Nighttime ecology: the 'nocturnal problem' revisited

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ABSTRACT: The existence of a synthetic program of research on what was then termed 'the nocturnal problem', and which we might now call 'nighttime ecology', was declared more than 70 years ago. In reality this failed to materialise, arguably as a consequence of practical challenges in studying organisms at night and concentration instead on the existence of circadian rhythms, the mechanisms that give rise to them, and their consequences. This legacy is evident to this day, with consideration of the ecology of the nighttime markedly under-represented in ecological research and literature. However, several factors suggest that it would be timely to revive the vision of a comprehensive research program in nighttime ecology. These include (i) that study of the ecology of the night is being revolutionised by new and improved technologies,; (ii) suggestions that far from being a minor component of biodiversity a high proportion of animal species are active at night; (iii) that fundamental questions remain largely unanswered as to differences and connections between the ecology of the daytime and nighttime; and (iv) that the nighttime environment is coming under severe anthropogenic pressure. In this article, I seek to re-establish 'nighttime ecology' as a synthetic program of research, highlighting key focal topics, key questions, and providing an overview of the current state of understanding and developments.

Introduction

More than 70 years ago, the American ecologist Orlando Park published the last in his series of papers addressing various aspects of what he termed the 'nocturnal problem' (Park et al. 1931, 1940a, 1940b, 1947; Park and Keller 1932; Park 1935, 1937, 1938, 1940, 1941a, 1941b; Park and Sejba 1935; Park and Strohecker 1936; Park and Noskin 1947). Of these, his sole authored 1940 paper is not only the longest but also the most significant. In this he sought to synthesise understanding of the ecology of the nighttime, including such issues as the environmental differences between daytime and nighttime, which animals were nocturnal or exhibited nocturnalism (by which he meant 'those general or specific activities initiated by, or enduring at night'), the advantages and challenges of being nocturnal, adaptations to nocturnalism, internal and environmental determinants of nocturnalism, and the contribution of nocturnal species to ecological communities. Park (1940) felt that this understanding had developed to the point that 'study of nocturnalism and its inter-relations is a comprehensive biological program'.

Park's vision for such a program failed, to this day, fully to materialise. There are number of possible explanations. These include that (i) ecologists themselves belong to a diurnal species and therefore have found it much easier, and may have had an innate proclivity, predominantly to focus on and study daytime phenomena; (ii) there seems to have been a widespread and long standing belief that in the majority of ecosystems most species are active and most ecological functioning occurs during daytime, and that nighttime is a relatively minor contributor (e.g., Crawford 1934); (iii) the technological challenges of studying ecological systems at night long remained too great, with the limited available techniques (e.g., making observations under various forms of artificial visible light; Finley 1959) having then unknown but likely problematic consequences; and (iv) attention grew, initially during a period when the fields of ecology and physiological ecology were regarded as largely synonymous (see Spicer and Gaston 1999), instead to focus on the existence of circadian rhythms, the mechanisms that give rise to them, and their consequences (e.g., Park 1941b; Calhoun 1944, 1945, 1946; Harker 1958; Panda et al. 2002; Yerushalmi and Green 2009).

This legacy is evident to this day. Only a small proportion of the papers published each year in any of the major journals in the field of ecology concern nocturnal phenomena. General monographs on nighttime ecology remain lacking. Standard recent ecology texts almost invariably use few nocturnal examples, make little or no mention of diel (daily) time partitioning by organisms, and typically do not include in their indices terms such as 'circadian', 'diel', 'night', 'nighttime' or 'nocturnal' (e.g., Begon et al. 2006; Cain et al. 2014; Krebs 2014; Molles 2016). Finally, there are seldom sessions at general ecology conferences, and indeed there are few dedicated conferences or workshops, that focus on nighttime ecology.

This is not, of course, to say that no ecological studies have been conducted at night. Many have. However, rather than that of a broader nighttime ecology these have predominantly been placed foremost in the contexts of the ecology of individual taxa (e.g., moths, owls, bats, primates), of particular habitats and regions (e.g., pelagic, arctic, antarctic) or of particular phenomena (e.g., interspecific competition, migration). Thus, whilst contributing to a general understanding of nighttime ecology, considerable work remains to be done to place them in a coherent framework focused on this topic.

As Park (1945) observed ‘Within biology, as facts accumulate about some central doctrine, or group of principles, and as these facts are collated and synthesized, there emerges a subscience which becomes recognizably distinct from its sister subsciences partially as a consequence of its technical content, and partially because of its point of view’. Now seems a good point at which to attempt to revive his (Park 1940) early vision of a synthetic research program in nighttime ecology. There are several reasons. First, study of the ecology of the night is being revolutionised by new and improved technologies that enable organisms to be observed, monitored and tracked at night under natural conditions (including camera traps, low light cameras, night-vision goggles, acoustic telemetry, PIT tags, satellite tags, laser scanning, radar, accelerometers; e.g., Chapman et al. 2011; Mizumoto et al. 2011; Walters et al. 2012; Brown et al. 2013; O’Connell et al. 2014; Puttonen et al. 2016; Meyer 2017; Linke et al. 2018). Many novel and important insights have already resulted. Second, some have argued that far from being a minor component of biodiversity a high proportion of animal species are nocturnal. Hölker et al. (2010) estimate that this is the case for 30% of all vertebrates and more than 60% of all invertebrates, which would make nocturnality the dominant way of life for animals. Third, fundamental questions remain largely unanswered as to the extent to which ecological principles derived (sometimes almost exclusively) from studies of diurnal organisms apply to nighttime ones, to which diurnal and nighttime communities are linked and influence one another, and to which, more generally, observations of ecological systems made during the day are shaped by processes operating at night (and vice versa). Finally, the introduction of artificial nighttime lighting, from streetlights and other sources, is disrupting natural diel light cycles, at least as perceived by many organisms, over increasingly large areas (Davies et al. 2014; Kyba et al. 2015, 2017; Falchi et al. 2016). This is having major ecological impacts on individuals, populations, communities and ecosystems (Gaston et al. 2013, 2014, 2017), but understanding of these effects, their mechanistic pathways, and their likely consequences is limited by knowledge of natural nocturnal states.

In this paper I seek to re-establish nighttime ecology as a synthetic research program. To do this, I (i) draw together current understanding of, and important knowledge gaps in, key issues on which such a program needs to be centred. In particular, to a large degree echoing those recognized by Park (1940) but not brought together since, I focus on environmental conditions, diel time partitioning, traits, community ecology and macroecology, and ecosystem functioning (fig. 1); (ii) bring together in one place example studies of these key issues, regardless of the context in which they were originally published (which are often diverse, including not just ecological and evolutionary research but also, for example, agricultural science, conservation biology and fisheries science); (iii) highlight some of the important linkages between these key issues (fig. 1, box 1); and (iv) consider the importance of anthropogenic pressures with respect to each of these key issues. These pressures have attained a significance that was virtually unrecognized in Park's time, but in many cases continues to receive rather limited attention.

