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PARTITIONING OF TIME AS AN ECOLOGICAL RESOURCE

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■ **Abstract** Animal species have evolved different diel activity rhythms that are of adaptive value. Theory suggests that diel temporal partitioning may facilitate coexistence between competitors and between predators and prey. However, relatively few studies demonstrate a temporal shift that is predation- or competition-induced. Recorded shifts are usually within the preferred activity phase of animal species (day or night), although there are some inversions to the opposite phase cycle. Temporal partitioning is not perceived as a common mechanism of coexistence. This rarity has been variously ascribed to theoretical considerations and to the rigidity of time-keeping mechanisms, as well as to other physiological and anatomical traits that may constrain activity patterns. Our decade-long study of spiny mice of rocky deserts demonstrates that, while different factors select for activity patterns, endogenous rhythmicity may be an evolutionary constraint.

INTRODUCTION

Different animal species are active during different parts of the diel cycle. Activity patterns have evolved to cope with the time structure of the environment, which changes with a 24 h periodicity (e.g., Daan 1981). These different activity patterns may have ecological implications and evolutionary significance, as well as physiological ramifications. Insight into the interplay between selective forces and evolutionary constraints at these different levels is crucial for understanding the evolution of activity patterns. The selective forces and constraints affecting evolution of activity patterns underlie the partitioning of time as a resource.

How time mediates ecological interactions and shapes the structure of ecological communities is still poorly understood (Jaksic 1982, Schoener 1986, Wiens et al. 1986). Theory postulates that temporal partitioning among competitors and between predators and their prey may promote coexistence in ecological communities (e.g., Schoener 1974a, Richards 2002, Wiens et al.1986). Although the role of temporal partitioning in structuring communities has never been a strong focus of ecology, over the years a number of studies have accumulated that attach

ecological significance to activity patterns (e.g., Kenagy 1973, Kunz 1973), as well as studies that record competition- or predation-induced shifts in activity patterns (e.g., Alanara et al. 2001, Fenn & MacDonald 1995).

On the other hand, much physiological, biochemical, and molecular research focuses on the evolution and maintenance of rhythms in activity, physiology, hormone concentrations, biochemistry, and behavior in animals (e.g., De Coursey et al. 1997, Gerkema 1992, Heldmaier et al. 1989, Horton 2001, Refinetti et al. 1992, Turek & Takahashi 2001). These circadian rhythms allow an animal to anticipate environmental changes and to choose the right time for a given response or activity (Aronson et al. 1993). The past decade has seen a surge of research into the nature of circadian rhythms, and, in particular, into mechanisms regulating them. In fact, in 1998 *Science* magazine listed breakthroughs in understanding diel rhythmicity among discoveries transforming our ideas about nature (*Science* Dec. 18:1998:2157–61). Mechanisms regulating circadian rhythmicity may affect the plasticity of response to ecological selective forces and hence the potential for evolving temporal partitioning among animal species.

Our goal here is to review the literature on the ecological significance of temporal partitioning and the physiological literature on the evolution and maintenance of activity rhythms. We aim to gain insight into the ecological significance of temporal activity patterns in light of the physiological literature, and to relate patterns to physiological, morphological, and behavioral adaptations to different activity phases. A close look at the interface between different scientific approaches and disciplines may yield insight into the evolutionary forces and evolutionary constraints at play. We also review a unique case of temporal partitioning among competing rocky desert rodents and point to general inferences that can be drawn from this system.

THE THEORETICAL USE OF TEMPORAL PARTITIONING AT THE DIEL SCALE

The time niche-axis may facilitate niche partitioning between co-occurring organisms. Different diel activity patterns may imply different use of resources or different levels of susceptibility to predation.

Among Competitors

Ecological theory has long considered niche differentiation in heterogeneous environments as a major mechanism of coexistence among competitors (e.g., MacArthur 1958, MacArthur & Levins 1967). Ecological separation is usually considered to involve habitat, food resources, and time axes, or a combination of them. In recent years a growing number of studies have suggested trade-offs in foraging ecology as a mechanism of coexistence (e.g., Brown 1996, Ziv et al. 1993).

Temporal partitioning on the diel scale may facilitate coexistence through avoidance of direct confrontation (interference competition) or through the reduction of

resource overlap (resource competition). Temporal partitioning is a viable mechanism for reducing resource competition under either of the following conditions:

- If the shared limiting resources differ between activity times, particularly for predatory species whose prey populations have activity patterns (Schoener 1974a; but see Palomares & Caro 1999); or
- If the limiting resources are renewed within the time involved in the separation (MacArthur & Levins 1967).

A theoretical model suggests that fairly severe resource depletion must occur before it is optimal to cease feeding in a patch frequented by competitors (Schoener 1974b). Based on this model, Carothers & Jaksic (1984) argued that interference competition must be more prevalent than resource competition in driving temporal partitioning. Interference competition and resource competition are not mutually exclusive, however: Temporal partitioning may be generated by interference and yet act to reduce resource overlap, or vice versa (Kronfeld-Schor & Dayan 1999).

Richards (2002) developed a theoretical model to investigate the conditions necessary for temporal partitioning to be an evolutionarily stable strategy. The model highlights how the optimal foraging decision of an individual may depend strongly on the state of the individual and also that of its competitor (Richards 2002).

In Predator-Prey Systems

Some times are more dangerous for activity than others owing to temporal variation in predator activity and predation risk (Lima & Dill 1990). A decrease in activity as well as inactivity in a refuge lower an animal's risk of predation by lowering chances of detection and the probability of encounter (Lima 1998, Skelly 1994, Werner & Anholt 1993). Because many animals experience predictable daily fluctuations in predation risk, they may evolve activity patterns that minimize mortality risks while maximizing foraging. Therefore, it has been suggested that temporal partitioning between predators and their prey at the diel scale may evolve as a mechanism of coexistence (Stiling 1999).

