Received: 30 May 2022 | Accepted: 21 December 2022

DOI: 10.1111/1365-2435.14255

Functional Ecology | BRITISH ECOLOGICAL SOCIETY

PERSPECTIVE

Circadian rhythms of hosts and their gut microbiomes: Implications for animal physiology and ecology

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Handling Editor: Johannes Rousk

Abstract

1. Daily light–dark cycles shape the circadian physiology and behaviour of nearly all organisms, with variation in circadian phenotypes having cascading effects on individual fitness, species interactions and species co-evolution.
2. Recent evidence that circadian rhythms in host immunity and metabolism are synchronised by the gut microbiota suggest that the circadian dynamics of gut microbes are a crucial component of their function. However, there remains little knowledge or understanding of the diurnal dynamics of gut microbiomes in natural populations or the consequences for host physiology and ecology.
3. Here, we summarise the hallmarks of gut microbiota oscillations reported to date and the mechanisms by which they synchronise rhythms in host immunity and metabolism. We outline the consequences for diverse biological processes such as host pathogen susceptibility and seasonal switches in metabolism, and discuss how the breakdown of these circadian interactions, for example during senescence or because of light pollution, may affect wildlife infection risk and disease.
4. We also provide practical guidelines for the measurement of microbial oscillations in wildlife, highlighting that whilst faecal samples of wild animals are rarely available over a 24-h period, characterising even parts of the gut microbial cycle can be informative.
5. An improved understanding of how gut microbial diurnal rhythms manifest in wildlife is essential to fully comprehend their role in shaping variation in host circadian phenotypes and the consequences for host physiology and ecology.

KEYWORDS
biological rhythms, circadian rhythms, gut microbiota, host-microbe interactions, immune function

1 | INTRODUCTION

Circadian rhythms shape diverse biological processes spanning individual physiology and behaviour, even influencing survival (Dodd et al., 2005; Libert et al., 2012; Spoelstra et al., 2016), species interactions (Bloch et al., 2017) and species co-evolution (Westwood et al., 2019). Whilst the evolution and genetic underpinnings of circadian rhythms have been relatively well studied (Mack et al., 2021; Patke et al., 2020; Young & Kay, 2001), the ecological drivers shaping variation and plasticity of animal circadian phenotypes across individuals and species remain poorly understood (Helm et al., 2017; Yerushalmi & Green, 2009). One overlooked factor influencing circadian phenotypes is the gut microbiota, the hyperdiverse suite of microbes that inhabit the intestinal tract. The gut microbiota is pivotal for the regulation of host metabolism, immunity and consequently organismal health (Sommer & Bäckhed, 2013). Removal of this microbial community dampens the circadian expression of both central and peripheral clock genes, even when light and feeding cues are maintained (Leone et al., 2015). Recent evidence suggests that these effects are mediated by specific gut microbes that oscillate over the day, and whose periodic interactions with the host are crucial for synchronising circadian rhythms in innate immunity (Brooks et al., 2021) and metabolism (Choi et al., 2021) and thus are key players in shaping host physiology and function.

The role of the gut microbiota in the regulation of circadian phenotypes has important implications for our understanding of diverse biological and ecological processes. For instance, the disruption of microbial oscillations is linked to organismal senescence (Paschos & FitzGerald, 2017), increased infection susceptibility (Xia et al., 2022), and metabolic disorders (Choi et al., 2021; Reitmeier et al., 2020), possibly via the dysregulation of circadian gene expression (Leone et al., 2015; Thaiss et al., 2016). These findings raise the possibility that gut microbial dysbiosis may be characterised by a lack of rhythmicity in the gut microbiome (e.g. Reitmeier et al., 2020) and negatively impact host health through their effects on host circadian rhythms. However, our knowledge about the interactions between the gut microbiota and host circadian rhythms is based almost exclusively on a relatively small range of captive model organisms and humans. To fully grasp the ecological relevance of these interactions, which could have profound ecological and evolutionary implications, requires a careful design of microbiome studies across diverse ecological contexts.

In this perspective, we summarise key findings on gut microbial oscillations derived from model systems and humans and outline how and why they are relevant to understanding diverse biological and ecological processes. We first review the hallmarks and known drivers of gut microbial oscillations that have been identified to date, and summarise how circadian crosstalk between hosts and microbes can regulate rhythms in host physiology, with a focus on how circadian host–microbe interactions influence host susceptibility to pathogens. We next provide six examples of diverse biological and ecological processes, such as pathogen susceptibility and biological senescence, that are likely to be mediated, at least in part, by circadian host–microbe interactions. We discuss how urban conditions (e.g. light pollution) or the study of species with noncircadian feeding strategies (e.g. ectotherms) can help us understand the adaptive significance of microbial oscillations. Finally, we apply this information to provide recommendations on how to advance our understanding of gut microbial oscillations and their relevance to host physiology and ecology from studying wildlife and their associated gut microbiota.

2 | HALLMARKS OF GUT MICROBIAL OSCILLATIONS

Gut microbial oscillations have been identified in both natural populations (e.g. humans and meerkats; Reitmeier et al., 2020; Risely et al., 2021) and captive cohorts (e.g. mice, chickens, and fish; Brooks et al., 2021; Hieke et al., 2019; Parris et al., 2019; Zhang et al., 2021). Other types of microbiomes also undergo diurnal oscillations, including cow rumen microbiomes (Ouyang et al., 2021; Shaani et al., 2018), fish skin microbiomes (Ellison et al., 2021), plant rhizosphere microbiomes (Hubbard et al., 2018), invertebrate microbiomes (Pfenning-Butterworth et al., 2022; Roeder et al., 2022), and coral microbiomes (Rosenberg et al., 2022), highlighting the ubiquity of diurnal rhythms across host-associated microbiomes.

