**p<.05**	**p<.05**	**p<.05**	*NS*	*NS*
13h00														*NS*	*NS*	**p<.05**	p<.1	*NS*	*NS*	*NS*	p<.1	*NS*	*NS*
14h00															*NS*	**p<.05**	**p<.05**	*NS*	*NS*	*NS*	p<.1	*NS*	*NS*
15h00																*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
16h00																	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
17h00																		*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
18h00																			*NS*	*NS*	*NS*	*NS*	*NS*
19h00																				*NS*	*NS*	*NS*	*NS*
20h00																					*NS*	*NS*	*NS*
21h00																						*NS*	*NS*
22h00																							*NS*

Appendix 2 – Statistical significance of One-Way Repeated-Measures ANOVA comparing the food consumption of the cats every hour.

	01h00	02h00	03h00	04h00	05h00	06h00	07h00	08h00	09h00	10h00	11h00	12h00	13h00	14h00	15h00	16h00	17h00	18h00	19h00	20h00	21h00	22h00	23h00
00h00	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
01h00		*NS*	*NS*	p<.1	**p<.01**	*NS*	*NS*	*NS*	**p<.05**	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	**p<.05**	*NS*	**p<.05**	**p<.05**	*NS*	*NS*	*NS*
02h00			*NS*	*NS*	**p<.05**	*NS*	*NS*	*NS*	**p<.05**	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
03h00				*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
04h00					*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	**p<.05**	**p<.05**	**p<.05**	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
05h00						*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	**p<.01**	**p<.01**	**p<.01**	**p<.01**	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
06h00							*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
07h00								*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
08h00									*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
09h00										*NS*	*NS*	**p<.01**	**p<.05**	**p<.01**	**p<.05**	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
10h00											*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
11h00												*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
12h00													*NS*	*NS*	*NS*	p<.1	**p<.05**	**p<.05**	**p<.05**	**p<.05**	*NS*	*NS*	*NS*
13h00														*NS*	*NS*	*NS*	**p<.05**	*NS*	**p<.05**	**p<.05**	*NS*	*NS*	*NS*
14h00															*NS*	p<.1	**p<.05**	p<.1	**p<.05**	**p<.05**	*NS*	*NS*	*NS*
15h00																*NS*	*NS*	*NS*	p<.1	*NS*	*NS*	*NS*	*NS*
16h00																	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
17h00																		*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
18h00																			*NS*	*NS*	*NS*	*NS*	*NS*
19h00																				*NS*	*NS*	*NS*	*NS*
20h00																					*NS*	*NS*	*NS*
21h00																						*NS*	*NS*
22h00																							*NS*

TRANSITION…

This first study validated the use of our tracking technologies as well as of adapted chronobiological parameters to assess the rhythm of cats living indoors at the cattery of Royal Canin. It gave us a first glimpse of the daily rhythmicity of the cat in these conditions, which showed a periodicity of 24 hours. Through this analysis, we also noted the futility of trying to categorise the cat as strictly diurnal or nocturnal, since bimodality characterises its locomotor and feeding rhythms, driven by crepuscular peaks. The impact of twilight therefore appears decisive in the daily pattern of cats. In order to investigate this effect as well as the daily rhythm of the cat on an annual basis, we conducted a second study on a population of indoor cats at the same cattery during the 4 seasons. This enables the study of seasonal impact, especially photoperiod duration, on the behaviour of indoor individuals. In addition, we this time standardised human intervention schedules so as to reduce human disturbance on the daily rhythms of the cats and recorded behaviour over longer periods (21-days).

ARTICLE 2

AIM: ASSESS SEASON IMPACT ON THE DAILY RHYTHMS OF INDOOR CATS

SEASONAL IMPACT ON LOCOMOTOR AND FEEDING RHYTHMS IN INDOOR CATS

Parker Marine*[a], Challet Etienne[a], Deputte Bertrand[b],
Ract-Madoux Brunilde[c], Faustin Marie [d], Serra Jessica[d]

[a] Institut des Neurosciences Cellulaires et Intégratives (INCI), CNRS, Université de Strasbourg, 8 allée du général Rouvillois, 67000 Strasbourg, France

[b] Ecole Nationale Vétérinaire d'Alfort (ENVA), 7 Avenue du Général de Gaulle, 94700 Maisons-Alfort, France

[c] Scientific consultant, Paris, France

[d] Royal Canin Research center, 650 avenue de la petite Camargue, 30470 Aimargues, France

*corresponding author: Parker Marine, marineparker@gmail.com

ABSTRACT

Different synchronisers can modify daily rhythms during an annual cycle. Nevertheless, the fluctuation of these external factors is often ignored in studies on the locomotor activity and feeding rhythms of the cats focused on single seasons. To fill this gap, the activity and feeding rhythms of six cats living in a cattery panel, receiving natural daylight, were followed during 3 weeks for each season. Although under minimal influence of seasonal fluctuations in ambient temperature and humidity, the cats nevertheless showed maxima in distance covered daily during spring and autumn, minima in both distance and food intake during winter. The rhythms followed 24 hours periodicity at all seasons and bimodality was detected in the activity and feeding rhythms of the cats, with decreased covered distance and food intake around mid-night and mid-day. These troughs were robust and stable across seasons, whereas the inter-seasonal differences in activity level resided in the peaks. However, the eating daily pattern was less impacted 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 impact seems 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.

Key words: *Cat, seasons, feeding pattern, locomotor activity, daily rhythms, crepuscularity*

1. INTRODUCTION

Understanding how cats daily and seasonally manage their locomotor activity and feeding behaviour under natural day-light would provide a strong basis for better management of their needs in different environments. While some authors consider the domestic cat as arrhythmic (Hawking et al., 1971; Kavanau, 1971), observations of individually housed cats (Kuwabara et al., 1986), feral, farm or free-roaming cats (Horn et al., 2011; Jones & Coman, 1982; Langham & Porter, 1991; Macdonald & Apps, 1978; Moon et al., 2013; Romanowksi, 1988) and suburban house cats (Barratt, 1997), lead other authors to classify the individuals as night-active. Yet, other studies suspect diurnality in a laboratory cat (Hawking et al., 1971) and pet cats (Horn et al., 2011), possibly because of diurnal human impact. While authors do not always agree on this chronotype classification of the cat, a simple diurnal-nocturnal dichotomy is not applicable to some species. Several mammals like the degu (*Octodon degus*), the golden spiny mouse (*Acomys russatus*), or the tayra (*Eirabarbara*) and grison (*Galictis*) can spontaneously shift from diurnal to nocturnal activity patterns under particular environmental conditions (Kas & Edgar, 1999; Kavanau, 1971; Shkolnik, 1971). Besides, the cat is known for its interindividual variability as well as its behavioural plasticity, sometimes influenced by human presence (Piccione et al., 2013). During previous analyses (Parker et al., 2018), chronotypes did not prove to be a pertinent categorisation, as the only difference appeared in more pronounced peaks at twilights in the nocturnal categorised individuals. It could therefore be doubtful whether the concept of diurnality or nocturnality is applicable to domestic cats. In fact, Aschoff (1962, as cited in Randall et al., 1987) rejected nocturnal versus diurnal labels because the same individual may exhibit different patterns on different occasions. Refinetti et al. (2016) more recently emphasised the idea that the diurnal-nocturnal dichotomy should not apply to the domestic cat, as their chronotype spread (measuring the variability of chronotypes among individuals) was the highest compared to 15 other mammalian species ranging from Indian field mouse to cows, meaning some cats are mostly active at day while others are mostly active at night.

As day-lengths and twilights (i.e. sunrise and sunset) vary across seasons, one could expect animal behaviours 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 behaviour. Twilight onsets vary across seasons, yet, regular peaks of activity in the cat near dawn and dusk, whether natural or artificial, have been described in many studies (Dards, 1979; Haspel & Calhoon, 1993; Izawa, 1983; Jones & Coman, 1982; Kappen et al., 2013; Kavanau, 1971; Kuwabara et al., 1986; Parker et al., 2018; Podberscek et al., 1991), showing a tendency towards being crepuscular.

Free-roaming cats are also subject to seasonal change. Romanowski (1988) first reported more locomotor activity in summer and spring, least in winter. These findings were later confirmed in

Brooklyn (USA) where a decline of the activity levels throughout autumn and an increase in spring was detected (Haspel & Calhoon, 1993). A decrease of the home ranges of farm cats in winter compared to other seasons was also reported in a Swiss mountainous area (Weber & Dailly, 1998). Dards (1979), witnessing similar variations in dockyard cats of Portsmouth (UK), considers these differences in activity patterns are probably due to differences in day length. In fact, Goszczyński (2009), who noted the fewest cats from November to March and the most in June and August in rural areas of central Poland, demonstrated that the density index correlated positively with average monthly temperature and with day-length. However, these seasonal variations in activity amount were also observed in laboratory conditions where temperature remained constant: during long-day conditions (8 hours of darkness, 16 hours of light), group housed neutered male cats showed higher total activity than cats under short-day conditions (16 hours of darkness, 8 hours of light), primarily due to an increase in dark period activity (Kappen et al., 2013).

Nevertheless, other publications reported different amounts in locomotor activity according to the season. Summer maxima and winter minima were indeed observed in feral cats in Australia, but along spring minima, assumably caused by emigration (Jones & Coman, 1982). In New-Zealand, the home ranges of adult feral males were larger in summer but also in winter (Langham & Porter, 1991). These last findings recall those of Horn et al. (2011) who observed greatest activities in “unowned” cats -i.e. not observed being fed or cared for by humans- in Illinois (USA) 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”. For their part, “owned” cats -i.e. fed and cared by humans and partly living in human dwellings- had slightly depressed activity in January-February but also in August-September.

While peaks of activity constantly occurred at dusk through the year in the results of Izawa on feral cats in Japan (1983), house cats in rural areas presented a two-peaked activity pattern in spring and summer in Poland (Goszczyński, 2009). These findings are in accordance with the observations of Jones & Coman in Australia (1982) where peaks occurred near dawn and dusk and lows occurred near midday during the warm season of the year. The cats however showed a more stable activity pattern throughout the day during the cold seasons. Feral cats in Japan shifted their active time seasonally from a nocturnal habit in summer to a more diurnal habit in winter (Izawa, 1983).

The plasticity of the behaviour of the cat, able to adjust to food availability to maintain its energy balance, is well suited to its life style as an opportunistic feeder. Therefore, its changeable activity rhythm is in accordance with the adaptability this predator must show regarding the variety of the rhythms of its preys (Konecny, 1987): rodent preys are usually nocturnal while most song birds are diurnal. It seems that no cyclicity has yet been clearly discerned regarding eating habits in cats so far.

For most authors, the feeding pattern of the cat is entirely random, some pointing out the large variability between individuals (Johnson et al., 1983; Kane et al., 1981; Mugford, 1977; Mugford & Thorne, 1980; Randall et al., 1985; Thorne, 1982). In fact, Thorne (1982) suggested that the cat has a behavioural repertoire containing different patterns of feeding, each being used when appropriate. The cat could therefore adapt its feeding behaviour according to the fluctuating seasonal conditions.

Photoperiod is known to cause physiological changes in seasonal mammals, including changes in body weight (Ebling, 2014). 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 the increasing photoperiod had significantly more chance to develop obesity at 9 years (Cave et al., 2018). Yet, 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 increased 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). Yet, a longer study on a larger and more varied population with *ad libitum* access to food (Serisier et al., 2014) found food intake was least in summer months and greatest during late autumn and winter, presuming feeding behaviour occurred in response to changes in energy for thermoregulation. Periods of peak and trough in food intake coincided with peaks and troughs in both temperature and daylight length.

Effects of the natural light-dark (LD) cycle 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 cats' activities had to be carried out by direct observation or in laboratories. Yet, as our understanding of the effect of photoperiod on the feeding and activity rhythm in domestic cats improves, this could be used to develop season-specific feeding and housing recommendations. 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.

2. MATERIAL AND METHODS

2.1. Animals and conditions

One group of 6 cats, 7 month-old at the beginning of the experiment, was studied. This group constituted in 5 spayed females and 1 castrated male of different breeds (Exotic shorthair, American shorthair, Selkirk rex and Selkirk straight shorthair).

They 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 22.5m² (6.4m (l) x 3.51m (w) x 2.60m (h)) as well as in an inner courtyard of 7m² (2.9m (l) x 2.4m (w) x 2.60m (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 (fig. 1). In the main room, the cats had free access to a wall shelf containing several hiding places and cushions and to an area containing several cat toys, a wall scratching post, a feeding area, a water bowl and a litter tray. In the courtyard, the cats had access to two cat trees containing cushions and another litter tray.

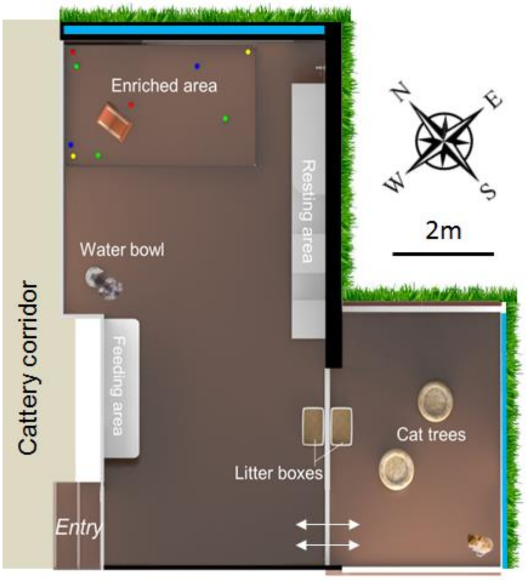

Figure 1 – Map of the study room (light blue lines represent the location of the bay windows)

The cats were exposed to natural light/dark cycle through large windows. The cycle averaged 14h21 of daily light period in spring, 14h56 of light in summer, 09h51 of light in autumn and 09h56 of light in winter.

2.2. Recording periods

The cats were observed continuously and simultaneously during 21 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 behaviour 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 days of recording took place after a week of habituation to let the cats acclimate themselves to the study conditions (feeding, human interventions, collars). In autumn, however, the locomotor activity recordings was restricted to a period between the 8th and 19th of November 2016 because of technical difficulties.

2.3. 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 animal caregivers entered the panel everyday 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 panel.

2.4. 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 consumptions (see Parker et al. 2018 for more details). These tags had no adverse effect on the physical condition of the animals and were accepted without behavioural disturbance. This protocol was approved by Royal Canin’s ethical committee.

2.5. Rhythm analyses

The same rhythm parameters were calculated and compared as in our previous study (Parker et al. 2018): the period (duration of a full cycle, ≈24h for a circadian rhythm) 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 (invariability between the days), Intradaily Variability (indication of the fragmentation of the rhythm) and onset of the least active 5 hours were calculated by the ActiWatch software (v. 7.31). 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 vs day hours), using the sunrise and sunsets hours as phase references. An individual was considered to show a tendency towards bimodality (period of 12 hours) when the magnitude of the 12h-peak was equal or superior to half of the 24h-peak (highest one) on its periodogram.

2.6. Statistical analyses

Every statistical comparison was made with Sigmaplot (v. 13.0, Systat Inc., San Jose, California, USA). The individuals being the same among the seasons, tests with repeated measures were conducted. One-way ANOVAs with repeated measures were performed to compare the daily covered distance and food consumption, 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 light 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 analyses of variances (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, as well as to compare the rhythm parameters according to the variable (activity versus feeding behaviour) and the data every 20 minutes when looking at the 16h 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 ± standard error, with a significance threshold of $p < .05$ (* when $.01 \leq p < .05$, ** when $.001 \leq p < .01$, *** when $p < .001$ 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. Low-case is not to be compared to upper-case letters and vice versa.

3. RESULTS

3.1. Body weight

The indoor cats significantly gained body weight throughout the seasons ($F_{3, 15} = 62.99$, $p < .001$). They were heavier in summer (2.85 ± 0.15 kg) compared to spring (2.53 ± 0.11 kg; Holm-Sidak post-hoc test, $p < .01$) 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, $p < .001$).

3.2. Locomotor activity and behaviour

3.2.1. Locomotor rhythm

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

The activity rhythm amplitude of the cats, on average of 618 ± 53 (fig. 2A), as well as the intradaily variability of the activity rhythm, on average of 1.42 ± 0.06 (fig. 2B), were impacted by the season ($F_{3, 15} = 18.79$, $p < .001$ and $F_{3, 15} = 3.63$, $p < .05$, respectively). The amplitude was the highest and lowest in spring and autumn, respectively (Holm-Sidak post-hoc test, $p < .01$) and intermediate in summer and winter (Holm-Sidak post-hoc test, $p < .01$). The IV values in winter were higher than in autumn (Holm-Sidak post-hoc test, $p < .05$).

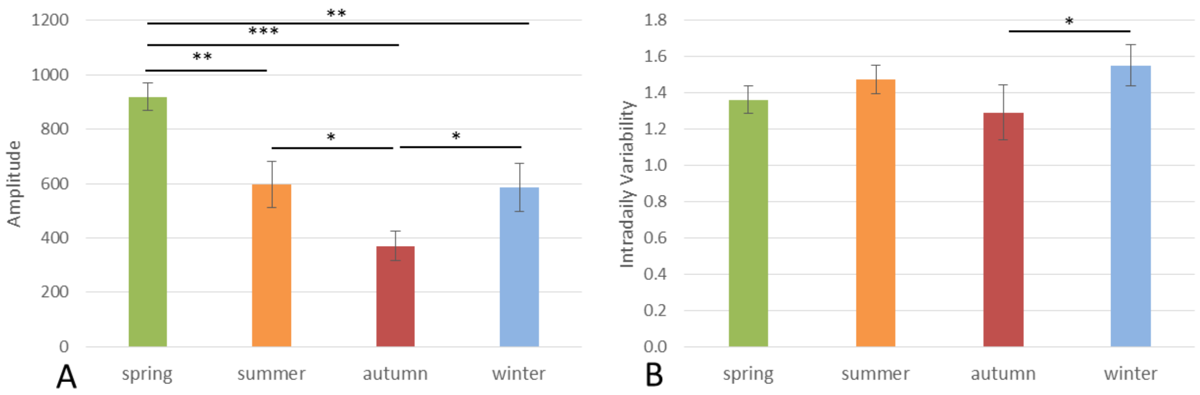

Figure 2 – Mean amplitude (A) and Intradaily Variability (B) of the activity rhythm of the cats (n = 6) according to the season. Error bars represent standard errors, (*) indicates p < .05, (**) indicates p < .01, (***) indicates p < .001.

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 ($F_{3,\ 15}$ = 2.55, p = .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.

3.2.2. Daily covered distance

The cats covered 2.11 ± 0.13 km per day, on average (fig. 3). This distance is impacted by the season ($F_{3,\ 15}$ = 32.82, p < .001), the cats covering the highest and least distance in spring and winter, respectively (Holm-Sidak post-hoc test, p < .001). Covered distance decreased in summer (Holm-Sidak post-hoc test, p < .01), but reached again the spring level in autumn.

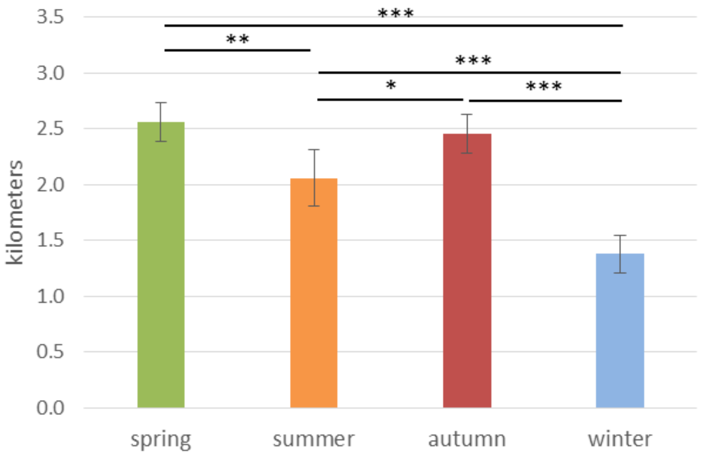

Figure 3 – Mean daily distance (km) covered by the cats (n = 6) according to the season. Error bars represent standard errors, (*) indicates p < .05, (**) indicates p < .01, (***) indicates p < .001.

3.2.3. Nocturnal versus diurnal activity rate

Daily, the cats covered significantly more distance during daytime than at night ($F_{1,\ 15}$ = 19.89, p < .01). There was an interaction between the lighting phase (day versus night) and the season ($F_{3,\ 15}$ =

8.71, p < .01). The cats covered significantly more distance during daytime than at night in spring (Holm-Sidak post-hoc test, p < .001) and summer (Holm-Sidak post-hoc test, p < .01), while daytime and night-time covered distances were very close in autumn or winter (Holm-Sidak post-hoc test, p > .1, fig. 4).

During daytime, the cats covered largest distance in spring (Holm-Sidak post-hoc test, p < .01), intermediate values in summer and autumn (Holm-Sidak post-hoc test, p < .01), and lowest distance in winter (Holm-Sidak post-hoc test, p < .01, fig. 4). At night, they covered significantly more distance in autumn than in winter (Holm-Sidak post-hoc test, p < .001), summer (Holm-Sidak post-hoc test, p < .05), and almost spring (Holm-Sidak post-hoc test, p = .075, fig. 4).

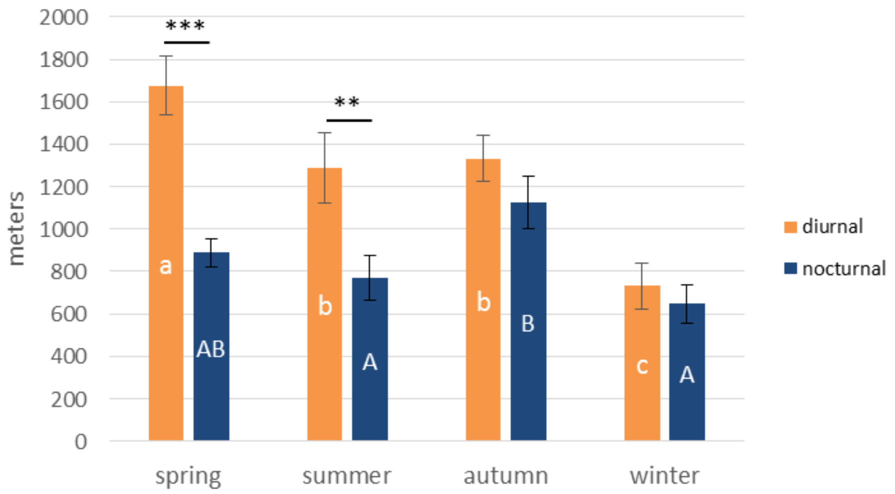

Figure 4 – Mean daily nocturnal and diurnal distance (m) covered by the cats (n = 6) according to the season. Error bars represent standard errors, (**) indicates p < .01, (***) indicates p < .001. Different letters represent a significant difference between data, similar letters represent a non-significant difference between data. Low-case is not to be compared to upper-case letters and vice versa.

Hourly, the cats also covered significantly more distance during daytime than at night ($F_{1, 15}$ = 13.79, p < .05). There was an interaction between the lighting phase (day versus night) and the season ($F_{3, 15}$ = 7.45, p < .01): they cover significantly more distance hourly at day than at night in spring (Holm-Sidak post-hoc test, p < .05), autumn (Holm-Sidak post-hoc test, p < .001) and winter (Holm-Sidak post-hoc test, p < .05, fig. 5).

During daytime, the cats covered significantly more distance hourly in autumn and spring (Holm-Sidak post-hoc test, p < .05), and less in summer and winter (Holm-Sidak post-hoc test, p < .01, fig. 5). 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 < .01, fig. 5).

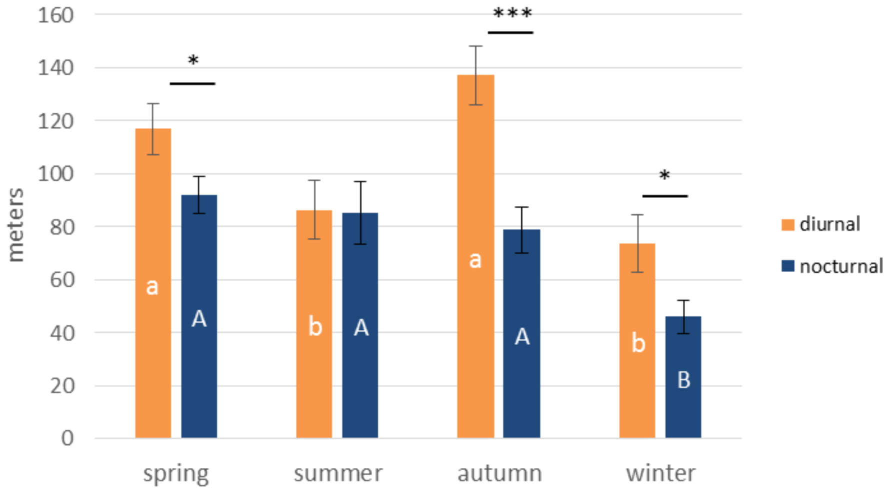

Figure 5 – Mean hourly nocturnal and diurnal distance (m) covered by the cats (n = 6) according to the season. Error bars represent standard errors, (*) indicates p < .05, (***) indicates p < .001. Different letters represent a significant difference between data, similar letters represent a non-significant difference between data. Low-case is not to be compared to upper-case letters and vice versa.

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, it took place at night for 5 cats (onset between 20:00 and 22:00), and during daytime for the one left (onset at 10:00).

3.2.4. Mean activity rhythm during the day

The hour of the day had an impact on the covered distance of the cats ($F_{23,\ 115}$ = 21.02, p < .001 in spring; $F_{23,\ 115}$ = 9.74, p < .001 in summer; χ^2_{23} = 83.34, p < .001 in autumn; χ^2_{23} = 104.03, p < .001 in winter).