TEMPORAL PARTITIONING IN NATURE

Temporal Partitioning Between Potentially Competing Taxa

Differing activity patterns of sympatric species have been viewed as ways to reduce interspecific resource and interference competition (Johnston & Zucker 1983). Many studies describe different diel activity patterns of potential competitors, many of which date to a time when patterns in ecological communities were not tested (Table 1). A study of four *Acacia* species in a highly seasonal savannah habitat in Tanzania stands out in this respect. Between dawn and dusk, pollen availability maxima (peaks of pollen release) were more regularly spaced than would be predicted by chance alone (Stone et al. 1996). Moreover, the summed

TABLE 1 Temporal partitioning between potentially competing taxa

Species	Observation	Reference
Sympatric congeneric lizards (*Ctenotus*)	The time niche axis is one of three on which these lizards subdivide environment and resources*	Pianka 1969
Great Basin kangaroo rats (*Dipodomys microps*), Merriam's kangaroo rats (*D. merriami*), little pocket mouse, (*Perognathus longimemberis*)	Aggressive interactions with *D. microps* drive *D. merriami* away, and this interaction reduces competition between *D. merriami* and *P. longimemberis*	Kenagy 1973
Twelve species of nocturnal rodents	Differences in time of daily activity between potential competitors	O'Farrell 1974
Hispid cotton rat (*Sigmodon hispidus*), fulvous harvest mouse (*Reithrodontomys fulvescens*)	Temporally partitioned in the Coastal Texas Prairie	Cameron et al. 1979
13 individual cotton rats in captivity	Interpreted as a means for reducing intraspecific competition	Johnston & Zucker 1983
California mouse (*Peromyscus californicus*), cactus mouse (*P. eremicus*), bannertail kangaroo rat (*Dipodomys spectabilis*), Fresno kangaroo rat (*D. nitratoides*)	Differences in response to lunar cycle may reflect temporal segregation among competitors	Lockard & Owings 1974, Owings & Lockard 1971
Cheetahs (*Acinonyx jubatus*), lions (*Felis leo*), spotted hyenas (*Crocuta crocuta*)	The activity pattern of cheetahs reduces kleptoparasitism and interference from lions and spotted hyenas	Mills & Biggs 1993, Palomares & Caro 1999, Schaller 1972
Bat communities	Interspecific differences in onset of activity and species-specific differences in activity times among bat species	Kunz 1973 and references therein
Different species of African dung beetles	Different species emerge from the soil at characteristic times of the day to fly and colonize freshly deposited dung of mammalian herbivores	Caveney et al. 1995

*While ecototherms may reduce food overlap by being active at different times, they may simply be choosing activity periods when their own metabolic performance is "optimal" (Huey & Pianka 1983), so that temporal partitioning of prey may be only an epiphenomenon (Carothers 1983).

activity of pollinators at each *Acacia* species clearly followed the temporal separation between species in pollen release, so the ecological consequences of temporal partitioning have actually been demonstrated.

The interest in the role of competition in evolution and in structuring communities also bears on scientific understanding of the evolution of activity patterns at broad taxonomic scales. For example, Wiens et al. (1986) suggested that mammals were restricted to nocturnal activity because of the largely diurnal activity patterns of dinosaurs, or that flying foxes (*Pteropus*) are constrained to nocturnality by competition with avian and mammalian frugivores. Testing evolutionary-scale patterns is difficult, sometimes impossible, particularly for extinct taxa. However, resource overlap and its partitioning can be studied among temporally partitioned extant taxa, although this has rarely been attempted.

It has often been suggested that raptors reduce competition by differing in activity time (reviewed by Jaksic 1982). Jaksic (1982) and Jaksic et al. (1981) found a high degree of overlap between prey of owls and diurnal raptors and suggested that owls evolved nocturnality in response to interspecific interference (Carothers & Jaksic 1984; Jaksic 1982; but see Simberloff & Dayan 1991). Huey & Pianka (1983), however, found that dietary overlap tended to be lower than expected among pairs of nocturnal and diurnal desert lizards with nonsynchronous activity.

In sum, only in a few cases is there statistical evidence for the occurrence of a meaningful pattern (Stone et al. 1996), or a strong resource-based test of the efficacy of temporal partitioning (Huey & Pianka 1983, Stone et al. 1996). Other studies have failed to demonstrate temporal partitioning or to establish ecological significance relating to interspecific competition (e.g., Cameron et al. 1979, Gabor et al. 2001, Kasoma 2000, Saiful et al. 2001, Saunders & Barclay 1992). However, it would be impossible to assess the prevalence of partitioning on the diel time axis on the basis of current evidence.

Temporal Partitioning Between Predators and Prey

Activity patterns of predators and their prey affect the level of predation risk. It has been suggested that, at the macroevolutionary scale, predator activity patterns track those of their prey. For example, around the Jurassic, insects evolved a waxy epicuticle that enabled them to become day-active; this probably set the stage for an evolutionary boom in diurnal reptiles (Daan 1981).

The bimodal activity pattern of three sympatric species of squirrels in Peninsular Malaysia was interpreted as a means to reduce predation by diurnal raptors that require good light and felids that are not active at these times (Saiful et al. 2001).

Greylag geese (*Anser anser*) on a Danish island responded more strongly to predator-like stimuli (overflying herons and helicopters) during moult when they are flightless, although real predators were absent, and foraged at night, possibly because such stimuli were lowest at night (Kahlert et al. 1996). Before moulting geese remained on the feeding grounds throughout the 24 h.

Fruit bats are active by day and at night on some small, species-poor Pacific islands such as Fiji. Wiens et al. (1986) suggested that they are constrained

elsewhere to fly only at night by the presence of predatory diurnal eagles. Although bats are nocturnal, many species emerge from roosts to forage during twilight. Field research on foraging by a maternity colony of Schneider's leafnosed bats (*Hipposideros speoris*) in Sri Lanka suggested that bats captured large numbers of insects that were only available or had marked peaks in abundance during twilight (Pavey et al. 2001).

To test the theory that insectivorous bats have selected for diurnality in earless butterflies, Fullard (2000) compared nocturnal flight patterns of three species of nymphalid butterflies on the bat-free Pacific island of Moorea with those of three nymphalids in the bat-inhabited habitat of Queensland, Australia. No differences were found, however. Fullard (2000) concluded that physiological adaptations constrain the butterflies to diurnal flight. Also, although predation is a very serious threat to microtine rodents (e.g., Jacobs & Brown 2000), studies of their activity patterns suggest that they did not evolve as a means of preventing predator temporal specialization (Halle 1993, Reynolds & Gorman 1994).

In sum, few descriptive studies actually deal with depicting differences in activity patterns between predators and their prey, perhaps because the significance of such separation is perceived as trivial. The scarcity of such studies may also stem from the fact that, during the heydey of descriptive studies of niche partitioning in ecological communities, the focus was on how potential competitors coexist, rather than on predators and their prey.

TEMPORAL SHIFTS IN ECOLOGICAL TIME

Experimental results are the most compelling type of evidence that can be generated in order to test whether differences in activity patterns can actually evolve as a mechanism for coexistence.

Temporal Shifts of Competitors

In the sandy habitats of the western Negev desert of Israel there coexist two species that partition activity times, with *Gerbillus pyramidum* active during the early hours of the night and *G. allenbyi* active during later hours of the night. Upon removal of *G. pyramidum*, the smaller *G. allenbyi* shifted its activity to the earlier hours of the night, suggesting that coexistence between the two species is due to a trade-off between the foraging efficiency of *G. allenbyi* and the dominance of *G. pyramidum* (Ziv et al. 1993). The shared limiting resources, seeds, are renewed daily by afternoon winds redistributing and exposing buried seeds (e.g., Kotler & Brown 1990).

