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Contents lists available at ScienceDirect

Animal Behaviour



journal homepage: www.elsevier.com/locate/anbehav

How coevolution in daily activity rhythms governs encounters between predator and prey

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A R T I C L E I N F O

Article history: Received 15 February 2024 Initial acceptance 20 June 2024 Final acceptance 21 October 2024 Available online xxx MS. number: 24-00089R

Keywords: activity pattern evolutionary game theory predator-prey coevolution risk allocation Predation risk in the wild varies across the day in a relatively predictable way, as a function of environmental conditions, such as light intensity and temperature, and of predator habits. Prey animals can thus adjust their own activity rhythm to avoid the most dangerous periods. We studied this situation in a coevolutionary perspective, considering that, if prey spread their activity across the day to counter predator temporal preferences, these preferences may in turn change to track prey activity. We therefore built a game-theoretical model to derive evolutionarily stable activity patterns for a predator constantly trying to maximize its chance of capture and a prey trying to minimize this probability. Key parameters concern circadian variations in environmental conditions and their influence on predator hunting efficiency and energy demands of the prey, which dictate its total amount of activity. The model predicts high levels of prey activity during periods of reduced predator efficiency. The predator may then either track these activity patterns will be synchronized. In the second one, they will exhibit strong temporal segregation. We show how these diverging scenarios emerge and how they can help to disentangle the wide variety of situations existing in the wild.

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Circadian variations in light intensity punctuate life in the upper layers of the oceans, in freshwaters and across continents (Nielsen, 1983; Rijnsdorp et al., 1981). Consequently, animals living in these environments have developed temporal specializations, with diurnal, nocturnal or crepuscular ways of life, or more complex activity patterns (Cox & Gaston, 2024; Kronfeld-Schor & Dayan, 2003). These specializations concern sensorial capacities, physiology and behaviour (Hall & Ross, 2007; Munz & McFarland, 1973). They may be strict or compatible with some level of plasticity (e.g. Fox & Bellwood, 2011; Villafuerte et al., 1993).

By driving encounters between individuals, temporal preferences mediate interactions between species (Rossa et al., 2021). Prey animals, in particular, are essentially vulnerable to predation during their own activity periods, because they then attend exposed areas and adopt conspicuous postures (e.g. Daly et al., 1992; Valeix et al., 2009). Each individual is thus subject to

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circadian variations in predation risk, jointly driven by its own activity patterns, those of its predators and fluctuations in environmental conditions (Esattore et al., 2023; Rickel & Genin, 2005). Variations in the level of risk form the temporal dimension of the landscape of fear, with which the animal must cope (Brown et al., 1999; Kohl et al., 2018; Palmer et al., 2017).

Adaptation of prey behaviour to temporal variations in predation risk is well documented (Ferrari et al., 2009), and the most convincing examples concern short-term responses to changes in the predation risk regime. Thus, Fenn and Macdonald (1995) observed rapid switches between diurnal and nocturnal ways of life in rats, when foxes, which hunt at night, were either introduced or removed from the environment. Similarly, the removal of two important nocturnal predators from the African savannah, the lion, *Panthera leo*, and the spotted hyaena, *Crocuta crocuta*, led some of their prey to transfer a large part of their activity to dark hours (Tambling et al., 2015). Reciprocally, predators can change their activity patterns to follow those of their prey. For example, jaguars, *Panthera onca*, in Costa Rica abruptly increase their activity at night when turtles come to lay eggs on beaches (Carillo et al., 2009), and

https://doi.org/10.1016/j.anbehav.2025.123078

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foxes can switch from mainly nocturnal to more diurnal habits in summer, when insects are abundant (Cavallini & Lovari, 1991). Not all species, however, are capable of such rapid adjustments in behaviour, because temporal specializations also involve specialized sense organs and physiological adaptations, which limit behavioural plasticity in both predator and prey (e.g. Monterroso et al., 2013).