Whilst much of what has been learnt about some of the key issues (e.g., time partitioning) has been derived from laboratory studies, here I will almost exclusively consider studies of wild organisms and field experiments. This is important because, for example, the patterns of diel activity of the same species in the laboratory and in the wild can sometimes be quite different (e.g., Blanchong et al. 1999; De et al. 2012; Tomotani et al. 2012; Fritzsche et al. 2017; Hoole et al. 2017); this is true of some model organisms for studying circadian rhythms in the laboratory, such as the golden hamster *Mesocricetus auratus* which is nocturnal in captivity but diurnal in the wild (Gattermann et al. 2008). As did Park (1940), I will also focus almost exclusively on animals, although, of course, plants typically exhibit different metabolic, physiological and functional activity, and different intraspecific and interspecific interactions, during daytime and nighttime.

Environmental conditions

The nighttime environment provides the ecological theater for the nocturnal play (sensu Hutchinson 1965). Its conditions and their spatial and temporal variation remain much less well quantified and understood than are those of the daytime environment. Indeed, as with the behaviour of nocturnal animals, knowledge of the nighttime environment itself has been improved with technological advances (remote sensing and night sky imagery, sensitive photometers and spectrometers, global environmental models; e.g., Foster et al. 2018; Román et al. 2018). Many of these advances have been made foremost in the context of studying animal vision systems, and have not been drawn into the context of nighttime ecology more broadly.

Perhaps critical to an understanding of nighttime ecology has been recognition that:

(i) light levels at nighttime vary over a similar range (four or so) of orders of magnitude as during the daytime, albeit at a markedly lower average intensity (Martin 1990).

(ii) the spectrum of light changes through the day, especially at twilight, providing potentially valuable biological cues. On a moonless night, as the sun drops from low on the horizon to below it, a clear sky changes from approximately white to reddish to blue and then back to reddish (Johnsen 2012); the moon has limited effect until late twilight, but then its phase and altitude significantly alter the colour and brightness of objects (Palmer and Johnsen 2015).

(iii) just as during the daytime, as well as reducing light intensity vegetation cover alters the spectral properties of the nighttime light environment, not only such that these changes are measurable but apparently sufficiently that they shape the most appropriate organismal vision systems (Veilleux and Cummings 2012).

In short, the nighttime environment is arguably, in terms of light alone, in relative terms as spatially and temporally complex as that of the daytime. Indeed, many assumptions as to the irrelevance, for example, of visually-oriented behaviours at nighttime (e.g. visual communication, camouflage) have proven to be incorrect (see Traits).

Of course, the nighttime environment differs from that of the daytime not just in terms of light; it is not daytime without the light. Over land, for example, nighttime also typically has lower temperatures than daytime with progressive cooling through the night; differs in surface wind speeds (and sometimes prevailing direction) and air turbulence (e.g., Lapworth 2005; He et al. 2013); and, largely driven by cooling of the atmosphere and lowering of saturation water pressure, differs in precipitation (e.g., Zhou and Wang 2017), humidity (e.g., Wang and Gaffen 2001), cloud cover and occurrence of fog (Eastman and Warren 2014). These differences influence, amongst others, the energetics of animals, their dispersal, and the effectiveness of their communication systems (e.g., Kerlinger and Moore 1989; Larom et al. 1997; McNab 2002; Müller-Schwarze 2006). Despite this, often profound, diel environmental variation, the modeling of the spatial distributions of animal species, for example, continues to focus heavily on average daily conditions rather than those prevailing at the time of day when individuals would tend to be most active.

The level and dynamics of environmental differences between daytime and nighttime are influenced by a variety of anthropogenic factors, including global climate change and land use change (e.g., Zhou et al. 2009; Betts et al. 2013; Song and Wang 2016). For example, global nighttime temperatures (and therefore daily minima) have increased more rapidly than have those during the daytime, and have contributed disproportionately to shifts in the more widely remarked daily mean temperatures (Karl et al. 1991; Davy et al. 2017). Daily and Ehrlich (1996) also argue that faced with tropical forest fragmentation nocturnal species fare better than do diurnal ones, because the contrasts between the environmental conditions in remnant forest patches and surrounding habitats (e.g., pastures) are far less extreme at night, enabling individuals to disperse between the patches much more readily.

Artificial sources also influence nighttime lighting regimes over large areas. Skyglow, caused predominantly by upwardly emitted artificial light being scattered in the atmosphere by water, dust, and gas molecules, extends conservatively over 23% of the global land surface (Falchi et al. 2016), and 100s of kilometers beyond urban sources (Luginbuhl et al. 2014). On clear nights it can readily attain levels that obscure the visibility of high proportions of stars (clear night starlight is ~0.001 lx) and can be sufficient to obscure natural light variation due to lunar cycles (full moonlight is ~0.1 lx; Davies et al. 2013). It is further amplified locally by cloud cover (Kyba et al. 2015), although this may limit its spatial propagation. Direct lighting is locally more intense (ground-level illuminance immediately under streetlights of ~10-40 lx usually declines to less than 1 lx a few meters away) but more constrained in extent, although an appropriate measurement is hard to make given that emissions in the horizontal plane (e.g., from vehicle headlights and poorly shielded street lamps) can carry over long distances and remote sensing measurements are typically taken closer to the vertical plane (Gaston et al. 2017). Widespread change from lamps of often narrow spectra (e.g., low pressure sodium) to ‘broad white’ lighting using light-emitting diodes (LEDs) is both exacerbating skyglow and increasing the intensity and extent of direct light emissions (Kyba et al. 2017).

Although largely unremarked, arguably overall the nighttime environment has actually been subject to more marked anthropogenic pressure than has that of the daytime. The former has experienced fundamental changes to light cycles and more pronounced temperature increases, whilst most other pressures are shared more equally between daytime and nighttime (e.g., habitat loss and fragmentation, chemical pollution);

pressures that are differentially expressed during the daytime include some forms of overexploitation (although much fishing and hunting, for example, is conducted during the night), and physical and noise disturbance (although given levels of anthropogenic noise will tend to carry further at nighttime than during the day time). Such differential impacts on the nighttime environment accentuate the present desirability of a new synthetic approach to the ecology of the nighttime.