The cue for a temporal shift may be aggressive interference but may also be resource level. Lockard (1978) found that, when food resources were low, bannertail kangaroo rats (*Dipodomys spectabilis*) not only were active under full moonlight but also showed sporadic diurnal activity.

Nectar is renewed within the diel cycle (e.g., Cotton 1998, Craig & Douglas 1984) suggesting that temporal partitioning may facilitate coexistence between nectarivorous species. Cotton (1998) found a hierarchy of dominance over resources between four territorial hummingbird species that is body-size related, with larger species foraging in richer patches. Cotton (1998) suggested that the small body size of some of the species enables them to exploit marginal resources that would not be profitable for individuals of the larger species. In New Zealand bellbirds (*Athornys melanura*), dominant individuals forage in the morning when nectar availability peaks, while subordinate males and females forage in the afternoons, with lower rewards, suggesting intraspecific temporal partitioning (Craig & Douglas 1984).

Arjo & Pletscher (1999) documented interference competition between coyotes and recolonizing wolves in Montana, with records of wolves killing coyotes, and found increased temporal partitioning and changes in coyote behavior after wolf recolonization, in particular in winter (Arjo & Pletscher 1999).

In brown trout (*Salmo trutta*), individuals differ in their daily activity patterns, with dominant individuals feeding mainly at the most beneficial times of dusk and the early part of the night, while more subordinate fish feed at other times (Alanara et al. 2001, Bachmann 1984, Giroux et al. 2000). Moreover, the degree of overlap in foraging times between high-ranking fish depended on energetic demands related to water temperatures. However, predation risk influenced choice of foraging times by dominant individuals, so temporal activity patterns may result from a complex trade-off between ease of access to those resources and diel variation in foraging risk (Alanara et al. 2001).

Temporal Shifts of Predators and Their Prey

Much literature documents how predation risk affects animal activity levels. Predation risk can limit prey activity time. For example, presence of diurnal predatory fish limits activity of large mayfly larvae (*Baetis tricaudatus*), otherwise aperiodic or weakly diurnal, to the night (Culp & Scrimgeour 1993). Hermit crabs (in particular *Coenobita rugosus* and *C. cavipes*) respond to human-induced disturbances in Mozambique mangroves by changing from a 24-h activity cycle to a nocturnal one (Barnes 2001). A diametrically opposite pattern obtains for bank voles (*Clethrionomys glareolus*), which were inactive at night and exhibited a peak of activity at dawn, but in presence of a weasel (*Mustela nivalis*) shifted to being active during both the day and night (Jedrzejewska & Jedrzejewski 1990).

Actual shifts to a different activity pattern are not common (Lima & Dill 1990), but some cases have been reported. Fenn & MacDonald (1995) discovered a population of commensal Norway rats (*Rattus norvegicus*), some members of which were conspicuously diurnal. An experiment revealed that rats shifted to diurnal activity in an area heavily populated by foxes (*Vulpes vulpes*), while in nearby experimental fox-free enclosures, they reverted to nocturnal activity.

Nocturnal Patagonian leaf-eared mice (*Phyllotis xanthophygus*) decreased their activity under high illumination and increased the number of diurnal activity bouts,

probably as compensation for reduced foraging (Kramer & Birney 2001). Daly et al. (1992) previously reported a similar pattern of increased crepuscular activity of Merriam's kangaroo rats (*Dipodomys merriami*) in response to full moonlight.

Pheidole titanis, ants that occur in desert and deciduous thorn forest in the southwestern United States and western Mexico, prey on termites during the day in the dry season. During the wet season these ants prey on termites at night, shifting their activity because of a specialist parasitoid fly diurnally active during this season (Feener 1988).

A similar pattern occurs in leaf-cutter ants (*Atta cephalotes*) at the tropical premontane wet forest at Parque Nacional Corcovado in Costa Rica (Orr 1992). These ants shift from nocturnal to diurnal activity in the presence of a diurnal parasitoid fly (*Neodohrniphora curvinervis*) (Orr 1992). In the presence of the parasitoid, daytime foraging ants were below the optimal size for foraging efficiency, but also smaller than the minimum size on which *N. curvinervis* will oviposit; nocturnal foragers were larger and within the optimal size range for foraging efficiency (Orr 1992).

Species that can be either nocturnal or diurnal can be used to test whether diel activity patterns respond to variations in predation pressure (Metcalfe et al. 1999). Many fishes can change their activity pattern from nocturnal to diurnal and vice versa, usually on a seasonal basis (Sanchez-Vazquez et al. 1996, Yokota & Oishi 1992). Changes in phasing related to variations in light intensity (Beers & Culp 1990), water temperature (Fraser et al. 1993), social effects (Anras et al. 1997), and nutritional status (Metcalfe & Steele 2001), have been reported. The flexibility in phasing can be an adaptive response to a relatively stable aquatic environment subjected to periodic changes in some biotic factors such as food availability or absence of predators (Sanchez-Vazquez et al. 1996). However, this flexibility in phasing may entail a cost in growth (Baras 2000) and in foraging efficiency (reviewed by Fraser & Metcalfe 1997).

Juvenile Atlantic salmon (*Salmo salar*) exhibit a temperature-dependent shift in the balance of diel activity: At higher temperatures they are found in foraging locations throughout both day and night but acquire most of their food by day when light enables them to forage more efficiently, but they are at greater risk of predation (Fraser & Metcalfe 1997). As temperatures drop they increasingly seek refuge during the day in crevices and emerge at night (Metcalfe et al. 1999). Higher temperatures imply greater energetic requirements, hence the diurnal activity at higher temperatures and more temperate zones. Increased food levels enabled juvenile salmon to minimize their exposure to predators by preferentially reducing daytime (in contrast to nighttime) activity (Metcalfe et al. 1999).

Moreover, the daily timing of activity in juvenile Atlantic salmon is related to the life-history strategy that they have adopted and their current state (body size/relative nutritional state). Salmon preparing to migrate to the sea, which would experience size-dependent mortality during migration, were more diurnal than fish of the same age and size that were delaying migration for a year (Metcalfe et al. 1998).

Dominant brown trout (*Salmo trutta*) preferred to forage during hours that are thought to minimize the predation risk incurred per unit of food obtained (Metcalfe et al. 1999). Thus risk of predation governs not only the activity patterns of dominant individuals, but also those of lower-ranking individuals that they displace (Alanara et al. 2001).