The proportion of gut microbes that show 24 h oscillating behaviour varies within and between species, with the proportion of operational taxonomic units (OTUs) being identified as oscillators ranging between ~10% and ~40% (Reitmeier et al., 2020; Thaiss et al., 2014; Zarrinpar et al., 2014). Oscillations in taxonomic composition translates into rhythms in gut microbial functional traits such as transcriptomes, metabolites and gene content (Kaczmarek et al., 2017; Leone et al., 2015; Thaiss et al., 2016), and in cow rumen microbiomes these functional shifts impact methane production (Shaani et al., 2018). Members of Clostridiales appear to undergo some of the strongest and most consistent oscillations in the gut microbiomes of mammals (Leone et al., 2015; Liang et al., 2015; Risely et al., 2021; Thaiss et al., 2016; Wu et al., 2018; Zarrinpar et al., 2014) and possibly birds (Hieke et al., 2019; Zhang et al., 2021), with Bacteroidales and Lactobacillales also tending to demonstrate oscillations in mammalian microbiomes. Overall, whilst these studies stem from a limited number of species, they highlight that diurnal rhythms of the gut microbiota are often very strong and explain more variation in composition than individual identity (Risely et al., 2021; Shaani et al., 2018; Wu et al., 2018; Zhang et al., 2021).

3 | DRIVERS OF GUT MICROBIAL OSCILLATIONS

Host genetics certainly regulate some facets of gut microbial oscillations. Mice lacking functional clock genes such as *Bmal1* and *Per1/2*, for instance, display disrupted gut microbial rhythms (Liang et al., 2015; Voigt et al., 2016). Individual bacterial taxa,

but also microbial composition and diversity, are under control from both the innate and adaptive arm of the host's immune system (Bolnick et al., 2014; Rakoff-Nahoum et al., 2004), which themselves are under genetic circadian control (Man et al., 2016; Scheiermann et al., 2018). Disruptions of gut microbiome oscillations under constant light or dark conditions, even when feeding schedules remain identical (Godinho-Silva et al., 2019; Jiang et al., 2020; Lee et al., 2022; Wu et al., 2018; Zhang et al., 2021), provide strong support for the role of a central circadian clock—which is largely entrained by light cues—in regulating rhythms in gut microbiota.

Feeding schedules and diet are also important for mediating microbial oscillations. Experimental high fat diets disrupt rhythms of murine gut microbiomes even when the timing of feeding is identical (Leone et al., 2015), and feeding drives a 10-fold change in absolute bacterial abundance in the murine gut microbiome (Thaiss et al., 2016). Initial evidence suggests that feeding schedules are equally important for driving microbial oscillations in wildlife. Peaks in foraging activity of wild meerkats, which are generally limited to early morning and evening due to hot temperatures during the middle of the day (Figure 1a), correspond to peaks in the absolute abundances of some abundant microbial taxa (Risely et al., 2021), with members of Clostridia in particular peaking strongly at dawn and declining in the afternoon (Figure 1b). Moreover, these oscillations have ripple-effects, which in turn structure the entire gut microbial community (Figure 1c). However, the extent to which gut microbial oscillations occur across natural populations is unclear due to a lack of studies, and the ubiquity of microbial oscillations in captive animals may be in part due to set feeding times that do not reflect natural foraging schedules of wild counterparts. For example, grazing animals may not have strongly structured feeding schedules across the day and therefore may not necessarily be expected to demonstrate microbial circadian rhythms.

4 | CIRCADIAN HOST-MICROBE CROSSTALK SHAPE CIRCADIAN PHENOTYPES IN IMMUNITY

Gut microbial oscillations are shaped by the intertwined actions of the host clock and feeding schedules. Yet, gut microbial oscillations themselves are a crucial component in the downstream synchronisation of multiple circadian phenotypes post-feeding. Whilst numerous molecules, microbial metabolites and bacterial proteins are involved in signalling pathways that mediate circadian rhythms in immunity, metabolism, and behaviour (reviewed in Choi et al., 2021; Teichman et al., 2020; Xia et al., 2022), we focus on two components of the immune system (antimicrobial peptides and secretory Immunoglobulin A) most thoroughly studied in the context of bacterial circadian rhythms and pathogen defence (Figure 2). The roles of gut bacteria in this crosstalk can be separated by gut biogeography: bacteria that colonise the mucosal gut lining, termed *mucosal commensals*; and bacteria that are mostly found in the gut lumen, termed *luminal bacteria* (Van den Abbeele et al., 2011). Mucosal commensals are distinguishable from luminal bacteria by having the biological architecture to anchor themselves to the host epithelial layer (Hedblom et al., 2018).