Diel time partitioning

Perhaps reflecting some persistent sense that the nighttime environment is a more challenging one for organisms and thus that activities during the night require more explanation, the issue of how organisms partition diel time for activity (fig. 1), and the mechanisms that determine this partitioning, have been argued to lie at the heart of the study of the ecology of the nighttime (Park 1940). This said, characterisation of this partitioning nonetheless remains extremely poor for the vast majority of species of animals, and often limited at best to broad extrapolations for entire taxonomic groups based on limited data. It is notable how frequently in recent years, often exploiting technological advances, unexpected levels of nighttime activity by particular species have been documented (e.g., Newman and Springer 2008; Le Bohec et al. 2003; Lambert et al. 2009; Mukhin et al. 2009; Regular et al. 2011; Zavalaga et al. 2011; Donati et al. 2012; Tan et al. 2013; Broekhuis et al. 2014; Berge et al. 2015; Tran et al. 2016). These include, for example, findings that cheetahs *Acinonyx jubatus* can be highly active foragers at night (Cozzi et al. 2012), that zooplankton undergo mass vertical migration (Last et al. 2016; Ludvigsen et al. 2018) and cormorants *Phalacrocorax carbo* dive (Grémillet et al. 2005) through the polar night, and that some dragonfly species migrate by night (Feng et al. 2006). The overall level of nighttime activity by animals is doubtless vastly underestimated; whilst activity of night active species in the daytime tends readily to be observed, the converse does not.

There are two prominent, and rather contrasting, perspectives on the consistency of diel time partitioning by animals, the current balance between which has yet adequately to be resolved. The first focusses on the degree to which this behaviour is phylogenetically conserved, and hence the accuracy with which extrapolation can be made from knowledge of individual species to entire clades. Diel activity patterns or temporal niches (e.g., diurnal, nocturnal, crepuscular, cathemeral) have been argued to be phylogenetically highly conserved (typically maintaining the ancestral condition). This has been shown within groups of mammals (Roll et al. 2006; de Oliveira et al. 2016), across all mammals (Bennie et al. 2014), and across tetrapods more widely (Anderson and Wiens 2017). However, I am not aware of such empirical analyses for other groups of organisms, although there are numerous examples in which all of the species in a clade exhibit the same broad type of diel temporal niche (e.g., within most families of birds). Some attention has been paid to examples of narrower clades that whilst predominantly showing one form of diel activity pattern have apparently undergone evolutionary transitions by species to others on one or more occasions. But again such studies tend to have been confined to vertebrates (e.g., Ankel-Simons and Rasmussen 2008; Gamble et al. 2015).

An alternative perspective focusses on evidence of the lability of diel temporal activity within a species. Seasonal switches may be quite common, with individuals typically being more diurnal when it is colder and more nocturnal when it is warmer (fig. 2 c & d, e & f; e.g., fish - Hautala 2008; mammals - Hayes and Krausman 1993; Maloney et al. 2005; Bourgoin et al. 2008; Zschille et al. 2009; Erkert et al. 2012; Hetem et al. 2012; Giné et al. 2015; Bu et al. 2016; Clemente et al. 2016; Hofmann et al. 2016; Davimes et al. 2017); the evolution of endothermy may have been associated with expanding daily activity into the night (Grigg et al. 2004). The degree of nocturnal activity of a species can also be dependent on life stage, age and/or body size, sex, migratory phase, density, lunar phase, habitat, weather, and timing of prey activity (table 1, fig. 2 a & b). The availability of nighttime seems likely also to be of widespread importance. Empirical examples are, nonetheless, very scant. Some species have been shown to exhibit less nocturnal activity at higher latitudes (e.g., Dreisig 1981; Theuerkauf 2009; but see Heurich et al. 2014). The distribution of the Indian crested porcupine *Hystrix indica* has also been found to be spatially constrained by the length of the night available for foraging (e.g., Alkon and Saltz 1988).

Interspecific competition has regularly been dismissed as a significant determinant of time partitioning behavior by species, principally on the grounds that there would be no energetic gain to individuals from not feeding during most periods, and hence such partitioning has been regarded as a rather unimportant dimension of niche differentiation (Jacksić 1982; Schoener 1986). Nonetheless, evidence has continued to accrue of taxonomically or functionally similar species apparently avoiding competition by differential use of different times (e.g., insects - Albrecht and Gotelli 2001; DeVries et al. 2008; Kamenova et al. 2015;

Żmihorski and Ślipinski 2016; mammals - Kronfeld-Schor and Dayan 2003; Gutman and Dayan, 2005; Hayward and Slotow 2009; Lucherini et al. 2009; Di Bitetti et al. 2010; Romero-Muñoz et al. 2010; Schwartz et al. 2010; Gerber et al. 2012; Scheibler et al. 2013; Ferreguetti et al. 2015; Sunarto et al. 2015; Monterroso et al. 2016; but see Vieira and Paise 2011; Guo et al. 2017). These are almost exclusively non-experimental studies, limiting the inferences that can be drawn. This includes the possibility of underestimating the likely occurrence of such partitioning effects by not accounting for those that involve 'apparent' competition (sensu Holt and Bonsall 2017). If time partitioning amongst species does occur with even moderate frequency this could have important implications for studies of co-occurrence and community structure that otherwise ignore this.

In contrast to interspecific competition, avoidance of predation has long been championed as an important driver of the nighttime activity of species. It has frequently been used to explain the ancestral or characteristic behaviour of entire taxonomic groups (e.g., Maor et al. 2017), and reciprocal coevolutionary changes in the diel activity of predators and prey have been argued to occur (e.g., Wu et al. 2018). There is much evidence for daytime predation risk driving greater nocturnal activity by prey species (e.g., crustaceans - Bishop and Wear 2005; insects - Culp and Scrimgeour 1993; fish - McCauley et al. 2012; Kadye and Booth 2014; amphibians - Barr and Babbitt 2007; birds - Keitt et al. 2004; mammals - Swarts et al. 2009; Zapata-Ríos and Branch 2016), and for nighttime predation risk driving less nocturnal activity (e.g., fish - Fraser et al. 2004; amphibians - Velo-Antón and Cordero-Rivera 2017; mammals - Fenn and Macdonald 1995; Monterroso et al. 2013; Bischof et al. 2014; Suselbeek et al. 2014; Tambling et al. 2015; Pavey et al. 2016; Zapata-Ríos and Branch 2016). By contrast, examples are rather scarce for no marked impacts of predation on levels of nocturnal activity (but see Mestre et al. 2013; Monterroso et al. 2013), although this could be subject to a 'file drawer' problem (sensu Rosenthal 1979).

Time partitioning behaviour observed in the wild may reflect underlying endogenous circadian rhythms, and/or the 'masking' of these by responses to other factors. The relative importance of these two is a critical mechanistic issue, but remains formally to be determined. However, the multiplicity of ways in which temporal switching of diel time partitioning occurs suggests that masking seems easily to be achieved, is likely often to be of adaptive significance, and that it is doubtless at least very widespread (Hut et al. 2012; Smarr et al. 2013).