Experimental release from predation risk is a strong test of the significance of predation on modulating activity patterns. The longnose dase (*Rhinichthys cataractae*) is one of the few nocturnal minnow species. Its nocturnal activity pattern is constrained by the risk of predation by diurnally or crepuscularly active predators (Culp 1988). After several months in the laboratory, these fish are asynchronous to each other in their activity pattern with many individuals active during daylight (Culp 1988). Like its nocturnal congeners, the longnose dace have significantly increased encounter rates and reactive distance and significantly decreased search time under twilight conditions compared to starlight (Beers & Culp 1990), so this nocturnal activity clearly has a fitness cost (Calow 1985).

Another interesting case is the diel periodicity of downstream drift of stream invertebrates (Muller 1974). In many invertebrate taxa and among some fishes, drift numbers are low during the day followed by dramatic increases at night (Flecker 1992), a pattern interpreted as an evolutionary response to minimize predation risk by visually hunting fishes. Prey size classes with the greatest risk of predation by size-selective predators exhibit the greatest propensity for nighttime drift (e.g., Allan 1984). A study of mayflies in a series of Andean mountain and piedmont streams revealed that mayfly activity was arrhythmic in fishless streams. A correlation was found between level of predation risk (number of predatory species and their abundance) and propensity toward nocturnal activity (Flecker 1992). Experimental exclusion of fish did not change the nocturnal drift pattern, suggesting that nocturnal activity has evolved as a fixed behavioral response to predation; apparently, this behavior can evolve rapidly because, in formerly fishless streams where trout (*Oncorhynchus mykiss* and *Salvelinus fontinalis*) were introduced, nocturnal peaks in drift were observed for the mayfly *Baetis* (Flecker 1992).

In New Zealand, native common river galaxias (*Galaxias vulgaris*) were replaced in many streams by introduced brown trout (McIntosh & Townsend 1995) that present a higher predation risk to *Deleatidium* mayfly nymphs during the day than at night, while common river galaxias present a similar risk throughout the diel cycle. Mayfly nymphs fed significantly more during the night in streams with introduced brown trout than in streams with native galaxias, a difference that reflects the diel variation in predation risk imposed by the fish (McIntosh & Townsend 1995).

It has been argued that prey activity influences the activity patterns of their predators (e.g., Halle 1993). Zielinski (1988) studied the influence of daily restricted feeding in foraging mustelids, and discovered that while activity of six (of seven) animals shifted in response to modified foraging cost, this shift mostly meant an expansion of foraging period. In only two individuals, both of them mink (*Mustela vison*), was there an increase in activity in the nonpreferred part of the diel cycle (Zielinski 1988).

On the Relative Rarity of Temporal Partitioning at the Diel Scale

Schoener (1974a), reviewing resource partitioning in ecological communities, found temporal partitioning to be significantly less common than habitat or food type partitioning. He argued that "in deciding to omit certain time periods, the consumer is usually trading something—a lowered but positive yield in the time period frequented by competitors—for nothing, no yield at all" (p. 33). Schoener (1974b) developed a theoretical model that predicts that temporal resource partitioning at the diel scale should be relatively rare, requiring severe depletion of resources before it is no longer optimal to feed in a period frequented by competitors.

An alternative hypothesis was presented by Daan (1981), who suggested that diurnal and nocturnal activity require different evolutionary adaptations and therefore closely related species, prime candidates for competition, are usually active during the same part of the diel cycle.

This hypothesis implies that animal species are evolutionarily constrained in their activity patterns (Daan 1981; Kronfeld-Schor et al. 2001a,b,c; Roll & Dayan 2002) and that the plasticity assumed by Schoener (1974a) in adapting to ecological settings is limited. In fact, zoologists recognize that different species tend to have taxon-specific activity patterns. For example, most birds are diurnally active, while most terrestrial amphibians are nocturnal (Daan 1981). A recent quantitative study reveals a strong relationship between between phylogeny (using taxonomic status as a surrogate) and activity patterns in rodents (Roll & Dayan 2002).

These patterns are also in accord with the fact that many recorded shifts in activity times or perceived patterns of temporal partitioning are contained within the preferred part of the diel cycle, whether day or night, although these are detectable only by detailed scientific research. This is in spite of the fact that temporal segregation within the preferred activity phase limits foraging times and hence energy intake of the competing species (see Schoener 1974a). The behavioral response of prey to predation risk is also more commonly manifested in a restriction, rather than shift, of activity times. Actual inversion of activity patterns is not commonly described, although such gross differences in activity patterns (day or night) can be easily discerned. It could be argued that temporal partitioning evolved in response to competitive pressures, but activity patterns may have since become "fixed" and are no longer amenable to manipulation ("ghost of competition past").

Little such general discussion of the potential use of temporal partitioning between predators and their prey is found in the ecological literature, although some authors have raised this issue regarding specific cases (e.g., Flecker 1992, Fullard 2000). For example, Flecker (1992) suggested that some antipredatory behaviors may become "fixed" or "hard-wired," presumably where there is a "prohibitively expensive cost" in assessing risk, meaning a high probability of mortality (Sih 1987). Thus, the general question raised regarding competitors is also relevant to predators and their prey. Specifically, the issue is what is the degree of flexibility of the adaptations to different activity patterns. Are ecological- and

evolutionary-level plasticity in the adaptations to activity patterns limited, and hence do they limit the use of the time axis in ecological separation?

In order to explore this issue, we review the literature on adaptations to diurnal and nocturnal activity, in particular that which relates to the evolution and maintenance of diel rhythmicity in animal species.

ADAPTATIONS TO NOCTURNAL AND DIURNAL ACTIVITY

Being active during night or day exposes animals to different challenges; meeting them requires different anatomical, physiological, and behavioral adaptations. For example, environmental conditions affect the activity of animal species, and may even drive them to invert their activity patterns. The bat-eared fox (*Otocyon megalotis*) of the South African deserts forages nightly in the summer when mid-day soil temperatures reach 70°C and diurnally in the winter when night air temperatures drop to −10°C (Lourens & Nel 1990). Desert seed-harvesting ants forage during the day in winter but avoid the heat of summer by foraging crepuscularly, nocturnally, or on cloudy days (Whitford et al. 1981).

Diurnal animals usually use vision for predation and visual pecking, while nocturnal animals use tactile probing, smell, and hearing. Communication is usually vocal and aromatic in nocturnal animals (and also, although rarely, luminescent). Nocturnal animals use camouflage for concealment from their diurnal predators during the day (e.g., moths and owls); diurnal animals use visual signals, e.g., aposematic coloration (Daan 1981).