Food intake introduces both nutrients and food-borne pathogens into the gut, therefore the upregulation of both metabolism and components of innate immunity during feeding is crucial for gut function and pathogen defence. During the active phase, when animals are awake and feeding, high densities of gut microbes are

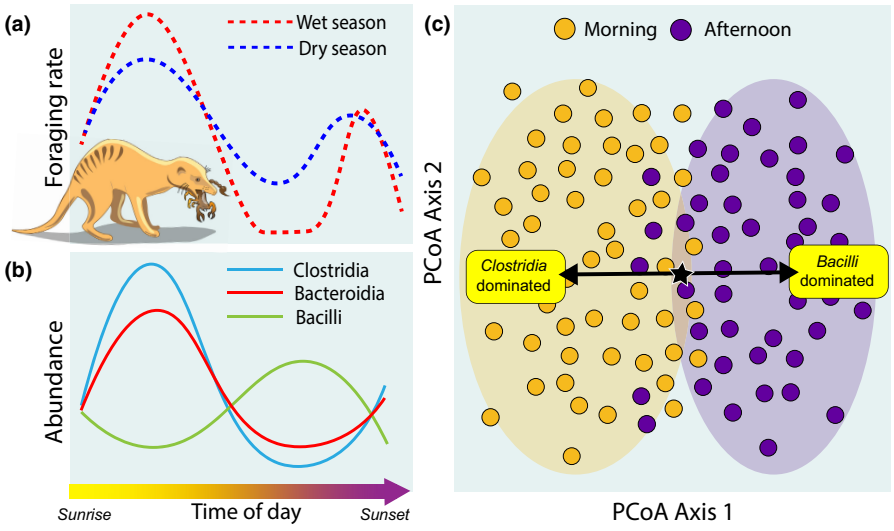

FIGURE 1 Conceptual figure representing meerkat foraging schedules and corresponding shifts in the gut microbiota, based on findings from (Risely et al., 2021). (a) Meerkats forage mostly in the morning and again before dusk to avoid the midday heat, although during the cool dry season they can also forage through the entire day; (b) Oscillations in selected taxa showing peaks in Clostridium and Bacteroides in the morning, and peaks in Bacilli in the afternoon, with abundances based on 16S copy number; (c) Diurnal shift in many taxa, especially Clostridium, cause community-wide structuring of the gut microbiota according to time of day, as represented by a PCoA plot.

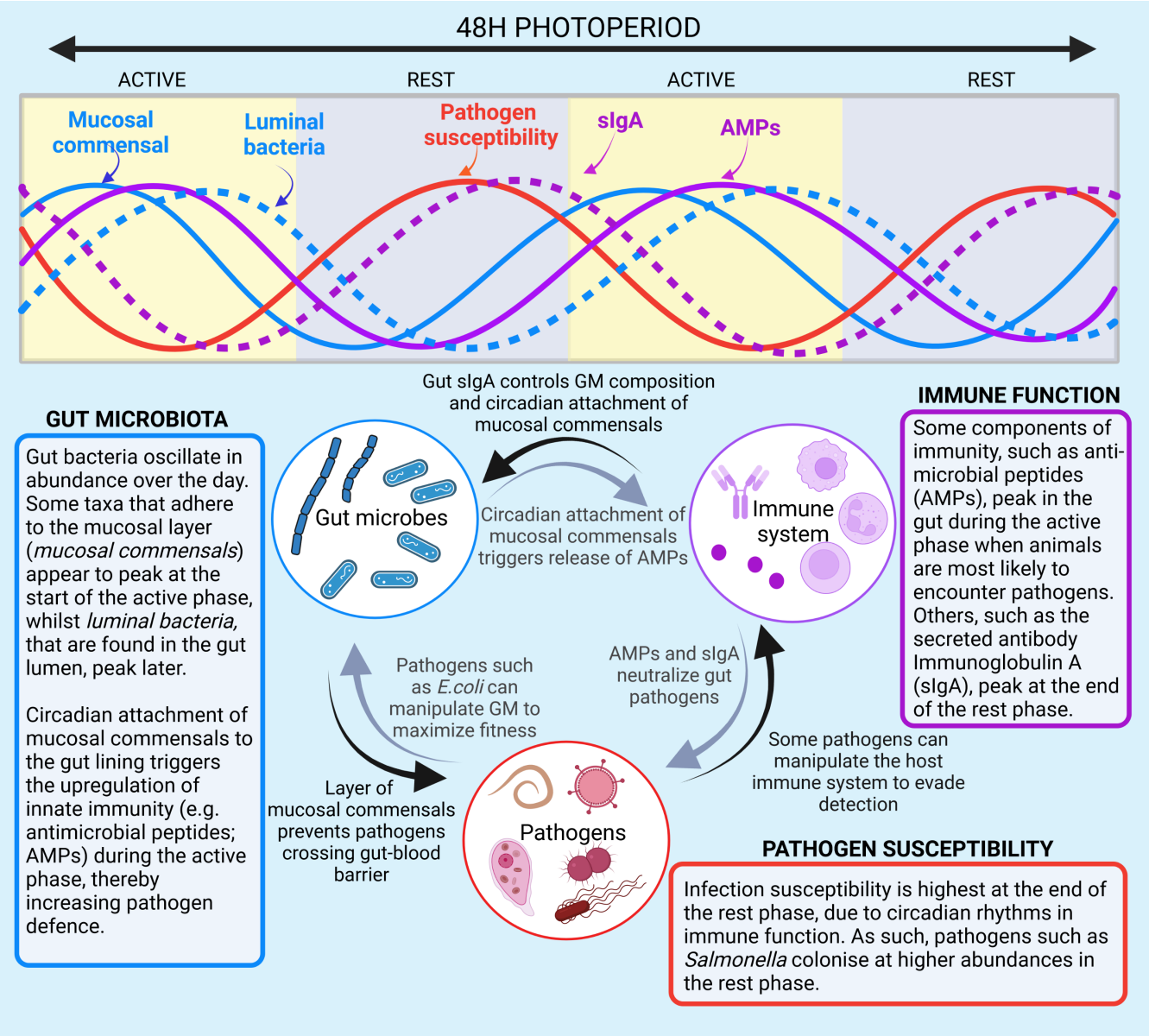

FIGURE 2 Summary of the circadian crosstalk between gut microbes, components of the host immune system, and pathogens, as characterised in laboratory mice (Brooks et al., 2021; Penny et al., 2022; Tuganbaev et al., 2020).