Ignorance of, or ignoring, the diel partitioning behaviour, and especially the usually more poorly known nighttime activity, of species may have important management and conservation implications. For example, it can result in biased assessments of the abundances of species, with implications for sustainable use, by failing to estimate these at the most appropriate times of day (e.g., Wolter and Frehof 2004; Waltert et al. 2006; Aguzzi and Bahamon 2009; Wrege et al. 2011), in key predatory species being overlooked for the biocontrol of pests (Woltz and Landis 2013), and in the failure correctly to identify patterns of habitat use (e.g., Johnson and Covich 2000; Elliott 2005) and thence to protect habitat that is important for species persistence (e.g., Austin et al. 2016).

Given the responsiveness of diel time partitioning behaviour to a variety of abiotic and biotic factors one would predict that it is sensitive to anthropogenic pressures. This has indeed proven to be the case. Change in the nocturnal behaviour of species has been documented as a consequence of provision of supplementary food sources, human recreational activity, hunting, fishing, persecution, predator control, occurrence of feral dogs, disturbance, logging, land use, habitat creation and the introduction of artificial nighttime lighting (table 2, fig. 2 g & h). In many of these cases the outcome has been for species to become more nocturnal in order better to exploit opportunities and/or avoid human activity, although artificial nighttime lighting tends to curtail the activity of nocturnal species (as well as extending into the natural nighttime period the activities of species that are not nocturnal; e.g., Bakken and Bakken 1977; Wolff 1982; Negro et al. 2000; Frank 2009). However, even within a population the extent of responses to anthropogenic pressures on the nighttime can be variable depending on the experiences of those pressures by individual animals (Kaczensky et al. 2006).

Being obligately limited in diel activity behavior will tend to make species more susceptible to some kinds of anthropogenic environmental pressures. For example, obligately diurnal or nocturnal mammals have been found to be more than twice as likely to respond to climate change (through local population extirpation, range contraction, range shift, and through directional change in abundance, phenology, body size or genetic diversity) as those with flexible activity times (McCain and King 2014). Conversely, as has been explored for fish under harvesting pressure, species with more flexible diel activity may experience marked directional selection over the timing of this activity as a consequence of anthropogenic pressures (Alós et al. 2012).

Traits

The challenges and opportunities of nighttime environmental conditions may not only shape the diel activity of animals, but also other traits that they exhibit (with presumably some interplay between diel activity and other traits; fig. 1). How the traits exhibited by night active species differ from those of other species, and most especially the differences in sensory systems and their relations to environmental conditions is the aspect of nighttime ecology that has received more attention than any other. Sensory systems are often under strong selection pressure because of the high energy costs associated with their maintenance (Niven and Laughlin 2008). A wide array of such systems has been argued either to be adapted for, or more specifically associated with, nocturnally active species (although interpretation is complicated because nighttime is not the only dark environment). More general systems adapted for night activity include visual (e.g., Hall and Ross 2006; Land and Nilsson 2012), olfactory (e.g., Healy and Guilford 1990; Cooper 1999), hearing (e.g., Fullard et al. 2000; Fullard and Napoleone 2001) and mechanosensory systems (e.g., Pohlmann et al. 2004; Seneviratne and Jones 2010; Mitchinson et al. 2011; Schwarz et al. 2011). There have been various attempts to use the morphological structure of associated organs to try and differentiate between, and enable inference about, species with different diel partitioning behavior (e.g., Bauer and Kredler 1993; Hall and Ross 2006; Schmitz and Motani 2011; Hall et al. 2012). Systems that are more specifically associated with night active species include echolocation (e.g., Speakman 1993; Thomas et al. 2004; Lindberg and Pyenson 2007), infra-red detection (Kurten and Schmidt 1982; Goris 2011) and electrosensing systems (Bullock et al. 1983; Pettigrew 1999). The relative importance of different sensory systems may vary even between closely related species with different daily activity patterns (e.g., Balkenius et al. 2006), although some species are able to use the nighttime without any apparent sensory adaptations (e.g., Kelber et al. 2011).

Whilst attention tends frequently to focus on other sensory systems, particularly striking has been growth in understanding of the role that vision plays for many night active species, including that (i) some species are able to use remarkably low light levels for, in some cases rapid and spatially accurate, visually orientated movement (e.g., Warrant 2004, 2017; Warrant et al. 2004; Somanathan et al. 2008; Last et al. 2016); (ii) for their size and metabolic rate nocturnal species visually sample the environment at lower rates, that is they have lower critical fusion frequencies (Healy et al. 2013); (iii) some species are able to see in colour even at low light levels (Kelber et al. 2002, 2003; Roth and Kelber 2004); (iv) there are nocturnal predators that attract prey using colour (Chuang et al. 2007); (v) there are prey that exhibit nocturnal camouflage (Hanlon et al. 2007); (vi) visual communication by animals at night is extensive (Penteriani and Delgado 2017); and (vii) vision can be important for species in groups for which other sensory systems have received most attention (e.g., spiders, electric fish, bats; Rydell and Eklöf 2003; Zhao et al. 2009; Fenk et al. 2010; Pusch et al. 2013).

A variety of non-sensory traits have been found to differ between groups of evolutionarily related nocturnal and other species, although tests of these relationships remain few and thus the extent and limits to their generality are almost invariably unclear. Many of these are related to the different thermodynamic conditions that pertain at night (although other explanations have also been proposed). For example, there is evidence that compared with their relatives species of nocturnal ectotherm have higher metabolic rates at low temperatures (lizards - Hare et al. 2010), metabolic rates that are more dependent on temperature (beetles - Lease et al. 2014), lower thermal tolerances (ants - Garcia-Robledo et al. 2018), larger body sizes (insects - Luff 1978; Dennison and Hodkinson 1983; Ottesen 1985; Caveney et al. 1995; Guevara and Avilés 2013; Medina and Lopes 2014; fish - Hernández-Serna et al. 2015; lizards - Meiri 2008), larger geographic range sizes (fish - Luiz et al. 2013), and can have different morphology (fish - Pulcini et al. 2008). Nocturnal endotherms also tend to have lower resting metabolic rates (birds - Bennett and Harvey 1987; McNab 1996; Duriez et al. 2010; mammals - Hildwein and Goffart 1975; McNab and Wright 1987). Although there are such differences, there is little evidence at present that grouping species within a taxon by their diel partitioning behaviour provides a strong prediction of the sets of traits that they are likely to exhibit (Pianka et al. 2017).

One might predict that given the marked anthropogenic changes to nighttime environments there is potentially strong selection on nocturnal traits. A broad suite of traits has been argued potentially to be influenced by artificial light at night, including photoperiod-dependent phenological traits, such as the timing of growth and reproduction (Hopkins et al. 2018). It is unclear to what extent some of the numerous phenotypic and evolutionary differences between rural and urban populations of species (McDonnell and Hahs 2015; Alberti et al. 2016, 2017; Johnson and Munshi-South 2017) are a consequence of differences in artificial nighttime lighting, but it could play an important role. The only clear demonstration of such effects to date has been reduced flight-to-light behaviour of individuals of the small ermine moth (*Yponomeuta cagnagella*) from light polluted sites compared with those from unpolluted ones (Altermatt and Eber 2016).