Following these observations, we studied how the activity rhythms of a predator and its prev should adjust to one another when the propensity of the predator to hunt during the most profitable periods and the propensity of its prey to precisely avoid the most dangerous moments are simultaneously taken into account. The outcome of a game between such diametrically opposed interests is far from obvious and raises intriguing questions concerning the real drivers of both predator and prey behaviour. Do we, for example, expect predators to be active when light conditions favour hunting or essentially prone to follow the activity patterns of their prey? Conversely, should prey leave their shelter when ambient conditions favour camouflage or when predators display only low levels of activity? To these regards, field studies reveal a striking variety of patterns, in virtually all types of ecosystems, which results in highly variable levels of correlation between predator and prey activity patterns, ranging from nearly perfect opposition (e.g. Bosiger & McCormick, 2014) to nearly perfect synchronization (e.g. Lang et al., 2019), through intermediate, partially overlapping, patterns (e.g. Arias-Del Razo et al., 2011). Exploring the joint evolution of predator and prey activity rhythms should thus help to interpret field observations dedicated to the temporal components of predator-prev interactions and help us to understand why they vary so much (Ito et al., 2021; Valleio-Vargas et al., 2022). The consequences for the dynamics of the whole community are also huge, the level of overlap between predator and prey activity patterns being determinant for both the temporal distribution of kills and the resulting rate of predation (e.g. Kohl et al., 2018; Valeix et al., 2009).

To investigate the coevolution of predator and prey daily activity rhythms, we built a game-theoretical model of activity spreading for a predator and a prey living in an environment where conditions vary in a marked manner between night and day. The modelling framework is provided by risk allocation theory (Lima & Bednekoff, 1999), a very influential piece of theory exploring how a prey animal subject to varying levels of predation risk should spread its activity over the day. There are however two fundamental differences between the present work and the original risk allocation model. First, daily variations in predation risk are not considered here as imposed by the environment, but as the outcome of a predator strategy also subject to natural selection. Second, predation risk explicitly incorporates two components, namely, the level of activity of the predator and its hunting efficiency. The first one is under predator control, the second one varies across day hours in an inexorable way.

THE MODEL

Our study is dedicated to daily activity patterns in a predator and its prey. These animals live in an environment where conditions, such as light and temperature, vary between night and day, which affects the hunting efficiency of the predator. Periods H and L, respectively, correspond to moments when this efficiency is high and moments when it is low. They, respectively, represent proportions p and 1 - p of total daytime T. Depending on the studied species, period H may correspond to night or to day.

As in the original risk allocation model (Lima & Bednekoff, 1999), $f_{\rm H}$ and $f_{\rm L}$ represent the proportions of time the prey devotes to feeding during periods H and L, respectively. Letting *e* be its instantaneous feeding rate, assumed to be equal between periods H and L, and ε its daily energy requirements, we have: $f_{\rm H} p e T + f_{\rm L} (1 - p) e T = \varepsilon$, which yields:

$$f_{\rm H} p + f_{\rm L} (1-p) = R,$$
 (1)

where $R = \epsilon/Te$ corresponds to the mean feeding rate that the prey must sustain over the day, directly driven by its energy needs, and $0 \leq f_{\text{H}}, f_{\text{L}}, R \leq 1$.

Still following Lima and Bednekoff (1999), we assume that, for the prey, the probability of failing to escape when under an attack is proportional to $f_{H,L}^2$. In the wild, high levels of activity do indeed induce disproportionate vulnerability due to conspicuousness (see Banks et al., 2000), which justifies the choice of an accelerating function linking risk of capture to prey activity level.