Retinas of nocturnal and diurnal mammals differ in their photoreceptors; adaptations to vision at a given light level tend to reduce efficiency of activity at other times (Jacobs 1993, Van Schaik & Griffiths 1996). For example, wild-caught antelope ground squirrels (*Ammospermophilus leucurus*) deprived of their suprachiasmatic nuclei [SCN, where the master circadian clock is located (Moore & Eichler 1972, Stephan & Zucker 1972)] behaved normally but became arrhythmic, enabling nocturnal Mojave Desert predators such as rattlesnakes, kit foxes, bobcats, coyotes, and barn owls to take advantage of their limited visual acuity at night and prey upon them (DeCoursey et al. 1997).

In sum, complex adaptations have evolved to accompany diurnal and nocturnal ways of life. Because of the major differences between night and day, particularly in light levels and ambient temperatures (Daan 1981), adaptations to a nocturnal way of life may differ dramatically from those for diurnal activity, and adaptations to a certain mode of activity may be deleterious for another.

DIEL RHYTHMS AND THEIR RELEVANCE TO ECOLOGY

An animal's behavior and physiology result from an integration between its endogenous circadian rhythms generated by an internal clock, direct response to environmental stimuli that mask the expression of the endogenous circadian rhythm

independently from the pacemaker, and the influence of the environment on its endogenous circadian clock (entrainment).

The Adaptive Value of Circadian Rhythms

Circadian rhythms allow animals to anticipate environmental changes: Physiological parameters such as body temperature, enzymatic activity, sensitivity of photoreceptors, and storage or mobilization of energy reserves have to be adjusted before the expected environmental changes actually take place. Furthermore, behavioral timing in feeding, reproduction, migration, etc., often precedes the external events (Gerkema 1992). It also allows the animal to choose the right time for a given response or activity without being easily misled by minor environmental disturbances (Aronson et al. 1993), thus contributing to their fitness (Bennet 1987, Daan & Aschoff 1982, Horton 2001).

The internal clock also ensures that internal changes (biochemical and physiological) are coordinated with one another (Horton 2001, Moore-Ede & Sulzman 1981, Turek & Takahashi 2001). In humans under circumstances where social and working routines are disrupted, such as shift-work and jet-lag, the clock may receive photic and nonphotic cues that potentially conflict, leading to circadian dysfunction and poor performance (e.g., Turek & Takahashi 2001).

One way to demonstrate that a character is adaptive is to look for loss or relaxation of this trait in environments lacking diel rhythmicity, where it has no apparent advantage (Horton 2001,Willmer et al. 2000). Subterranean mole rats (*Spalax ehrenbergi*) that live in constant darkness are predominantly diurnal during winter and predominantly nocturnal during summer (Kushnirov et al. 1998). Brazilian cave catfishes (*Pimelodella kronei*, *P. transitoria*, and *Trichomycterus* sp.) showed some degree of rhythmicity (circadian, ultradian, and/or infradian) (Trajano & MennaBarreto 1995, 1996). Most cave-dwelling millipedes (*Glyphiulus cavernicplu sulu*, Cambalidae, Spirostreptida) that occupy the deeper recesses of a cave show circadian rhythmicity (Koilraj et al. 2000). The hypogean loach (*Nemacheilus evezard)*, shows a circadian rhythm of body temperature, with individually varying periods (Pati 2001). Other species, such as the European blind cave salamander (*Proteus anguinus*), have lost their circadian rhythmicity (Hervant et al. 2000). It has been hypothesized that the retention of some rhythmic component reflects the importance of maintaining internal temporal order or the ability to measure seasonal changes in photoperiod (Goldman et al. 1997, Horton 2001).

Plasticity of Diel Rhythms (Laboratory Experiments)

Under constant laboratory conditions, the period of circadian rhythms is usually in the range of 24 h. This fact implies that changes in the physical environment must synchronize or entrain the internal clock system regulating circadian rhythms. In order for the internal timing mechanism to be adaptive, the internal clock should respond to highly predictive environmental cues and not to less predictive ones (Daan & Aschoff 2001).

One of the most important and predictable cues in the environment is the day/night cycle, which allows the development of relatively rigid internal circadian programming of behavior and physiology as an adaptive strategy. The endogenous circadian rhythm is an intrinsic and relatively inflexible component of the organism's physiology and behavior that is common to the species (Daan 1981). At the individual level, this internal component is adjusted to its specific environment based on individual experience with the temporal organization of the environment: Events related to food availability, territory, predation, inter- and intraspecific competition, and temperature affect behavior over the course of the day. Thus, the overt activity rhythms result from the output of the endogenous clock, a direct response to environmental stimuli, and the influence of the environment on the endogenous clock.

The effect of nonphotic stimuli on activity patterns of animals is of special significance to the evolution of temporal partitioning in communities. The ability to respond to nonphotic cues is what provides animal species with some flexibility to respond at the ecological timescale to competition or to predation pressures by shifting diel rhythms.

In the absence of the light-dark cycle (in constant light or dark), nonphotic stimuli such as activity, wheel running, food availability, and social stimuli, can entrain the endogenous circadian clock located in the SCN (e.g., Mistlberger 1991, Mrosovsky 1988) or mask the endogenous circadian system (e.g., Eckert et al. 1986, Gattermann & Weinandy 1997, Refinetti et al. 1992). Masking (Aschoff 1960) is defined as "any process that distorts the original output from the internal clock whether this originates from inside or outside the body" (Minors & Waterhouse 1989). As soon as the masking effect is removed, the underlying circadian rhythm is revealed (Waterhouse et al. 1996).

Under field conditions, light-dark cycles are present for most species. When both light and a nonphotic stimuli are presented, the nonphotic stimulus may be confronted by photic input, so that the perceived shift is a masking effect (Gattermann & Weinandy 1997, Refinetti 1999, Refinetti et al. 1992) or downstream to the clock (Kas & Edgar 1999). Alternatively, it may be blocked by the photic stimulus (Honardo & Mrosovsky 1991, Maywood & Mrosovsky 2001). In any of these cases, the effect of the nonphotic stimulus will disappear when the stimulus is ended (e.g., Blanchong et al. 1999, Kas & Edgar 1999, Kronfeld-Schor et al. 2001a) and will not cause a phase-shift of the circadian system.

A molecular mechanism involving clock gene expression for the interaction between photic and nonphotic circadian clock resetting stimuli was recently suggested. The sensitivity of the circadian pacemaker to light and nonphotic stimuli is phase-dependent. Light causes a phase shift only when given during the subjective night, while nonphotic stimulus causes a phase shift when given during the subjective day (e.g., Hut et al. 1999). Maywood & Mrosovsky (2001) showed in the laboratory that at any phase of the cycle, light and nonphotic stimuli have convergent but opposite effects on the circadian clock gene expression.