Community ecology and macroecology

All else being equal, one might expect that, based on the relative durations of nighttime and daytime, similar numbers of animal species and individuals in communities would be nocturnal as diurnal (Park 1941a). Of course, a number of factors could readily and substantially distort such symmetry, including phylogenetic, thermal and seasonal constraints. The role of seasonality is potentially particularly significant, shortening the numbers of hours that are dark during the warmer months at higher latitudes.

In practice, variation in the relative frequency in communities of nocturnal species and individuals remains remarkably poorly understood. Global macroecological studies of lizards (of which most species are diurnal) and of mammals (of which most species are nocturnal), based on geographic range maps, have shown that the frequency of nocturnal species tends to be lower when nighttime temperatures are low (e.g. at higher latitudes and elevations), and higher when daytime temperatures are high (e.g. in deserts), and when periods of nighttime are longer and those of twilight shorter (Bennie et al. 2014; Vidan et al. 2017).

Local studies of the relative frequency of nocturnally active species and individuals are also surprisingly scarce. Setting aside those groups for which the majority of species share a diurnal or a nocturnal temporal niche (e.g. birds, mammals), probably the most research has been conducted into fish assemblages. Here, daytime and nighttime assemblages seem often to be similar in richness and abundance or greater numbers are active in the nighttime (e.g., Robblee and Zieman 1984; Layman 2000; Arrington and Winemiller 2003; Dulčić et al. 2004; Correa et al. 2008; Castillo-Rivera et al. 2011; Roach and Winemiller 2011; Matheson et al. 2017). But this can be reversed, with daytime assemblages being larger than nighttime ones (e.g., Rooker and Dennis 1991; Rooker et al. 1997; Nagelkerken et al. 2000), and some have argued that this is the norm (Helfman 1978). Those studies that have been conducted for more speciose taxonomic groups have mostly been for arthropods, and suggest that, in general, similar numbers of taxa and individuals are active during the daytime and at night, or greater numbers are active during the daytime (e.g., Williams 1959; Dondale et al. 1972; Janzen 1973; Vickerman and Sunderland 1975; Basset et al. 2001, 2003). The principal exception is for arid areas with high daytime temperatures, where nocturnality tends to be most prevalent (e.g., Vonshak et al. 2009), but studies in other environments have also found such outcomes (e.g. Costa and Crossley, 1991).

On the basis of present information it is impossible to provide a reliable evaluation of what proportion of animal species are nocturnal at local, regional or global scales. Hölker et al. (2010) attempt a global calculation based on the rather scant available estimates for major animal groups, concluding that >60% of all invertebrates (the vast majority of animal diversity) are nocturnal. This appears to be based on a quite liberal interpretation of nocturnal activity, and if so is probably strongly influenced by organisms that have a nocturnal stage in their lifecycle, even if the adult form is not nocturnal. If this figure is broadly correct then, given all of the associated uncertainties, it may not be that different from Park's (1941a) expectation of rough equality amongst numbers of species that are nocturnal and that are not.

In all environments there is usually substantial turnover in the identities of the species that are active between daytime and nighttime, with some evidence that this is higher when the differences in temperatures are greater (Basset et al. 2001, 2003). In some systems at least, there may also be marked shifts in the trophic composition of assemblages between daytime and nighttime (e.g., Castillo-Rivera et al. 2011).

The introduction of artificial nighttime lighting can have profound effects on the structure of local ecological communities, including changes in species composition and abundance, and in fluxes of individuals (Davies et al. 2012, 2017; Meyer and Sullivan 2013; Hölker et al. 2015; Spoelstra et al. 2015). There is evidence that at broader spatial scales it may also alter the proportions of species present with different kinds of diel time partioning behaviour (Bennie et al. 2014).

Ecosystem functioning

The general role of biodiversity and individual species in levels of ecosystem functioning, and the marked partitioning of activity of individual species between periods of the day, suggest that the functioning of ecological systems may be strongly partitioned between day and night. Some key forms of ecosystem functioning that were thought predominantly to occur during the daytime have been found to have strong nighttime components (e.g., evapotranspiration - de Dios et al. 2015; O'Keefe and Nippert 2018; decomposition in arid environments - Gliksman et al. 2016; tropical seed dispersal - Santana et al. 2016). Given the marked differences in environmental conditions and community structures between daytime and nighttime it is almost inevitable that ecosystem functioning will also differ. These differences include in such diverse phenomena as the functional composition and redundancy of assemblages (e.g., Houadria et al. 2016), the structure of interaction networks (e.g., Remmert 1969; Devoto et al. 2011), and the cycling of materials (e.g., Wilson and Xenopoulos 2013).

The asymmetries in global climate warming between daytime and nighttime have important consequences for ecosystem functioning. For example, increased nighttime temperatures have been linked to spatially and temporally divergent responses of vegetation growth and carbon sequestration (Alward et al. 1999; Peng et al. 2013; Xia et al. 2014; Anderegg et al. 2015), changes in yields of some crops (Peng et al. 2004), differences in microbial activity (Freixa et al. 2017) and soil respiration (Xia et al. 2009), and increased top-down control of plant diversity (Barton and Schmitz 2018). Fundamentally, the temperature dependence of respiration is likely to mean that carbon fluxes are profoundly influenced by any diel asymmetry of warming. Given this apparent importance of nighttime temperature changes, it is of concern that the vast majority of ecological experiments into the impacts of climate change have typically assumed that daytime and nighttime temperature changes are the same.

Changes in nighttime lighting conditions through the introduction of artificial sources has been shown to result in changes in disparate components of ecosystem functioning, including the trophic structure of species assemblages (Davies et al. 2012), the balance of bottom-up and top-down control in communities (Bennie et al. 2015; Sanders et al. 2018), carbon cycling (Hölker et al. 2015), pollination (Macgregor et al. 2015; Knop et al. 2017) and seed dispersal (Lewanzik and Voigt 2014). For example, Davies et al. (2012)

found that, both at night and during the day, predator and scavenger invertebrates were more abundant under streetlights than between them.

Some of the responses of ecosystem function to temperature change and to artificial nighttime lighting can be very similar, begging questions as to the extent to which these drivers have been sufficiently differentiated in some (non-experimental) studies, and whether they are synergistic. A study of the combined effects of nighttime warming and artificial light pollution on a visually foraging ladybeetle predator species, found that these had non-additive effects which together caused much lower abundances of aphid prey (Miller et al. 2017).