At 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 (fig. 6). 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 at 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).

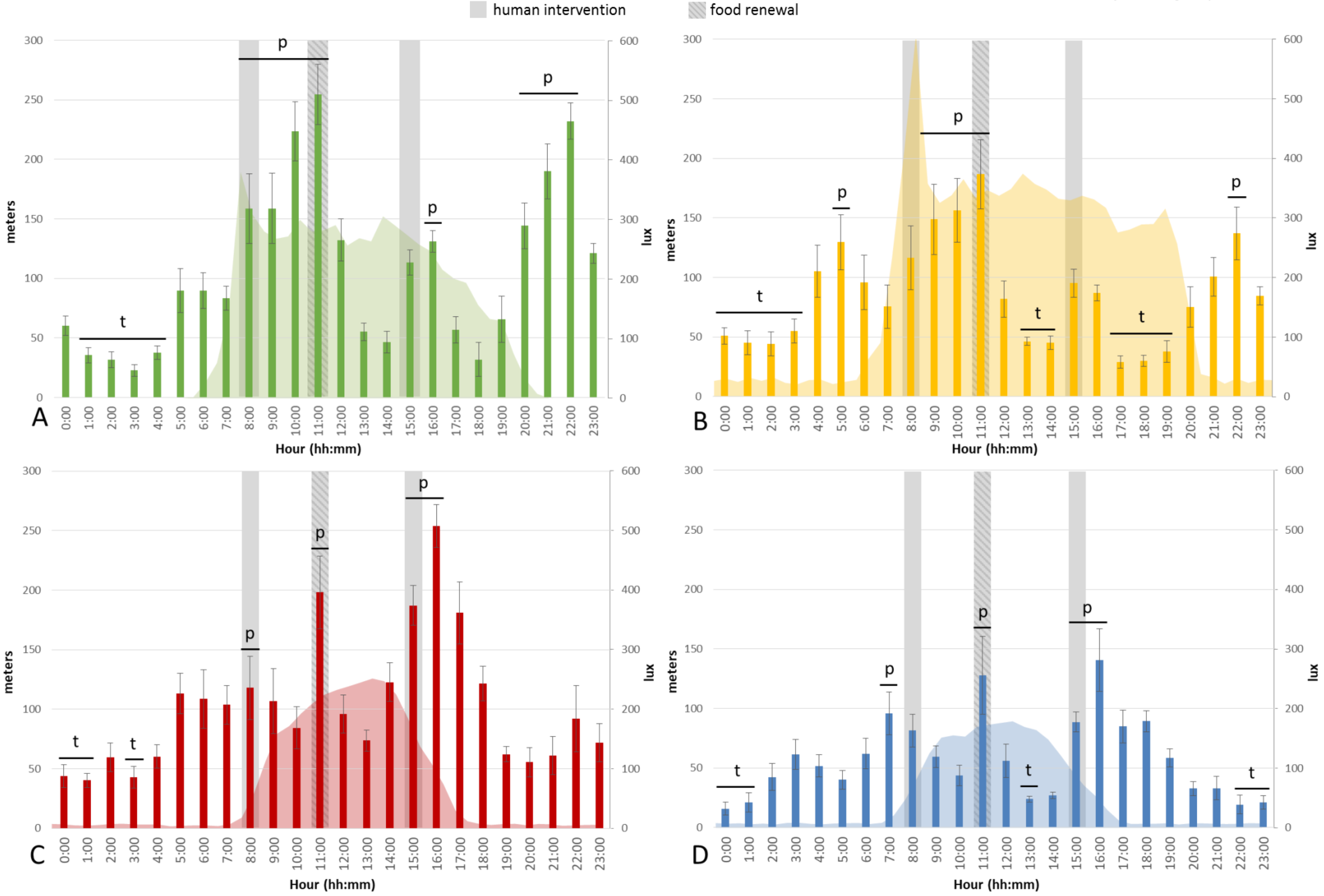

Figure 6 – Mean distance (m, bars) covered by the cats (n = 6) and luminosity (lux, area) every hour (hh:mm) in spring (green, A), summer (yellow, B), autumn (red, C) and winter (blue, D). Error bars represent standard errors, (p) indicates a significant peak, (t) indicates a significant trough.

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 (fig. 7): in spring, the evening peak is significantly higher than during the other seasons (Holm-Sidak post-hoc test, p < .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 < .001). In winter, the least active season, the peaks are less pronounced.

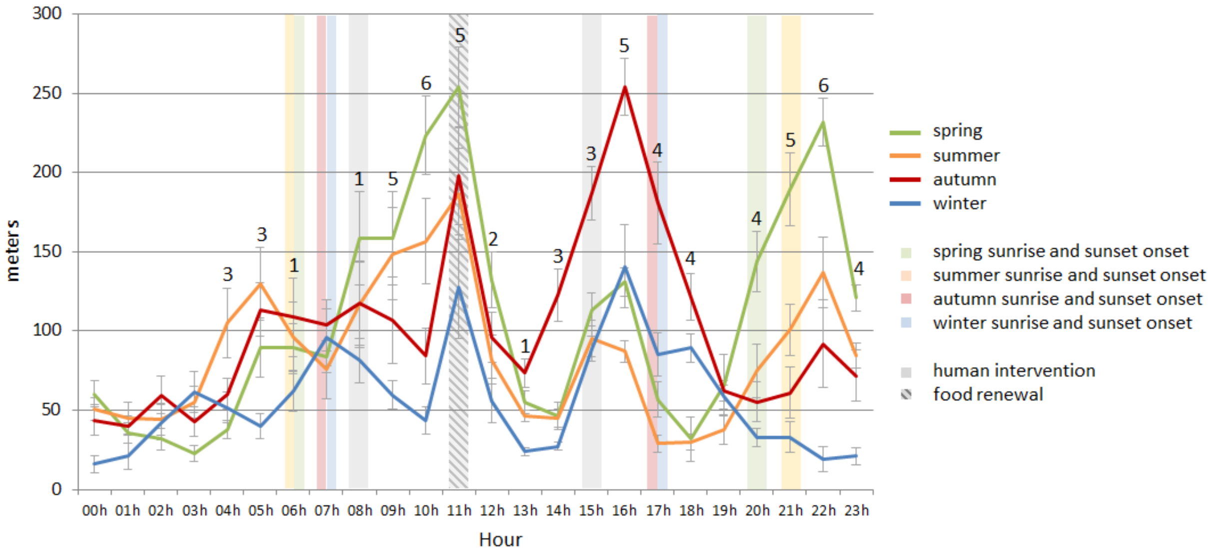

Figure 7 – Mean distance (m) covered every hour by the cats (n = 6) throughout the day according to the season. Error bars represent standard errors, 1/2/3/4/5/6: one/two/three/four/five/six significant difference(s) among the seasons.

3.2.5. 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 (20min) between 15:00 and 17:00 (fig. 8A). 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 < .001).

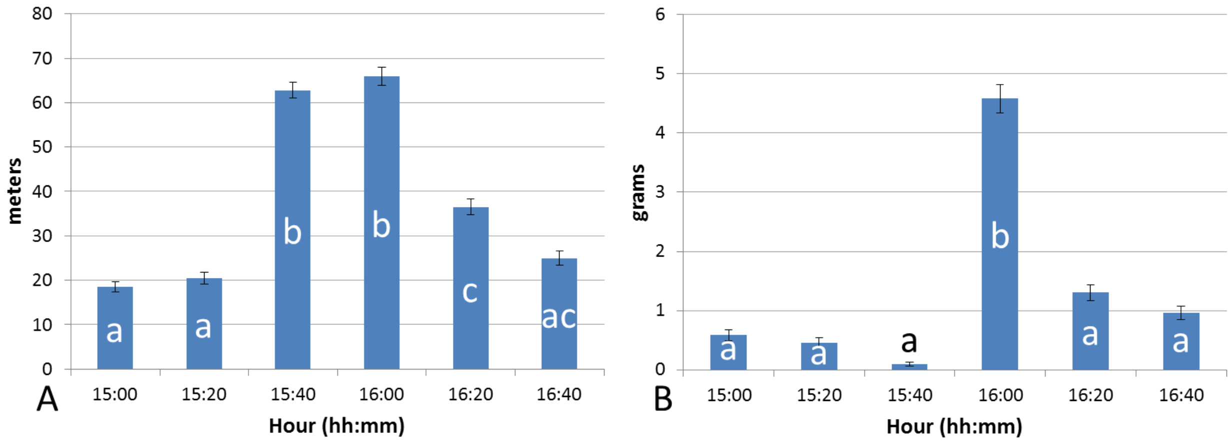

Figure 8 – Mean covered distance (m, A) and food intake (g, B) of the cats (n = 6) every 20min between 15:00 and 17:00. Error bars represent standard errors. Different letters represent a significant difference between data, similar letters represent a non-significant difference between data.

3.3. Feeding rhythm and behaviour

3.3.1. Feeding rhythm

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

The amplitude of their feeding rhythm, of on average 178 ± 24 (fig. 9), was impacted by the season ($F_{3,\ 15}$ = 5.81, p < .01), being higher in winter than in spring (Holm-Sidak post-hoc test, p < .05) and in summer (Holm-Sidak post-hoc test, p < .05).

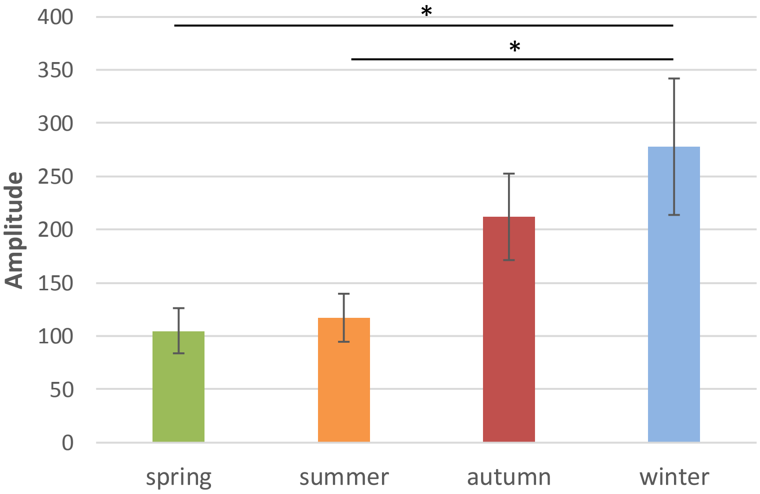

Figure 9 – Mean amplitude of the feeding rhythm of the cats (n = 6) according to the season. Error bars represent standard errors, (*) indicates p < .05.

The interdaily stability of the feeding rhythm of the cats averaged 0.34 ± 0.04 (fig. 10A). It was impacted by the season ($F_{3,\ 15}$ = 7.08, p < .01), with higher values in autumn than in summer (Holm-Sidak post-hoc test, p < .01), spring (Holm-Sidak post-hoc test, p < .01) and almost winter (Holm-Sidak post-hoc test, p = .088). The intradaily variability of the feeding rhythm averaged 1.92 ± 0.09 (fig. 10B). It was also impacted by the season ($F_{3,\ 15}$ = 6.53, p < .01), being the lowest in autumn (Holm-Sidak post-hoc test, .01 < p < .05).

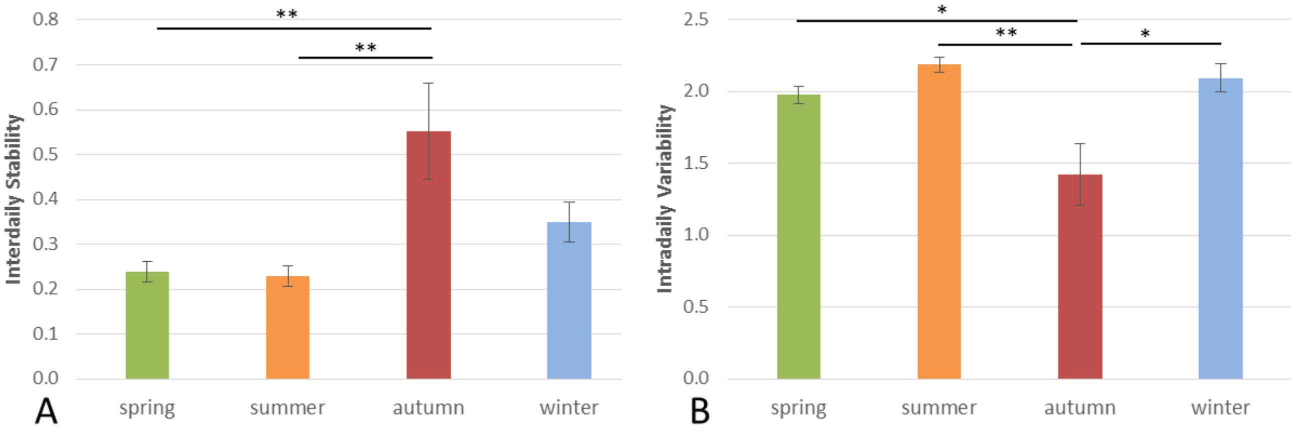

Figure 10 – Mean interdaily Stability (A) and Intradaily Variability (B) of the feeding rhythm of the cats (n = 6) according to the season. Error bars represent standard errors, (*) indicates p < .05, (**) indicates p < .01.

Many cats show tendencies towards bimodality in their 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.

3.3.2. *Daily food consumption*

The cats ate on average 53.9 ± 2.1 g per day without significant changes across the seasons ($F_{3, 15}$ = 3.37, $p > .05$ among seasons). However, season had an impact on the amount of ingested food by kilogram of the weight of the cats ($F_{3, 15}$ = 10.99, $p < .001$, fig. 11). It was significantly lower in winter than in spring (Holm-Sidak post-hoc test, $p < .001$) or summer (Holm-Sidak post-hoc test, $p < .01$).

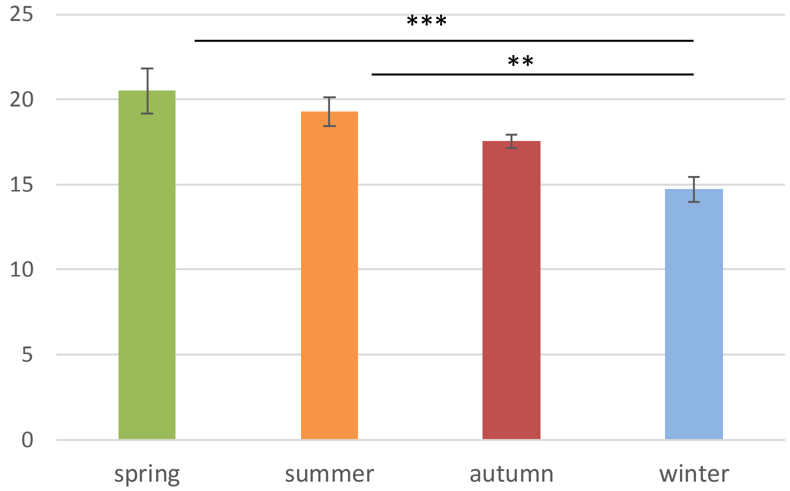

Figure 11 – Mean relative daily food consumption (grams per kilogram of cat weight) of the cats (n = 6) according to season. Error bars represent standard errors, (**) indicates p < .01, (***) indicates p < .001.

3.3.3. *Nocturnal versus diurnal consumption*

The lighting period (night versus day) had no impact on the daily nor on the hourly mean consumption of the cats ($F_{1, 15}$ = 2.59, $p = .169$ and $F_{1, 15}$ = 1.03, $p = .357$, respectively).

In spring and winter, the 5 hours during which the cats eat 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).

3.3.4. *Mean feeding rhythm during the day*

The hour of the day had an impact on the food intake of the cats (χ^2_{23} = 81.67, $p < .001$ in spring; χ^2_{23} = 81.95, $p < .001$ in summer; χ^2_{23} = 64.89, $p < .001$ in autumn; χ^2_{23} = 83.51, $p < .001$ in winter).

At all season, 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; fig. 12). 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.

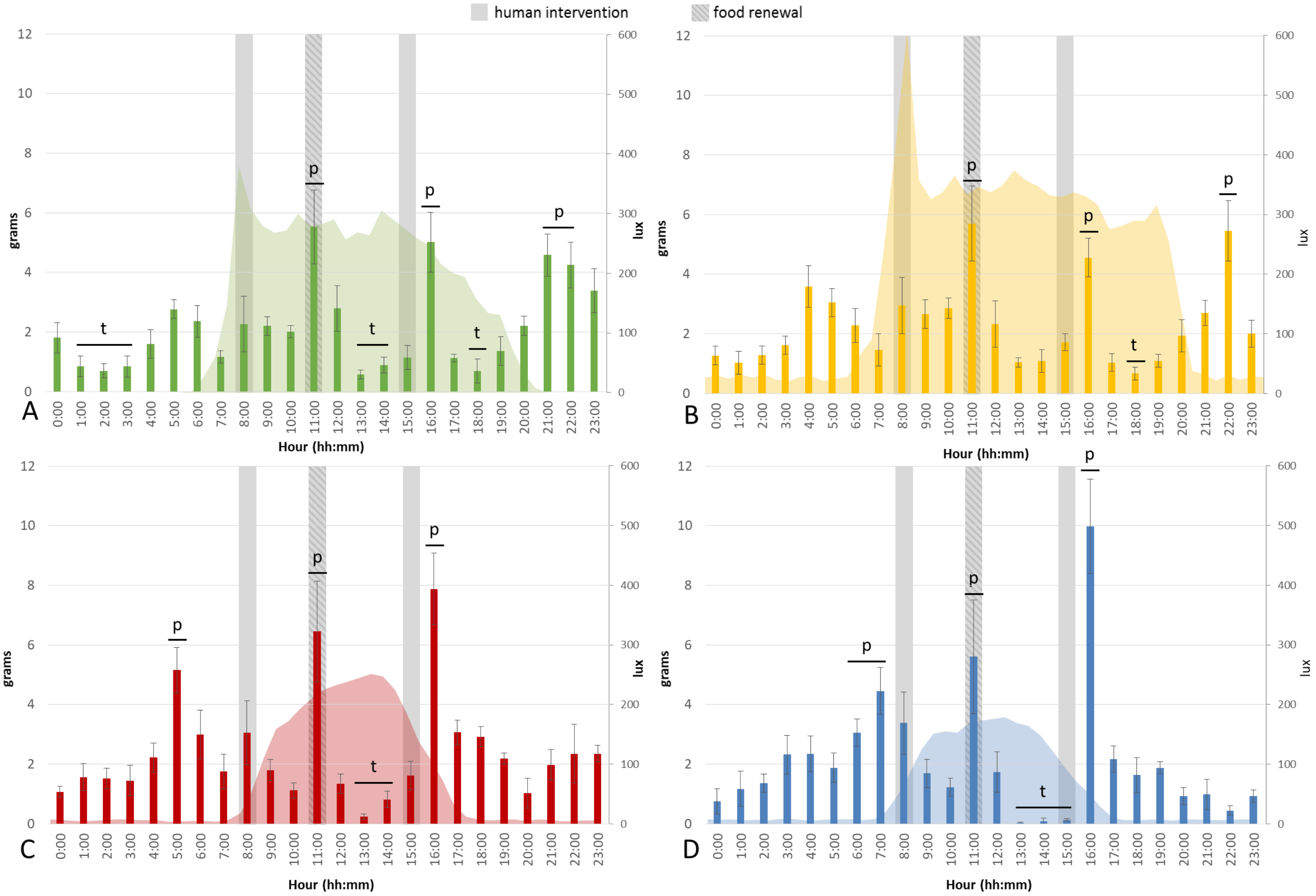

Figure 12 – Mean food consumption (g, bars) of the cats (n = 6) and luminosity (lux, area) every hour (hh:mm) in spring (green, A), summer (yellow, B), autumn (red, C) and winter (blue, D). Error bars represent standard errors, (p) indicates a significant peak, (t) indicates a significant trough.

There are fewer differences in the hourly consumption among the seasons, especially at 11:00 when no significant difference stands out (fig. 13). 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.

At all seasons, the cats ate the least in the middle of the night and in the middle of the day. It is interesting to see it even goes towards no consumption during the mid-day trough in winter.

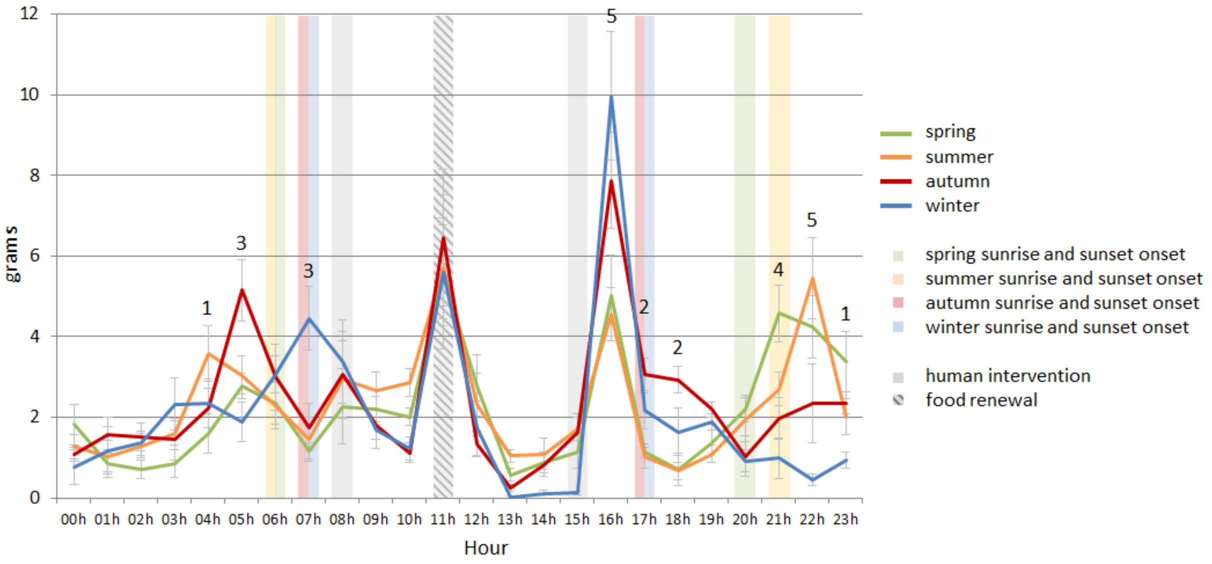

Figure 13 – Mean food consumption (g, every hour) of the cats (n = 6) throughout the day according to the season. Error bars represent standard errors.
1/2/3/4/5: one/two/three/four/five significant difference(s) among the seasons.

3.3.5. Examination around the 16-hour activity peak

The cats ate significantly more at 16:00 compared to the preceding 60 minutes or following 40 minutes (Holm-Sidak post-hoc test, p < .001, fig. 8B).

3.4. Feeding versus locomotor activity rhythm

The amplitude of the locomotor activity rhythm was significantly higher than that of the feeding rhythm (618 ± 53 versus 178 ± 24, respectively, $F_{1, 15} = 38.77$, $p < .01$) and the intradaily variability (IV) of the locomotor activity rhythm was significantly lower than that of the feeding rhythm (1.42 ± 0.06 versus 1.92 ± 0.09, respectively, $F_{1, 15} = 58.47$, $p < .001$). There was an interaction between the rhythm type (feeding versus activity) and the season ($F_{3, 15} = 19.63$, $p < .001$ for the amplitude; $F_{3, 15} = 3.76$, $p < .05$ for the IV, Tab. 1): the amplitude was higher and the IV lower in the locomotor activity rhythm than in the feeding rhythm of the cats in spring (Holm-Sidak post-hoc test, p < .001), summer (Holm-Sidak post-hoc test, p < .001), winter (Holm-Sidak post-hoc test, p < .01, p < .001, respectively), but not in autumn (Holm-Sidak post-hoc test, p = .103, p = .335, respectively).

No significant difference stood out between the feeding and the locomotor activity rhythms regarding their interdaily stability ($F_{1,\ 15} = 1.80$, p= .237). However, there also was an interaction between the rhythm type and the season ($F_{3,\ 15} = 6.05$, $p < .01$) so that the IS was higher in the locomotor activity rhythm than in the feeding rhythm of the cats in spring and summer (Holm-Sidak post-hoc test, $p < .01$, $p < .05$, respectively), but not in autumn or winter (Holm-Sidak post-hoc test, p = .156, p = .777, respectively).

	Variable	Amplitude		IS		IV	
	Rhythm	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

Table 1 – 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)

4. DISCUSSION

This study enabled us to assess the locomotor activity and feeding rhythms of the same individuals, under similar housing conditions, during continuous 24h-recording throughout a complete annual cycle. Contrary to previous statements about behavioural arrhythmicity in the cat (Hawking et al., 1971; Kavanau, 1971) or random patterns of eating (Kane et al., 1981; Johnson et al., 1983; Randall et al., 1985; Thorne, 1982; Mugford & Thorne, 1980), in our study, using precise automatic tracking technology during 21-day long protocols, we showed that cats moved and ate with 24-hour cyclicity at every season. Few cats in similar study conditions (Parker et al., 2018) did not show this daily rhythmicity in their feeding behaviour. Nevertheless, this might be due to the shorter duration of data recording in that previous work. In fact, when we calculated rhythmicity of our present cats over a seven-day or even 14-day period, this rhythmicity was not always detected. This strongly suggests the importance of recording the cat's behaviour over long periods in order to detect its rhythmicity. Thus, it might be suspected the so-called arrhythmicity in Hawking et al. (1971) and Kavanau (1971) was a result of too short recording periods on single individuals.