According to their model, under natural conditions, the animal is exposed to light only during the day, and any phase shift that may have been caused by a nonphotic stimulus will be blocked by the light stimulus. During the night animals in their natural habitats are not normally exposed to light, and nonphotic stimulus is not expected to cause a phase shift during the night in the absence of light. Interactions between light and nonphotic stimuli that fit this model were reported in several laboratory experiments (e.g., Mistlberger & Antle 1998, Mistlberger & Holmes 1999, Mrosovsky 1991, Ralph & Mrosovsky 1992, Weber & Rea, 1997).

The mechanisms determining diurnal, nocturnal, or crepuscular activity are still unknown (Kas & Edgar 1999, Novak et al. 1999). The internal clock, located in the SCN, is necessary and sufficient for the generation of mammalian circadian rhythms (Moore & Eichler 1972, Stephan & Zucker 1972), but the neuronal and metabolic activity within the SCN and the response to light (Inouye & Kawamura 1979, Sato & Kawamura 1984, Schwartz et al. 1983), and the clock gene expression (Novak et al. 2000, Mrosovsky et al. 2001) are similar in nocturnal and diurnal species, indicating that the center managing activity is located downstream from the core pacemaker.

Unstriped Nile rats (*Arvicanthis niloticus*) in the laboratory show a diurnal rhythm (Blanchong et al. 1999). However, introducing a running wheel to their cage induces an abrupt dramatic change in the basic pattern of activity within one day to a more nocturnal one (Blanchong et al. 1999). A similar effect of a running wheel was described for the diurnal *Octodon degus* (Kas & Edgar 1999), which inverted its activity rhythm in 24 to 48 h (Stevenson et al. 1968). An abrupt change in activity rhythms was also described in cotton rats (*Sigmodon hispidus*), where a variety of distinctly different patterns coexist, and individuals frequently switch from one kind of pattern to another (Johnston & Zucker 1983). Such an abrupt shift without evidence of phase transients (progressive changes in rhythm phase during the course of a phase shift, Kas & Edgar 1999) typical to the process of entrainment suggests that the mechanisms determining the overt diurnal or nocturnal activity rhythm in these species are separate from phase control mechanisms within the circadian pacemaker and that nonphotic stimuli can modulate the mechanisms that determine phase preference (Kas & Edgar 1999). Phase relation of *Fos* expression in the ventrolateral preoptic area (which appears to be the site that integrates circadian and homeostatic signals that influence the sleep-wake cycle) and that of the SCN differ between diurnal and nocturnal rodents exposed to the light-dark cycle, and this fact raises the possibility that the functional outcome of SCN inputs to the ventrolateral preoptic area differs in these two groups of animals, reflecting their activity patterns (Novak et al. 1999).

In nocturnal animals the internal clock period is shorter than 24 h, while in diurnal animals it is longer. Exposure to constant light lengthens and shortens the period of the internal clock of nocturnal and diurnal species, respectively. It was speculated that, as day length changes seasonally, these differences allow

diurnal animals to track dawn whereas nocturnal animals track dusk (Pittendrigh & Daan 1976). Several species of rodents expressing shifts from nocturnal to diurnal activity and vice versa have a longer circadian period under constant light conditions than under constant dark, typical of nocturnal animals, even when they are diurnally active [*Arvicanthis ansorgi* (Challet et al. 2002), *Octodon degus* (Lee & Labyak 1997), *Arvicanthis niloticus* (Katona & Smale 1997)]. This fact further supports the hypothesis that the mechanisms determining the overt diurnal or nocturnal activity rhythm in these species are separate from phase control mechanisms within the circadian pacemaker.

Food has a separate entrainable oscillator outside of the light-entrained SCN (reviewed by Stephan 2001, but see Refinetti 1999). Having two separate oscillators with weak coupling may be adaptive, because food sources may shift suddenly, whereas seasonal changes in sunrise and sunset are gradual. This will enable animals to reset the phase of the food entrainable oscillator without shifting the phase of all the circadian system (Stephan 2001). The same reasoning holds for other nonphotic cues affecting activity. At any rate, under natural field conditions the internal circadian clock is primarily entrained by the steadily and reliably occurring light/dark cycle (Gattermann & Weinandy 1997). Thus, it appears that nonphotic stimuli such as food availability, predation, inter- and intraspecific competition, and temperature can cause the animal to shift its activity time without shifting the endogenous circadian clock. In such cases an animal will be active opposite or out of phase to its endogenous circadian rhythm.

For most animals under natural conditions the timing of sleep and wake (rest and activity) is in synchrony with the circadian control of the sleep/wake cycle and all other circadian-controlled rhythms. Humans have the cognitive capacity to override their endogenous circadian clock and its rhythmic output (Turek & Takahashi 2001). We showed here several examples of other species shifting their activity time without shifting their endogenous circadian clock and its rhythmic output. In humans, disturbed circadian rhythmicity has been associated with many mental and physical disorders and can have a negative impact on human safety, performance, and productivity (Turek & Takahashi, 2001). Among the very few studies of animals that shift their activity times, no other differences in diurnal rhythms were found between nocturnally and diurnally active individuals (Blanchong et al. 1999, Kronfeld-Schor et al. 2001a, Weber & Spieler 1987), suggesting that in these cases, the activity-rest cycle is indeed out of synchrony with all other circadian clock–controlled rhythms. Thus the daily optimal temporal arrangement with environmental events and/or the internal temporal order of physiological and biochemical processes may be out of synchrony. As in humans, such a shift may entail severe costs.

In sum, it appears that circadian rhythmicity may limit the response to nonphotic cues such as ecological interactions. The cost of a shift may be considerable in terms of the physiology and ecology of living organisms. Thus the plasticity of use of the time niche-axis at the diel scale may be severely constrained.

SPINY MICE OF ROCKY DESERTS: AN ECOLOGICAL/EVOLUTIONARY CASE STUDY OF TEMPORAL PARTITIONING

Activity Patterns

An excellent model system for the study of the role of temporal partitioning and the evolution of activity patterns is found in a hot rocky desert near the Dead Sea. The common spiny mouse (*Acomys cahirinus*) and the golden spiny mouse (*A. russatus*) coexist in rocky habitats (Kronfeld-Schor et al. 2001a; Shkolnik 1966, 1971) where they overlap in microhabitat use, home ranges, food habits, and reproductive period (Kronfeld et al. 1994, 1996; Kronfeld-Schor & Dayan 1999; Shargal et al. 2000). These species have attracted attention (e.g., Fluxman & Haim 1993; Haim & Borut 1981; Shkolnik 1971; Shkolnik & Borut 1969; Zisapel et al. 1998, 1999) owing to their unique temporal activity patterns: The common spiny mouse is active during the night, as are most desert rodents, whereas the golden spiny mouse is active during the day.