The instantaneous probability of capture is also proportional to the hunting effort of the predator which, by increasing its own level of activity and dedicating more attention to hunting, increases its chance of success (Williams et al., 2014). α_H and α_L represent the predator hunting efforts during periods H and L, respectively. These variables are not independent of one another because hunting is costly and the predator is limited by the total quantity of energy it can invest in hunting every day, with no guarantee of success (Scantlebury et al., 2014). For the sake of simplicity, we assume this quantity to be a constant. We thus have:

$$\alpha_{\rm H} p T + \alpha_{\rm L} (1-p) T = E, \qquad (2)$$

where *E* is the daily quantity of energy invested in hunting by the predator. This equation becomes:

$$\alpha_{\rm H} p + \alpha_{\rm L} (1-p) = K, \qquad (3)$$

where K = E/T.

Finally, the instantaneous probability of capture is proportional to the predator hunting effort, $\alpha_{H,L}$, to the probability for the prey of failing to evade captures, $f_{H,L}^2$, and to a parameter measuring the effects of environmental conditions on predator hunting efficiency. This parameter is set equal to 1 during periods H, and to *r* during periods L, with $r \leq 1$.

The mean risk of capture calculated over the day is thus proportional to the following quantity:

$$F = \alpha_{\rm H} f_{\rm H}^2 p + \alpha_{\rm L} f_{\rm L}^2 r (1-p)$$

$$\tag{4}$$

(see Lima & Bednekoff, 1999).

The principle of our model is that predator—prey relationships are driven by the antagonistic interests of the predator, which tries to capture the prey, and of the prey, which tries to avoid capture. The predator activity rhythm thus corresponds to the set of $(\alpha_{\rm H}, \alpha_{\rm L})$ values, denoted by $(\alpha_{\rm H}^*, \alpha_{\rm L}^*)$, which maximizes quantity *F*, and the prey activity rhythm to the set of $(f_{\rm H}, f_{\rm L})$ values, denoted by $(f_{\rm H}^*, f_{\rm L}^*)$, which minimizes this quantity. The coevolutionary equilibrium is reached when both predator and prey strategies reach evolutionary stability (Maynard Smith, 1982).

PREDATOR AND PREY ACTIVITY PATTERNS

Optimal Strategy of the Prey

Differentiating quantity *F* with respect to $f_{\rm H}$ and $f_{\rm L}$ subject to condition (1) leads to three possible situations for the strategy of the prey (see demonstration in Supplementary Material):

(i) If
$$\alpha_{\rm H} > \frac{rpK}{(R - (1 - p))(1 - p) + rp^2}$$
 and $R > (1 - p)$,
 $f_{\rm L}^* = 1$ and $f_{\rm H}^* = \frac{R - (1 - p)}{p}$. (5)

In this situation, the high level of risk prevailing during period H leads the prey to be as active as possible during period L ($f_L^* = 1$). It cannot, however, fulfil its daily requirements during this period only, because $(1 - p)f_L^* < R$, and must therefore remain partially active during period H ($f_H^* > 0$).

(ii) If
$$\alpha_{\rm L} > \frac{(1-p)K}{rp(R-p) + (1-p)^2}$$
 and $R > p, f_{\rm H}^* = 1$ and
$$f_{\rm L}^* = \frac{R-p}{(1-p)}.$$
 (6)

This is the opposite situation. The prey avoids as much as possible being active during period L, which is the most dangerous. It is thus fully active during period H ($f_{\rm H}^* = 1$) and partially active during period L ($f_{\rm L}^* > 0$).

(iii) In all other cases,

$$f_{\rm H}^* = \frac{Rr}{\frac{\alpha_{\rm H}}{\alpha_{\rm L}}(1-p) + rp} \text{ and } f_{\rm L}^* = \frac{R}{\frac{\alpha_{\rm L}}{\alpha_{\rm H}}rp + (1-p)}.$$
(7)

In these situations, predation risk is more balanced between periods H and L and the prey spreads its activity more evenly between periods H and L. Increasing the relative level of danger during either period leads the animal to progressively transfer its activity to the other one ($f_{\rm H}^*$ increases when $\alpha_{\rm H}$ decreases or r increases and $f_{\rm L}^*$ increases when $\alpha_{\rm L}$ or r decreases).