Under wild conditions, mammals react to a combination of 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 for these animals. With negligible impact of seasonal variations in ambient temperature and humidity, the cats of our study still showed daily covered distance being subject to seasonal fluctuations with autumn and spring maxima and winter minima. We could therefore consider that natural luminosity, in particular the related day-length, is a powerful external rhythm-synchronizer, i.e. *zeitgeber*, in the domestic cat as well.

While spring maxima and winter minima were also detected in free-roaming cats (Dards, 1979; Goszczyński, 2009; Haspel & Calhoon, 1993; Romanowski, 1988; Weber & Dailly, 1998), autumn maxima have not yet been reported in the 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 places in the afternoon. This timing is particular during early-sunset seasons, as it constitutes a combination of two positive influential factors on the cats' activity: impact 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, in the same way sex differences happened during the peak hours in our previous study (Parker et al., 2018), the enhanced activity during the most active seasons in the present study seems primarily due to higher peaks of covered distance: in spring, the spontaneous sunset peak is higher than during the other seasons. In winter, the least active season, peaks are less pronounced, reminding the result of Goszczyński (2009) where cats showed a more stable activity pattern throughout the day during the cold seasons. In the outskirts of Champaign-Urbana (USA), lessened activity in pet ("owned") cats compared to feral ("unowned") cats also resulted in more consistent activity pattern during the day (Horn et al., 2011). This might be the reason why the afternoon peak we find in autumn is less significant in winter, despite the also advanced hour of sunset.

The season had no impact on the daily food consumption of the cats. Be that as it may, as the cats significantly gained weight during our 1-year study, we looked at the amount of food eaten by kilogram of weight of the cats. In that case, the cats ate significantly less in winter than in spring and summer. These findings are in accordance with the studies of Kappen et al. (2012, 2013) who observed lesser energy intake in short day conditions or winter compared to long-day conditions or summer, and Bermingham et al. (2012) who measured less dietary energy intake during winter than in summer. Serisier et al. (2014), who found food intake was least in summer months and greatest during late autumn to winter, suppose ambient temperature, daylight length, or a combination of the two, are responsible for these differences, so that this feeding behaviour occurred in response to changes in energy for thermoregulation or activity (which was not measured). Yet, diets differed in a number of ways including energy content, ingredients, and macronutrient levels in their study, while we used the same *ad libitum* dry food for all seasons. More importantly, most of the cats in Serisier et al. (2014; 30 out of 38) had free access to an outdoor part (14m²) larger than their indoor part (13m²), while the individuals of the current study only received few fresh air through narrow gaps underneath and on the top of windows in a 7m² inner courtyard, smaller than the temperature-controlled main area (22.5m²). It therefore seems daylight length played a more important role in the behaviour of the cats in the present study. Nevertheless, the more contrasted warm or cold outdoor temperatures during the Mediterranean summer or winter might have impacted the reduced locomotor activity we detected during both those seasons.

While free-roaming cats are more frequently described as nocturnal in the literature (Barratt, 1997; Horn et al., 2011; Jones & Coman, 1982; Langham & Porter, 1991; Macdonald & Apps, 1978; Moon et al., 2013; Romanowksi, 1988), the individuals of our study were more diurnal than nocturnal in their locomotor rhythm. As suggested in the study of Horn et al. (2011) where pet cats were diurnal whereas feral cats were nocturnal, our findings may be due to human influence, the interventions of the caretakers happening only at daytime and having already been described in the literature as positive modulators of the activity of the cats (Parker et al., 2018; Piccione et al., 2013; Randall et al., 1987). 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 day-hours than during night-hours at all seasons except in summer. In fact, in summer, the diurnal locomotor activity was lessened, with significant activity troughs in the afternoon. The cats may associate long photoperiods with high ambient temperature and adopt reduced locomotor activity in consequence, as activity troughs have been proposed to be a response to an increase in ambient temperature (Aschoff, 1966; Konecny, 1987). This emphasises, once more, the difficulty to categorise the cat as purely nocturnal or diurnal, its daily peaks and troughs seeming more suited to describe its daily activity pattern. Actually, our results indicate that total activity is increased primarily by an increase in diurnal activity: while the diurnal hourly covered distance during the most active seasons (spring and autumn) are larger than during the less active seasons, the nocturnal hourly covered distance are more similar among the seasons, except in winter where it is still the lowest. Contrary findings in Kappen et al. (2013), where 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.

The locomotor rhythm of the cat 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) resulted in a weaker assessed locomotor rhythm, as discussed earlier. This could also justify the similar amplitude, stability and variability between the feeding and locomotor activity rhythms at 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. The young age of the individuals at the beginning of the study may be responsible: 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. (2018) was higher than for the young cats of this study.

Except in autumn, the locomotor behaviour of the cats was more rhythmic than their eating behaviour. Already noted during our previous study (Parker et al., 2018), this reminds us of the opportunistic nature of this solitary hunter. In the wild, the various rhythms of the numerous small preys may result in flexibility in its eating patterns to adapt to the daily rhythms of its preys, as suggested by Konecny (1987). Compared to their activity pattern, fewer differences according to the season were observed in the feeding pattern of the cats. In particular, no significant 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 seems the impact of human interactions and food renewal is stronger than seasonal daylight fluctuations on the feeding behaviour of the cats.

At all seasons, a positive modulator of activity and food consumption 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, since they prefer to consume freshly killed carcasses rather than carrion in the wild (Bradshaw et al., 1996). As the caretakers entered the panel for the last time between 15:45 and 16:00, the cats also started to be more active during this intervention and 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 no stimulations subsisted from the caretakers, redirected their behaviour towards eating for a moment. This suspected “appetite-trigger” should be further investigated with visual observation of the behaviour of the cats.

In Japan, peaks of activity and consumption in feral cats constantly occurred at dusk through the year (Izawa, 1983). Likewise, in our conditions where the cats received natural daylight modulations, their locomotor activity and food intake were increased around sunset whatever the season. However, the sunset peak timings differed between the warm and cold seasons: it happened at the end of sunset in spring and summer, at its beginning in autumn and winter. As previously discussed, the last human intervention happening right before sunset in the short-day seasons, the cats may have started their sunset peak at that time and not dissociate it. Besides, in autumn and winter, the 16:00-consumption peak 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 other human intervention schedules to investigate this hypothesis. Nonetheless, these findings reflect the crepuscular activity of the species often characterised in the literature (Dards, 1979; Haspel & Calhoon, 1993; Izawa, 1983; Jones & Coman, 1982; Kavanau, 1971; Kuwabara et al., 1986; Parker et al., 2018; Podberscek et al., 1991). While this crepuscular-related activity persisted through the process of domestication and is inherited from its ancestor for which the availability of its nocturnal and diurnal preys was increased at twilights, it is interesting to see the individuals still express it in conditions where food is made available *ad libitum*. It therefore seems this behaviour is intrinsic to the species.

The activity and food intake of the cats are lessened in the middle of the night and in the middle of the day, where they even almost stopped eating between 13:00 and 15:00 in winter, reminding us of the highly diminished consumption of the cats at the same hours in our previous study (Parker et al., 2018). The absence of significance of these troughs of locomotor activity in spring and autumn might be due to the general enhanced activity during these more active seasons. The cats therefore show mainly two peaks and two troughs of activity and food intake during the day, as in the 5 years-old cats of our previous study (Parker et al., 2018). 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 (Goszczyński, 2009; Jones & Coman, 1982) 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 (Johnson et al., 1983; Parker et al., 2018; Randall et al., 1985; Refinetti et al., 2016; Thorne, 1982), we encountered a great interindividual variability during our study: for example, some cats showed lesser reaction to human presence, others showed higher sunset or sunrise peaks. Nevertheless, the activity and feeding patterns of the cats are more homogenous in the daily troughs, differing mainly at peak hours.

Although the results observed in domestic cats do not appear to be as dramatic as those reported in other seasonal mammals, we demonstrated that activity and feeding patterns are different according to the long-day and short-day seasons, 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. (2018) and give evidence of the role of twilights on the feeding and activity pattern of the cats. Then, the annual changes of day-length affected dominantly 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*. The patterns of the cat, however, could also be modified by study conditions, such as food and care conditions: 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 behaviour of the species as well as reactivity to human activity, by being more active at day, again highlighting the behavioural plasticity of the domestic cat. These findings suggest feline housing and nutrition strategies may need to adapt to a seasonal basis in the domestic cat, to ensure that space and availability meet demand at different times of the year. Finally, sex impact could not be assessed in this study because of the too weak sex ratio (five females and one male). Whether the sex of the cats affects their behaviour and daily rhythms throughout the seasons would constitute a relevant study.

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TRANSITION…

This second study confirmed the impact of twilight on the daily behaviour of indoor cats which we detected during our first study. Indeed, crepuscular peaks in locomotor activity and food intake rose around dawn and dusk according to the season and rhythm bimodality persisted through the seasons. Seasonal fluctuations in photoperiod also resulted in lower daily covered distance and food intake in winter. This demonstrates daylight works as a major *zeitgeber* in cats as the study emphasises its impact in conditions where ambient temperature and humidity remained constant across the seasons. The daily patterns of the cats were impacted by human presence, resulting in more diurnal activity. In our last and following article, we investigated further again the impact of environmental cues on the locomotor activity and food intake of domestic cats, by conducting the same study, in summer, on cats living outdoors. With comparisons between the behaviours of indoor and outdoor individuals, we expect to determine how the housing conditions affect the daily patterns of the cats.

ARTICLE 3

AIM: ASSESS THE HOUSING CONDITIONS IMPACT ON THE DAILY RHYTHMS OF INDOOR AND OUTDOOR CATS

COMPARISON OF LOCOMOTOR AND FEEDING RHYTHMS BETWEEN INDOOR AND OUTDOOR CATS LIVING IN CAPTIVITY

Parker Marine[a]*, Serra Jessica[d], Deputte Bertrand[b],
Ract-Madoux Brunilde[c], Faustin Marie[d], Challet Etienne[a]

[a] Institut des Neurosciences Cellulaires et Intégratives (INCI), CNRS, Université de Strasbourg, 8 allée du général Rouvillois, 67000 Strasbourg, France

[b] Ecole Nationale Vétérinaire d'Alfort (ENVA), 7 Avenue du Général de Gaulle, 94700 Maisons-Alfort, France

[c] Scientific consultant, Paris, France

[d] Royal Canin Research center, 650 avenue de la petite Camargue, 30470 Aimargues, France

*corresponding author: Parker Marine, marineparker@gmail.com

ABSTRACT

The plastic nature of cat behaviour allows this "friendly symbiont" of humans to adapt to various housing conditions. As daylight has been proven to play a role in the rhythms of the cats, one could wonder if other environmental factors affect its patterns. Yet, how their activity and feeding rhythms are impacted by the environment they live in is not clear and most studies conducting this comparison did not use standardised conditions between the populations. In our study, we compared the behaviour of cats living in a 29 m² indoor room and cats living in a 1145 m² outdoor enclosure. We tracked them simultaneously in summer for 21 days, using advanced tracking technologies. Both populations received daylight but only the outdoor population was exposed to weather fluctuations. The cats were fed the same diet. Bimodality was detected in the activity and consumption rhythms of indoor as well as outdoor cats, while twilight triggered crepuscular peaks. Daily, the outdoor population covered more distance and consumed more food than the indoor population, but displayed less rhythmic behaviours, assumedly because of rhythm disruptors met in outdoor conditions whereas the indoor population was less disturbed in their everyday life. The cats were more active at night outdoors than indoors, reflecting exploratory behaviour which may be inhibited indoors. The indoor individuals had feeding rhythms more affected by human interactions and ate more frequently than the outdoor individuals.

Key words: *Cat, housing, feeding pattern, locomotor activity, chronobiology*

1. INTRODUCTION

The cat is a domestic animal in the sense of being a "friendly symbiont" of humans (Downs, 1960, as cited by Randall et al., 1985), not as dependent on humans as the dog, for instance. Still, it constitutes one of the most frequent pets with 13.5 million individuals in France in 2017 (Statista 2018). Yet, how its daily activity is affected by different housing conditions, which is of importance for the maintenance of its well-being, is not fully clear. Most of chronobiological studies are conducted on laboratory animals to enable proper assessment of the rhythms displaying an oscillation of about 24 hours, called circadian rhythms (*circa* meaning “around”, *dies* meaning “day”). Indeed, circadian rhythms, controlled by endogenous oscillators, including a master clock located in the hypothalamic suprachiasmatic nucleus (SCN) (see Golombek & Rosenstein, 2010), are unambiguously detected when animals are studied in conditions with no synchronization to environmental time cues (called “zeitgebers”), i.e. in periods of constant darkness or constant light. In such laboratory conditions, the locomotor activity of the cat has been described as arrhythmic by Hawking et al. (1971) and Kavanau (1971), but the small sample size (n = 1) and short recording period (8 and 7 days in Hawking et al. (1971) and Kavanau (1971), respectively) make this conclusion doubtful. During more reliable conditions, circadian rhythms were discerned in the cat (Johnson et al., 1983; Kuwabara et al., 1986), while cats in isolation from humans and human noises exhibited random patterns of activity in constant light but free-running circadian rhythms in constant darkness (Randall et al., 1985). Nevertheless, confinement in cages and controlled conditions in laboratories can erase the effects of external factors determining the natural patterns in animals. Besides, Randall et al. (1985) admitted discovering the problem of what the adequate *zeitgeber* in different light/dark cycles is for this species.

From an ecological perspective, the "highly adaptable and opportunistic species" (Kavanau, 1971) might be predicted to respond with ultradian cycles in a complex environment and exhibit less rigid relation to light/dark transitions. Therefore, in studies conducted in more natural conditions, the question is less about circadian rhythmicity than about nocturnal or diurnal activity patterns. Indeed, the light/dark cycle, recognised as the most potent cue for circadian entrainment in most organisms, can lead to chronotype (i.e. propensity to be more nocturnal or more diurnal) categorisation. Light also suppresses locomotor activity in some mammals (nocturnal species) but promoting it in others (diurnal species, Redlin, 2001). The activity pattern of the cat has most often been described as with a tendency towards nocturnality (Barratt, 1997; Haspel & Calhoon, 1993; Johnson et al., 1983; Jones & Coman, 1982; Kanarek, 1975; Kuwabara et al., 1986; Langham & Porter, 1991; Macdonald & Apps, 1978; Moon et al., 2013; Romanowski, 1988; Walls, 1942). Other authors detected diurnality; however human interventions or daily feeding conditions were often proposed to be responsible for this timing (Dards, 1979; Hawking et al., 1971; Kappen et al., 2013; Kavanau, 1971). In fact, Aschoff (1962, as cited in Randall et al., 1987) rejected nocturnal versus diurnal labels because the same individual may exhibit different patterns on different occasions. Some studies indeed observed either variability among the chronotypes of the different individuals (Horn et al., 2011; Panaman, 1981; Piccione et al., 2013; Randall et al., 1985) or shifts according to the season (Izawa, 1983). This nocturnal/diurnal distinction may therefore not always be applicable and the undecided literature lets us believe the cat may not fit to it. Be that as it may, crepuscularity seems to best characterise the activity pattern of the cat, with regular peaks occurring near twilights, whether natural or artificial (Dards, 1979; Goszcynski, 2009; Haspel & Calhoon, 1993; Horn et al., 2011; Izawa, 1983; Jones & Coman, 1982; Kappen et al., 2013; Kavanau, 1971; Konecny, 1987; Kuwabara et al., 1986; Parker et al., 2018; Podberscek et al., 1991; Randall et al., 1987).

There is evidence that different factors such as interaction with competitors and/or with conspecifics, and food distribution interact with photoperiod in the determination of the daily rhythm in the cat. Aside for a high interindividual behavioural variability cited in several studies (Johnson et al., 1983; Parker et al., 2018; Randall et al., 1985, 1987; Thorne, 1982), the behavioural plasticity of the cat is claimed to be responsible for the plurality of findings about its rhythms.

Randall (1985, 1987), referring to the “friendly symbiosis” between cats and humans, pointed out that both food intake and activity in cats are influenced by humans, which can thus be a potent stimulus in determining the pattern of cat activity. High influence of human presence and care on the amount of activity was also reported in pet cats (Piccione et al., 2013).

The housing conditions of cats may affect the feeding behaviour of the cats. Under *ab libitum* diet, cats kept in outdoor individual pens in summer and winter had higher energy requirements than when kept indoors, possibly reflecting the wider ambient temperature range they were exposed to (Bermingham et al., 2012). The housing conditions may also be a significant factor modulating their activity rhythm. Differences in home range size, habitat use and activity patterns between “owned” individuals -i.e. fed and cared by humans and partly living in human dwellings- and “unowned” individuals -i.e. not observed being fed or cared for by humans- were observed on the outskirts of Champaign-Urbana (Illinois, USA, Horn et al., 2011). “Unowned” cats were more active than “owned” cats throughout the year and were more nocturnal in their diel activity, possibly reflecting activity patterns of their prey. Diel activity of “owned” cats, for their part, was more consistent throughout the day, leading the authors to speculate supplemental feeding and the availability of reliable shelter lessens the need for “owned” cats to correspond activity with prey activity patterns. The increased activity in early morning and during evening is considered to come from the availability of the preys in “unowned” cats but from the activity of the owner in “owned” cats. In another study, the activity patterns of one group (B), living in large house, having free access to a large garden (2000-2500 m²) and kept outside at night was compared to another group (A) which had access to a smaller garden (20-40 m²) only during 1 h in early morning (Piccione et al., 2013). Group B was also mainly nocturnal and displaying an active lifestyle, along presenting a more robust daily rhythmicity than group A which was mainly diurnal and also more active when their owners were home compared to when they were away. The authors believe restricted activity and exercise area, human care and cleaning, can be cause of shifts in diurnal/nocturnal active phase and generate weaker rhythms.

However, a longer and continuous recording period (10 days in total or 4 recordings per week in Piccione et al. (2013) and Horn et al. (2011), respectively) and an improved standardisation between the two groups (feeding and living conditions were different between the compared groups for both studies), combined with a feeding behaviour assessment would allow a better understanding of the housing impact on cats. For this purpose, we investigated factors influencing the daily rhythmicity of locomotor activity and feeding behaviours in cats by using chronobiological tools to compare two populations of cats living in two different housing conditions but experiencing similar feeding and caring conditions.

2. MATERIAL AND METHODS

2.1. Animals and conditions

The indoor population was constituted of two groups of neutered domestic cats (*Felis catus*): group A consisted in 6 females and 2 males, group B of 3 females and 5 males. They were aged from 1 to 2 years-old and belonged to 6 different breeds: American shorthair, British longhair, British shorthair, Exotic shorthair, Selkirk rex and Selkirk straight shorthair. The individuals of both groups have been living together for four months prior to the beginning of the study. They were housed at Royal Canin's cattery located in the South of France (Aimargues, Guard). Each group lived in an indoor heated main area of 58.4 m^3 (L=6.4 m, l=3.51 m, H=2.6 m) and an inner courtyard of 18.1 m^3 (L=2.9m, l=2.4 m, H=2.6 m). This courtyard received fresh external air through narrow gaps underneath and on the top of windows, separated from the main area with hermetic cat flaps (fig. 1). In the main room, the cats had free access to a wall shelf containing several hiding places and cushions, an area containing several cat toys, a wall scratching post, a feeding area, a water bowl and a litter tray. In the courtyard, the cats had access to two cat trees containing cushions and another litter tray. The indoor cats had 3.6 m^2 available per individual.

The outdoor population was constituted of one group of 27 cats (15 neutered females, 9 castrated males and 3 intact males) aged from 1 to approximately 12 years old, all belonging to European breed. The cats came from different origins: 20 were previously feral and 7 were previously pet cats before arriving at the shelter. They had been living together for at least one month prior to the beginning of the study. The individuals were housed in an outdoor enclosure with grass, shrubs and trees, of about 1145 m^2 at the shelter AVA (Aide aux Vieux Animaux) located in the North of France (Cuy-Saint-Fiacre, Normandie). Within the enclosure, cats had also access to two chalets containing shelves with cat baskets, 9 kennel areas filled with clean straw, two litter areas, two drinking areas containing two stainless-steel water bowls each and two feeding areas, each containing 8 doors giving access to two feeding bowls (fig. 1). The outdoor cats had 42.4 m² available per individual.

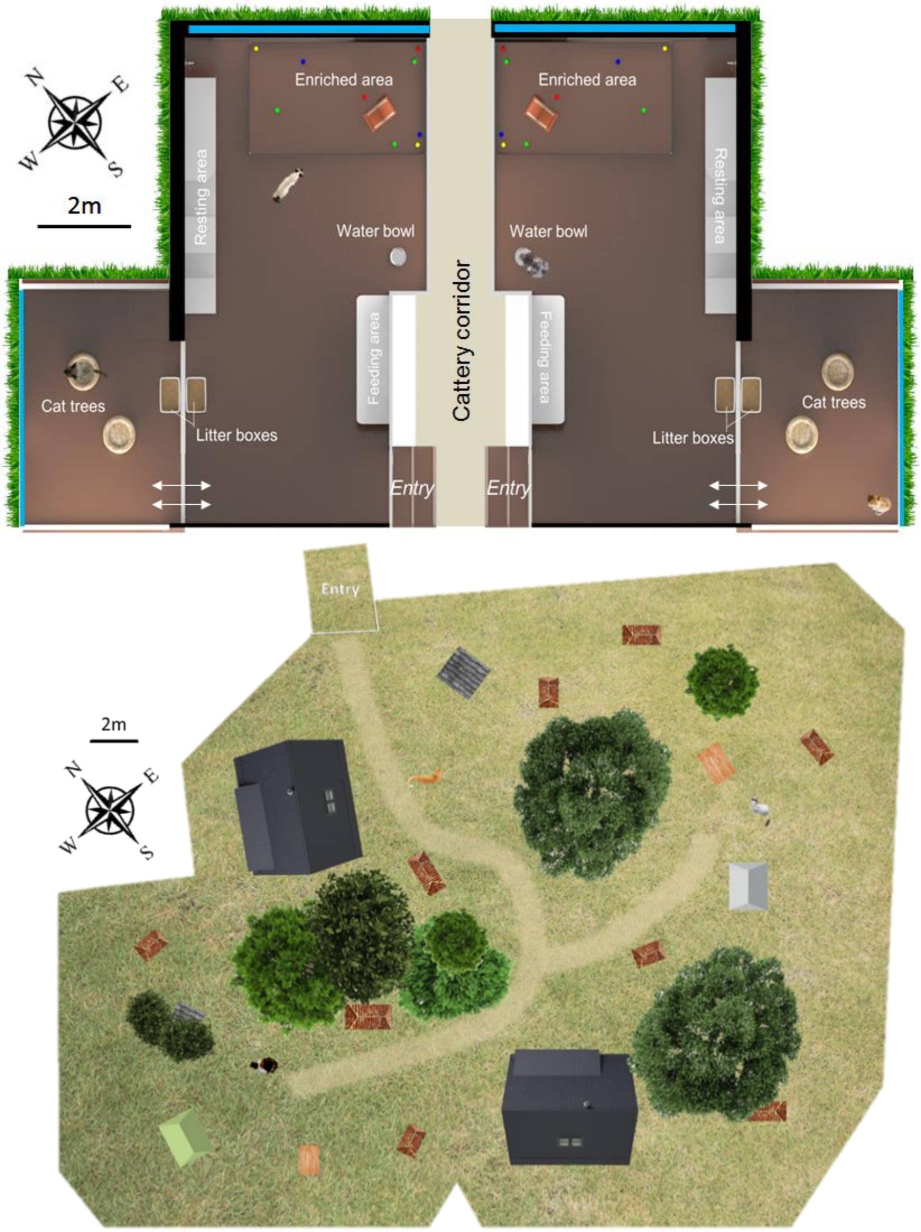

Figure 1 – Maps of the indoor panels (top) and outdoor enclosure (bottom)

The indoor cats were exposed through large windows to natural light/dark cycle, with an average of 14h56 of light per day, daily varying on average from 21 to 608 lux (fig. 2). Ambient temperature and relative humidity were controlled in the main room, varying on average from 22.8 to 23.2°C and from 60 to 66%, respectively. The outdoor individuals were exposed to climate conditions, receiving on average 15h36 of light per day with ambient temperature daily varying on average from 12.8 to 30.9°C, humidity from 44 to 95% and light from 7 to 2283 lux (fig. 2).

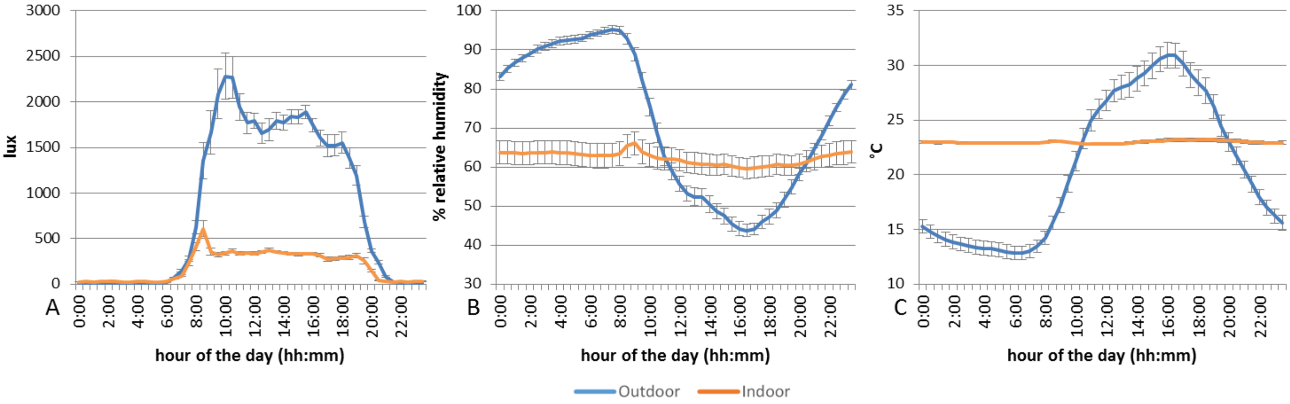

Figure 2 – Mean daily luminosity (lux, A), ambient temperature (°C, B) and relative humidity (%, C) according to the housing condition (indoor versus outdoor). Error bars represent standard errors.