Conclusions

Several important conclusions arise from this synthesis:

- The failure to realize Park's (1940) original vision of a comprehensive research program in nighttime ecology has hindered recognition of the general ecological importance of the night.
- The ecology of the nighttime should neither be underplayed nor treated as something unusual or odd. It is a substantial component of the ecology of the earth.
- If similar studies of many topics were to be conducted during the daytime or the nighttime, those for the nighttime would continue often to contribute proportionally much more to overall ecological understanding.
- There are important questions, particularly concerned with the links between the different key issues in nighttime ecology highlighted in this paper (box 1), that remain essentially unanswered.
- The potential for a 'golden age' of nighttime ecological research is undoubtedly with us. There is huge, as yet largely untapped, opportunity to exploit technological advances for conducting studies of the ecology of the nighttime. Only recently have costs reduced sufficiently to enable some technologies to be used very widely (e.g., camera traps) and this has yet to happen for others (e.g., starlight cameras).

- It is unclear why issues of time partitioning have become so much more heavily associated with nighttime than daytime ecology. Animals use the nighttime in as varied a manner as they do the daytime.
- With species trait combinations well established as being central to much ecosystem function and process, it important to understand better how and why non-sensory traits differ between animals that are most active at different times of day.
- It is time that the long-standing questions of how similar are the species richness, abundance and biomass of animal communities between daytime and nighttime, and how these interact, are properly answered. These are fundamental characteristics of ecological systems.
- Opportunities to observe nocturnal ecology under natural light cycles are fast disappearing. The ecology of the nighttime is under intense anthropogenic pressure, and arguably more so than that of the daytime, albeit the two are intimately linked. This gives the development of a synthetic research program in nighttime ecology an imperative that has previously been lacking. Estimates that skyglow presently influences the nighttime over a quarter of the land surface are conservative and rates of increase in this coverage are high, and in some regions (e.g., Europe, eastern North America) unpolluted skies are largely gone.

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Box 1. Some important questions regarding the key issues about nighttime ecology highlighted in this paper and their linkages. Numbers refer to linkages in fig. 1.

Environmental conditions

- Is the nighttime environment under greater anthropogenic pressure than that of the daytime?

Time partitioning

- How well does conventional categorization of diel partitioning behavior (e.g. diurnal, nocturnal, crepuscular, cathemeral) reflect the variety of behaviours actually exhibited?
- What is the relative importance of endogenous circadian rhythms and the 'masking' of these by responses to other factors in shaping observed diel activity patterns? (1,3,4)

Traits

- How well does the diel activity of a species predict the suite of non-sensory traits that it possesses? (5)
- How do differences in the traits of day active and night active communities influence ecosystem function? (8)
- How widespread are evolutionary responses of traits to anthropogenic pressures on the nighttime, particularly artificial lighting? (2)

Community dynamics

- What is the relative species richness, abundance and biomass of day active and night active animals, and how does this relate to environmental conditions? (9)
- How are the community dynamics of day active species influenced by night active ones, and vice versa?
- Do differences in daytime and nighttime community dynamics select for different traits? (6)

Ecosystem functioning

- What is the relative contribution of daytime and nighttime to the overall delivery of different ecosystem functions and processing?
- Do differences in the dynamics of day active and night active communities change ecosystem functioning? (7)
- How important is differential anthropogenic nighttime warming in changing ecosystem functioning? (10)

Table 1. Examples of variation in degree of nighttime activity by species as a consequence of intrinsic or extrinsic factors.

Species	**Trait**	**Variation**	**Source**
Pararge xiphia, *Hipparchia semele* [butterflies]	age/size	Diurnal foraging of larvae ceased at large sizes while nocturnal foraging remained constant or increased	Berger and Gotthard (2008)
Atlantic salmon *Salmo salar*	age	Parr predominantly active at night, young-of-the-year equally active during day and at night	Imre and Boisclair (2004)
Atlantic salmon *Salmo salar*	size	Young-of-the-year predominantly diurnal in early summer and nocturnal in late summer	Johnston et al. (2004)
Brown bear *Ursus arctos*	age	Younger individuals more nocturnal	Hertel et al. (2017)
European polecat *Mustela putorius*	sex	Females predominantly diurnal and crepuscular, males nocturnal	Marcelli et al. (2003)
American mink *Neovison vison*	sex	Females predominantly diurnal, males nocturnal	Zschille et al. (2009)
Pantala flavescens [dragonfly]	migratory phase	Migrates at night	Feng et al. (2006)
North American nesting birds	migratory phase	Many species that migrate partly or exclusively at night are strictly diurnal foragers	Beauchamp (2011)
Field vole *Microtus agrestis*	density	Predominantly diurnal during density peaks, nocturnal during population declines, and diurnal	Halle and Lehmann (1992)

		at low density and early increase phases	
Pimelodus maculatus [fish]	lunar phase	Nocturnal migratory movement lessened during new moon	Bizzotto et al. (2009)
59 nocturnal mammal species	lunar phase	Across all species, moonlight suppressed activity	Prugh and Golden (2014)
Red brocket deer *Mazama americana*, Paca *Cuniculus paca*, Nine-banded armadillo *Dasypus novemcinctus*, Greater long-nosed armadillo *Dasypus kappleri* [prey of Puma *Puma concolor*]	lunar phase	Paca and armadillos more active on darker nights, and all species avoided brighter times of night regardless of moon phase	Pratas-Santiago et al. (2017)
Leopard *Panthera pardus*	habitat	Nocturnally active in savannah, diurnal and crepuscular in forests	Jenny and Zuberbühler (2007)
Golden-lined rabbitfish *Siganus lineatus*	habitat	Diurnal forager on boulder-shoreline, nocturnal on reef	Fox and Bellwood (2011)
Mulloway *Argyrosomus japonicus* [fish]	weather	Diurnally active during non-rain conditions, more nocturnal after rainfall	Payne et al. (2015)
Andean cat *Leopardus jacobita*	timing of prey activity	Timing of activity similar to that of main prey mountain vizcacha *Lagidium viscacia*	Lucherini et al. (2009)
Jaguar *Panthera onca*, Puma *Puma concolor*	timing of prey activity	Timing of activity similar to main prey species, Armadillo *Dasypus novemcinctus* and Paca	Harmsen et al. (2011)

Agouti paca respectively

Table 2. Examples of changes to nighttime activity of species as a consequence of anthropogenic opportunities and pressures.