Optimal Strategy of the Predator

Differentiating quantity *F* with respect to $\alpha_{\rm H}$ and $\alpha_{\rm L}$ subject to condition (3) leads to the following possibilities for the behaviour of the predator (see demonstration in Supplementary Material):

(i) If
$$f_{\rm H}^2 > f_{\rm L}^2 r, \alpha_{\rm H}^* = \frac{K}{p}$$
 and $\alpha_{\rm L}^* = 0$ (8)

(ii) If
$$f_{\rm H}^2 < f_{\rm L}^2 r, \alpha_{\rm H}^* = 0$$
 and $\alpha_{\rm L}^* = \frac{K}{(1-p)}$ (9)

(iii) If $f_{\rm H}^2 = f_{\rm L}^2 r$, $\alpha_{\rm H}^*$ and $\alpha_{\rm L}^*$ are not uniquely defined because the chance of capture is the same during periods H and L. The success of the predator then does not depend on its behaviour.

The predator will thus concentrate its activity during the period when the prey is most vulnerable, the vulnerability of the prey being equal to $f_{\rm H}^2$ during period H and to $f_{\rm L}^2$ *r* during period L.

Coevolutionary Equilibrium

A coevolutionary equilibrium is met when predator and prey simultaneously achieve maximum fitness (i.e. $(\alpha_H, \alpha_L) = (\alpha_H^*, \alpha_L^*)$ and $(f_H, f_L) = (f_H^*, f_L^*)$), and the corresponding equilibrium point is evolutionarily stable (Maynard Smith, 1982). Using evolutionary game theory, we were able to show that, for all possible sets of environmental conditions, one unique coevolutionary equilibrium exists (see Supplementary Material). This means that, for a given set of parameters, concerning both the environment and the biology of the species under study, one and only one set of behavioural strategies concerning daily activity patterns is expected to be encountered in nature, for both the predator and its prey.

Nevertheless, depending on environmental conditions, two radically different situations emerge. Fig. 1 illustrates the influence



Figure 1. Activity patterns as a function of predator efficiency ratio between periods L and H. *r* represents the relative efficiency of the predator during period L, compared to period H. When conditions begin to significantly penalize the predator during period L (r < 1), the prey progressively transfers its activity towards this period and the predator follows this pattern (synchronization scenario: when r decreases, f_L and α_L increase in a proportional way). When *r* is low, the prey is fully active during period L and the predator concentrates its whole activity during period H (temporal segregation scenario: $f_L = 1$ and $\alpha_L = 0$). Parameter values: mean daily energy expenditure rate sustainable by the predator: K = 0.6, mean feeding rate that the prey must sustain over the day: R = 0.8, proportion of total daytime corresponding to period H: p = 0.5.

of parameter r on the predicted activity rhythms in both predator and prey. In particular, it shows how this parameter governs transition between the two scenarios. Figs. 2 and 3 show examples of activity patterns corresponding to each of these scenarios and Table 1 highlights the fundamental differences between them.

Scenario 1: synchronization of activity patterns

If
$$\sqrt{r} > \frac{R - (1 - p)}{p}, f_{L}^{*} = \frac{R}{(1 - p) + p\sqrt{r}}$$
 and
 $f_{H}^{*} = f_{L}^{*} \sqrt{r} = \frac{R\sqrt{r}}{(1 - p) + p\sqrt{r}}$
(10)

$$\alpha_{\rm L}^* = \frac{K}{(1-p) + p\sqrt{r}} \text{ and } \alpha_{\rm H}^* = \alpha_{\rm L}^* \sqrt{r} = \frac{K\sqrt{r}}{(1-p) + p\sqrt{r}}$$
(11)

When conditions do not differ between periods H and L (i.e. when r = 1), both predator and prey display constant levels of activity (i.e. $f_{\rm H}^* = f_{\rm L}^*$ and $\alpha_{\rm H}^* = \alpha_{\rm L}^*$; see Fig. 1). Then, a decreasing value of r progressively leads the prey to lower its activity during periods H and transfer it to periods L, to benefit from relative safety. The predator then tracks the activity of its prey, its level of activity during each period being proportional to that of the prey (see equations 10–11). We therefore call this situation the synchronization scenario (see Figs. 1 and 2). We note that, while predation risk still culminates during periods H, captures mostly occur during periods L, because most encounters take place then (see Fig. 2, Table 1).