Because of technical difficulties and unapproachable cats (outdoor), we could not record enough data for every individual. For our analyses, we were able to use the recordings of 15 indoor cats (6 females and 1 male of group A, 3 females and 5 males of group B) and only 8 outdoor cats (2 sterilised females, 4 castrated males and 2 intact males). The health of the individuals was regularly monitored.

2.2. Recording periods

The locomotor activity and feeding behaviour of the cats were continuously recorded during 21 days between July 11th and 31st 2016. Cats were subjected to a week of habituation prior to the 3-week recording period, in order to acclimate themselves to the study conditions (feeding conditions and areas, human interventions, collars).

2.3. Feeding and human intervention

The cats were fed *ad libitum* with an extruded dry diet (Fit32 (3859kcal/kg), Royal Canin, Aimargues, France) throughout the study. 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 meals.

Human interventions were standardised, i.e. happened at the same schedule every day. The animal caregivers entered the panel or enclosure to clean the facilities, interact with the cats and check the good functioning and state of the protocol conditions: between 08:20 and 08:50, between 11:15 and 11:45 and between 15:45 and 16:00 indoors, between 09:15 and 09:30, between 11:15 and 11:45 and between 16:30 and 16:45 outdoors.

2.4. Tracking technologies

Indoors, 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 episodes (passive RFID and electronic scales). They continuously provided us with distance covered by each cat every 10 minutes and time and weight of consumptions (see Parker et al. 2018 for more details). Outdoors, the same tags were incorporated into specifically designed collars to protect them from weather fluctuations. These collars were attached to adjustable break-away collars. An habituation period allowed us to assess the tags and collars had no adverse effect on the physical condition of the animals and their functioning and correct fitting were checked every day. Preliminary observations were conducted before the study to ensure that the feeding devices did not impact the behaviour of the cats. This protocol was approved by Royal Canin's ethical committee and by the ethic regulations of the shelter AVA.

2.5. Rhythm analyses

Using the covered distance and food intake of each cat every 10 min, the same rhythm parameters were calculated and compared as in our previous study (Parker et al. 2018). The period (duration of a full cycle, ≈24h for a circadian rhythm) 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, Actimetrics, Wilmette, Illinois, USA, extension of Matlab v. R2013a, Mathworks, Natick, Massachusetts, USA). The Interdaily Stability (IS), Intradaily Variability (IV) and onset of the least active 5 hours (L5) were calculated by the ActiWatch software (v. 7.31, CamNtech Ltd, Papworth Everard, UK). IS quantifies the degree of resemblance between activity patterns of individual days, IV quantifies the fragmentation of periods of rest and activity and L5 onset yields the time when starts the sequence of the 5 least active hours in the 24-hour average activity profile. A strong and robust rhythm was 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 consumption/activity by hour and by day according to the light condition (night hours vs day hours), using the sunrise and sunsets hours as phase references. An individual was considered to show a bimodal pattern when the magnitude of the 12h-peak was equal or superior to half of the 24h-peak (highest one) on its periodogram. Finally, we used the 10-min periods data to calculate how many times the cats moved and ate in an average day, in both housing conditions.

2.6. Statistical analyses

Every statistical comparison was made with Sigmaplot (v. 13.0, Systat Inc., San Jose, California, USA). T-tests and Mann-Whitney Rank Sum tests (when the data passed Shapiro-Wilk test for normality or Brown-Forsythe test for equal variance) were performed to compare the daily data and rhythmic parameters according to the population. A one-way ANOVA with repeated measures was performed to compare the distance covered by the outdoor population according to the hour of the day. The distance covered hourly by the indoor population, as well as the hourly food consumption of the two populations not following statistical normality or homogenous variances, Friedman analyses of variances (ANOVAs) with repeated measures were conducted for these data. Two-way ANOVAs were performed to compare the data according to the hour and population (indoor versus outdoor) and Two-way ANOVAs with repeated measures were completed to compare the rhythm parameters according to the variable (activity versus feeding behaviour) as well as the total and hourly covered distance and food consumption according to the light phase. Holm-Sidak post-hoc tests were performed with the ANOVAs and Tukey post-hoc tests with the Friedman ANOVAs. Results are given as mean ± 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 $p < 0.001$ on graphs). Box plots represent first (Q1), second (median) and third quartile (Q3), minimum, and maximum of the data, as well as the smallest data superior to the low frontier (LF=Q1-1,5*(Q3-Q1)) and the highest data inferior to the high frontier (HF=Q3+1,5*(Q3-Q1)).

3. RESULTS

3.1. Locomotor activity and behaviour

3.1.1. Locomotor rhythm

All the individuals irrespective of their housing conditions had 24h periodicity in their activity rhythm.

The activity rhythm amplitude and interdaily stability of the cats were significantly higher indoors than outdoors ($t_{21} = -2.83$, $p < .05$; Mann-Whitney, U = 16.0, $p < .01$; respectively, fig. 3).

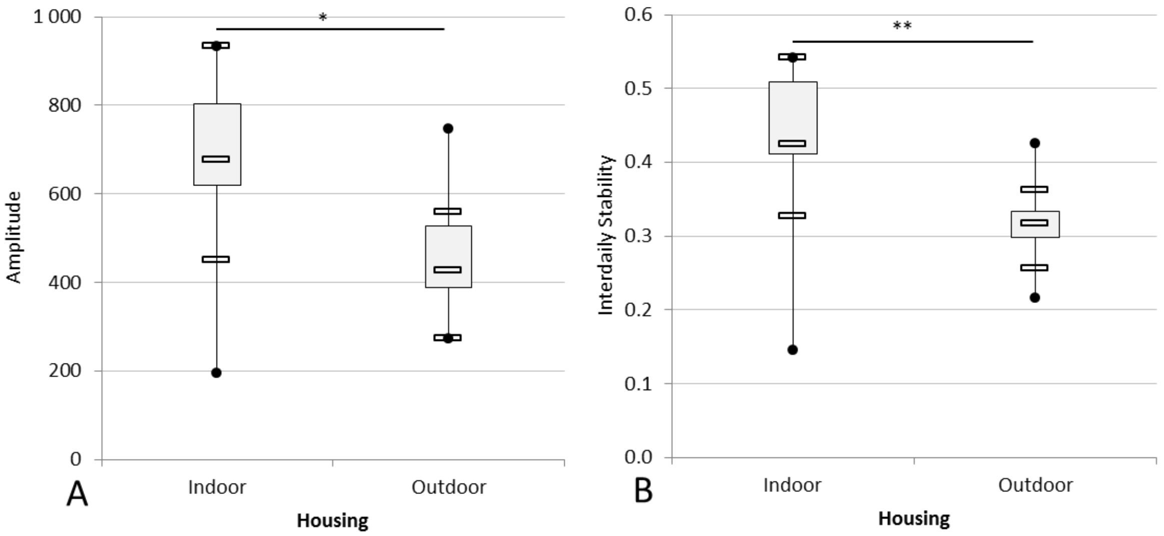

Figure 3 – Mean amplitude (A) and Interdaily Stability (B) of the activity rhythm of the cats according to their housing condition (indoors (n = 15) versus outdoors (n = 8)). Box plots represent first (Q1), second (median) and third quartile (Q3), minimum, and maximum of the data, as well as the smallest data superior to the low frontier (LF=Q1-1,5*(Q3-Q1)) and the highest data inferior to the high frontier (HF=Q3+1,5*(Q3-Q1)). (*) indicates p < .05, (**) indicates p < .01.

The intradaily variability of the activity rhythm did not differ significantly between the two populations (1.36 ± 0.05 indoors versus 1.47 ± 0.05 outdoors, $t_{21} = 1.42$, $p = .172$).

Many cats showed bimodality in their activity rhythm. Twelve out the 15 cats indoor (80%) and 5 out 8 cats outdoor (63%) displayed a bimodal activity rhythm: the peak of their activity periodogram at 12 hours was higher than half of their 24-hour peak. The others cats showed unimodal rhythms.

3.1.2. Daily covered distance and frequency of activity

The cats covered on average 3.01 ± 0.25 km per day. The outdoor cats covered significantly more distance per day than the indoor cats ($t_{21} = 6.33$, $p < .001$; fig. 4).

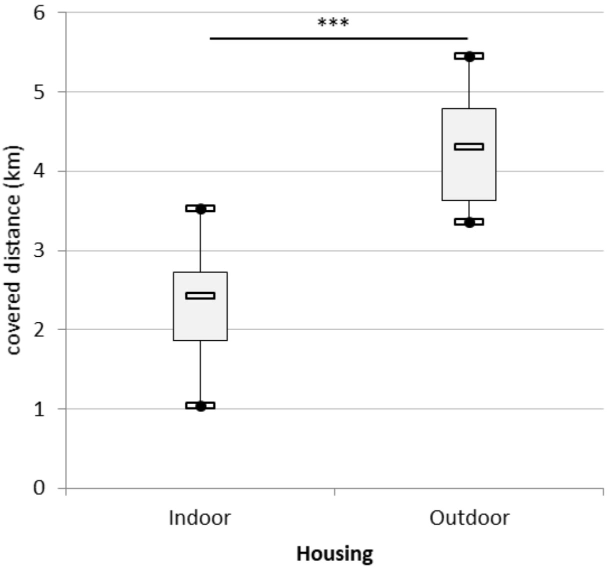

Figure 4 – Mean daily distance (km) covered by the cats according to their housing condition (indoors (n = 15) versus outdoors (n = 8)). Box plots represent first (Q1), second (median) and third quartile (Q3), minimum, and maximum of the data, as well as the smallest data superior to the low frontier (LF=Q1-1,5*(Q3-Q1)) and the highest data inferior to the high frontier (HF=Q3+1,5*(Q3-Q1)). (***) indicates p < .001.

The outdoor population tended to move more frequently than the indoor one (108.8 ± 1.5 10-min periods per day versus 101.0 ± 0.6, respectively, $t_{21} = -1.906$, $p = .070$).

3.1.3. Nocturnal versus diurnal activity

Daily, the cats covered significantly more distance during daytime (1983 ± 165 m) than at night (1028 ± 102 m, $p < .001$), regardless of their housing conditions ($F_{1,\,21} = 125.98$, $p < .001$, fig. 5).

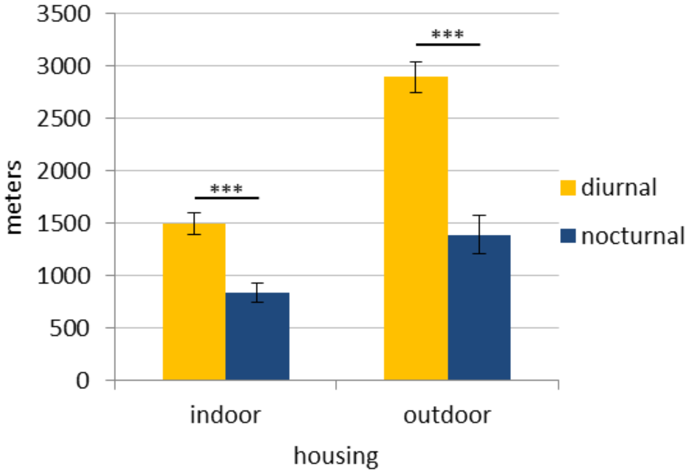

Figure 5 – Mean daily nocturnal and diurnal distance (m) covered by the cats according to their housing conditions (indoors (n = 15) versus outdoors (n = 8)). Error bars represent standard errors, (***) indicates p < .001.

However, the difference between nocturnal and diurnal period was not statistically significant as far as the hourly covered distance is concerned ($F_{1,\ 21} = 2.16$, $p = .157$).

Most of the indoor cats (60%) had their 5 least active hours during the night, whereas the outdoor cats had their 5 least active hours either at midday or at night (Tab. 1).

		Onset of the Least active 5 hours		
		Middle day (12:00 – 14:00)	Afternoon (16:00 – 17:00)	Night (23:00 – 1:00)
Housing condition	Indoors (n = 15)	++	++++	+++++++++
	Outdoors (n = 8)	++++		++++

Table 1 - Time of onset of the Least active 5 hours of the cats according to their housing condition. (+) represents one cat.

3.1.4. Mean activity rhythm during the day

The hour of the day had an impact on the covered distance of the cats ($F_{23,\ 161} = 7.05$, $p < .001$ outdoors; $\chi^2_{23} = 246.70$, $p < .001$ indoors).

Indoors, the cats were more active from the first human intervention to the second (between 08:00 and 12:00), as well as after sunset (between 21:00 and 23:00) and before sunrise (at 05:00; fig. 6A). They covered significantly less distance in the middle of the night (between 01:00 and 04:00) and between the end of human activity in the cattery and sunset (between 17:00 and 19:00).

Outdoors, the cats significantly increased their locomotor activity during human interventions (at 09:00, 11:00 and 16:00, fig. 6B). They were also more active after the sunset (at 22:00). Outdoor cats were significantly less active in the middle of the night (between 01:00 and 03:00) and in the middle of the day (at 13:00 and 15:00).

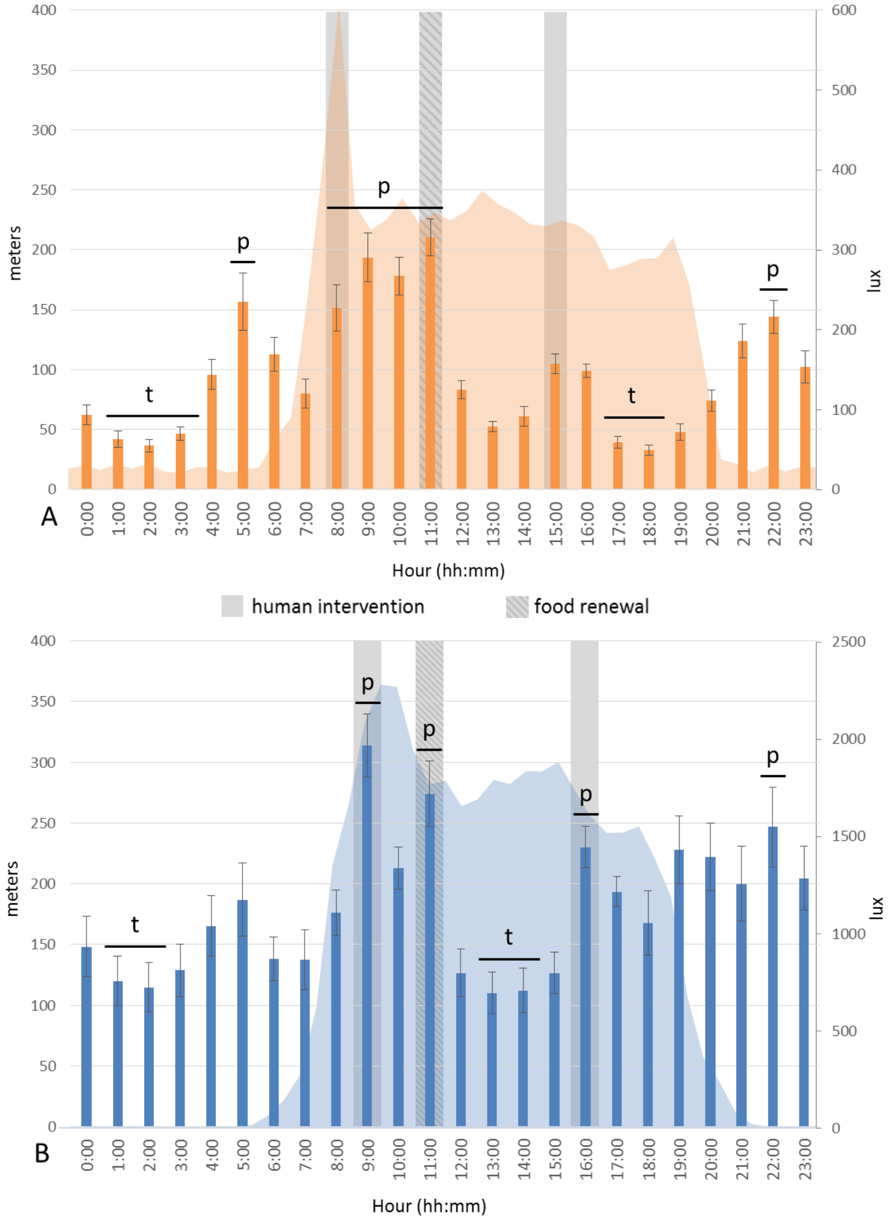

Figure 6 – Mean covered distance (m, bars) and luminosity (lux, area) during a day cycle of the cats, indoors (A, n = 15) and outdoors (B, n = 8). Error bars represent standard errors, (p) indicates a significant peak, (t) indicates a significant trough.

The outdoor cats covered significantly more distance than the indoor cats at several occasions during the day and especially during the evening and night (fig. 7).

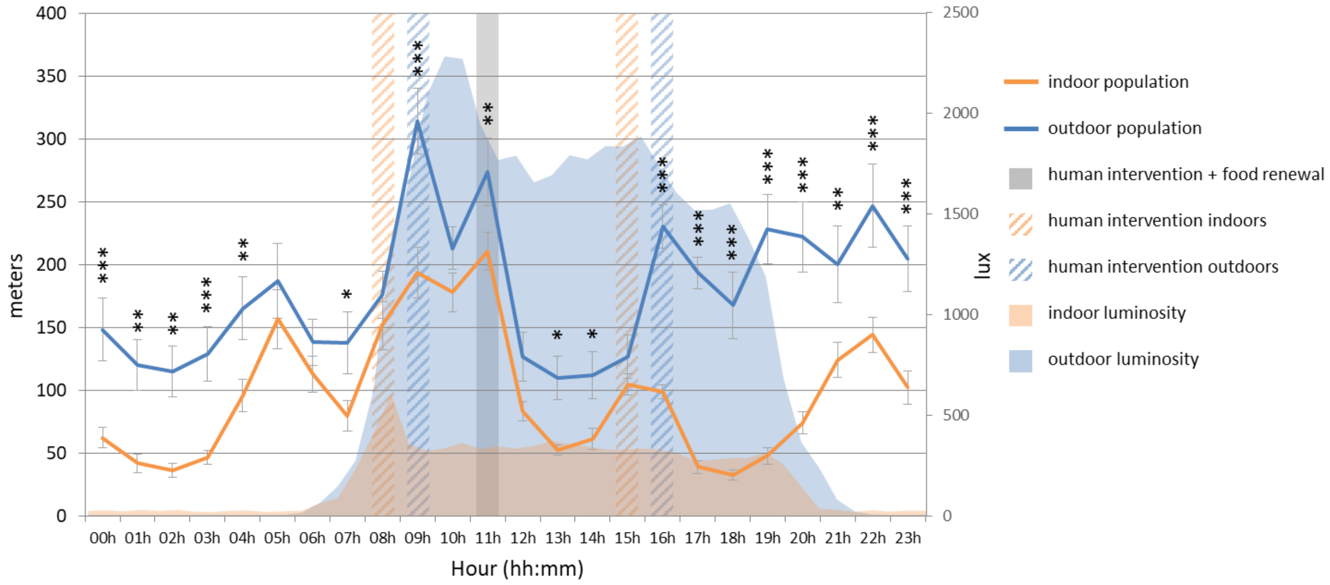

Figure 7 – Mean covered distance (m, bars) and luminosity (lux, area) during a day cycle according to the housing condition of the cats (indoors (n = 15) vs outdoors (n = 8)). Error bars represent standard errors, (*) indicates p < .05, (**) indicates p < .01, (***) indicates p < .001.

3.2. Feeding rhythm and behaviour

3.2.1. Feeding rhythm

All indoor cats and 5 outdoor cats ate with a 24h-cyclicity, the 3 other outdoor cats were arrhythmic.

The amplitude of the feeding rhythm of the indoor cats (132 ± 20) did not differ significantly from that of the rhythmic outdoor cats (102 ± 31, $t_{18} = 0.76$, p = .457) but the indoor cats showed a significantly higher interdaily stability than the outdoor cats ($t_{21} = -2.88$, p < .01, fig. 8).

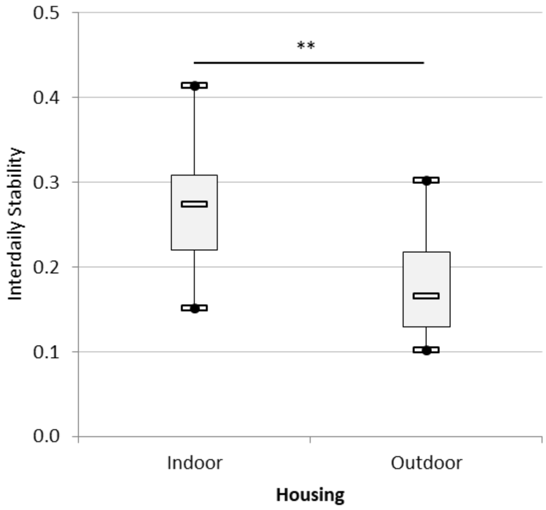

Figure 8 – Mean interdaily stability of the feeding rhythm of the cats according to their housing condition (indoors (n = 15) versus outdoors (n = 8)). Box plots represent first (Q1), second (median) and third quartile (Q3), minimum, and maximum of the data, as well as the smallest data superior to the low frontier (LF=Q1-1,5*(Q3-Q1)) and the highest data inferior to the high frontier (HF=Q3+1,5*(Q3-Q1)). (**) indicates p < .01.

The intradaily variability of the feeding rhythm did not differ significantly according to the housing condition of the cats (2.09 ± 0.04 indoors versus 2.06 ± 0.06 outdoors, $t_{21} = -0.46$, p = .652).

Most of the indoor cats (12/15, 80%) showed tendencies towards bimodality in their feeding rhythm while the remaining indoor cats displayed unimodal feeding rhythmicity. In contrast, six out of eight outdoor cats (76%) showed either unimodal feeding rhythm (3/8) or arrhythmicity (3/8). Only two outdoor cats (25%) displayed a bimodal feeding rhythmicity.

3.2.2. Daily food consumption and frequency of food intake

The cats ate on average 61.1 ± 2.3 g per day. The outdoor individuals ate significantly more food than the indoor cats ($t_{21} = 2.21$, $p < .05$; fig. 9).

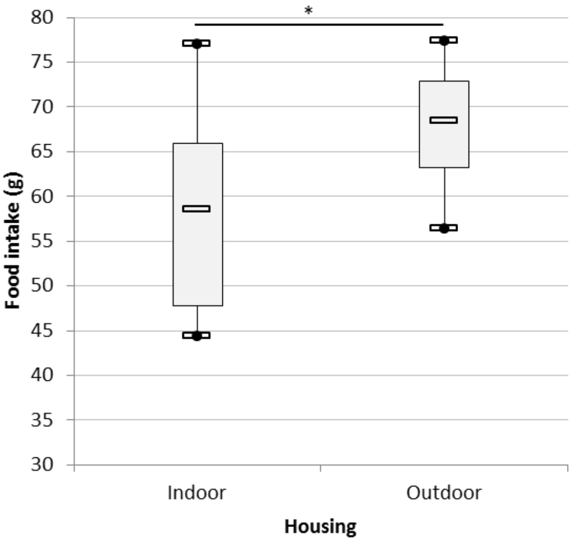

Figure 9 – Mean daily food consumption (g) of the cats according to their housing condition (indoors (n = 15) versus outdoors (n = 8)). Box plots represent first (Q1), second (median) and third quartile (Q3), minimum, and maximum of the data, as well as the smallest data superior to the low frontier (LF=Q1-1,5*(Q3-Q1)) and the highest data inferior to the high frontier (HF=Q3+1,5*(Q3-Q1)). (*) indicates p < .05.

It is worth pointing out that indoor cats only tended to eat more frequently and during a global longer period of time than outdoor individuals (11.5 ± 0.2 10-min periods per day versus 9.3 ± 0.2, respectively; $t_{21} = 1.97$, $p = .063$).

3.2.3. Nocturnal versus diurnal consumption

Daily, the cats ate significantly more during daytime (40.1 ± 2.3 g) than at nighttime (20.9 ± 1.7 g, $F_{1, 21} = 57.36$, $p < .001$), be it indoors (Holm-Sidak post-hoc test, $p < .01$) or outdoors (Holm-Sidak post-hoc test, $p < .001$, fig. 10A). Hourly, food consumption tended to be higher during daytime (2.6 ± 0.1 g per hour) than nighttime (2.4 ± 0.2 g per hour, $F_{1, 21} = 3.18$, $p = .089$, fig. 10B).

There was a significant interaction between housing condition and period of the day in the daily and hourly comparisons ($F_{1, 21} = 11.73$, $p < .01$; $F_{1, 21} = 5.89$, $p < .05$; respectively): the outdoor group ate significantly more than the indoor group at day/day hours (Holm-Sidak post-hoc test, $p < .001$, $p < .05$, respectively) but not at night/night hours (Holm-Sidak post-hoc test, $p = .150$, $p = .192$, respectively).

Also, the more diurnal hourly consumption was significant in the outdoor group (Holm-Sidak post-hoc test, $p < .05$) but not indoors (Holm-Sidak post-hoc test, $p = .591$).