tolerated because they generate metabolites and nutrients, which are absorbed into the bloodstream through the gut lining (Figure 2a). To lower infection risk, most luminal bacteria are kept away from the mucosal layer by allowing only specific mucosal commensals to adhere to the gut lining (Brooks et al., 2021; Tuganbaev et al., 2020). This function is largely performed by segmented filamentous bacteria (SFBs), a group of host-adapted, commensal bacteria related to *Clostridium* that are found across vertebrate and invertebrate hosts (Hedblom et al., 2018). The physical interaction between mucosal commensals and host epithelial cells at the start of the active phase triggers the mass release of components of innate immunity, including antimicrobial peptides (AMPs; Brooks et al., 2021; Thaiss et al., 2016) that together protect the host against a broad range of pathogens during feeding (Brooks et al., 2021). Mice lacking SFBs, but with an otherwise normal gut microbiome, do not release AMPs until SFBs are introduced via co-housing with mice with SFBs (Brooks et al., 2021), demonstrating that the rhythmic attachment of mucosal commensals is key for regulating rhythms in gut immunity. Mucosal commensals also trigger the release of major histocompatibility complex (class II)-mediated cytokines (Tuganbaev et al., 2020), which, whilst part of the adaptive arm of the vertebrate immune system, act to modulate the innate immune response (Cyktor & Turner, 2011).

Maintaining a high level of immune control across a 24-h period is energetically expensive, and prolonged inflammation can cause immunopathology (Labrecque & Cermakian, 2015). Many aspects of innate immunity are therefore downregulated during the rest phase when the host is less likely to encounter pathogens (Figure 3b). This

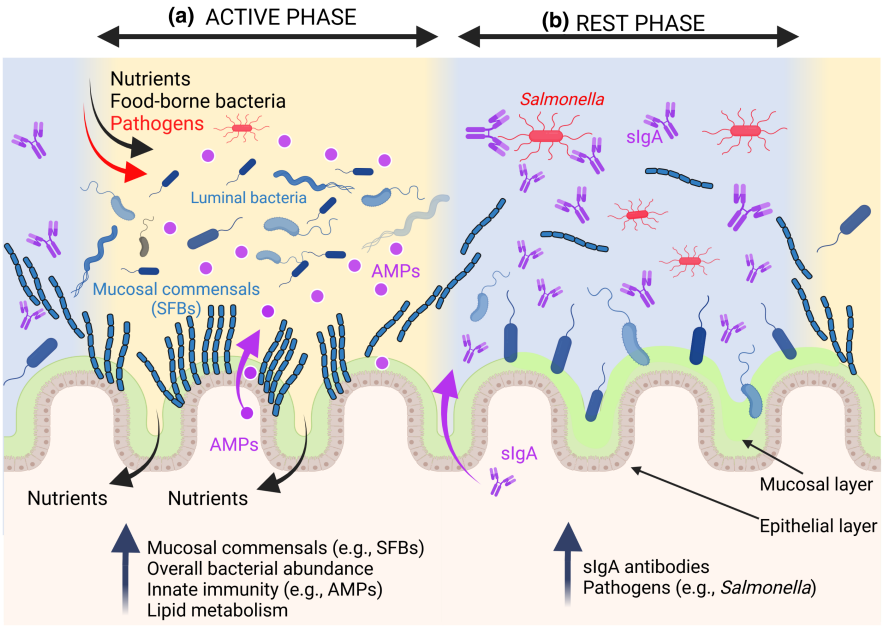

FIGURE 3 Diurnal rhythms and gut geography of the microbiota, host immunity and pathogen abundance across (a) the active phase and (b) the rest phase, as characterised in laboratory mice (Brooks et al., 2021; Penny et al., 2022; Tuganbaev et al., 2020). AMPs, anti-microbial peptides; SFBs, segmented filamentous bacteria

leads to higher host susceptibility to pathogens during the rest phase (Comas et al., 2017), with pathogens such as *Salmonella* able to colonise at higher relative abundances compared to the active phase (Bellet et al., 2013). The downregulation of innate immunity in the gut is preceded by the detachment of mucosal commensals from the mucosal layer, thereby triggering a reduction in the number of AMPs secreted into the gut. In the absence of nutrients from food, the gut bacterial population declines, and remaining bacteria migrate to the gut epithelium to feed on the mucosal layer, replacing the protective layer of commensals (Brooks et al., 2021; Thaiss et al., 2016) (Figure 3b).