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Figure 2. Daily activity patterns of predator and prey: synchronization scenario. The prey is more active during period L, when predator efficiency is low, than during period H. The predator follows the same pattern, tracking the activity of its prey, and being finally more active when its efficiency is lower. Predator and prey activity levels are proportional to one another during both periods and captures mainly occur during period L. Parameter values: K = 0.6, R = 0.8, p = 0.5, r = 0.5. Time is measured in arbitrary units (100 units per day).



Figure 3. Daily activity patterns of predator and prey: temporal segregation scenario. The prey displays maximum activity level during period L, when predator efficiency is low. It is nevertheless forced to be partially active during period H to fulfil its needs, and the predator concentrates its whole activity during this period. All captures therefore occur during period H. Parameter values: K = 0.6, R = 0.8, p = 0.5, r = 0.2. Time is measured in arbitrary units (100 units per day).

Table 1

Key convergence and divergence points between the two scenarios

Scenario	1: Synchronization	2: Temporal segregation
Period with maximum prey activity ($f_{\rm H}$ or $f_{\rm L}$)	Period L	Period L
Period with maximum predator activity (α_H or α_L)	Period L	Period H
Period with maximum predation risk (proportional	Period H	Period H
Period with maximum effective capture rate (proportional to $\alpha_{\rm H} f_{\rm H}^2$ or to $\alpha_{\rm L} r f_{\rm L}^2$)	Period L	Period H

Scenario 2: temporal segregation

If
$$\sqrt{r} \le \frac{R - (1 - p)}{p}, f_{L}^{*} = 1 \text{ and } f_{H}^{*} = \frac{R - (1 - p)}{p}$$
 (12)

$$\alpha_{\rm L}^* = 0 \text{ and } \alpha_{\rm H}^* = \frac{K}{p}$$
 (13)

In this situation, the high difference in predatory efficiency between periods H and L leads the prey to be fully active during periods L, while the predator begins to concentrate its whole hunting effort during periods H, exploiting the remaining prey activity that takes place then (see Figs. 1 and 3). Predator and prey activity patterns now exhibit temporal segregation, but segregation is not total, and captures occur when they overlap, that is, during period H (see Fig. 3).

In summary, the temporal segregation scenario will be privileged when predator hunting efficiency is particularly low during periods L, but the energy requirements of the prey nevertheless force it to be partly active during periods H. Otherwise, the synchronization scenario will prevail and most activities and encounters will take place during periods L.

DISCUSSION

Using game theory, we studied how daily activity rhythms should settle down when predator and prey respond to each other in an adaptive way. For all possible sets of environmental conditions, one joint stable equilibrium was identified. Nevertheless, depending on conditions, two types of situations emerged, corresponding to distinct scenarios of reciprocal adjustments in daily activity patterns. These scenarios share important features: in both cases, predation risk culminates when environmental conditions favour the predator (periods H) and the prey is less active during these periods. These trends should thus always be present. There are, however, essential differences between the two scenarios and, hence, a potential multiplicity of situations in the wild.

In the first scenario, the predator tracks the activity of its prey. It is thus drawn to be mostly active when its own efficiency is reduced, and this tendency is strengthened when the difference in efficiency between both kinds of periods increases. In other words, the less efficient the predator is during periods L, the more active it is during these periods, because it follows the rhythm of its prey (see equation (11); Fig. 1). This synchronization pattern, however, is only expected to occur when the difference in predator hunting efficiency between periods remains relatively low (see condition (10)).