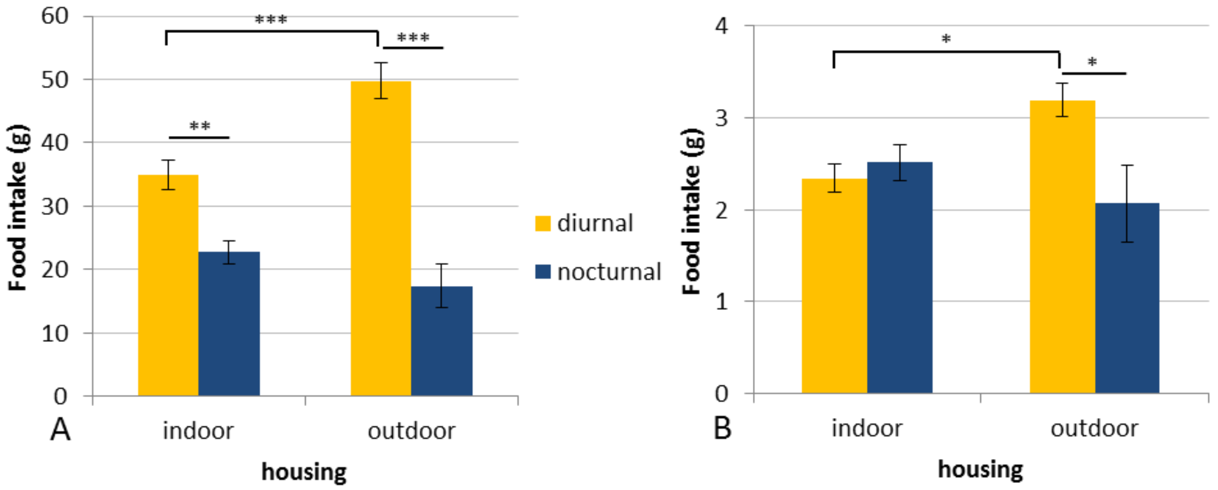

Figure 10 – Mean daily (A) and hourly (B) nocturnal and diurnal food intake (g) of the cats according to their housing condition (indoors (n = 15) versus outdoors (n = 8)). Error bars represent standard errors, (*) indicates p < .05, (**) indicates p < .01, (***) indicates p < .001.

The indoor cats (60%) had their 5 least active hours either during the night (47%) or in the middle of the day (33%), whereas most of the outdoor cats had their 5 least active hours at night (Tab. 2).

		Onset of the Least active feeding 5 hours			
		Morning (05:00 – 06:00)	Middle day (11:00 – 12:00)	Afternoon (17:00)	Night (23:00 – 02:00)
Housing condition	Indoors (n = 15)	+	+++++	++	+++++++
	Outdoors (n = 8)	++	+		+++++

Table 2 - Time of onset of the Least active feeding 5 hours of the cats according to their housing condition. (+) represents one cat.

3.2.4. Mean feeding rhythm during the day

The hour of the day also had an impact on the food intake of the cats ($\chi^2_{23} = 57.31$, $p < .001$ outdoors; $\chi^2_{23} = 183.72$, $p < .001$ indoors).

The indoor cats ate significantly more at 05:00 (before sunrise), 11:00 (when food was renewed and humans interacted with the cats), 16:00 (after the last human intervention) and between 21:00 and 23:00 (after sunset, fig. 11). The cats ate significantly less between 01:00 and 03:00 (in the middle of the night), at 13:00 (middle of the day) and 18:00 (before sunset).

The food intake of the outdoor cats was significantly higher at 16:00, during the last human intervention in the enclosure, and significantly lower at 00:00 (fig. 11).

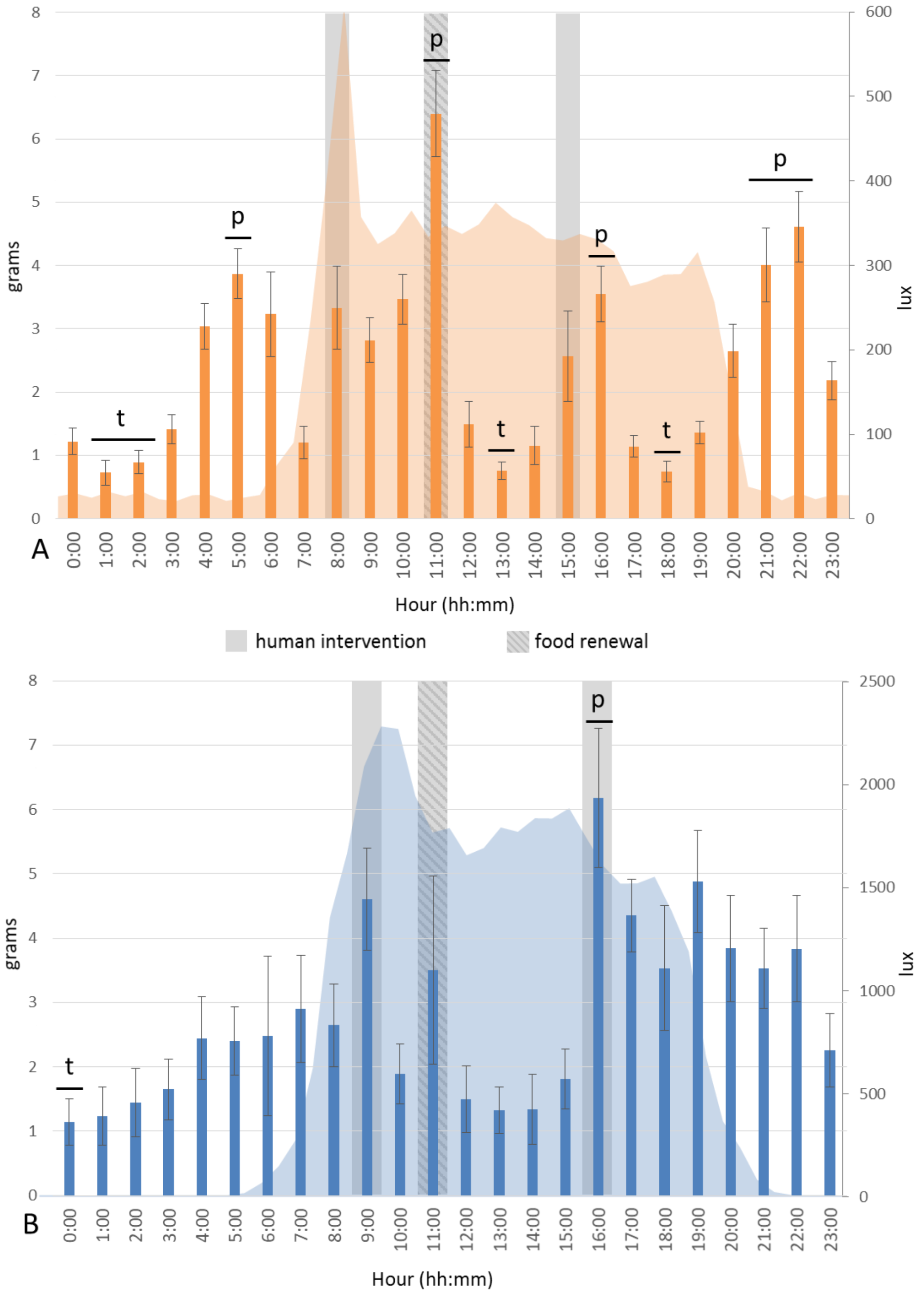

Figure 11 – Mean food consumption (g, bars) and luminosity (lux, area) during a day cycle of the cats, indoors (A, n = 15) and outdoors (B, n = 8). Error bars represent standard errors, (p) indicates a significant peak, (t) indicates a significant trough.

The outdoor cats ate significantly more than the indoor cats at 07:00, 09:00 (during the first outdoor human intervention) and from 16:00 to 20:00 (fig. 12). The indoor cats ate significantly more than the outdoor cats at 10:00 and at 11:00, when food was renewed (fig. 12).

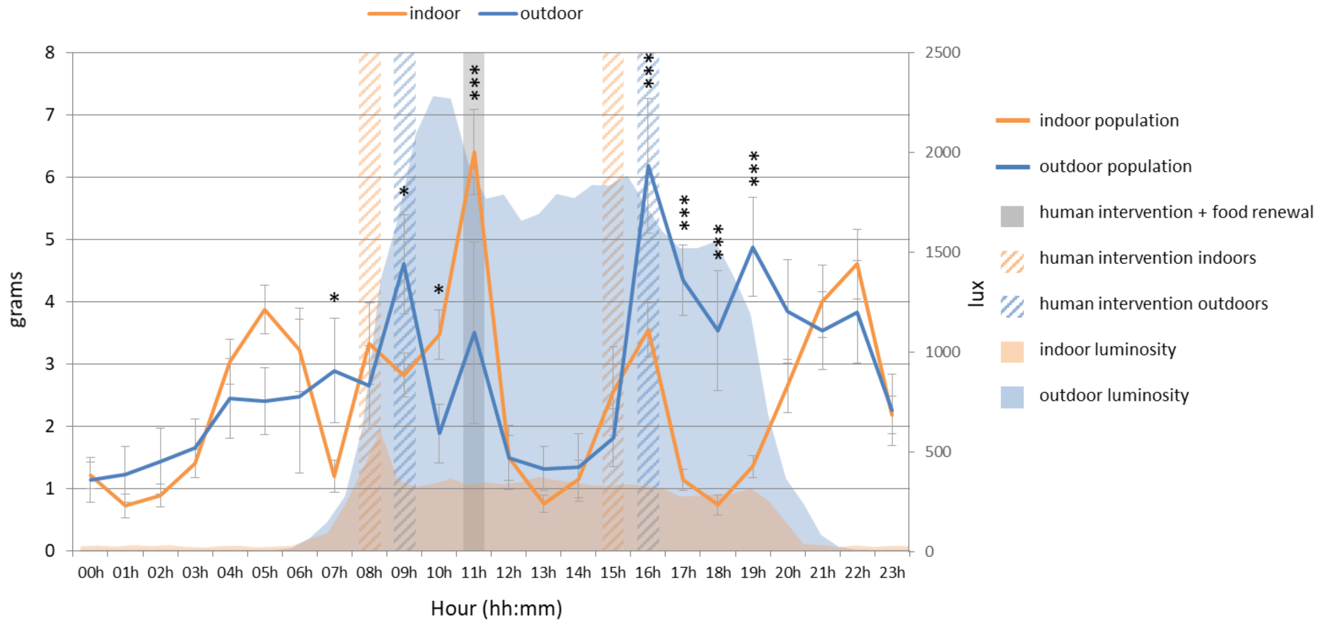

Figure 12 – Mean food consumption (g, every hour) of the cats throughout the day according to their housing condition (indoors (n = 15) versus outdoors (n = 8)). Error bars represent standard errors, (*) indicates p < .05, (***) indicates p < .001.

3.3. Eating versus locomotor activity rhythm

The amplitude and interdaily stability of the locomotor activity rhythm were significantly higher than those of the feeding rhythm of the cats (600 ± 41 versus 112 ± 16, $F_{1, 21} = 199.90$, $p < 0.001$; 0.39 ± 0.02 versus 0.24 ± 0.02, $F_{1, 21} = 69.39$, $p < 0.001$; respectively; Tab. 3) and the intradaily variability of the locomotor activity rhythm was significantly lower than the intradaily variability of the feeding rhythm (1.40 ± 0.04 versus 2.08 ± 0.03, respectively, $F_{1, 21} = 257.62$, $p < .001$), be that indoors and outdoors (Holm-Sidak post-hoc test, $p < .001$ for all).

	Variable	Amplitude		IS		IV	
	Rhythm	locomotor	feeding	locomotor	feeding	locomotor	feeding
Housing condition	Indoors (n = 15)	674 ± 47	132 ± 20	0.43 ± 0.023	0.27 ± 0.02	1.36 ± 0.05	2.09 ± 0.04
	Outdoors (n = 8)	461 ± 52	75 ± 23	0.32 ± 0.02	0.18 ± 0.03	1.47 ± 0.05	2.06 ± 0.06

Table 3 - Mean ± SE of Amplitude, Interdaily stability (IS) and Intradaily Variability (IV) according to the rhythm (locomotor versus feeding) and the housing condition of the cats.

4. DISCUSSION

This study enabled us to compare the feeding and locomotor activity rhythms of cats according to their housing condition, one population living in an outside enclosure of about 1100 m², the other in indoor panels of about 30 m² each. Although our study conditions prevent the assessment of circadian rhythms in our cats (i.e. no recordings of free-running behaviour in constant darkness or constant light conditions), we were able to determine that a great majority of cats moved and ate with 24-hour cyclicity, thus following day-length periodicity. The arrhythmicity in the eating behaviour of three outdoor individuals must be put in parallel with the weaker rhythms we detected in this housing condition. Lessened rhythmicity in cats living in larger outdoor environment differs from the findings of Piccione et al. (2013) who observed a more robust daily rhythmicity in cats having *ad libitum* access to a large outdoor garden compared to cats having access to a small one, one hour a day. This could be due to unstandardised conditions in the study of Piccione et al. (2013) where owners interacted at will with their pets when at home. Moreover, the indoor population of our study received little disturbance in their daily activity, apart from the three daily standardised human interventions, human noise in the cattery, behaviour of their conspecifics, and the weather fluctuations on the other side of the windows, whereas, in addition to what received the indoor cats, the outdoor population was exposed to direct weather fluctuations, a larger number of conspecifics with varied experience and even occasional fauna living in the enclosure. All these stimuli may constitute rhythm disruptors outdoors that were not met indoors.

On a daily basis, the outdoor population covered more distance than the indoor population, as observed in Horn et al. (2011) and Piccione et al. (2013). Knowing that this population was housed in an enclosure about 39 times larger than the indoor panels and that feral cats and free-roaming pet cats can cover up to 1.7 km between diurnal locations (Jones & Coman, 1982) and 2.3 km from their home (Metsers et al., 2010), respectively, such results were expected. Furthermore, the activity of these predators may be enhanced by an outdoor environment large enough to run through it and giving access to numerous stimuli such as tall grass, insects, even small rodents or birds, which can also explain the tendency of the outdoor cats to move more frequently than the indoor cats. Both populations covered more distance during the photophase than during the scotophase, but the long photoperiod met at this season (around 15h indoors and 15h30 outdoors) could be responsible for this finding as the difference is not detected when looking at the hourly covered distance. Our cats were thus not necessarily more active at day hours than at night hours, despite diurnal human impact, possibly because of nocturnal activity outdoors and diurnal activity troughs indoors.

As observed in previous studies (Parker et al., 2018; Piccione et al., 2013; Randall et al., 1987), the activity of the cats increased during human presence. They were also more active when sunset ended and prior to sunrise indoors, reminding the findings of many studies where peaks of activity rose around twilight (Dards, 1979; Goszczynski, 2009; Haspel & Calhoon, 1993; Horn et al., 2011; Izawa, 1983; Jones & Coman, 1982; Kappen et al., 2013; Kavanau, 1971; Konecny, 1987; Kuwabara et al., 1986; Parker et al., 2018; Podberscek et al., 1991; Randall et al., 1987). Relative troughs in activity were detected in the middle of the night and in the middle of the day for both populations. This echoes with our previous findings in similar indoor conditions (Parker et al., 2018) as well as with lowest activity or observability of cats at midday in two studies on the activity of cats during day hours. Rhythm bimodality is therefore met in both populations.

The main difference between the daily activity patterns of the two populations resides in the evening and at night when outdoor cats were significantly more active than the indoor group, whereas differences between the two populations were less pronounced from morning to end of afternoon. This reminds the higher levels and more prolonged nocturnal activity in the “unowned” cats (Horn et al., 2011) and cats having access to an outdoor garden (Piccione et al., 2013). In fact, the outdoor group stayed active after the afternoon human impact, whereas the indoor group seemed to show a longer midday activity trough where activity is low from 12:00 to 20:00 except at the moment humans enhance it. This could represent a preservation of nocturnal exploratory behaviour when cats live in an outdoor environment. Also, the increase of activity during the morning human intervention was more pronounced outdoors, possibly because the cleaning staff did not interact with the indoor cats at 08:00 whereas interactions happened outdoors at 09:00.

In accordance with the results of daily locomotor activity, the daily food intake of the cats was larger outdoors (around 260 kcal ingested per day), where energy requirements should be higher, than indoors (around 223 kcal ingested per day). Nevertheless, confirming previous results mentioned in the introduction (Bermingham et al., 2012), the indoor individuals tended to eat more frequently than the outdoor ones. Once again, the more confined area the indoor population lives in may be the reason of this tendency: the feeding area being closer to the cats during the day, i.e. more easily accessible, and distractions being less frequent, the cats may eat more often indoors than in a large outdoor enclosure.

Crepuscular peaks of food intake rose indoors around twilight, as previously observed in Parker et al. (2018). In accordance with the literature (Johnson et al., 1983; Parker et al., 2018; Randall et al., 1985), humans induced consumption in the cat, resulting in higher diurnal than nocturnal food intake. Also, food intake of the indoor population was most affected by humans and food renewal at 11:00. More pronounced human impact indoors could be predicted, as the indoor individuals were more familiar and interacting with the caregivers than the outdoor ones. Also, humans represented a more accessible stimulus in about 30 m² than in about 1100 m². This could also result from longer time necessary outdoors to renew the food, compared to indoors where humans were thus available longer. Only one consumption peak was significant in the outdoor daily pattern, during the last hour humans were present in the enclosure. The locomotor behaviour of the outdoor cats is thus more impacted by humans than their eating behaviour. The less rhythmic feeding pattern outdoors may explain the lack of significance in the consumption peaks and troughs in this population. Still, as found in our previous study (Parker et al., 2018), the least active 5 hours of food intake indicated the cats ate the least in the middle of the day and in the middle of the night in both populations.

The moment outdoor cats ate more than indoor cats resided mainly at 09:00 when humans entered the panel for the first time of the day and more interestingly at the end of the day, between 16:00 and 20:00. During this end of afternoon, the outdoor population did not diminish their consumption after the last human-induced peak of the day whereas the indoor population did. In accordance with these observations, evening L5 are never found outdoors and coincide with their indoors activity trough occurring at the same time. This comparison reminds us of the difference in activity patterns in the evening and night between the two populations, but this time, the feeding pattern difference is shorter in time, the cats recovering similar rhythm from 20:00. It seems cats are prone to exploratory behaviour, more than eating behaviour, in outdoors nocturnal environment.

Once again (Kuwabara et al., 1986; Parker et al., 2018; Randall et al., 1987; Refinetti et al., 2016), bimodality, indicated by the periodograms, is an important characteristic of the activity and feeding pattern of the cats and does not vary markedly according to the housing condition. The locomotor activity behaviour of the cats is systematically more rhythmic than their eating behaviour (Parker et al., 2018) and to corroborate with Johnson et al. (1983), Randall et al. (1985, 1987), Refinetti et al. (2016), Thorne (1982) and our previous results (Parker et al., 2018), variability is detected among the individuals of a same group, as demonstrated with variable patterns (variable L5 for example), although some aspects are common among individuals, such as crepuscular and human influence that affected all the individuals.

To conclude, on one hand, similarities are observed between the two populations. Human impact is systematic and even results in more diurnal eating behaviour. It is interesting to see that daylight impacts both populations, as twilight contributes to crepuscular activity and eating peaks and both outdoor and indoor cats decrease activity and food intake in the middle of the day and in the early afternoon. Daylight variations, more than humidity or temperature variations, therefore seem to play a major role in shaping the activity and feeding patterns of the domestic cat. On the other hand, differences according to the housing condition are flagrant: although we could have expected more robust daily rhythms when individuals are exposed to daily fluctuations in humidity and temperature, the outdoor cats are less rhythmic than the indoor cats, supposedly because of more rhythm disruptors in their environment. In their larger enclosure, they cover more distance, feed more and are more active than the indoor population mainly in the evening and night hours, reflecting nocturnal exploratory behaviour. The indoor individuals, on their part, may inhibit nocturnal behaviour without any environmental stimulation and develop a more rhythmic routine with higher daily human impact on their eating behaviour and more frequent meals. Such observations should be taken into account in cat housing procedures in order to better fit to their lifestyle.

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DISCUSSION

Biological rhythms constitute few studies in the scientific literature about cat ethology and vice versa. This scarcity may come from the difficulty to analyse rhythms in a species showing high interindividual variability and from the common idea that the rhythms of the cat are rather random. In fact, due to the opportunist and plastic nature of the cats, their daily rhythms are flexible and enable individuals to adapt to very diverse living conditions. The preservation of traits from their wild nature, such as crepuscular activity peaks, combined with additional stimuli coming from their domestication (i.e. human impact, captivity), make the cat an interesting model to examine.

A proper analysis of daily rhythms requires reliable and complex recording tools providing large and objective numbers of data. During this PhD, we first validated a new way to analyse daily locomotor and feeding rhythms in the cat using precise 24h/24 automatic recording technologies (i.e. UWB and passive RFID) and specific chronobiological parameters in a colony of 14 cats living in an indoor environment at the cattery of Royal Canin (≈2x30 m²; Aimargues, France) on a continuous 7-day recording period (article 1). Then, using the same technologies, we aimed to explore the impact of different environmental cues on their rhythms. In this context, we explored the effect of seasonal fluctuations in photoperiod on the daily behaviour of 6 indoor individuals, recording their behaviours during 21-day long protocols at each season (article 2). Finally, we compared the daily rhythms of cats, during 21 days in summer, according to their housing condition: 15 living indoors, 8 others in a large outside enclosure in the shelter Aide aux Vieux Animaux (AVA, Cuy-Saint-Fiacre, France).

COMMON RHYTHMICITY AMONG INDIVIDUALS

Although our study conditions prevented the assessment of clear circadian rhythms in our cats (i.e. no recordings in constant darkness or constant light conditions), we demonstrated 24-h periodicity in the locomotor behaviour of every population of cats, i.e. in 43 individuals in total (young adults or adults, at every season, indoors or outdoors). The cats therefore followed day-length periodicity, strongly suggesting daylight constitutes a major *zeitgeber* in these populations, as suspected in previous chronobiological studies which detected circadian activity rhythms in the cat (Johnson et al., 1983; Randall et al., 1985). Besides, by providing *ad libitum* feeding conditions, we prevented food-anticipatory activity in the cats, thus eliminating the possibility of a *zeitgeber* caused by daily scheduled feeding (Mistlberger, 1994).

We emphasised bimodality in the activity and feeding patterns of our individuals, as already observed in laboratory (Randall et al., 1987; Refinetti et al., 2016), and free-roaming cats (Goszczyński et al., 2009). Even though more than two peaks appear in the daily activity and feeding patterns of our cats, they are bimodal and not ultradian rhythms of period of six hours or less. Indeed, if the cats showed the latter, significant peaks would rise in the periodograms around six hours or at lower periods. This was not the case, i.e. based on their periodograms, the cats showed only significant peaks at 24 hours and shorter ones at 12 hours. Therefore, we conclude the cats of our three studies presented two main daily troughs in their locomotor and eating behaviours: in the middle of the night and in the middle of the day. To recall, lowest activity or observability at midday had already been reported in studies on day hours (Konecny, 1987; Kunz & Todd, 1978), while a large amount of sleep occurring from 09:00 to 15:00 in laboratory cats (Kuwabara et al., 1986). Some indoor individuals even almost stopped eating between 11:20 and 15:00 h in our first study and between 13:00 and 15:00 h in winter in our second study. These findings resemble those of Peachey & Harper (2002) who noticed that some individually housed cats, exposed to darkness between 19:00 and 06:00 h, stopped eating between 15:00 and 17:00. The last human intervention in our studies, happening around 15:30, could explain why our cats began to eat again after 15:00 h.

The two main activity/eating periods of these double-peaked behavioural patterns corresponded to dawn and dusk. As already observed in the literature (Dards, 1979; Goszcynski et al., 2009; Haspel & Calhoon, 1993; Horn et al., 2011; Izawa, 1983; Jones & Coman, 1982; Kappen et al., 2013; Kavanau, 1971; Konecny, 1987; Kuwabara et al., 1986; Podberscek et al., 1991 Randall et al., 1987), we can thus deduce crepuscularity was expressed in the rhythmic behaviours of our cats. Indeed, this impact of twilight we detected in our first study was confirmed by our second one, as the timings of enhanced activity and food intake changed from one season to another, following the timings of sunrise and sunset according to the season. This is in accordance with previous findings where peaks of activity and food consumption constantly occurred at dusk through the year in free-roaming cats in Ainoshima Island (Izawa, 1983). We demonstrated that annual changes of day-length affect dominantly the duration of active period while sunrise and sunset peaks remained at each season.

The many authors who reported peaks of activity at dawn and dusk characterised these specific moments as key periods in biological and ecological processes such as prey activity, food condition, body temperature, or colonic motility (Goszczyński et al., 2009; Izawa, 1983; Jones & Coman, 1982; Konecny, 1987; Randall et al., 1987). This crepuscular-related activity seems therefore to have through the process of domestication and to be inherited from its ancestor for which the availability of its nocturnal and diurnal preys was likely increased at twilights. It is interesting to see the individuals still express this in conditions where food is made available *ad libitum*. It thus seems this crepuscular behaviour is intrinsic to the species. The preservation of such a trait represents an undoubted advantage for animals if they need to go back to a wild lifestyle, which is often observed in the domestic cat. This hunting behaviour is also blatant in the playing behaviour of pet cats while it is less visible in dogs, emphasising once more the lessened impact domestication had on the domestic cat. Bimodality and crepuscularity, met at every season and in indoor and outdoor populations, seem therefore the best way to categorise the activity and feeding rhythms of the cats.

In our first study, we used actogram characteristics, Least active 5 hours (L5) values and the rate of activity and food consumption according to the period of the nycthemeron (day versus night) to see if the categorisation of our individuals was pertinent regarding typical chronotypes (nocturnal versus diurnal). Interindividual variation occurred in this classification and the main difference between diurnal and nocturnal categorised individuals resided in more pronounced peaks of activity and food consumption at twilights in the latter. The activity and food consumption troughs were similar between the two types of categorised individuals. Therefore, as no general pattern emerged according to the chronotype categorisation, we concluded that the nocturnal/diurnal dichotomy does not fit to the domestic cat, in accordance with several authors who rejected these labels for the species (Aschoff, 1962, as cited in Randall et al., 1987; Hawking et al., 1971; Randall et al., 1987; Refinetti et al. 2016).