Shkolnik (1966, 1971) repeatedly trapped all individual *A. cahirinus* from a joint habitat, a rock pile, and after several months he began to trap *A. russatus* individuals during the night. This shift implies that the two species compete and that temporal partitioning is a mechanism of coexistence between them (Shkolnik 1971). A recent study with replicated experimental and control enclosures revealed that, while *A. russatus* shifted their activity also into the night in absence of their congener, their diurnal foraging activity remained high (Gutman 2001).

In the past decade we have been investigating the effect of the ecological and environmental challenges of diurnal and nocturnal activity on spiny mouse populations. We studied the costs incurred in diurnal and nocturnal activity and the evolutionary constraints involved in the shift from nocturnal to diurnal activity patterns.

Temporal Partitioning as a Mechanism of Coexistence

Experimental results suggest that temporal partitioning is a mechanism for coexistence between spiny mice (Shkolnik's 1966, 1971), although the actual limiting resource remains to be studied. In the Negev Desert, Abramsky et al. (1992) demonstrated that shelters limit common spiny mice on slopes covered with small stones. However, the Ein Gedi terrain is rich in boulders, and shelter is abundant for the low spiny mouse populations (Kronfeld-Schor & Dayan 1999). In disturbed areas near human settlements where food availability is high, their population densities increase, suggesting that food may be limiting (Kronfeld-Schor & Dayan 1999), as in other desert rodent communities (e.g., Heske et al. 1994, Rosenzweig & Abramsky 1997). Alternatively, the temporal shift results from interference competition but does not actually reduce resource overlap.

The species overlap in food habits, with a preference for arthropods (Kronfeld-Schor & Dayan 1999). In the field, the arthropod component in the diet of both

species was low in winter but extremely high in summer (Kronfeld-Schor & Dayan 1999). Thus during winter both species overlap in a largely vegetarian diet.

In winter the two species showed trade-offs in foraging efficiency: The common spiny mouse is a "cream skimmer," a relatively inefficient forager with high giving-up densities, and a habitat generalist; the golden spiny mouse is a habitat specialist that compensates for this restricted niche by foraging very efficiently to low giving-up densities (Jones et al. 2001).

In summer, however, a predation-induced shift in foraging of both species increased the overlap in foraging behaviors between them (Jones et al. 2001). Moreover, an experimental study during summer suggests that foraging trade-offs are not a viable mechanism of coexistence between the two species (Gutman 2001). However, during summer both species turn primarily insectivorous. Because the arthropod prey of *A. cahirinus* and *A. russatus* are likely to show diurnal patterns in availability, temporal partitioning could well promote resource partitioning and coexistence, particularly in summer (Jones et al. 2001, Kronfeld-Schor & Dayan 1999).

Resource competition may be mediated by interference competition, but the evidence for this phenomenon among spiny mice is equivocal (Gutman 2001, Pinter et al. 2002). A possible cue for the displacement of the golden spiny mice from nocturnal to diurnal activity is chemical signals released by common spiny mice (Haim & Fluxman 1996).

Anatomical, Behavioral/Ecological, and Physiological Adaptations

At Ein Gedi, the average maximal temperature in January is 20°C, and the average minimal temperature is 13°C. In July, the average maximal temperature is 38°C, and the average minimal temperature is 28°C (Jaffe 1988). During the day *A. russatus* avoid the heat behaviorally by remaining in the shade (Kronfeld-Schor et al. 2001b, Shkolnik 1971), reducing mid-day activity (Kronfeld-Schor et al. 2001a), and/or using evaporative cooling, which uses water, a scarce resource in the desert. Nevertheless, *A. russatus* has low water requirements owing to their ability to reduce water loss in the feces (Kam & Degen 1993) and to produce highly concentrated urine (Shkolnik 1966, Shkolnik & Borut 1969).

We found no significant differences in water turnover between the species in all seasons, reflecting adaptations of *A. russatus* to water conservation (Kronfeld-Schor et al. 2001c). In summer, energy expenditure of *A. russatus* tended to exceed that of *A. cahirinus*. Energy requirements of *A. cahirinus* in winter were double those of *A. russatus* and may reflect the cost of thermoregulating during cold nights (Kronfeld-Schor et al. 2001c).

A. russatus has evolved some adaptations to diurnal activity, such as dark skin pigmentation and a high concentration of ascorbic acid in its eyes (Koskela et al. 1989). However, it also retained the retinal structure of a nocturnal mammal (Kronfeld-Schor et al. 2001b). Moreover, it has a similar potential for nonshivering

thermogenesis (NST) to that of its nocturnal congener (Kronfeld-Schor et al. 2000), which is exposed in winter to much lower ambient temperatures and spends more energy on thermoregulation (Kronfeld-Schor et al. 2001c), suggesting that, in terms of NST *A. russatus* still displays its nocturnal legacy. The degree of NST capacity should be related to the most extreme cold conditions that an animal is expected to encounter. Since reaching maximal NST capacity requires at least several days (Heldmaier et al. 1981), it is crucial that animals not be misled by warm spells within the cold period and reduce their NST capacity. Control of NST capacity by day length obviates this problem, but it also implies that an animal that has shifted to activity in a warmer environment but with the same day length may retain its original cold-adapted NST capacity for an extended period (Kronfeld-Schor et al. 2000).

Ecological Interactions as Selective Forces

The few case studies that concern activity patterns of rodents and their predators take only one predator species or one functional group of predators into account (Halle 1993). General indirect evidence for the evolutionary significance of predation include spines on spiny mouse rumps and a histological mechanism for tail loss (Shargal et al. 1999). In order to gain insight into the evolution of activity patterns of spiny mice, we considered predation risk by owls, snakes, foxes, and diurnal raptors, (Jones et al. 2001).

A. cahirinus reduced their foraging in response to predation risk by owls in open habitats and during moonlit nights (Mandelik et al. 2002). Interestingly, golden spiny mice reduce their daytime foraging following full moon nights, a legacy of their nocturnal activity (Gutman 2001). Also, in response to owl calls, the level of stress hormones of *A. cahirinus* increased (Eilam et al. 1999), and their motor behavior changed with rising illumination levels. Predation risk by owls is a cost during the night, in particular in open habitats, and in particular during moonlit nights.

Nocturnal Blanford's foxes (*Vulpes cana*) prey upon spiny mice, although they constitute only a small portion of their diet (Geffen et al. 1992). Spiny mouse foraging patterns were not clearly affected by the presence of fox feces (Jones & Dayan 2000), and we view risk of predation by foxes as merely reinforcing a pattern driven by risk of owl predation.