Species	**Anthropogenic change**	**Effect**	**Source**
Black bear *Ursus americanus*	provision of supplementary food sources	Greater nocturnal activity in areas with garbage	Beckmann and Berger (2003)
Southern stingray *Dasyatis americana*	provision of supplementary food sources	Greater diurnal activity in supplementary feeding area	Corcoran et al. (2013)
Bobcat *Lynx rufus*, Coyote *Canis latrans*, and Mule deer *Odocoileus hemionus*	human recreational activity	Greater nocturnal activity by Bobcats in sites with higher human recreation	George and Crooks (2006)
Mediterranean mouflon *Ovis gmelini musimon* x *Ovis* sp.	human recreational activity	Greater nocturnal activity in area with intense tourism	Marchand et al. (2014)
Leopard *Panthera pardus*	human recreational activity	Greater nocturnal activity in presence of tourist activity	Ngoprasert et al. (2017)
Puma *Puma concolor*	hunting	Greater crepuscular and nocturnal activity in areas with less protection from hunting and logging	Paviolo et al. (2009)
Brown bear *Ursus arctos*	hunting	Greater nocturnal activity during hunting season	Ordiz et al. (2012)
Mediterranean mouflon	hunting	Greater nocturnal	Marchand et al. (2014)

Ovis gmelini musimon x *Ovis* sp.		activity in hunted areas	
Audouin's gull *Larus audouinii*	fishing	Greater nocturnal activity when greater nocturnal fishing fleet activity	Oro (1995)
Coral reef fish	fishing	Greater diurnal activity of nocturnal species on predator depleted reefs	McCauley et al. (2012)
African wild dog *Lycaon pictus*	persecution	Greater proportion of hunts under moonlight when human presence and persecution greater	Rasmussen and Macdonald (2011)
Dingo *Canis lupus dingo*	predator control	Less active at dusk and more active before dawn at sites where numbers controlled	Brook et al. (2012)
Eight carnivore species	feral dogs	Greater dusk activity by Ring-tailed mongoose *Galidia elegans* in presence of dogs	Gerber et al. (2012)
10 mammal species	feral dogs	Greater nocturnal activity by mountain tapir *Tapirus pinchaque*, and greater diurnal activity by Andean bear *Tremarctos ornatus* and Little red brocket deer	Zapata-Ríos and Branch (2016)

		Mazama rufina, when dogs present.	
Hainan Eld's deer *Cervus eldi hainanus*	disturbance	Greater nocturnal activity when living amongst villagers	Pan et al. (2011)
European Red deer and North American Elk *Cervus elaphus*	disturbance	Greater nocturnal activity in region with greater human disturbance	Ensing et al. (2014)
Red fox *Vulpes vulpes*	disturbance	Decrease in diurnal activity in areas with higher levels of human disturbance	Díaz-Ruiz et al. (2015)
Collared brown lemur *Eulemur collaris*	disturbance	Decrease in diurnal activity in areas with higher levels of human disturbance	Donati et al. (2015)
12 carnivore species	disturbance	Decrease in diurnal and increase in nocturnal activity by Puma *Puma concolor*, Bobcat *Lynx rufus* and Coyote *Canis latrans* in areas with higher levels of human disturbance	Wang et al. (2015)
Seven bat species	logging	Early night activity reduced in logged compared with control	Castro-Arellano et al. (2009)

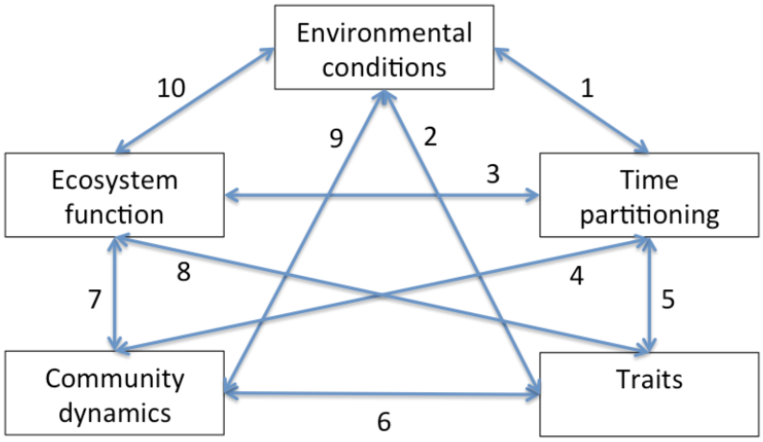
		forest for three species	
Spotted hyena *Crocuta crocuta*	land use	Greater nocturnal activity with increased livestock grazing	Boydston et al. (2003)
Serval *Leptailurus serval*	land use	Greater nocturnal activity on intensively farmed land	Ramesh and Downs (2013)
Japanese sika deer *Cervus nippon*	land use, feral dogs	Greater nocturnal activity with more agricultural land, forestry area, natural grassland, subalpine vegetation and greater dog density	Agetsuma et al. (2016)
White seabream *Diplodus sargus*	habitat creation	Greater nocturnal activity on artificial compared with natural reefs	Koeck et al. (2013)
Santa Rosa beach mouse *Peromyscus polionotus leucocephalus*	introduction of artificial nighttime lighting	Fewer food patches exploited with artificial lighting	Bird et al. (2004)
Common spiny mouse *Acomys cahirinus* and Golden spiny mouse *Acomys russatus*	introduction of artificial nighttime lighting	Nocturnal species decreased activity and foraging with artificial lighting; diurnal species did not respond	Rotics et al. (2011)
15 bat species	introduction of artificial nighttime lighting	Activity in early night of some species influenced by artificial lighting	Lacoeuilhe et al. (2014)

House mouse *Mus musculus*	introduction of artificial nighttime lighting	Activity and foraging reduced by artificial lighting	Farnworth et al. (2016)

Figure 1: The key issues in nighttime ecology highlighted in this paper, and some key questions concerning these and their linkages (see Box 1).

Figure 2: Examples of how levels of nighttime activity by species change with environmental factors. Mulloway *Argyrosomus japonicus* [fish] in southeastern Australia during (a) non-rain period and (b) rain period (acoustic accelerometer data with activity in $m.s^{-2}$; data from Payne et al. 2015); ant *Messor capitattus* in northeastern Spain (number of individuals observed at baits, standardised to the maximum hourly activity recorded) in (c) spring and (d) summer (data from Cros et al. 2016); Short-beaked echidna *Tachyglossus aculeatus* in western Australia (accelerometer data; frequency of activity per hour) in (e) spring and (f) summer (data from Clemente et al. 2016); and Dingo *Canis lupus dingo* in north and central Australia on properties that (g) did not control and (h) did control the species (camera trap data - proportion of records; data from Brook et al. 2012). Time in hours from midnight.