Still, it remains of interest to compare the nocturnal or diurnal predominance in cat behaviour according to the season or the housing conditions, as shifts have been observed in other mammals (Cochran, 1987; Merrill & Mech, 2003; Rattenborg et al., 2004) and even in some feral cats (Izawa, 1983). A great majority of the cats we studied covered more distance during day hours than during night hours. Nevertheless, the food intake varied little according to photophase. This underlines the lessened rhythmicity in the eating compared to activity pattern of the cats: daylight seemed to play a less important role in their food consumption than other factors such as human impact or food renewal. The feeding behaviour of the cats of our studies therefore appears to partly dissociate from their locomotor activity. One could wonder if this is due to the *ad libitum* diet they received and if the activity of cats hunting in the wild would corroborate their feeding habits in a greater way than in our study conditions. This could also illustrate frequent exploration behaviour with fewer meal than locomotor activity episodes. The limited impact of daylight on the feeding patterns of the cats emphasises, once more, the difficulty of categorising the cat as purely nocturnal or diurnal, its daily peaks and troughs seeming more suited to describe its daily activity pattern. Furthermore, we consider human impact played an important role in the tendency of the cats towards diurnality, the interventions of the caretakers happening only at daytime and having already been described in the literature as modulators enhancing the activity and food consumption of the animals (Horn et al., 2011; Piccione et al., 2013; Randall et al., 1985, 1987).

We consider the systematic lessened rhythmicity of the feeding behaviour of our cats is related to the opportunistic nature of this solitary hunter, as it must display flexibility in its eating patterns to adapt to the daily rhythms of its preys. Besides, the feeding rhythm of the cats was more variable within a day (i.e. high Intradaily Variability) than their activity rhythm. This difference could be expected, as the feeding pattern of the species has previously been characterised as scattered throughout the day (Bradshaw & Thorne, 1992; Kane et al., 1981; Mugford, 1977; Mugford & Thorne, 1980; Peachey & Harper, 2002; Thorne, 1982), likely reflecting a daily pattern of multiple kills of small prey items in their ancestor, a solitary territorial predator.

As expected, the diurnal human activity in the enclosure or rooms influenced the behaviours of the different populations we studied: cats increased their locomotor activity and food consumption during or after human interventions. The possibility that human interventions play the role of a *zeitgeber* in the daily rhythms of the cat can therefore not be excluded. In fact, we suspect less standardised and more scattered human interventions during the first study (first indoor population), contrary to during the following two others, caused higher variability in the locomotor rhythm of the cats. Also, in our seasonal study (second article), we noticed this human impact was particularly strong at moments when humans interacted with the animals, compared to moments when human intervention only consisted in cleaning of the rooms (first intervention of the day). Besides, in our housing study (third article), the increase of activity and food intake during the morning human intervention was more pronounced outdoors, where interspecific interactions happened, contrary to indoors. It therefore seems it is not only human presence by itself but rather the interspecific interactions which trigger movements and food consumptions in the cats. In order to assess the behaviour of cats without human disturbance, it would be interesting to conduct similar protocols with human interventions happening at various randomised times or even transiently (e.g. for one day) without any human interventions, within the limits of ethics regarding the well-being of the animals.

When looking into more detail at the locomotor and feeding afternoon peak, we observed in our second study that the indoor cats moved to interact with the humans and then, when no stimulations subsisted from the caretakers, redirected their behaviour towards feeding for a moment. In fact, the moment when owners or caregivers feed their cats is a key event in the human-cat relationship. The duration and frequency of the eating behaviour in cats have been reported to increase by approximately 24-fold in the presence of a familiar person (Damasceno et al., 2016). This suspected "appetite-trigger" may be a product from the latest effects of domestication, pet cats becoming more and more dependent on humans for their food resources. It would be interesting to further study this human effect on the feeding behaviour of cats by comparing it in feral and pet cat populations.

Finally, we observed during our housing study (third article) that, put aside the first human intervention which differed in interspecific interactions between the sites (see above), human impact was more pronounced in our indoor population compared to our outdoor population. We suspect this was due to increased familiarity with the caregivers indoors, compared to outdoors. Indeed, different trainees were recruited at each season for studies at the shelter AVA, while the staff was persistent throughout the year at the cattery of Royal Canin. To support this hypothesis, a study demonstrated cats being petted by a familiar person showed higher arousal compared to when petted by an unfamiliar person, supposedly as a result of food or affection expectation (Slingerland et al., 2008). The higher human impact indoors may also come from longer availability from the caregivers during human interventions and in a smaller area compared to outdoors where longer time was necessary to carry out the different tasks in the large enclosure.

A great interindividual variability was observed in the eating and activity behaviour of our populations, as regularly found in the literature (see **Appendix 2** for illustration example). In our first study, some variation seemed to come from the sex of the individuals: the males tended to be more active, more rhythmic in their behaviours and ate more than the females. Other variability came from the group the individuals lived in: one group was more active than the other. This possibly happened because they had been living together for a longer time than the less active group and may therefore have shown less avoidance behaviour, as they had more time to accommodate to group behaviour. Also, in every population we studied, some cats showed lesser reaction to human presence and others showed higher sunset or sunrise peaks.

Be that as it may, it is noteworthy that similarities persisted across the individuals. Mainly, the activity and feeding troughs around mid-day and mid-night were robust across the seasons, sex, housing conditions and individuals, whereas differences in behaviour levels according to these variables resided in the peaks. We also noted that cats of a same group showed very similar rhythms, while cats between the groups acted more differently. This interactive aspect of the species living collectively may confer an evolutionary advantage as it allows the individuals to adjust their behaviour to various living conditions, evoking the adaptive behaviour already recognised in studies on the species. In fact, variations in the habits of the cats according to environmental conditions in our studies illustrate this plasticity rather than interindividual variability.

As a first illustration of this plasticity, the cats changed their activity and feeding patterns according to the season in a similar way across the individuals (second article). For instance, they diminished their daily covered distance in winter, when day-length was the shortest. In accordance with previous publications demonstrating cats are sensitive to photoperiod (Dawson, 1941; Leyva et al., 1989; Michel, 1993), this gives, once more, evidence of the impact of day-light length on the locomotor behaviour of cats, as this was the only varying environmental factor among the different season protocols.

Besides, the individuals showed maxima in covered distance during spring and autumn and minima in both distance and food intake during winter. In other cats exposed to seasonal fluctuations, spring activity maxima and winter minima had already been reported (Dards, 1979; Goszczyński, 2009; Haspel & Calhoon, 1993; Romanowski, 1988; Weber & Dailly, 1998), but not autumn maxima. This finding in our study comes from the imposing afternoon activity peak at this season and we consider human impact played a role in this distinction. Indeed, the afternoon human intervention and the upcoming sunset, two activity-enhancing factors, being close in time at this season, the combination of the two seems to have resulted in a single massive activity peak instead of two (see fig. 6 in the article “Seasonal impact on locomotor and feeding rhythms in indoor cats”). This combination was also met in winter, however the cats did not show such a high afternoon peak, demonstrating human impact was this time weaker against the general lessened activity at this season. Besides, this reminds a more stable activity pattern throughout the day during the cold seasons in free-roaming cats in rural areas of central Poland (Goszczyński, 2009).

The cats of our studies ate the least in winter, which concurs with the studies of Kappen et al. (2012, 2013) and Bermingham et al. (2012). Different findings, i.e. food intake maxima during late autumn to winter, in Serisier et al. (2014), may come from the more various diets in their study conditions, while our individuals received the same diet throughout the protocols and were more impacted by photoperiod alone. Also, the cats in the study of Serisier et al. (2014) had access to outdoor rooms. As the cats of our seasonal study received negligible impact of seasonal ambient temperature or humidity variations, we consider once more that natural luminosity, in particular the related photoperiod, a powerful *zeitgeber*, is the driving factor for these seasonal changes in behaviour in the domestic cat.

The same protocols were conducted on the outdoor population. Unfortunately, no statistical analyses could be conducted because of recording and other technical difficulties resulting in the impossibility to compare more than two (for locomotor behaviour) or three (for eating behaviour) similar outdoor individuals according to the season. We would have expected to find more pronounced seasonal differences in this population, more exposed to weather fluctuations (e.g. in ambient humidity and temperature), compared to the indoor population. Nevertheless, the less rhythmic outdoor behaviour caused by numerous rhythm disruptors (see below) may have made difficult the distinction of seasonal influence on the rhythms of the cats.

During the third article of this PhD, where we compared the behaviour of the indoor cats of the second study with other individuals living in an outdoor enclosure, the animals showed different behaviours according to their housing condition. Daily, the outdoor population covered the most distance and ate the most compared to all the indoor populations we studied (corroborating Horn et al., 2011 and Piccione et al., 2013). Knowing free-roaming cats can cover home-ranges of 3.45 ha (30 times the outdoor enclosure; Kitts-Morgan et al., 2015), this finding is probably mainly due to the surface difference between the two sites: the outdoor enclosure was about 39 times larger than each indoor room. Outdoor environment may also promote the activity of this hunter, giving access to numerous arousing cues such as tall grass, insects, even small rodents or birds. This can also explain the tendency of the outdoor cats to have moved more frequently than the indoor ones. Besides, as the outdoor individuals were exposed to greater fluctuations in ambient temperature, lighting and humidity, they may have needed to change spots more frequently than the indoor individuals in order to maintain comfort.

The more confined area the indoor individuals lived in may also be the reason why they tended to eat more frequently than the outdoor ones. Indeed, the feeding area being closer to the cats during the day, i.e. more easily accessible, and distractions being less frequent, the cats may have eaten more often in a confined indoor room than in a large outdoor enclosure. This emphasises the implication of the housing condition on the risk of obesity in domestic cats.

The locomotor rhythm of the outdoor population had lower amplitude, the lowest Interdaily Stability (IS) among all populations, as well as higher Intradaily Variability. Lessened amplitude and IS were also detected in their feeding rhythm. Supplementary daily behaviour disruptors were met outdoors compared to indoors, such as direct weather fluctuations, a larger number of conspecifics from various different backgrounds and even occasional fauna living in the enclosure. We suspect all these environmental cues may constitute rhythm disruptors outdoors that were not met indoors.

In addition, the main difference between the daily activity patterns of the two populations resided in the evening and at night. At that time of the day, outdoor cats were significantly more active than the indoor group, whereas differences between the two populations were less pronounced from morning to end of afternoon (see fig. 7 in article “Comparison of locomotor and feeding rhythms between indoor and outdoor cats living in captivity”). This reminds the higher levels and more prolonged nocturnal activity in the “unowned” cats in Horn et al. (2011) and the more nocturnal activity of cats having access to an outdoor garden in Piccione et al. (2013). In fact, the indoor group we studied seemed to show a longer midday activity trough where locomotor behaviour was low from 12:00 to 20:00, except at the moment humans enhanced it, whereas the outdoor population remained active after the afternoon human impact. This could represent a preservation of nocturnal exploratory behaviour when cats live in an outdoor environment. Horn et al. (2011) speculated that supplemental feeding and shelter availability were factors explaining the lower need for “owned” cats to correspond their activity to that of their prey, hence nocturnal activity. This explanation seems contradicted in our study, as the outdoor individuals were fed *ad libitum* and had access to numerous shelters in their enclosure. Besides, they ate significantly more during day hours than during night hours, demonstrating their nocturnal behaviour consisted more in locomotor activity than in feeding behaviour. These differences between the two populations may also partly come from their ability to adopt a similar behaviour within a group, which we presumably identified in our first study.

METHOD INTERESTS & LIMITATIONS

As we discussed, for a proper assessment of daily rhythms, the use of objective and accurate recording methods is crucial. Direct observations are not adapted to such studies as they prevent observations to be precise and over long periods, day and night. Automatic recording devices, providing a great and continuous number of data, thus consist in the most reliable tool.

In order to rigorously track the locomotor activity and feeding behaviour of the cats we studied, we used Ultra-Wide-Band (UWB) technology and passive Radio Frequency Identification (RFID) coupled with weighing scales, respectively. The UWB technology had previously been validated as a promising way to track the activity of indoor cats at the cattery of Royal Canin Research Centre, allowing precise real-time automatic recording of the location of each group member (Parker et al., 2017). Until today, the continuous monitoring of the behaviour of cats round the clock and with precision was extremely difficult, if not impossible. Contrary to GPS tracking collars or accelerometers, UWB tags and their long-life batteries enable collecting data with high temporal frequency and over long periods (up to 1 year or more). The analysis opportunities offered by UWB technology therefore opened the way to a great number of new ethology studies with more precision than ever and thus strengthen the scientific methods ethologists can use to better apprehend animal behaviour. Indeed, during our studies, it generated more than 1400 data per day and cat, which resulted in more than 30 200 data per 21-day protocol for one individual. This massive data set allows high significance in the statistical analyses and the continuity of the data is essential for reliable daily rhythm measurements. Also, this advantage of having objective and accurate data which are not influenced by the presence of an observer is particularly significant concerning avoidant individuals which were met in the outdoor cats during this PhD.

The food intake measure, using automatic weighing and passive RFID, has very few limitations. It records the identity of the individual, the time of food consumption and the amount of kibbles eaten with precision. While one could presume that one or two feeding areas are too few to match the needs of a species characterised as solitary, it has been demonstrated that members of a colony can organise themselves to access resources (Damasceno et al., 2016). Nevertheless, as the automatic feeding devices of the indoor groups were individual specific -each collar could only open one specific trapdoor-, some cats managed to force the opening of other traps than their own and steal the food of their conspecifics during the first protocol (spring) of our seasonal study. After assessing this problem, we noticed these “thieves” had preferential spots to eat (traps closer to the ground for example) and shifted the assigned doors accordingly. No stealing behaviour was observed since then. This however is the reason why we only compared six and not 15 cats during our seasonal study (second article). This problem was not met in the outdoor group, as the system of traps, open, differed in a way that every cat could have access to any door, the device automatically recording which individual was eating. Nonetheless, with this automatic recording without visual confirmation, we were not immune to cats taking kibbles out of the device without eating them and/or leaving them to another individual. Besides, as a cat had to wear a collar in order for its food intake to be recorded, part of the consumptions of the outdoor individuals were not recorded (e.g. unapproachable individual, loss of the collar). However, we ensured that the food quantity stock in the devices was always more than sufficient to give *ad libitum* access to every cat. This also helped lessening the need for cats to perform hunting activities, the feeding devices always containing left food when we renewed the daily rations, and prevented, as evoked earlier, a *zeitgeber* caused by food-anticipatory activity to influence the daily rhythms of our cats. Nevertheless, the necessity for the cats to enter their heads inside the feeding devices compartments in order to eat may not represent a natural eating behaviour for them, as the lack of visibility can induce a feeling of vulnerability (not being able to predict the arrival or presence of competitors or danger for example). Yet, we made sure this feeding system did not prevent any of our individuals from eating and no visual indices of stress behaviour have been observed at the feeding devices.

This PhD used pioneer technologies and therefore prototypes in the outdoor environment. Consequently, unexpected incidents happened. The weather in Normandy greatly varies from frost, rain, wind or heat from direct exposition to the sun. These conditions had been considered in the manufacture of the collars and feeding devices. Still, (parts of) the feeding devices broke down and had to be frequently repaired, which sometimes forced us to delay or even cancel outside recordings. The softwares specially developed for the recording of the outdoor group feeding behaviour were also prototypes. A number of modifications of configuration and algorithms have been considered and made throughout the studies in order to make sure the recorded data corresponded to the real food consumptions. Maintenance over time was necessary, as bugs could not be predicted and improvements were still to be identified. Several problematic events have been encountered and resolved throughout the PhD.

The captive cats we studied were fed their entire daily ration of food in a stable morning hour (between 11:15 and 12:00). This regular schedule was chosen to enable a comparison between seasons and between sites and was adapted to their welfare: Stella et al. (2014) reported a consistent husbandry routine promotes welfare in captive cats. Our conclusions however have to consider scheduled human presence as a possibly determining factor in the rhythm of the cats, as evoked earlier. In order to compare the data of the indoor and outdoor cat groups in a standardised manner, we made sure the protocols were synchronised. This necessity was difficult to set up as environmental and human conditions varied between the two study sites. For example, the caregivers of Royal Canin and the shelter AVA do not work at the same schedule, while we needed to find similar intervention timetables in the panels/enclosure. Furthermore, the enclosure of the outdoor cats being considerably larger than the rooms of the indoor cats, time needed to fulfil the numerous tasks (resupply the food in the devices, weigh and resupply the water, weigh the cats, check the loss of collars, the condition of the cats, feed the ones that stopped eating dry food, …) was different according to the study site.

On one hand, at the cattery of Royal Canin, the loss of collars was not a significant issue as classic clasps were used, with the tracking tags attached to it. On the other hand, anti-strangulation clasps were used for the outdoor population in order to prevent the risks of life in an outdoor enclosure containing trees or shrubs and many elements to climb up to (**See appendix 3**). Even though solid clasps were chosen, some outdoor cats detached their collars during the protocols and provoked data loss. We made sure they recovered them as soon as possible in order to limit the loss of data to a minimum. Also, outdoors, we chose to respect animal welfare by not using electrified fences and some cats figured out how to escape the enclosure. After observation, this problem seemed rather impossible to prevent, the motivation of the individuals enabling them to always find a way to escape, climbing the wire fencing and jumping outside the enclosure despite the anti-escape system put in place. Fortunately, these individuals were rare and did not diminish our sample sizes drastically.

Even though part of the outdoor population in the enclosure was afraid of humans and approaching these cats was very difficult or impossible, we managed, with the help of my trainees, to get close to most possible in order to equip them. Still, for the protocols to study a significant number of individuals, cats from outside the enclosure had to be recruited. However, in order to take part in the studies, they had to tolerate: eating only dry food, living with conspecifics (including intact males), human contact, outside living conditions (strong health). Contrary to the groups of the second indoor population (second and third articles) which remained stable between protocols, the outdoor cat population thus varied: some new individuals were added to the enclosure and some were taken out because of health or behavioural reasons expressing maladjustment to the study conditions (e.g. reclusion, agonistic behaviour, stress). The time separating each protocol from another however enabled the cats to acclimate to the potentially new organisation of the group. Another difficulty came from some animals which stopped eating, had thus to be fed individually and could no longer provide any reliable food consumption data. Nonetheless, we made sure the feeding of these individuals was isolated from the rest of the group so that the feeding behaviour of the latter was not biased.

On one side, the indoor cats mainly consisted of different breeds, same age and same extraction individuals. On the other side, the shelter AVA taking in animals from every type of background, the outdoor cats were mainly of European breed, different ages and from various origins, i.e. former house/flat cats, feral, or of unknown background. This heterogeneity of individuals allowed a more exhaustive analysis but also brought more difficulty in behavioural studying by adding different parameter levels to take into account. Unfortunately, the impacts of age, breed, sexual status and extraction were not assessable as they were related to the site impact (indoors versus outdoors) and because the too small number of individuals of some categories prevented proper statistical comparisons. Furthermore, the rare intact males may affect the dynamics of the others. In future analyses, consideration (including multifactorial analysis) of the different characteristics of the individuals would bring interesting and more detailed insight on the variety of behavioural patterns. Although the populations (mainly neutered individuals) and study sites (closed enclosure/rooms) prevent the generalisation of our findings to overall cat populations, our studies still concerned a significant part of them and provided a design better suited to scientific analyses. Nowadays, more and more pet cats live in captivity with lessened outdoor access, especially in areas where their impact on the neighbouring fauna becomes problematic.

As evoked earlier, technical unpredictable difficulties with the recording system sometimes resulted in data loss about the locomotor behaviour of the cats; especially outdoors. Some difficulties also occurred in the recording of the feeding behaviour of outdoor cats because of the occasional breakdown of the outdoor feeding devices prototypes. This resulted in too few outdoor animals (two or three) in common among seasons to enable proper rigorous comparisons and is the reason why we focused our second article on seasonal impact indoors, where the data of more animals were available at each season. For the third article, where we compared the behaviour of indoor and outdoor individuals, we chose to use summer data as this season did not suffer major data loss.

PERSPECTIVES

During the first year of study of this PhD, the main objectives were to characterise the activity and feeding behaviours and rhythms of the domestic cat according to the site (indoors/outdoors) and the season (spring/summer/autumn/winter) under *ad libitum* dry food. Nevertheless, a great part of cat owners feed their pet with wet food before going to work and/or when coming back from it. No longitudinal study has really evaluated the impact of this human-induced feeding rhythm on cats. During the second year, we thus attempted to assess if wet food, added to the original dry *ad libitum* diet of the cats at different times during the day, impacted their locomotor and feeding behaviours and rhythms. By studying the impact of wet food distribution once or twice a day on their behaviour, we expected to be able to assess the repercussion of the typical diet encountered by cats living with their owners. That way, we would be able to study the impact of the time of food distribution on the behaviour of the cats and to compare it in different conditions. This study would, for the first time, bring knowledge about the impact of mixed feeding on the daily activity and feeding rhythms of the cats throughout the seasons, indoors and outdoors.

The working hours of the caregivers had to be taken into account when deciding the timings of wet food distribution conditions. We had to choose the earliest and latest hours of their schedule, which did not correspond the best to the typical wet food distribution of cats living with owners (before leaving to work and after coming back from work). Yet, the chosen wet food distribution hours consisted in a pertinent parameter regarding different impacts of the diet timing on the rhythm of the cats, one being in the morning and the other in the afternoon. The cats were fed *ad libitum* the same extruded dry diet as during the first year protocols (Fit32 (3895kcal/kg), Royal Canin, Aimargues, France), but this time, various distributions of wet food (Gastro Intestinal Moderate Calorie (709kcal/kg), Royal Canin, Aimargues, France) were added to their diet (see **Appendix 4**). Distribution of wet food occurred: between 9:00 and 10:00 and between 15:00 and 16:00 during the first condition (“double”); between 9:00 and 10:00 only during a second condition (“morning”); between 15:00 and 16:00 only during a third condition (“afternoon”). During a last condition (“null”), no distribution of wet food was operated. One protocol (at one season) consisted of the following of the four conditions. Each condition lasted 10 days (3 days of habituation for the cats to acclimate to the diet conditions, followed by 7 days of recording) and their order was randomised at each season and for each population to eliminate an order effect. The wet food was made available for one hour each time so that each cat had enough time to eat it (especially outdoors, as only 16 cats could eat at the same time) and the food did not deteriorate (e.g. desiccation, insect intrusion). As during the protocols of the first year, in each trap, the cats could choose between two steelyards (see **Appendix 5**). Outside wet food distribution hours, both steelyards were filled with dry food. During wet food distribution hours, one steelyard stayed filled with kibbles whereas the other was filled with wet food.

The side where the wet food was provided was randomised at each protocol in order to eliminate a laterality effect, the food being poured as many times in the left steelyards than in the right steelyard in each condition period.

Unfortunately, some technical difficulties prevented the proper analyses of the data of these protocols for them to be used in the report of this PhD. Some steelyards of the outdoor feeding stations broke, or sometimes the whole devices stopped working. Also, rats started to eat from the food provided to the cats outdoors and impacted our feeding and locomotor data. Delay in data acquisition and data processing prevented proper analyses within the time frame set for this thesis, still, analysis will be performed in the near future.

The findings of our studies as well as the difficulties we met gave us an idea of how protocols should be conducted in the future for the proper assessment of the behaviour and rhythms of cats. Firstly, as required in any scientific study, the larger and more constant sample across the conditions, the best. In our studies, we suffered from data loss due to exited or not yet included individuals in some protocols. It would therefore be judicious to be able to choose animals with robust health, high intraspecific and study conditions tolerance. We still suggest keeping outdoor and indoor populations in order to enrich our knowledge on the behaviour of the domestic cat in a more generalizable way.

The indoor population we studied for the first article covered less daily distance and ate less than the indoor population of our second article. The first population being 5 years-old and the second 1-2 years old, this suggests a predictable age effect on locomotor activity. Also, age seemed to have an impact on the feeding rhythm of the indoor cats of our second study, as it grew stronger along the seasons. As the cats acquired their adult age during this year, we suspect they may have developed a feeding routine in relation to the daily food renewal and appetite-enhancing human interventions which were standardised at each season. In keeping with this hypothesis, the amplitude of the feeding rhythm of the first indoor population (first article) was higher than the one of the young adults of the second indoor population (second and third articles). Age effect being a pertinent aspect to study, individuals of different age categories should be used in future studies, with similar sample size per age category. The same should be applied for the study of sex, breed, sexual status and origin effects on the behaviour of cats.

Ad libitum dry diet should be provided as a base, considering it allows the animal to have direct control over the timing and size of their meals. Wet food, as during our second year of protocols, could be implemented in their diets in order to investigate the impact of humidity variations as well as the appetence of food on the behaviour of the cats. It should be provided so that every individual has time to have access to it. As for the distribution timings, it would be interesting to provide wet food at times when we observed peaks of food consumption (around twilight for instance) but also at times when we noted feeding troughs, in order to assess to what extent the cats can modify their feeding patterns. The implementation times should be randomised.

We have suggested the size of the enclosure was responsible for differences in the behaviour of the outdoor population compared to the indoor one. In order to better apprehend the impact of the housing conditions on the behaviour of cats, it would be pertinent to observe them in a more standardised manner, with, for example, the comparison of two sizes of outdoor enclosure and indoor rooms. The different areas (e.g. providing water, food, litter, shelter) should also be standardised in number and location. Outdoors, precaution should be taken to prevent animal intrusion and cat evasion.