The saw-scaled viper (*Echis coloratus*) is active during the summer. *A. cahirinus* have evolved relative immunity to its venom; a single snake bite is not lethal for individuals of this species (Weissenberg et al. 1997). A repeated strike, however, will kill them, so risk of predation by this snake remains a consideration for spiny mice. Predation by vipers is a threat primarily under boulders during the day (where these nocturnal sit-and-wait predators rest curled up) and during the night, both under and between boulders and in open areas, habitats where snakes are either lying still or actively moving at night (H. Hawlena, unpublished data; Mendelssohn 1965). Both *A. cahirinus* and *A. russatus* reduced their foraging in

sheltered microhabitats in summer and shifted their foraging activity to more open microhabitats in summer, the viper activity season (Jones et al. 2001). Thus, in summer the response to risk of predation by vipers counters the response to risk of predation by owls during the night (see also Kotler et al. 1992) and that of physiological stress during the day.

In sum, predation pressures clearly affect activity levels of spiny mice. Although they do not appear to cause an inversion in activity patterns, they confer a cost on both diurnal and nocturnal activity that varies seasonally.

Diel Rhythms as an Evolutionary Constraint

In the field spiny mice temperature rhythms are generally compatible with their activity patterns (Elvert et al. 1999). However, immediately upon removal to the laboratory, individuals of both species exhibited typical nocturnal temperature rhythms, and *A. russatus* individuals displayed nocturnal activity rhythms or were active both during the light and dark periods (Kronfeld-Schor et al. 2001a). Immediate inversion of the phase preference without evidence of a phase shift that would be expected in the case of true entrainment (Deacon & Arendt 1996) indicates that the diurnal activity of *A. russatus* in the field and their overt temperature rhythms are merely a masking effect. Furthermore, in the laboratory the presence of *A. cahirinus* provoked a change in daily rhythms of body temperature and urine volume. Lesion of *A. russatus* pineal gland resulted in diminution of urinary 6-sulfatoxymelatonin (6SMT) and modification of body temperature and urine volume rhythms. However, the modifications in body temperature and urine volume provoked by the presence of *A. cahirinus* were similar in pineal-lesioned and sham-operated *A. russatus*, and the presence of *A. cahirinus* did not affect glucose uptake of the SCN in pineal-lesioned and sham-operated *A. russatus*, indicating that the effect of *A. cahirinus* presence on *A. russatus* is a direct, pineal-independent effect (Zisapel et al. 1998, 1999). Thus, many generations of selection for diurnal activity in golden spiny mice have not caused a shift in their underlying rhythmicity. The diel rhythms that normally enable mammals to respond to environmental stimuli appropriately (e.g., Rusak 1981, Ticher et al. 1995) appear to lack the plasticity required to enable *A. russatus* to adapt to community-level interactions, even at this evolutionary scale.

These results suggest that, although the time axis may well be significant for ecological separation, the evolution of temporal partitioning may be severely constrained. If *A. russatus* are indeed constrained in terms of their rhythm biology to their legacy as nocturnal mammals, then they must be paying a price for being active at a phase opposite to their natural rhythm. The rich literature on human shiftworkers suggests that this type of shift, to the diametrically opposite part of the diel cycle, entails severe costs in health and performance (Van Reeth 1998).

In sum, ecological and physiological costs and constraints affect the activity patterns of spiny mice as well as their behavior and their space use. Interspecific competition drives golden spiny mice to invert their activity patterns. This

nonphotic cue, however, does not affect circadian rhythmicity, so golden spiny mice in nature are active against their native clock cycle. Circadian rhythms and NST capacity are regulated by photic cues that appear to override nonphotic cues in various biological systems for adaptive purposes; this rigidity implies that animals are not misled by minor environmental disturbances. It also implies that these aspects of animal physiology, as well as morphological traits that relate to their senses, may well act as evolutionary constraints limiting the use of the diel niche axis in structuring ecological communities.

Predation risk of owls, snakes, foxes, and probably also diurnal raptors affects microhabitat use and activity levels and consequently carries a cost, but it does not actually cause an inversion in activity patterns. Moreover, risk of predation by different predators may have opposing effects on activity and foraging and also an affect that opposes that of physiological costs and constraints. Our research so far suggests that, not only are the activity patterns and foraging microhabitat affected by ecological and physiological costs and constraints, but so is the community structure of these rocky desert rodents.

SUMMARY AND PROSPECTS FOR RESEARCH

Temporal partitioning between competitors and between predators and their prey is a significant mechanism of coexistence in some ecological communities. However, relatively few animal species invert their activity patterns as a result of interspecific or intraspecific interactions into the opposite activity phase. Most studies that suggest competition- or predation-induced segregation of activity patterns deal with temporal shifts within the normal nocturnal or diurnal activity time. Such temporal partitioning implies a cost in the overall reduction in activity times (see Schoener 1974a).

Although the time axis may well be significant for ecological separation among competitors and between predators and their prey, the evolution of temporal partitioning may be severely constrained. Physiological adaptations, among which are circadian rhythms, may limit the plasticity of activity patterns of animal species. Research at the interface between chronobiology, animal physiology, and ecological-evolutionary selective forces (see also Marques & Waterhouse 1994) may provide valuable insight into the evolution of activity patterns and of temporal partitioning (Kronfeld-Schor et al. 2001a).

Study of rhythm physiology may provide insight into the conditions under which phase shifts occur and the mechanism involved. In-depth ecological research of communities where temporal partitioning has evolved may provide insight into the selective regimes that have generated temporal segregation as a mechanism of coexistence. Is temporal partitioning a last-resource mechanism of coexistence where other mechanisms fail? Do some taxa have greater evolutionary plasticity than others? Are some environments (e.g., aquatic habitats) more conducive to shifts in activity patterns than others? How does phenotypic plasticity in the response of species to ecological interactions translate into phase shifts and the

evolution of different activity patterns? Does history play an important role? Is the time elapsed since selective pressures began a major component in the likelihood of the evolution of temporal segregation?

The majority of animal species have evolved to be active either by day or by night, and it is now difficult to tease apart the evolutionary forces that have selected for their diel activity patterns. Particularly significant for research of the selective forces affecting activity patterns are taxa that can be either nocturnal or diurnal (Metcalfe et al. 1999). These are amenable to manipulative experiments with varying levels of predation risk and interspecific competition.

The remarkable advances in our understanding of the physiology of diel rhythms coupled with a growing understanding of how ecological communities function offers a wonderful opportunity for gaining ecological-evolutionary insight into the role of time as a niche axis.

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