When this difference becomes important (see condition (12)), the activity level of the prey during periods L reaches its maximum

value. The prey thus becomes time-limited with respect to its energy requirements during these periods and is forced to complete its foraging activity during periods H. Concomitantly, the predator begins to concentrate its hunting activity during these moments, its efficiency during periods L being too low. Time limitation in prey is thus the ultimate outcome of predator avoidance strategies, and the predator exploits this time limitation. Predator and prev activity periods are then highly desynchronized, but encounters nevertheless occur when they overlap, that is, when predator efficiency is high, predator activity is at its maximum and prey activity is at its minimum.

The two scenarios thus differ with respect to the predicted level of synchronization between predator and prey activity patterns and with respect to the main driver of predator temporal preferences. In the first case, the predator tracks the activity of its prey and activity patterns are synchronized. In the second one, the predator responds to differences in environmental conditions and chooses the periods favouring hunting success. Activity patterns then exhibit temporal segregation. To our knowledge, this is the first time such a dichotomy emerged from a game-theoretical model of predator and prey temporal activity patterns. It can be brought together with the idea that, when selecting a hunting site, a predator may either favour a site that favours hunting, or favour a site where prey abound ('prey catchability' versus 'prey abundance' hypothesis; Davidson et al., 2012).

The idea that the activity patterns of predators can converge with those of their prey is well documented. Felids, for example, demonstrate a striking diversity of temporal preferences within species, but across populations, and local activity patterns of predators mirror those of their prey (jaguars: Harmsen et al., 2011; lynx: Heurich et al., 2014; leopards, Panthera pardus: Jenny & Zuberbühler, 2005). These studies do not show that prey temporal patterns reflect predator avoidance strategies, nor do they show that predators are drawn to hunt during periods that are suboptimal for them. There are, however, interesting results in this direction. For instance, Harmsen et al. (2011) showed that jaguars in the tropical forests of Belize hunt armadillos less during the clearest nights, although moonlight is suspected to help them detect their prey. The likely explanation is that armadillos respond to this increased vulnerability by reducing their own activity level, which, in turn, leads jaguars to hunt less during the periods that should benefit them. Similarly, Lang et al. (2019) identified prey activity as the main driver of temporal preferences in a wide range of diurnal raptor species. Some raptors, in particular, are expected to be essentially efficient at dawn, when dim light allows them to approach undetected (Beauchamp & Ruxton, 2008). They could nevertheless be drawn to be mostly active several hours later, under full daylight, to follow the activity patterns of their avian prey (Lang et al., 2019).

Synchronization between predator and prey activity patterns thus seems to be widespread. It nevertheless concerns predator species that retain a significant part of their hunting capacities when conditions are not optimal, which corresponds to some level of plasticity in temporal preferences, reflecting polyvalent sensorial systems (see Heurich et al., 2016; Monterroso et al., 2013), as illustrated in our model by a relatively high value of parameter *r*.

Reciprocally, temporal segregation between predator and prey is documented in situations where predators display marked preferences for certain times of the day and prey mainly restrict their activity outside these periods, taking advantage of temporal refuges (Kohl et al., 2018; Smith et al., 2019). Thus, Courbin et al. (2018) demonstrated that plains zebras, Equus quagga, leave their open grazing and drinking areas at nightfall, when lions begin ambushing. They then find shelter in more closed habitats, which greatly enhances their survival. Similarly, many coral reef fishes forsake activity at dusk and retreat into shelters within the reef to avoid nocturnal predators that take advantage of low light levels to hunt (see Bosiger & McCormick, 2014; Rickel & Genin, 2005). Risk avoidance strategies in prey can thus lead to temporal segregation between prey and their predators.