Despite higher infection susceptibility during the rest phase, animals are not altogether undefended. In mice, a key gut antibody, secretory immunoglobulin A (sIgA), is upregulated during sleep (Penny et al., 2022; Figure 3b). sIgA, the secreted form of IgA, is secreted by mucosal membranes and is present across all mammals and bird species (Macpherson et al., 2012; Pietrzak et al., 2020). It acts as bridge between innate and adaptive immunity, being able to distinguish between gut commensals and noncommensals (Huus et al., 2021). During the rest phase, upregulated sIgA neutralises noncommensals and their toxins that are tolerated during the active phase. Thus, IgA ensures that any potential pathogens introduced during the active phase are neutralised during the rest phase. Another function of sIgA is to bind to beneficial mucosal commensals and control their adhesion to the mucosal layer (Donaldson et al., 2018; Huus et al., 2021), and it is therefore a key agent in triggering the circadian cycles of the gut microbiota at the start to the active phase (Penny et al., 2022). A peak in sIgA just prior to the start of the active phase is likely involved in bringing mucosal commensals back to the epithelial layer to begin the circadian cycle anew, although the exact mechanisms are still unknown. Interestingly, sIgA secretion is controlled by food intake rather than the master clock, with food intake appearing to repress sIgA levels (Penny et al., 2022) in order to increase tolerance to gut bacteria during the active phase.

5 | RELEVANCE OF MICROBIAL OSCILLATIONS TO OUTSTANDING QUESTIONS IN ECOLOGY AND EVOLUTION

A major objective for future investigations on the daily rhythms of the gut microbiome is to quantify their prevalence and strength across diverse host species and elucidate their relevance to host physiology and ecology. Below, we provide six examples of biological and ecological processes of which our understanding may be advanced by the integration of gut microbial oscillations (Figure 4).

5.1 | How might gut microbial rhythms reflect host ecology and evolution?

Evidence that the gut microbiome is both modulated by the master clock and in turn synchronises peripheral and central circadian clocks via its responses to environmental cues has important implications for our understanding of how circadian phenotypes manifest across and within species. Comparative studies of gut microbial rhythms within and between species may elucidate in which ecological and evolutionary contexts, respectively, we may expect to observe gut microbial oscillations. Such comparisons can suggest which circadian phenotypes (e.g. metabolic, immune, behaviour) or

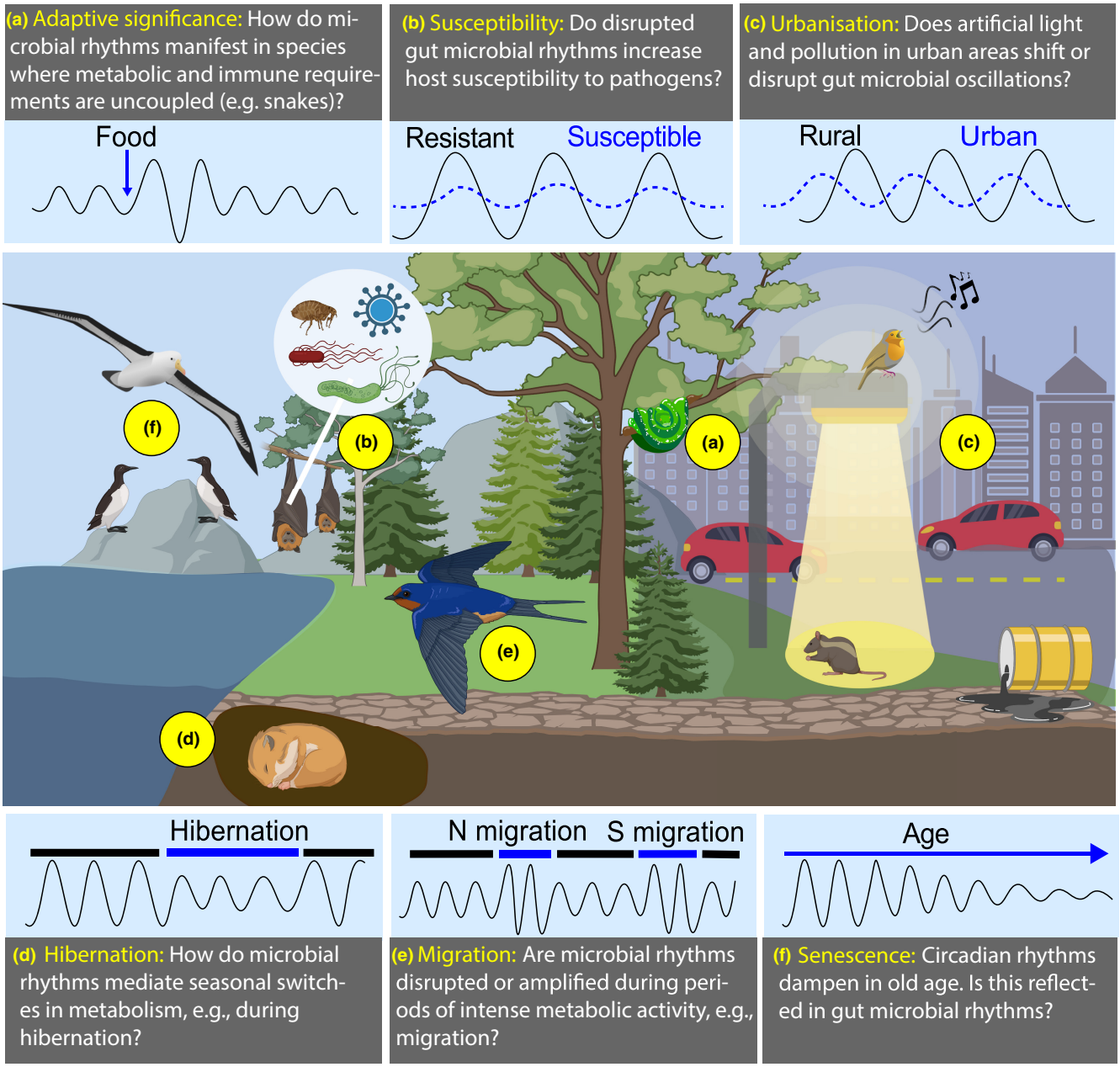

FIGURE 4 The involvement of food intake and gut microbial oscillations in mediating both metabolism and innate immunity raises several questions regarding their function across a range of ecological contexts. The figure visualises the predicted rhythms of mucosal commensals in the context of: (a) adaptive significance; (b) pathogen defence; (c) urbanisation; (d) hibernation; (e) migration (N = north, S = south); and (f) senescence