Figure 1



Environmental conditions
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Ecosystem function
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Time partitioning
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Community dynamics
Traits
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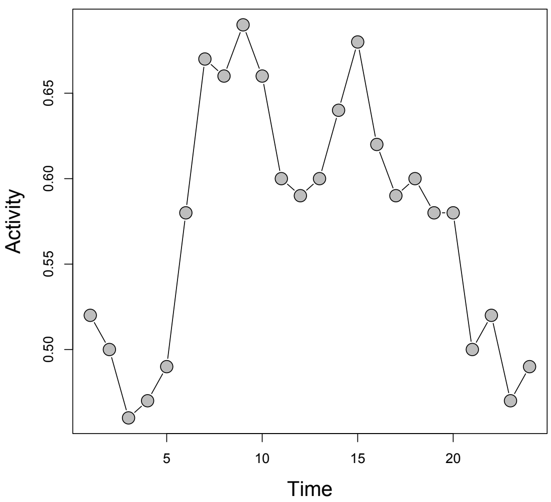
Figure 2

(a)



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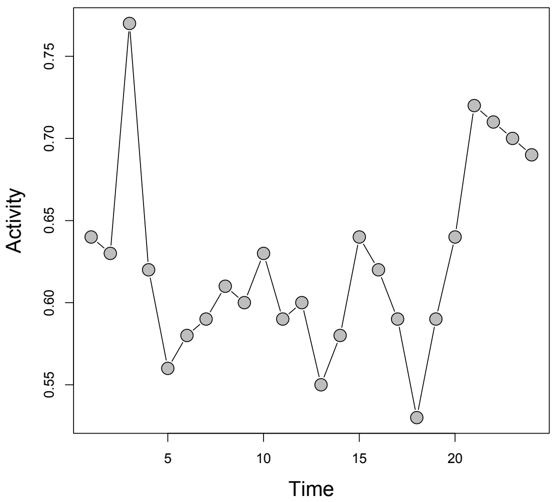

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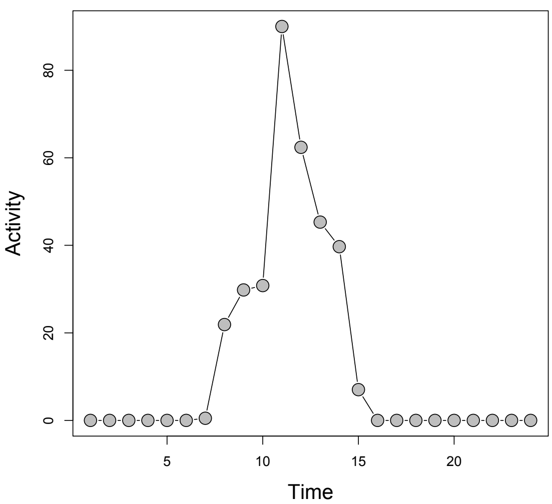

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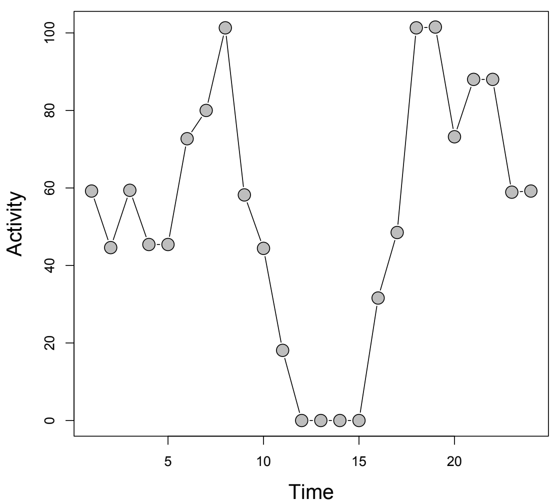

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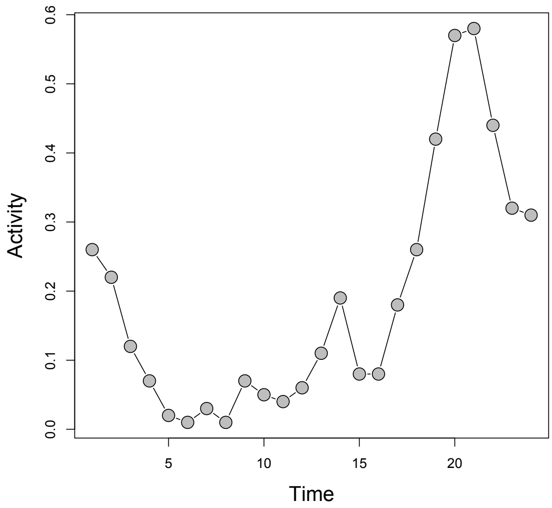
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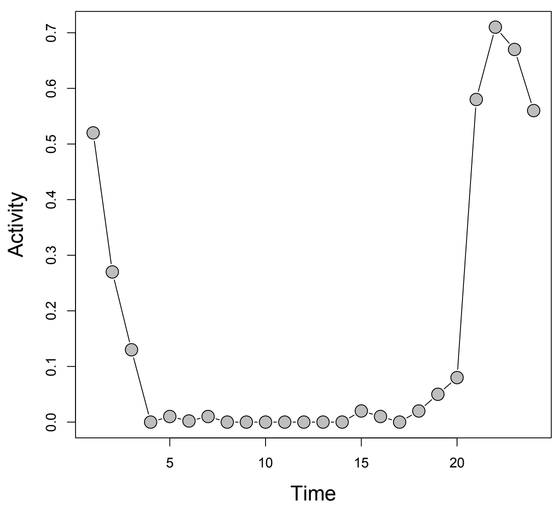
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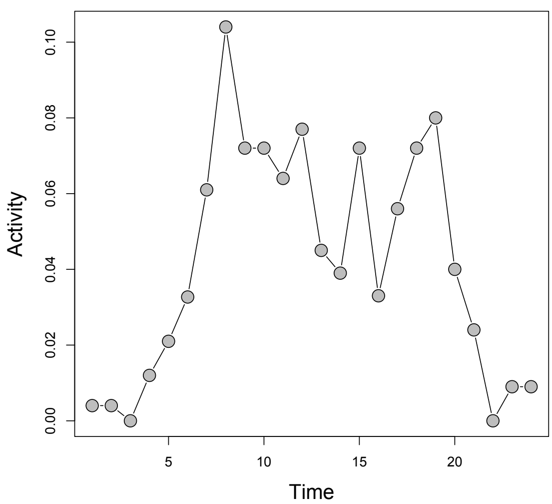
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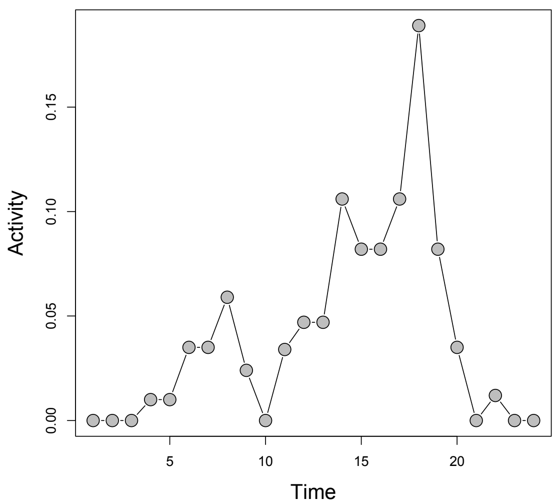
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