These risk avoidance strategies do not, however, prevent high predation rates, because activity periods of predator and prey, in spite of being highly separated, overlap, Mechanisms of very different nature may produce this. Competition for feeding sites is one of them. Imposed by dominant individuals within the group, as in passerine flocks (Krams, 2000), or by members of dominant species, as in herbivore herds attending waterholes (Valeix et al., 2007), it constrains some individuals to extend their foraging activity during the most dangerous hours of the day, providing easy prey to predators. Competition for shelters may also leave some individuals exposed to predation when they cease foraging, as in tropical fishes inhabiting coral reefs (Holbrook & Schmitt, 2002). Another possibility for predators is to exploit transition periods, by ambushing their prey when the prey leave their feeding areas to attend sheltered resting places, as in pumas, Puma concolor, hunting vicuñas, Lama vicugna (Smith et al., 2019; see also Kohl et al., 2018). Finally, individuals with high energy needs, such as young fishes during growth (Metcalfe et al., 1998) or small birds in winter (van der Veen, 1999), may be unable to feed enough during safe periods and forced to remain active during the most dangerous moments. Nocturnal animals will then substantially contribute to the diet of diurnal predators (e.g. Boal & Giovanni, 2007). In all these situations, predators achieve high capture rates while retaining temporal preferences that differ from those of their prev. The selection pressures induced by these lifestyles will then contribute to maintain divergence in the anatomical structure involved in temporal specializations, which may explain discrepancies existing in the wild in this regard between predator and prey species (see Wu et al., 2018).

Permeability between the synchronization and the temporal segregation scenarios is also possible. Photoperiod, as well as individual energy needs, vary over seasons, which corresponds to variations in parameters *p* and *R* in our model, and may induce shifts between the two situations. Thus, diurnal passerines may be forced to extend their daily foraging time in winter, because energy needs rise, and endure a higher level of predation risk (see van der Veen, 1999). Variations in lunar luminosity can also alternately favour the synchronization and the desynchronization scenario across successive nights, because variations in nocturnal luminosity affect predator hunting efficiency (Prugh & Golden, 2014), which corresponds to varying values of *r* in our model (see Penteriani et al., 2013). Finally, the propensity of a predator to follow the activity patterns of its prey may vary with density in the prey population. When prey abound, risk dilution among them, associated with high chance of encounter for the predator, may decorrelate activity patterns, the predator having little need to track the activity of its prey (see Eriksen et al., 2011).

Many factors also obviously contribute to make real situations more complex than the one described here. One of them is the fact that prey feeding rate may, as predator efficiency, vary across the day, either because food is not always present or because environmental conditions also influence prey searching efficiency. In this situation, synchronization between activity patterns should be reinforced if both predator and prey foraging efficiencies culminate at the same time, as demonstrated by Kotler et al. (2002). Reciprocally, temporal segregation will be favoured if a forager encounters its resource when the efficiency of its own predators declines (see De Vos et al., 2015). Finally, activity patterns within guilds of predators exhibit a complexity that not only reflects adjustments to prey activity patterns, but also responses to the presence of other

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predatory species, which may trigger various types of temporal adjustments (e.g. Harmsen et al., 2009; Lucherini et al., 2009; Rossa et al., 2021; Roth & Lima, 2007). The mechanisms highlighted in the present study should thus interact with other kinds of interspecific relationships to determine temporal patterns of activities at the food web scale.

Author Contributions

Etienne Sirot: Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **Frédéric M. Hamelin:** Writing – review & editing, Methodology, Investigation, Formal analysis, Conceptualization. **Thomas Benoit:** Methodology, Investigation, Formal analysis, Conceptualization.

Data Availability

No data were used for this research.

Declaration of Interest

The authors declare they have no conflicts of interest.

Acknowledgments

We thank Oswald Schmitz and two referees for their helpful comments.

Supplementary Material

Supplementary material associated with this article can be found at https://doi.org/10.1016/j.anbehav.2025.123078.

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