species traits (e.g. sociality, diet, nocturnality) are associated with gut microbial oscillations.

The observed correlation between feeding, metabolism, and immunity is expected to be the norm for species that have circadian feeding schedules, given that feeding introduces both nutrients and pathogens to the gut. However, the entrainment of peripheral circadian rhythms in immunity and metabolism may be microbiota-independent in species where metabolic requirements are not circadian, as well as in species where metabolic requirements and pathogen exposure are uncoupled. For example, ectotherms exhibit circadian rhythms in body temperature and activity (Bartell et al., 2004; Oishi et al., 2004; Tawa et al., 2014), and have some level of circadian cycles in metabolism (Roe et al., 2004) and immunity (Singh et al., 2020; Tripathi et al., 2015), but feeding patterns are often not circadian (e.g. for large reptiles such as snakes and crocodiles that are infrequent feeders). In these cases, does the gut microbiota undergo diurnal oscillations, and is the entrainment of innate immunity completely independent of the gut microbiota (Figure 4a)? Evidence from Burmese pythons suggests that shifts in the postprandial gut microbiota last for many days (Costello et al., 2010), although this study did not record time sample collection, obscuring whether feeding shifted microbial rhythms as well as composition.

In social or gregarious animals, microbiota are often shared (Sarkar et al., 2020) and pathogen exposure is high (Kappeler et al., 2015; McCabe et al., 2015; Yarlagadda et al., 2021). Peaks in pathogen exposure or activation of immunity may therefore not be limited to mealtimes. This raises the question as to whether social animals have altered circadian rhythms in immune function compared to solitary species, and whether such adaptations are mediated by the gut microbiota. Moreover, investigating microbial oscillations across latitudes and in environments with extreme light or temperature conditions (e.g. cave, arctic, or desert animals) will help uncover the precise contribution of these or other environmental stimuli to the initiation of microbial rhythms.

5.2 | How might gut microbial rhythms relate to pathogen susceptibility?

In mice, gut microbial oscillations reduce host susceptibility to gut pathogens during the active phase (Godinho-Silva et al., 2019) by triggering the release of AMPs into the gut (Brooks et al., 2021). Reducing the absolute abundance of mucosal commensals increases host susceptibility to pathogen infection and also diminishes circadian rhythms in susceptibility (Brooks et al., 2021), demonstrating that the rhythmic activity of specific gut mucosal commensals governs microbiome-mediated pathogen defence. In humans, arhythmic gut microbial communities have been linked to disease (Reitmeier et al., 2020). These findings suggest that individuals with disrupted gut microbiota rhythms (e.g. due to gut dysbiosis) may be more susceptible to infection (Figure 4b).

Circadian rhythms in animal susceptibility, pathogen reproduction and transmission are well documented (Martinez-Bakker & Helm, 2015; Westwood et al., 2019), with hosts and pathogens having coevolved defensive and offensive rhythms, respectively (Westwood et al., 2019). Nevertheless, many fundamental questions remain entirely unanswered: Do gut microbial rhythms protect the host against a broad range of pathogens, or are they only effective for specific gut pathogens? Judging by the role of microbial rhythms in the release of AMPs, which are effective against a wide range of pathogens (Huan et al., 2020) microbial rhythms likely protect the host against a broad range of pathogenic agents entering the gut. However, the gut is not the only entry point of pathogens and it remains to be seen whether microbial rhythms also play a role in pathogen defence more generally.

5.3 | How might urbanisation (e.g. light pollution) alter gut microbial rhythms?

Constant light or dark leads to a loss of microbial rhythms in chickens (Zhang et al., 2021) and mice (Wu et al., 2018), and this alteration is in part due to sensory signalling from the brain rather than changes to feeding times (Lee et al., 2022). Light-induced loss of microbial rhythms causes changes to gut function that promote disease (Wei et al., 2020), and these findings provide some of the strongest evidence that gut microbial rhythms are directly linked to health and disease, and at least partially independent from feeding schedules. The repercussions of artificial light and urbanisation on wildlife ecology, physiology and evolution are well documented (Johnson & Munshi-South, 2017; Sanders et al., 2021); yet, whilst there is evidence that light and even noise pollution are associated with changes in gut microbiota composition (Berlow, Wada, et al., 2021; Jiang et al., 2020) the role of the gut microbiota in mediating the downstream effects of urbanisation on ecological communities remains unknown.