The locomotor rhythm amplitudes, determining how much of the activity is actually rhythmic, were lower in the first indoor population (first article) and in autumn in the second indoor population (second article). While one could deduce lower rhythmicity in the cats from these findings, we consider short recording periods of the locomotor activity during these studies (i.e. 7 days during the first, 12 during the second) are responsible (see **Appendix 7**). Therefore, these periods should be long enough to allow proper estimation of the rhythmicity of the cats. We preconize a minimum of 21 days of recordings, as this duration was enough to detect rhythmicity in every indoor individuals of our study, but not outdoors. Also, as during the studies of this PhD, the recordings should take place at every season to get a view of the behaviour of cats on an annual basis.

We have established human interventions impact considerably the behaviour of the cats, provoking peaks in locomotor activity and food intake. In order to eliminate this effect (possible *zeitgeber*) for a better assessment of the spontaneous behaviour of the animals, one could argue we should study them in conditions without any human impact. However, aside technical complications, these conditions would not be ethically adapted to domestic cats over several days, as the welfare of some depends on regular human contact. Taken this into consideration, human interventions should happen transiently (for one day) or at randomised timings to erase their impact on the activity and feeding patterns of the cats. Also, the interspecific interactions (e.g. the behaviour humans should adopt) should be standardised as much as possible between seasons and populations.

The locomotor activity and feeding rhythms of the populations we studied showed high bimodality. Yet, some of the parameters we used to measure these rhythms were more fitted to unimodal patterns. For rhythms analyses to be more adapted to the cat, new chronobiological tools should be developed, taking into account their tendency towards two main daily peaks and troughs in activity and food intake (see **Appendix 7**).

Among other benefits, the tracking technologies we used during this PhD were chosen for their precision and automatism. We however discussed the limitations we met regarding the robustness of the devices. This was due to harsh weather conditions and the fact that we used prototypes. For further analyses, it would therefore be optimal to use more solid feeding devices (i.e. more adapted to outdoor conditions) and more reliable network and software with regular checking of their well-functioning (e.g. memory availability, ongoing of recordings). Also, it would be more convenient to find a way for the outdoors collars to open less easily, while keeping anti-strangling guarantee.

The automatic technologies we used allow having objective and accurate data which are not influenced by the presence of an observer. Nonetheless, they cannot inform about the actual behaviour the animal is showing when he moves or eats. This is why supplemental video analyses should be conducted to further study the behaviour of the animals. Visual observation could, for instance, inform about what activities cats express when outdoors (e.g. hunting, more frequent changes of resting spots, running), compared to indoors. In that context, the assessment of the use of resources other than food (e.g. resting, hiding or lighted areas) through time would constitute valuable insight.

Randall et al. (1985) indicated low light, during dark phases, impacts the rhythm of laboratory cats. Natural nocturnal ambient light (e.g. from the moon) could therefore constitute another environmental cue influencing the behaviour of outdoor individuals and should be investigated.

During our studies, we used the UWB technology to provide us with the distance covered by the individuals. The software related to this technology can however also calculate other variables from the coordinates of the individual such as time spent in specific areas, number and duration of intra and interspecific contacts and interindividual distance. These would be interesting to investigate for a more complete behavioural study. We could, for example, expect different use of the indoor rooms or outdoor enclosure according to the hour of the day, the season or the population. Furthermore, it would be interesting to measure the time spent in the indoor area where the individuals receive external air from gaps under bay windows (see fig. 1 of article “Comparison of locomotor and feeding rhythms between indoor and outdoor cats living in captivity”), in order to investigate the impact of these small outdoor fluctuations on their behaviours and rhythms. Moreover, as the cats live collectively, there is no doubt their interindividual interactions and relations impact their behaviour. For instance, we noticed a young intact male (Bounty) from the outdoor population, showed lessened and more nocturnal activity, while an older intact male (Merlin) which showed agonistic behaviour towards Bounty, was more active and diurnal in its activity (**See Appendix 6**). As the younger showed fearful behaviour towards the older, we wonder if Bounty adapted its activity pattern in order to avoid Merlin. Also, as the number and duration of interactions with humans vary across the individuals, this variable should be taken into account in the analyses of the behaviours of the cats, even with more standardised interspecific interactions.

CONCLUSION

During this PhD, through articles and scientific communications (see **Appendix 8**), we aimed to characterise the locomotor and feeding daily rhythms of the domestic cat under different living conditions (i.e. at every season, outdoors and indoors), in order to clarify the heterogeneous findings about its behaviour in the literature. Our main findings clearly demonstrate the cats follow 24-h periodicity, indicating that photoperiod is a decisive factor in the behaviour of the cat. This was confirmed by seasonal changes in activity and food intake amount, as well as in the related daily patterns, in indoor cats only receiving seasonal fluctuations of daylight. This does not mean however that they adopt clear nocturnal or diurnal patterns. In fact, this PhD gave evidence about the irrelevance of binary chronotyping for the domestic cat. Nevertheless, human interventions impacted the rhythms of the cats and we surmise their diurnal schedules resulted in more enhanced cat activity and food consumption at day than at night in our studies. As predicted, the cats showed multimodality in their daily patterns. In fact, we revealed that the best way to characterise the activity and feeding rhythms of the species relies on bimodal and crepuscular patterns. Indeed, be that outdoors or indoors, major peaks of food intake and locomotor activity rose around dawn and dusk, outside any human influence. Also, troughs were detected twice in the day, in the middle of the night and of the day, corroborating previous publications. This was expressed in individuals under *ad libitum* food whereas crepuscular behaviour in the domestic cat is considered to come from an adaptation towards the life rhythms of its diurnal and nocturnal preys in the wild. This rhythmicity, which shifted according to the twilight timings at each season, therefore seems intrinsic to the species and persisted through domestication. Besides, the feeding rhythm of the cats was more variable than their locomotor activity rhythm, recalling the opportunistic character of this hunter. Also, the plasticity of the species was confirmed. For instance, the cats adapted differently to their housing conditions: outdoors, environmental factors resulted in weaker daily rhythms and more nocturnal exploratory behaviour, compared to indoors where the cats were more prone to routine. To conclude, domestic cats enjoy great flexibility in their behaviour. Despite domestication, they stay adapted to life outdoors with the preservation of ancestral traits of an outdoor predator, as visible in crepuscular peaks of activity showing in indoor controlled conditions. Still, they are also fit to indoor life, showing tolerance to different housing conditions and integrating human proximity in their everyday life. This explains the multiplicity and durability of cat populations on Earth, ranging from pet cats living in apartments to feral cats roaming through hectares of nature.

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APPENDIX

APPENDIX 1 – Published article validating the UWB technology (Parker et al., 2017)

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Feline research

Accuracy assessment of spatial organization and activity of indoor cats using a system based on ultrawide band technology

Marine Parker [a,*], Sarah Lamoureux [a], Benjamin Allouche [a], Jean-Alain Brossier [a],
Mickaël Weber [a], Alexandre Feugier [a], Delphine Moniot [a], Bertrand Deputte [b],
Vincent Biourge [a], Jessica Serra [a]

[a] *Royal Canin Research Center, Aimargues, France*
[b] *National Veterinary School at Alfort ENVA, Maisons-Alfort Cedex, France*

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ABSTRACT

The study of mammalian societies and other similar social groups requires identification of group members and documentation of their spatial organization. Ultrawide band technology is a pioneering research technique that allows real-time automatic recording of the location of each group member. Cats living in a group were equipped with active transponders on their collars over a 2-week period. Cats traveled on average 965 ± 360 m per day, spending 30% ± 7% of their time moving. Their activity was characterized by 4 peaks of activity: 2 in the morning, another in the midafternoon, and the last at sunset. They spent most of their time in resting places, only 1 hour in the feeding area and a few minutes in the drinking and elimination areas. They interacted on average 53 ± 9 times with each other during the 24 hours they spent together per day and 32 ± 7 times with humans. This approach provides a new system to monitor groups of animals more accurately than Global Positioning System technology in indoor environments and in a much more convenient way than passive radiofrequency identification.

Introduction

Spatial distribution and social interactions of mammals or insects are typically investigated by human observers scoring behaviors in real time or from video data. The latter process, even with modern techniques based on digital image analysis, is time consuming and demanding in terms of data storage. Video recording is also fastidious and difficult to implement with animals similar in appearance or in conditions of low light or darkness. Another alternative is to follow the animals using Global Positioning System (GPS) trackers that can be very useful for long distances. This concept is based on the receiver-satellite distance estimated from the time taken by the signal to travel from the satellite to the GPS receiver. By monitoring feral cats with GPS collars in open landscapes, Recio et al. (2010) were able to determine their home ranges. Nevertheless, these technologies are unsuited to indoor environments. Furthermore, commercial GPS tracking collars also have data storage constraints, hindering collecting data with high temporal frequency (e.g., every 15 minutes or less) if animals are followed during long periods (up to 1 year or more).

Radiofrequency identification (RFID) technology represents an interesting alternative as it allows the storage of a hypothetically infinite quantity of data with excellent spatial resolution (<1 cm). In previous studies, passive RFID tags were chosen because of their miniaturized size and unique ability to yield accurate information about spatial distribution (Kritzler et al., 2006; Want, 2006; Serra et al., 2012). However, the tag must be close enough to the reader/antenna to be detected, and only 2 dimensions are documented. Furthermore, many RFID readers must be used to cover the spatial domains of interest. To overcome this limitation, some studies have developed a mobile reader able to cover the desired area of interest (Moreau et al., 2011), whereas others have used a large quantity of readers to cover larger areas (Kritzler et al., 2007).

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[*] Address for reprint requests and correspondence: Marine Parker, Royal Canin Research Center, 650 Avenue de la Petite Camargue, 30470 Aimargues, France. Tel: +33 6 73 33 40 12.
E-mail address: marineparker@gmail.com (M. Parker).

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Ultrawide band (UWB) may be a more suitable technology to track animals in an indoor environment as the reader can be spatially dissociated from the tag: the tag emits a signal that can be detected by triangulation by a remote reader. Thus, the UWB technology represents an innovative solution to mitigate the accuracy of GPS systems and the spatial constraints imposed by passive RFID.

The objective of this research was to use UWB technology to simultaneously localize, with maximum accuracy, a group of cats 24 hours a day, during a 2-week period and to automatically infer behavioral parameters.

Materials and methods

Animals

A group of 6 European breed cats, aged 3, was studied: 4 spayed females (Farfale, Farfouille, Ficelle, and Fleurette) and 2 castrated males (Falstaff and Farwest). They lived indoor at the Royal Canin's cattery (Aimargues, France) and were observed continuously during 14 days. They all wore UWB tags on their collars during the entire period and were housed under natural light conditions with ad libitum access to food and water, a temperature of 20-21°C in the room and a relative humidity of 20%. The group was fed an extruded dry diet (Fit 32; Royal Canin, Aimargues, France). Staff entered the cat housing facility every day around 06:00 hours to clean the facility, between 08:00 and 09:00 hours and between 14:00 and 15:00 hours to interact with the cats. Cats showed no clinical symptoms of disease over the duration of the study. Each movement was recorded during the entire study and analyzed by software specially developed for this purpose.

Experimental device

Experimental setup

The room was divided into 2 parts, an indoor heated main area of 22.5 m^2 and an outdoor courtyard of 7 m^2. Different areas were defined as static areas in the software's parameters to quantify the time spent in each of them (Figure 1): the feeding area, the drinking area, the seat, 2 litter trays, the wall shelf containing several hiding places and cushions, the enriched area, and the cat trees also containing cushions.

UWB antennas (Ubisense, Paris, France)

With a detection range of 60 m, 7 antennas were placed in corners of the rooms ensuring a perfect coverage. UWB technology uses the principles of active RFID system. Active UWB tags emit a signal detected by UWB readers. By contrast with passive RFID, active RFID does not require closeness between the reader and the tag. It also allows automatic recording, in real time, during a theoretical infinite period, and in 3 dimensions (x, y, and z), each tag's location. The accuracy at the location was analyzed by the manufacturer and was on average 12 cm with a median of 10 cm.

Tags

The 7000 series compact tags were UWB devices certified European Conformity and Federal Communications Commission Part 15.519 (Ubisense, Paris, France). Their dimensions were: width = 38 mm, length = 39 mm, height = 16.5 mm, and weighed 25 g, approximately 0.6% of the cat's weight. The frequency of RFID UWB was 6-8 GHz. The Ubisense tags and readers used extremely low-power radio transmitters and met all applicable European Union requirements, including those for human exposure to electromagnetic radiation.

Figure 1. Experimental setup in 2 rooms. The main one (around 22.46 m^2: 6.4 m [length] × 3.51 m [weight] × 2.60 m [height]) contains an enriched area (with toys), a feeding area, a resting area (big elevated shelf), a drinking area, and a litter; the other, an inner courtyard (around 7 m^2: 2.9 m [length] × 2.4 m [weight] × 2.60 m [height]) contains another litter, 2 cat trees, and a big seat.

Tags were fixed to each cat's collar, and humans wore a specific tag attached to a thin cord around their neck every time they entered the cat housing facility.

Data processing

Detection algorithm and extraction of each cat's position

The litter boxes, shelf, seat, cat trees, drinking and feeding areas, and the enriched area were not moved during the protocol and defined as static areas. Cats and humans were considered as virtual dynamic areas surrounding the tag in a 15 cm radius (Figure 2).

Data were recorded every 0.9 seconds, during a 2-week period (April 22-May 5, 2013), whenever the subject wearing the tag moved. Data were stored in a SQL server database, and all the computations were done with C++ language with Microsoft.Net development platform.

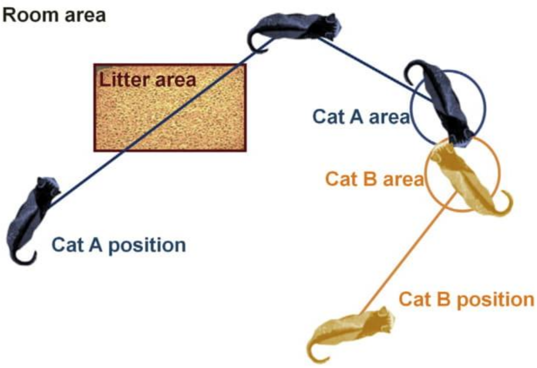

Figure 2. Schematic representation of a static area (litter area) and of dynamic areas (cats) around tags.

Extracted variables

Mean traveled distance per day and per hour. The mean traveled distance per day designates the distance traveled by an individual during the collection period, divided by the number of collection days. To infer daily activity patterns, we also calculated the mean traveled distance per cat and per hour on a 24-hour period.

Mean locomotor activity rate. Locomotor activity rate was calculated on a daily basis from the time spent traveling (i.e., the transponder is moving) compared with the time spent motionless. The algorithm did not take into account the moving artifacts because of activities such as autogrooming, eating, or other static behaviors.

Time spent in the different areas. The time spent in different areas designates the time a cat spent in each defined area per day (enriched, feeding, drinking, litter tray, shelf, cat trees, and seat).

Mean number and duration of intraspecific contacts. A contact was defined as a social proximity between 2 cats, as close as 30 cm, every time a cat's tag entered in another virtual dynamic cat area. From those data, we extracted the number of intraspecific contacts and their duration, defined as the amount of time a cat spent in another cat area.

Mean number and duration of interspecific contacts. The number of interspecific contacts was the number of times a cat area entered in a human area (as described before) and the duration as the amount of time a cat spent close to a human.

Results

Mean traveled distance per day

Overall, the 6 cats traveled on average 965.34 ± 359.51 m (standard deviation) per day (Figure 3). Huge differences in travel distances were observed between cats.

Mean traveled distance by hour

The traveled distance per hour was characterized by 4 peaks. The first at 06:00 hours (around 48 ± 39 m), and the second, between 08:00 and 09:00 hours, representing the highest level of locomotor activity (around 91 ± 33 m and 96 ± 31 m), both coinciding with the technicians' entrance to the room. The third happened in the early afternoon between 14:00 and 15:00 hours (around 42 ± 18 m), the fourth at sunset (around 21:00 hours, 50 ± 28 m) (Figure 4).

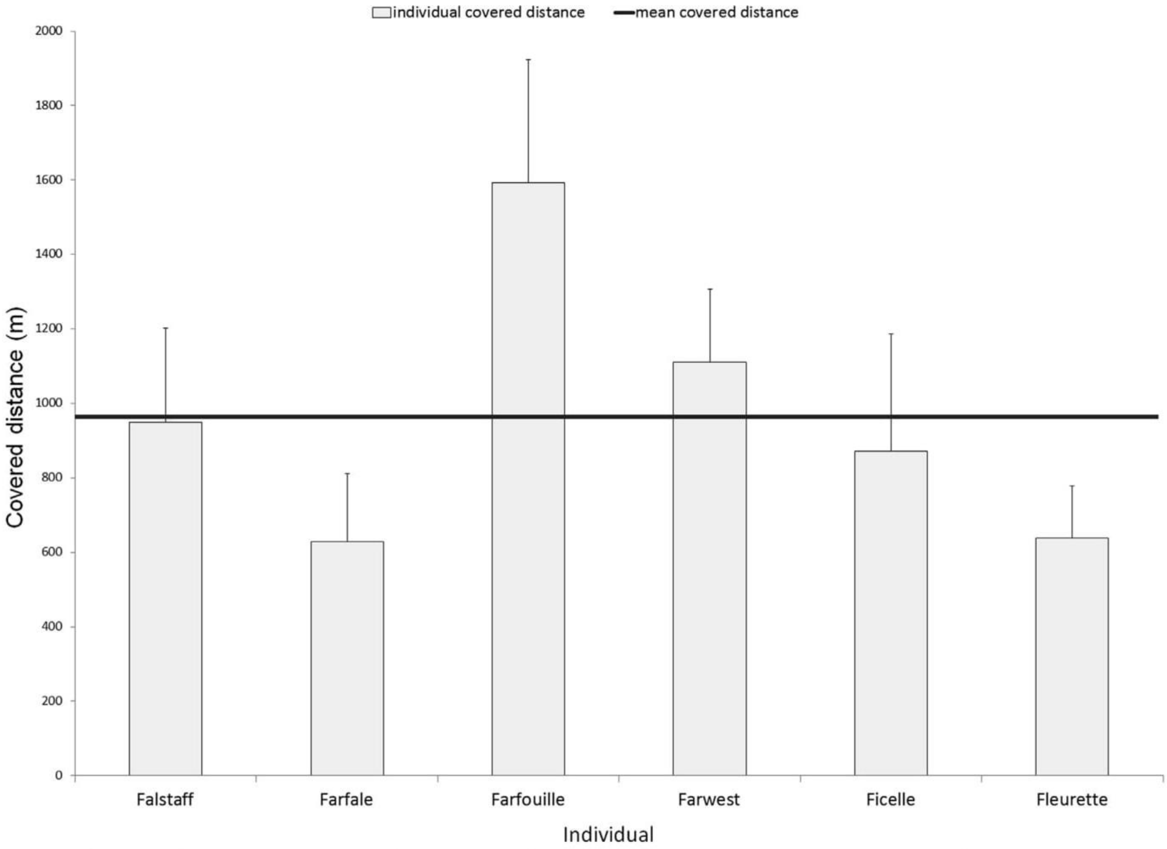

Figure 3. Mean traveled distance (m) per day. Data are presented as mean ± standard deviation.

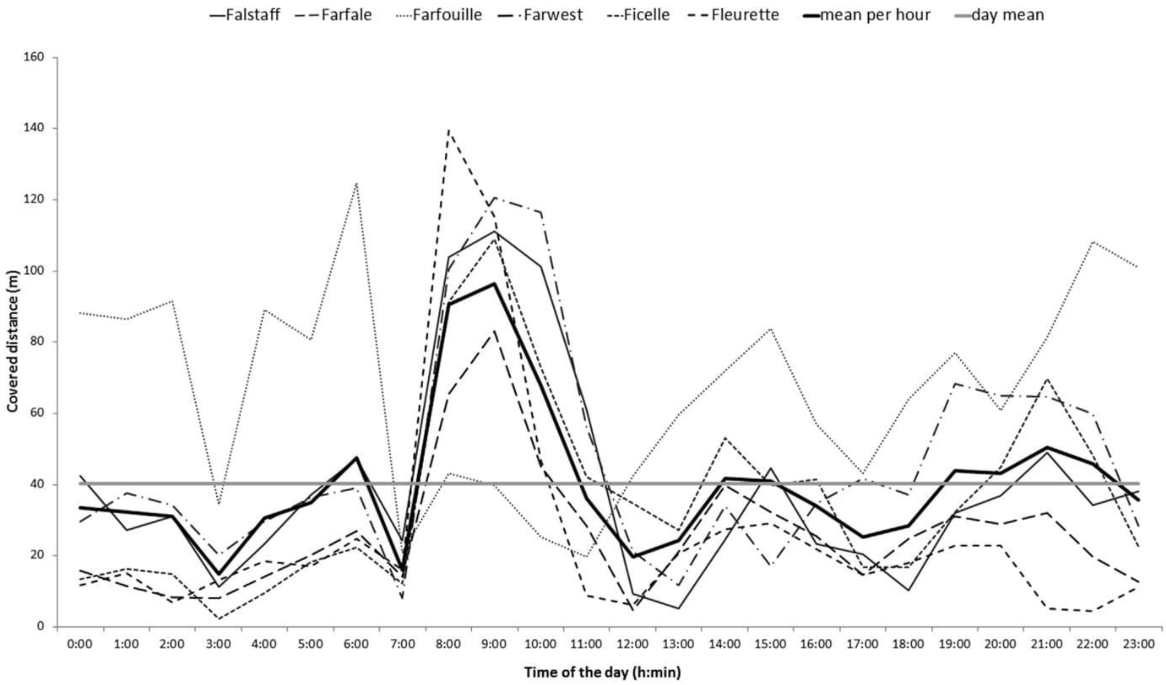

Figure 4. Mean traveled distance (m) by hour on an average day. The bold line illustrates the mean per hour, and each other line represents a cat.

Mean locomotor activity rate

Cats spent on average 30.37% ± 6.81% of their time moving. The differences of locomotor activity between cats were not as marked as those observed for the mean traveled distance, ranging from 21% to 41% of time spent moving.

Use of space

Cats spent around 15 hours 40 minutes per day on the wall shelf and on cat trees (on average, 11 hours 22 minutes ± 3 hours 54 minutes and 4 hours 10 minutes ± 2 hours 14 minutes, respectively; Figure 5). The seat was mostly avoided (7 ± 8 minutes). The cats spent on average 1 hour 25 minutes in the other areas (enriched area: 1 hour 04 minutes ± 19 minutes; feeding area: 1 hour 03 minutes ± 34 minutes; drinking area 10 ± 4 minutes; and litter trays: 8 ± 2 minutes).

Mean number and duration of contacts per day

Intraspecific

One cat interacted on average 53 ± 9 times with a conspecific per day (Figure 6A) (which means more than twice an hour). Fleurette was the most selective cat with a marked preference for Farwest.

Each member of the group got in contact during 17 minutes 57 ± 2 minutes 03 with another member per day on average. The variability was low among cats (Figure 6B).

Interspecific

On average, cats made contact 32 ± 7 times/day with humans (Figure 6A). Falstaff and Ficelle approached humans the most. The others did so less frequently, especially Fleurette who had the lowest score.

On average, cats made contact 4 ± 1 minute/day with humans (Figure 6B).

Discussion

The real-time monitoring provided by UWB technology enabled us to examine animal distribution and locomotor activity with an unmatched accuracy (15 cm) compared with all other current positioning systems. Other research has been carried out with video tracking, and our UWB accuracy was about the same as that using video tracking (Royal Canin, internal study data not presented). This technology makes 24-hour observations with a high acquisition rate and nearly unlimited data collection. Furthermore, the long-life batteries of the tags allow the recording of 3-dimensional locations during long periods without disturbing the animals.

This technology has been long awaited by ethologists as it enables them to conduct long-term behavioral studies. In this 2-week study, cats spent on average 30% of their time moving and traveling. In a study by Podberscek et al. (1991) using written observations, cats living in a space of 6.3 m^2 spent 24.5% of their time in locomotor behavior. This could suggest that the more space cats have the more active they are. The cats of this study are most active in the early morning (first peak of activity around 06:00 hours, second between 08:00 and 09:00 hours), early afternoon (third peak between 14:00 and 15:00 hours), and at sunset (final peak around 21:00 hours).