Urbanised environments offer the rare opportunity to experimentally contrast the impact of changes to abiotic (e.g. light, temperature) and biotic (e.g. diet, pathogen pressure) conditions on microbial circadian rhythms compared with nonurban environments (Johnson & Munshi-South, 2017). How might the interacting pressures faced by urban-adapted species affect the gut microbial diversity, rhythms and function (Figure 4c)? Initial evidence from across phylogenetically-diverse species suggests that urbanisation is associated with a more 'humanised' gut microbiota, with a higher proportion of opportunistic pathogens (Alpízar et al., 2021; Berlow, Phillips, et al., 2021; Dillard et al., 2022; Fackelmann et al., 2021; Murray et al., 2020; Ruiz-Calderon et al., 2016). Disentangling which urban characteristics are predominantly associated with changes to the gut microbiota and their rhythms is challenging and may differ between species, yet recent evidence from wild great tits indicate that multiple urban factors act together to generate shifts in microbial composition (Maraci et al., 2022).

5.4 | How might seasonal life-history events affect gut microbial rhythms?

Many species undergo striking changes in life-history strategies between seasons, with hibernation and long-distance migration representing two of the most extreme life-history responses to seasonal changes in climate. Seasonal shifts in gut microbiome composition and function have been well described (Baniel et al., 2021; Carey et al., 2013; Ren et al., 2017; Risely et al., 2018; Smits et al., 2017; Wu et al., 2017), but emerging evidence suggests that changes in function may be mediated via increasing or decreasing the amplitude of host circadian rhythms (Huang et al., 2022). In giant pandas, seasonal switching of diet from bamboo leaves to shoots causes an increase in the bacterial metabolite butyrate in the gut microbiota, and when transferred to mice, this causes the upregulation of the clock gene *Per2*, which increases lipid production and fat deposition in spring (Huang et al., 2022). This study does not measure gut microbial oscillations directly however, and it is unclear whether microbial rhythms also increase in amplitude during spring.

In addition to seasonal diet switches, seasonal changes to life history stages that involve metabolic restructuring such as hibernation (Figure 4d), migration (Figure 4e), and even reproduction may also be paired with changes to the amplitude of their gut microbial rhythms. Shifts in the gut microbiota during hibernation adaptively

lower metabolism and recycle nitrogen (Regan et al., 2022; Sommer et al., 2016; Wiebler et al., 2018), yet whether these functional changes interact with or are mediated by diurnal rhythms is uncertain. Seasonal switches in strategies may take more unpredictable and fascinating forms. For instance, the circadian rhythms of some arctic-breeding shorebirds become uncoupled from environmental cues during breeding due to pressures of incubation and predators, with social cues becoming the dominant form of entrainment (Bulla et al., 2016). How might such changes be reflected in the gut microbiome?

5.5 | How might gut microbial rhythms relate to the rate of senescence?

Organismal senescence is characterised by a progressive dampening of circadian rhythms across host and gut microbial phenotypes (Patke et al., 2020; Thompson et al., 2020; Wilmanski et al., 2021). For example, older chimpanzees exhibit weaker diurnal oscillations in glucocorticoid excretion than younger counterparts (Thompson et al., 2020). Across species, senescence is delayed by diet restriction—the restriction of food availability as an adult (Regan et al., 2020), providing a link between feeding schedules and senescence. The benefits of diet restriction are mediated in part via the gut microbiota (Choi et al., 2021), with circadian pulses in feeding and consequent gut microbiota rhythms together maintaining robust host circadian rhythms into old age which may delay senescence (Manoogian & Panda, 2017; Paschos & FitzGerald, 2017). Therefore, the long-term disruption or alteration of the gut microbiota, for example due to infection or pollution, might lead to increased rates of organismal senescence even where robust circadian rhythms in foraging and activity are maintained.

Since circadian rhythms decline in amplitude in old age, the prediction is that microbial oscillations should decline in old age (Figure 4f). In wild meerkats, the only study to test this question, there was little evidence for microbial senescence. Old meerkats demonstrate microbial rhythms that were as strong as those of younger individuals (Risely et al., 2021), despite old (and generally dominant) individuals generally losing body condition (Thorley et al., 2020) and having higher rates of telomere loss (Cram et al., 2018). However, physiological senescence may be mitigated in part by the benefits of group living in this species (Gaillard & Lemaître, 2020).

Although age-dependent changes to gut microbial composition are known from a variety of wildlife species (Barbosa et al., 2016; Risely et al., 2022; Sadoughi et al., 2022), it remains unknown how changes in composition relate to changes in rhythms. Exploiting systems with high survival rates that have previously been used to model senescence and demography, such as seabirds (Fay et al., 2018; Patrick & Weimerskirch, 2015) or long-lived mammals (Robinson et al., 2012), may help clarify this question. Simultaneously, interpretation of findings needs to consider whether these changes in rhythms are mediated by shifts in diet during ontogeny or waning host immunity in old age.

6 | BEST PRACTICES FOR STUDYING GUT MICROBIAL RHYTHMS IN WILDLIFE

Field ecologists face a number of challenges that may have acted to delay the integration of circadian rhythms into field ecology, such as limited availability of study animals across a 24-h period. Such practical limitations put constraints on which species are suitable to investigate these questions. Nevertheless, any study system where variation exists in the timing of sample collection can be harnessed to advance our understanding of this topic. For instance, the link between gut microbial oscillations and host health can be deduced from cross-sectional data on humans (Reitmeier et al., 2020), a species that usually defecates once a day, shows a highly skewed distribution in timing of defecation (Reitmeier et al., 2020), and has high individual variation in gut transit times (Asnicar et al., 2021), and therefore represents a typically challenging species to study. Below, we outline important considerations for the study of circadian rhythms and the gut microbiome in field systems.

6.1 | Considering host ecology and physiology

The decision when to sample will depend on both the ecology and physiology of the focal host, and knowledge of these processes are crucial for the accurate interpretation of findings. Gut physiology and diet of many large herbivores might mean constant influx of plant matter of low nutritional quality, which also take longer to digest. In contrast, carnivores might eat more sporadically but often large volumes of energy rich food with shorter gut transit times. As such, faecal microbiome composition may reflect gut conditions from minutes to days before the sample was collected, depending on the species. There is also substantial variation in gut transit times between individuals: in humans, gut transit times vary from 0.5 days to over 4 days, with transit time strongly linked to gut microbiome composition (Asnicar et al., 2021). Nevertheless, species that have known foraging schedules and that can be sampled before and after their first foraging bout of the day are ideal subjects to study these questions.

6.2 | Targeting key markers

A common obstacle in identifying meaningful associations between the gut microbiota and host physiology is the sheer diversity of gut microbial communities and available physiological markers. Future studies on nonmodel organisms may therefore benefit from focusing on the key taxa and physiological markers identified from experimental studies to date. Mucosal commensals, and in particular segmented filamentous bacteria (SFBs), which are found across vertebrates (Hedblom et al., 2018), play a fundamental role in mediating physiological homeostasis and immunomodulation by attaching to the intestinal epithelium at the start of the active phase. The identity and oscillations of these specific commensals are therefore likely to

be disproportionally important for identifying associations between the gut microbiota and host physiology in natural populations. In addition, gut sIgA and AMPs are two facets of immunity that have been strongly implicated in circadian interactions with the gut microbiota, whilst the microbial metabolites butyrate, flagellin, and LPS have been implicated in circadian interactions that regulate metabolic signalling pathways and innate immunity (Wang et al., 2017). Applying these physiological markers may therefore be particularly suitable for determining whether mechanisms identified in laboratory systems have broad biological relevance for natural populations.

6.3 | Quantifying the gut microbiome

Absolute microbial abundance varies across the day (Liang et al., 2015; Roeder et al., 2022; Thaiss et al., 2016). Interpretations based solely on compositional data might thus misrepresent gut microbial rhythms. Compositional data is undoubtably meaningful to summarise changes to the overall community structure throughout the day, but quantifying absolute abundances in bacterial load is particularly valuable for identifying the oscillations of specific taxa, and especially rare taxa whose relative abundance might be particularly biased by fluctuations in abundant taxa. Applying an internal reference standard on weighed faecal samples is one option to quantify absolute ratios of 16S copy number (Harrison et al., 2021; Risely et al., 2021). Whole-genome metagenomics or quantification of absolute bacterial abundance via flow cytometry are more advanced methods for quantifying absolute abundances, but samples should still be weighed and DNA concentration measured (Lloréns-Rico et al., 2021).

6.4 | Identifying mucosal commensals

Pairing sequencing-based methods with more traditional microbiology methods such as culturing and (optical or electron) microscopy may also be particularly informative for identifying key mucosal commensals that adhere to the gut mucosal layer. Whilst these techniques require dissection of the host, exploiting frozen specimens to isolate and identify mucosal commensals on the ileum lining is one option and would be helpful for distinguishing between luminal and mucosal bacteria. Gut microbiome culturing is increasingly accessible and with appropriate conditions can be used to isolate a large proportion of gut microbial members (Lagier et al., 2016; Pereira & Cunha, 2020), yet some key taxa, such as SFBs, unfortunately appear to be highly resistant to culturing (Hedblom et al., 2018). Nevertheless, other mucosal commensals, such as the human commensal *Bacteroides fragilis*, can be cultured. Culturing key microbes have the additional advantage in that isolated microbes can form the basis for experimental probiotics that allow for the manipulation of the gut microbiome to better understand the causal effects of the gut microbiome on circadian phenotypes.

7 | CONCLUSIONS

Microbial diurnal rhythms are likely widespread and pivotal for mediating physiological homeostasis and pathogen defence, yet their study has been neglected in wild populations. Whilst the mechanisms underpinning the circadian crosstalk between the host immune system and the gut microbiota is a rapidly evolving area of research, key commensal taxa that rhythmically attach to the host intestinal epithelium play a critical role in triggering the upregulation of innate immunity and metabolism at the start of the active phase. A future focus on how gut microbiomes change over the day across host species with diverse biology (e.g. ectotherms, hibernating animals) and ecology (e.g. social animals, urban wildlife) will advance our understanding of their function and adaptive significance, and may illuminate the processes underpinning the breakdown of gut microbiota function during infection, senescence, and global change.

AUTHOR CONTRIBUTIONS

Alice Risely and Dominik W. Schmid conceived and wrote the initial draft of manuscript. Nadine Müller-Klein, Simone Sommer, Pablo Capilla-Lasheras, and Davide M. Dominoni significantly contributed to the ideas and manuscript editing. All authors contributed critically to the ideas and drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

We thank editors and two reviewers for their constructive comments on the manuscript. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST

All authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

No data were analysed.

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How to cite this article: Schmid, D. W., Capilla-Lasheras, P., Dominoni, D. M., Müller-Klein, N., Sommer, S., & Risely, A. (2023). Circadian rhythms of hosts and their gut microbiomes: Implications for animal physiology and ecology. *Functional Ecology*, *00*, 1–12. https://doi.org/10.1111/1365-2435.14255