The first and third peaks coincide with the presence of cleaning or animal technicians. The second and highest peak of activity coincides with both the presence of animal technicians and food delivery. These observations suggest that the animals' rhythm of locomotor activity is affected by human activity. The evening peak occurs around sunset. This crepuscular activity underlines that, despite a mainly diurnal locomotor activity matching with food delivery and interactions with humans, the cats of this study still

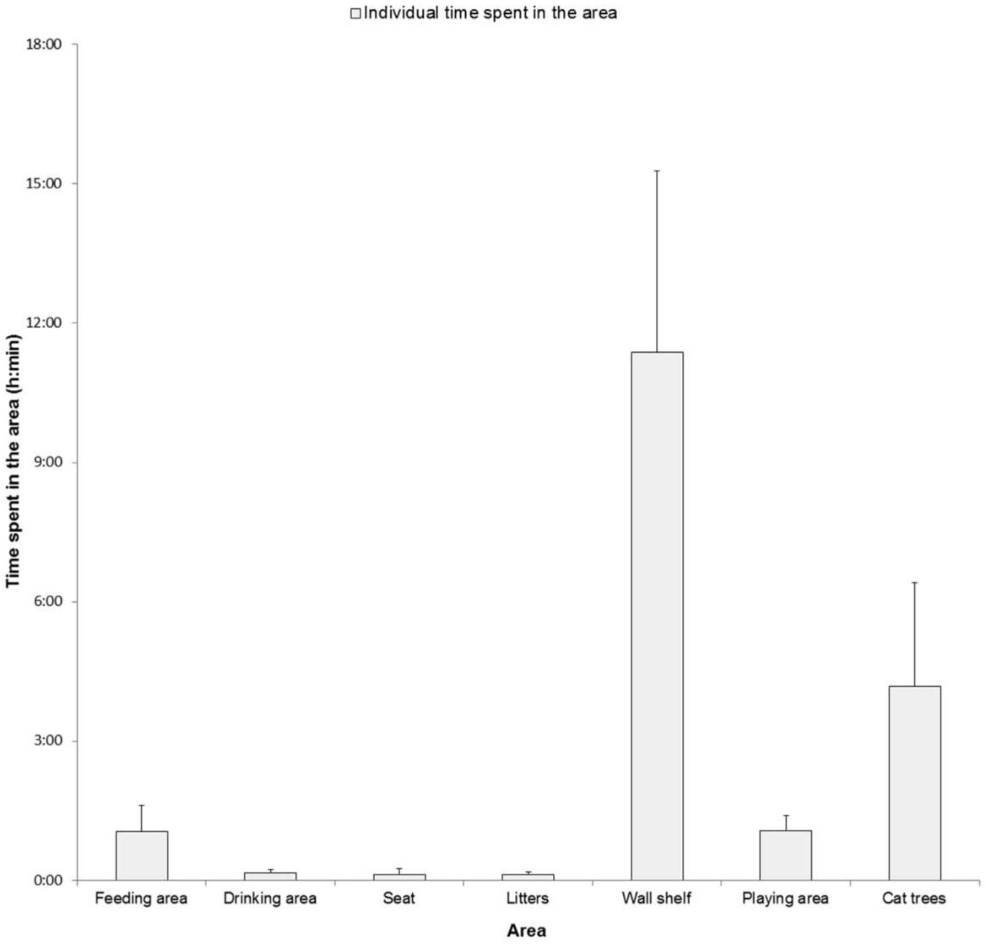

Figure 5. Mean time spent in the different areas per day. Data are presented as mean ± standard deviation.

maintain a spontaneous night locomotor activity. This observation corroborates those found in feral cats: without human disturbance, the felines showed moderate day activity and were mainly active at night (Alterio and Moller, 1997).

The number of intraspecific contacts estimated by our software showed that cats of this group interact in a selective way with their conspecifics. Interestingly, the most selective cat, Fleurette, who interacted very poorly with other cats, except Farwest, is the only cat not genetically related to the rest of the group. This result corroborates those of Bradshaw and Hall (1999) and Curtis et al. (2003) who found that cats spent less time in physical contact and showed less affiliative behaviors of proximity with unrelated individuals than with their littermates.

The cats spent around 15 hours 40 minutes (65%) per day in the resting areas, which corroborate the works of Sterman et al. (1965) and Jouvet (1967) reporting that laboratory cats spend approximately 55%-70% of their time sleeping. The cats in our study spent most of their time on the wall shelf and in the cat trees. They showed very little interest in the seat, an open space without hiding opportunities or comfort (no cushion). Studies have demonstrated a diminution of stress in cats when hiding places were provided (Rochlitz, 2000; Vinke et al., 2014). Our observation could also be due to difference in height (Podberscek et al., 1991), the seat being lower than the other resting places. Welfare is a major concern for domesticated cats, and our system may help to assess the relative usefulness of different furniture to enrich our pets' environment.

The use of the UWB technology has enabled us to define with great accuracy and objectivity different behavioral parameters of cats living in an indoor group. UWB technology allowed us to collect information regarding activity rate (46%), daily distance covered (965 m), favorite places (hidden and elevated), asymmetric interactions, and daily rhythmicity. In future studies, this new approach of tracking should help in comparing cats' behaviors in different conditions and enhance knowledge of the behavior of cats living in a community.

Acknowledgments

We thank all those who were involved in this project, particularly Sandrine Vialle who offered her continuous support, all the research technicians of the cattery who contributed to the protocol, and the manager of the cattery Sandrine Michel.

Ethical considerations

The protocol was reviewed and approved by the Royal Canin ethical committee.

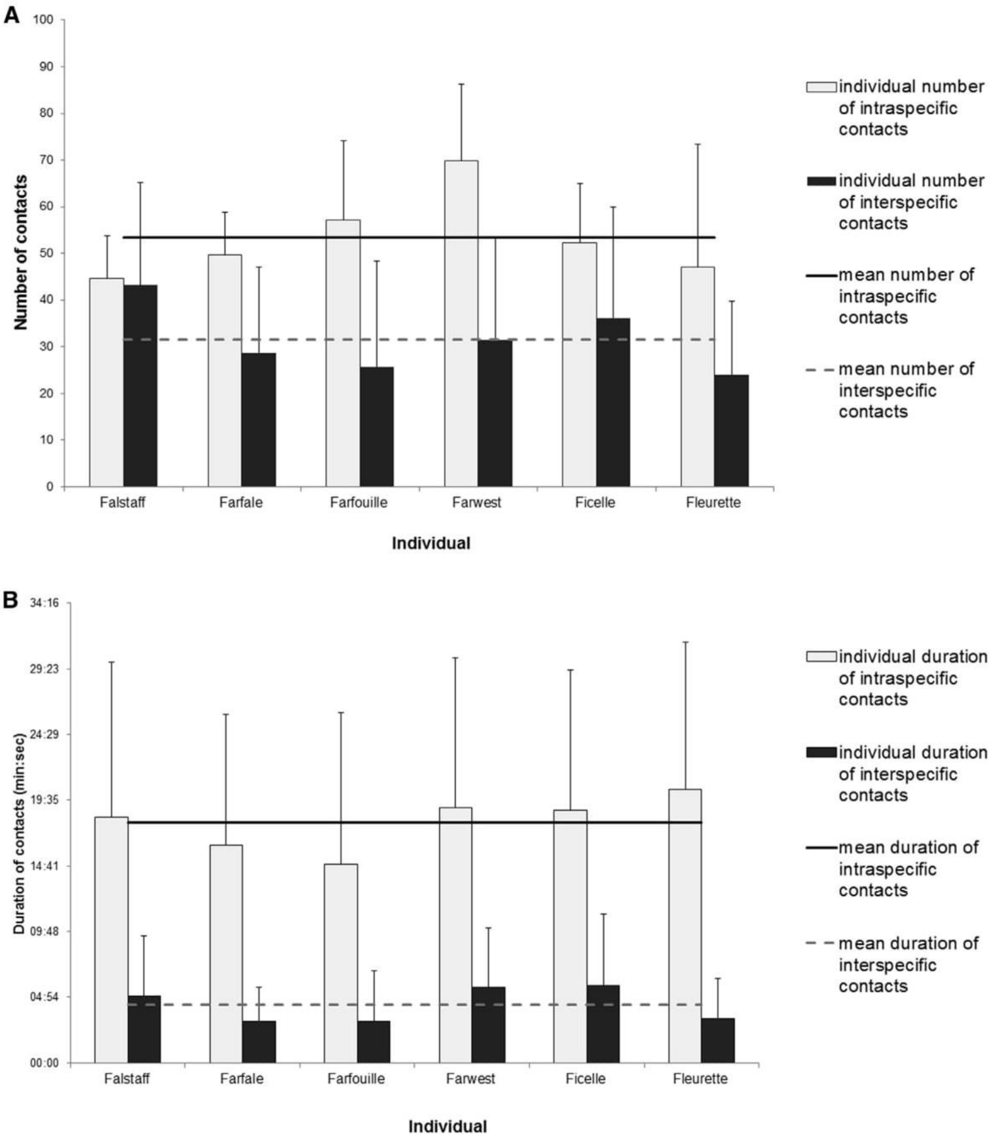

Figure 6. (A) Mean number and (B) duration (minutes:seconds) of contacts per day. Data are presented as mean ± standard deviation.

Conflict of interest

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

Authorship

The idea for the article was conceived by Jessica Serra. The experiments were designed by Jessica Serra, Benjamin Allouche, Jean-Alain Brossier, Mickaël Weber, Delphine Moniot, and Vincent Biourge. The experiments were performed mostly by Marine Parker (80%) and Jessica Serra (20%). The data were analyzed mostly by Marine Parker (80%), Sarah Lamoureux (10%), and Alexandre Feugier (10%). The article was written by Marine Parker and Jessica Serra (equal contribution). This study has been funded by Royal Canin.

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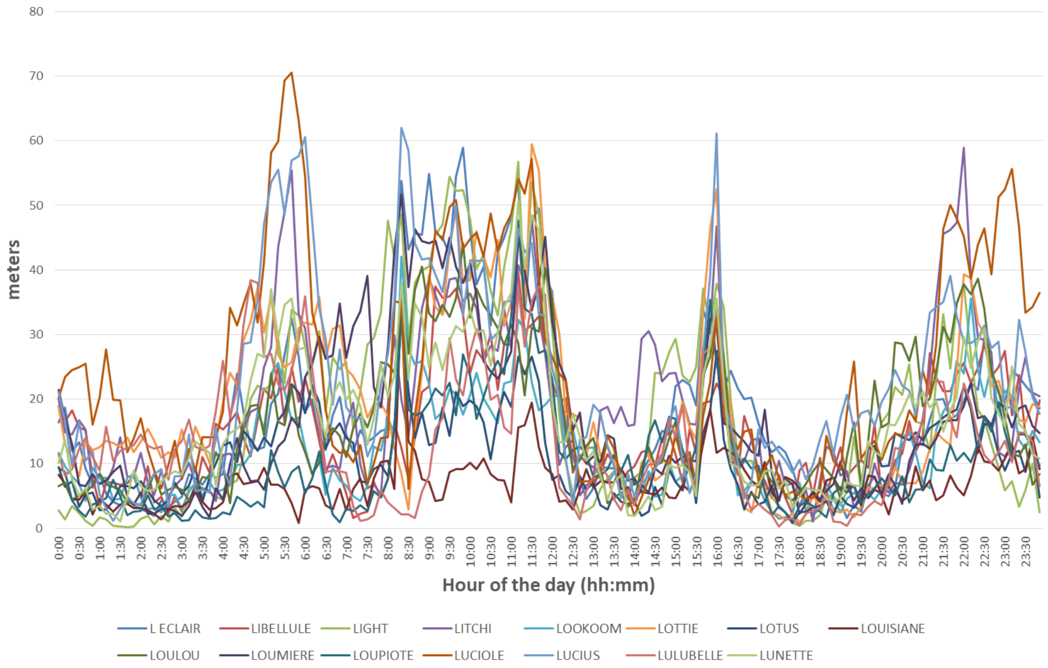
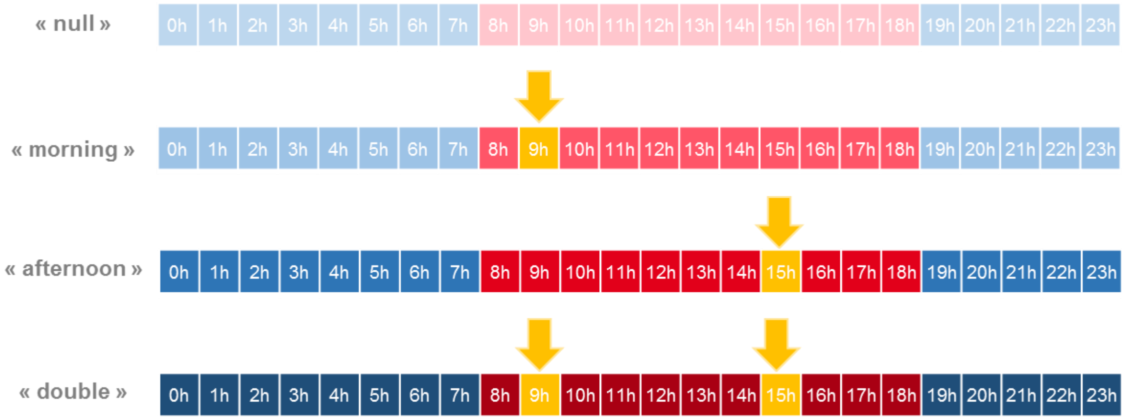
APPENDIX 2 – Mean covered distance (m) every 20 min throughout the day indoors in summer



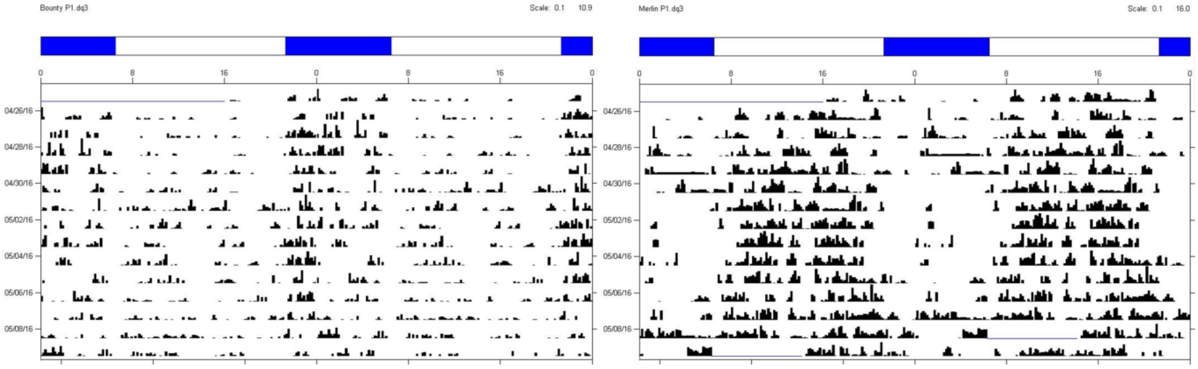
APPENDIX 3 – Indoor (left) tracking tag and outdoor (right) tracking collar

APPENDIX 4 – Mixfeeding protocols: daily wet food distributions (illustrated by yellow arrows and hours) according to the condition (“null”, “morning”, “afternoon”, “double”).



APPENDIX 5 – Pictures of the feeding devices indoors (top) and outdoors (bottom)

APPENDIX 6 – Actogram of Bounty (left) and Merlin (right) in spring 2016



APPENDIX 7 - Rhythm measurement of the cat

Actograms proved to be an efficient way to determine if a cat was more or less rhythmic, the main number of peaks during the day, as well as their tendencies towards more nocturnal or diurnal behaviours. This also helped categorise or characterise individuals for which the chronobiological parameters were ambiguous.

From the periodograms, we chose to measure the robustness and periodicity of the rhythms by using typical parameters such as the rhythm amplitude and period, respectively. These measurements were precious to determine periodicity, arrhythmicity and bimodality in the rhythms of the cats: a highest (i.e. of highest amplitude) peak at 24 hours in the periodogram indicated the rhythm of the individual followed 24-hour periodicity; a second peak at 12-hours, almost as high as (superior or equal to half of) the 24-hour one, indicated the rhythm of the cat showed bimodality; small peaks of low amplitude at several different hours in the periodograms indicated the cat was arrhythmic (**Fig. 1**).

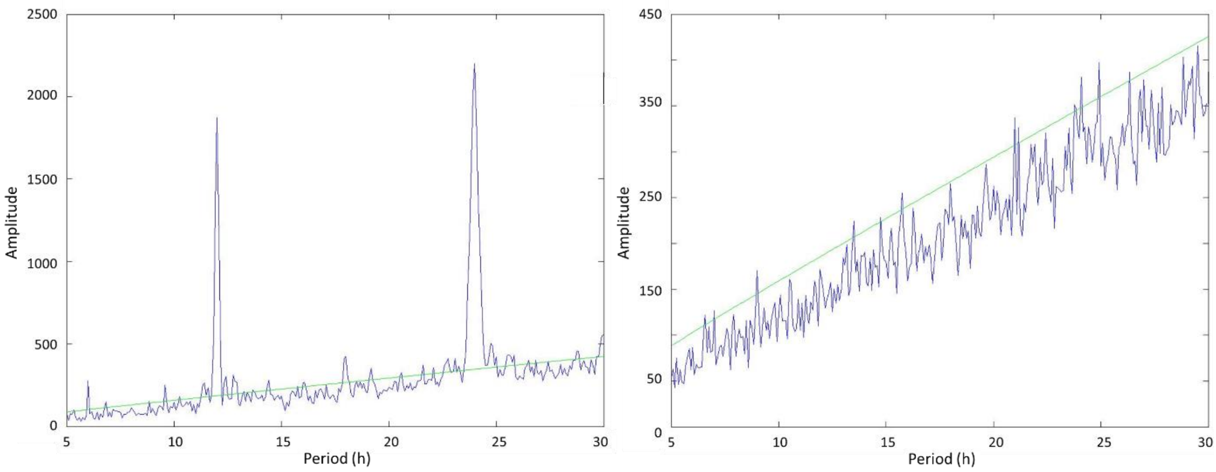


Figure 1 – Periodograms of the bimodal rhythm (left) and arrhythmicity (right) of two individuals

Also, the amplitude we used, a measure of how much of the behaviour that does occur is actually rhythmic, proved to be an efficient tool in comparing the robustness of the rhythm according to the individuals or situations. We also used variables adapted to more disturbed daily rhythms than typical circadian rhythms, such as interdaily stability (IS), intradaily variability (IV) and the least active 5 hours (L5), developed by Witting et al. (1990).

The IS measured the stability of the activity/consumption onset and offset between the days, i.e. the coupling between environmental cues (i.e. daylight) and the rhythm of the cats. It often worked in pair with the rhythm amplitude. For instance, it agreed on defining the rhythm of the nocturnal categorised individuals (first article) or indoor individuals (third article) as more stable/robust than the rhythm of the diurnal categorised ones or outdoor individuals, respectively. Nevertheless, the IS sometimes compensated the lack of significance between the amplitudes of two rhythms, or at other times did not significantly differ while the amplitude did. This is why a combination of the two parameters constitutes a powerful tool to determine and compare the rhythmicity among groups.

The IV measured the fragmentation of the rhythms on a daily basis. High IV corresponded to rhythms with scattered periods of activity/consumption throughout the day, whereas low IV corresponded to more gathered periods of activity/consumption. On one hand, this index is usually paired with the quality of a rhythm, as more scattered daily patterns result in lower rhythmicity. On the other hand, the IV was less efficient to compare the rhythmicity in our studies, as it was the least frequently significant parameter: it did not vary significantly between the sex, the chronotype categorisation or the housing condition. In our seasonal study, it showed the locomotor rhythm of the cats was more variable in winter than in autumn, which did not entirely corroborate with the other parameters we used. Still, when indicating the feeding rhythm was the least variable in autumn, it did corroborate with the IS findings. We would not affirm the IV is the most reliable tool to compare the rhythmicity of domestic cats, however, it gives information about the spreading of behaviour during the day.

The L5 have proved to be a pertinent rhythmic parameter (i.e. phase-marker) to compare in our study. They were efficient in determining the main daily troughs in the activity and feeding behaviour of our cats, while confirming the rhythm bimodality we detected via the periodograms. Their onset regularly occurred at two moments during the day: in the middle of the day or in the middle of the night, as discussed earlier. However, L5 were originally established for the analyses of unimodal rhythms, whereas the locomotor activity and feeding rhythms of the cats showed strong bimodality. This means daily L5 are not single in the cats: the detection of L5 happening in the middle of the day for an individual, for example, does not mean it did not also show a second mid-night trough of locomotor activity/food consumption. Plus, we are not certain the number of least active hours, five, is the most pertinent choice. We were not able to find, in the literature, why five hours were originally chosen for this chronobiological measure. To better match the bimodal rhythm of the domestic cat, it would be convenient to develop a way to detect two and not only one period of low activity/consumption.

Also, limitations were met in the use of the software providing IS, IV and L5. For example, too many zeros in the data would result in absurd variables, so we had to add 1 to every food intake raw data (the cats eating less frequently than moving). Plus, the loss of data during a day constrained in the data suppression of the entire day when the data loss happened.

The choice of using ANOVAs to compare the covered distance and food intake of the cats at every hour of an average day was efficient to visualise the main peaks and troughs in their behaviour. This method was more useful than simple activity profiles which are usually used in chronobiology, as it allowed to detect significant differences among hours and to establish a general view of the locomotor activity and food consumption daily patterns. It also helped to identify the moments when groups significantly showed different activity/food intake amounts, as in the more pronounced nocturnal exploratory behaviour outdoors compared to indoors (third article), for instance.

Finally, as evoked in the discussion section, we were able to evaluate the effect of the recording period duration on the reliability of the chronobiological measurements. The longer the recording period, the more rhythmicity was detected in the individuals. More precisely, the number of days of data impacted the amplitude of the rhythm, based on repeatability of a similar pattern, but not the IS or IV which are based on the onsets between the days and pattern within a day, respectively. Previously, it was already suspected that the arrhythmicity in the behaviour of cats in Hawking et al. (1971) and Kavanau (1971) was a result of too short recording periods. In our analyses, we first noticed the rhythms of the indoor individuals of our first study, for which we recorded behaviour during 7 days, were weaker than those of the indoor individuals of our second study, for which we recorded behaviour during 21 days. Also, some cats of the first study were arrhythmic in their feeding behaviour while none of the cats of the second study were, at any season. Then, we observed weaker rhythms in the locomotor behaviour of the indoor cats in autumn (second article), where we lost 9 days of locomotor activity data, compared to the other seasons. Finally, when measuring the rhythms of the same indoor population on 7 or 14 days periods, as a test, we found arrhythmicity in the behaviour of several cats, whereas every individual was rhythmic when we used 21 days of data. This strongly suggests the importance of recording the behaviour over long periods in order to detect its rhythmicity.

APPENDIX 8 – Scientific communications during the PhD

- Parker, M., Lamoureux, S., Allouche, B., Brossier, J. A., Weber, M., Feugier, A., Moniot, D., Deputte, B., Biourge, V., & Serra, J. (2017) Accuracy assessment of spatial organization and activity of indoor cats using a system based on UltraWide Band technology. *Journal of Veterinary Behavior: Clinical Applications and Research*, 21, 13-19

- Parker, M., Serra, J., Deputte, B., Ract-Madoux, B., Faustin, M., Challet, E. (2017) Activité et consommation de chats vivant en enclos extérieur, selon la saison (**poster**), *L'Animal en Marche*, Nanterre (FR)

- Parker, M., Serra, J., Deputte, B., Ract-Madoux, B., Faustin, M., Challet, E. (2017) Activity and feeding behaviour of indoor and outdoor cats throughout the seasons (**poster**), *Colloque d'EcoPhysiologie Animale (CEPA)*, Strasbourg (FR)

- Parker, M., Serra, J., Deputte, B., Ract-Madoux, B., Faustin, M., Challet, E. (2018) Locomotor activity and feeding rhythms of indoor and outdoor cats living in captivity (**oral presentation**), *Colloque de la Société Française pour l'Etude du Comportement Animal (SFECA)*, Rennes (FR)

- Parker, M., Serra, J., Deputte, B., Ract-Madoux, B., Faustin, M., Challet, E. (2018) Locomotor activity rhythm of indoor and outdoor cats living in captivity (**oral presentation**), *European Conference on Behavioural Biology (ECBB)*, Liverpool (UK)

Université de Strasbourg

Marine PARKER

ETHOLOGIE ET RYTHMES BIOLOGIQUES DU CHAT

CNRS
ROYAL CANIN

Résumé

Les rythmes biologiques aident les organismes vivants à programmer la plupart des processus comportementaux dans la fenêtre temporelle la plus appropriée. Les résultats de la littérature sur la rythmicité du chat domestique sont rares et conflictuels. Pour approfondir nos connaissances sur le sujet, nous avons utilisé de récentes technologies de télémétrie pour enregistrer et caractériser les rythmes journaliers d'activité locomotrice et de prise alimentaire chez des chats en fonction des saisons et de leurs conditions d'hébergement. Les rythmes des chats étaient modifiés par la photopériode et la présence humaine. Suivant une périodicité de 24 heures, ils ont affiché une bimodalité dans leurs rythmes quotidiens, avec des creux d'activité locomotrice et de consommation au milieu de la journée et de la nuit. Les deux périodes principales d'activité/alimentaires correspondaient à l'aube et au crépuscule à chaque saison, indépendamment de leur horaire, confirmant la nature intrinsèque crépusculaire de l'espèce. Le rythme alimentaire des chats était plus variable au cours du cycle que celui de leur activité locomotrice, rappelant ainsi le caractère opportuniste de ce prédateur. Les chats ont présenté une plasticité comportementale caractérisée par des rythmes plus faibles et un comportement d'exploration plus nocturne en milieu extérieur qu'en milieu intérieur, au sein duquel ils étaient plus enclins à la routine. Nos résultats ouvrent la voie au développement de solutions nutritionnelles et à des recommandations d'hébergement adaptées aux rythmes du chat en respectant les besoins physiologiques de l'espèce.

Mots-clés : Rythmes circadiens, prise alimentaire, activité, bimodalité, saison, plasticité comportementale

Abstract

Biological rhythms are of importance for living organisms as they help to schedule most behavioural processes within the most suitable temporal window. Literature on daily rhythmicity is scarce and conflicting regarding domestic cats. To sharpen our knowledge on the subject, we used advanced telemetry technologies to record and characterise the daily rhythms of locomotor activity and feeding in cats according to the seasons and housing conditions. The cats were sensitive to photoperiod and to human presence. Along 24-hour periodicity, they displayed bimodality in their daily patterns, with mid-day and mid-night troughs of locomotor activity and food consumption. The two main activity/eating periods corresponded to dawn and dusk at each season, regardless of the twilight timings, confirming the crepuscular intrinsic nature of the species. The feeding rhythm of the cats was more variable daily than their locomotor activity rhythm, recalling the opportunistic character of this predator. Cats displayed plasticity in their behaviour, such as weaker daily rhythms and more nocturnal exploratory behaviour outdoors, compared to indoors where they were more prone to routine. Our results open new avenues for developing nutritional and housing guidelines fitted to the rhythms of the cats according to their way of life.

Keywords: Circadian rhythms, food intake, locomotor activity, bimodality, season, behavioural plasticity