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Gerbils and Heteromyids – Interspecific Competition and the Spatio-Temporal Niche

Yaron Ziv[1*] and Jeffrey A. Smallwood[2]

1 - Dept. of Ecology & Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA

2 - Dept. of Integrative Biology, University of California, Los Angeles, CA 90024-1606, USA

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* Corresponding author

1. INTRODUCTION

Competition theory has had a major influence on ecological thought for at least the last sixty years with a special focus during the late 50's through the 70's (e.g., Hutchinson 1957, MacArthur and Levins 1964, Schoener 1974a). This led to the extensive development of niche theory (e.g., Hutchinson 1957, Pianka 1974, Whittaker and Levin 1975), linking competition pressures with observed resource use by competitors, both inter- and intraspecific (see Colwell and Fuentes 1975, Giller 1984 for reviews). As a result, terms such as niche release, niche shift and niche expansion are used to describe a species response to its competitor's presence or absence. Dissimilarity between competing species in their foraging behavior or habitat use is sometimes called "niche differentiation". Previous theoretical (e.g., May 1973) and experimental (e.g., Park 1962) studies on inter-specific competition concluded that niche differentiation is necessary for competitive coexistence in interactive communities (i.e., communities that are mainly influenced by density-dependent processes such as competition and predation). As a result, the way in which ecologically-related species partition resources to avoid competitive exclusion has attracted the attention of ecologists for many years (e.g., MacArthur 1958, Schoener 1974a, 1974b, 1986a).

Schoener (1974a) reviewed 81 studies on the relationship between competing species. He found that three major resource-partitioning dimensions may allow for niche differentiation between the species (see also Schoener 1986a for a more recent review): food, habitat (or space in general), and time (all corresponding to the "separation components" suggested by MacArthur in a series of papers: e.g., MacArthur 1964, MacArthur and Levins 1964, MacArthur et al. 1966). He concluded that "habitat dimensions are important more often than food-type dimensions, which are important more often than temporal dimensions".

Among the three resource-partitioning dimensions, time has received the least attention (Schoener 1974a, 1986a). Theory seems to justify that because "no energetic gain can be derived from not feeding during most time periods," and "the relative rarity of experimentally produced shifts along time and diet dimensions is, in general, consistent with foraging theory"

(Schoener 1986a). Some studies, however, did focus on temporal partitioning (Shkolnik 1971, Menge and Menge 1974, Kotler et al. 1993). These studies encouraged us to reevaluate the role of the temporal axis in niche partitioning. They also suggested that we should adopt a mechanistic approach that takes into consideration the complexity of species coexistence via the role of the limiting factor and the environmental heterogeneity (e.g., Price 1986, Schoener 1986a, Rosenzweig 1991). Note that this does not change the fact that observing a pattern is usually the first step toward understanding ecological processes. Here we focus on two such mechanistic approaches: a "theory of habitat selection" (Rosenzweig 1981) and "mechanisms of coexistence on a single resource" (Brown 1986).

Rosenzweig (1981) developed a theory of habitat selection for two competing species, which he calls "isoleg theory". The theory builds on the intraspecific selection theory of Fretwell and Lucas (1970, Fretwell 1972), and optimal patch use theory (e.g., Rosenzweig 1974, Charnov 1976, Brown 1988). The theory assumes that individuals of each competing species choose the habitat set that maximizes their fitness, and that the densities and distributions of each species affect this choice. In a practical sense, the theory of habitat selection allows one to map behaviors (i.e., different habitat preferences) onto a set of coordinate axes of population densities. As a result, it provides a way to incorporate niche relationships into a single two-dimensional picture (e.g., shared-preference vs. distinct-preference models; see Rosenzweig 1985, 1991 for reviews). We can use this approach to move from the fundamental to the realized niche (Hutchinson 1957) of a given species by looking at the species behavior with and without its competitor. It allows us to understand how the primary preference of each species (i.e., its resource preference in the absence of the competitor) for the competitively-limiting factor changes in a density-dependent manner. This may also allow us to hypothesize about the mechanism of coexistence between the competing species based on their community organization.

Studying mechanisms of coexistence on a single resource, Brown (1986, 1989a, 1989b) suggested that each mechanism of coexistence is composed of two essential features (see also

Kotler and Brown 1988): a) an environmentally heterogeneous resource axis (e.g., Levins 1979, Chesson and Warner 1981), and b) an evolutionary trade-off between the abilities of the coexisting species to utilize various parts of this axis (e.g., Stewart and Levin 1973, Kotler and Brown 1990). These two features may provide a variety of mechanisms to give each species a relative advantage over its competitor under different sets of conditions. Hence, each may reproduce and maintain a non-decreasing population size (e.g., Brown et al. 1994). Furthermore, this approach may allow us to explain competitive coexistence even when only a single limiting resource is involved (Vance 1984, Brown 1986).

Many studies show that competitive relationships play an important role in organizing rodent communities (e.g., Grant 1972, Brown et al. 1986, Frye 1983, Price 1986, Kotler and Brown 1988, Brown 1989b, Abramsky et al. 1991). In the following sections we review two studies on competing rodent species. These studies emphasize spatial and temporal partitioning. The first study focuses on the significance of the daily temporal axis between two gerbil species in Israel. The second study focuses on the contribution of the seasonal temporal axis between two species of pocket mice in Arizona. Both studies treat coexistence by examining how shared-preference habitat selection affects the competitive trade-off between the species. The gerbil study relies on manipulation experiments, while the pocket mouse study analyzes patterns of distribution.

2. GERBILS AND DAILY TEMPORAL PARTITIONING

The sandy habitats of the western Negev Desert in Israel are inhabited by up to 5 gerbil species (Zahavi and Wharman 1957). The most common species of this community are *Gerbillus allenbyi* (Allenby's gerbil; 26 g) and *G. pyramidum* (Egyptian sand gerbil; 40 g). These two species are nocturnal, inhabiting burrows during the day and consuming and collecting seeds and vegetative material while foraging during the night. Both species are mostly granivorous and have similar diets (Bar et al. 1984), and their densities are correlated with the productivity of seed-producing annual plants (Abramsky 1988). Habitat selection of *G. allenbyi* and *G. pyramidum* (Rosenzweig and Abramsky 1986, Abramsky and Pinshow 1989) and the amount of time they are active (Mitchell et al. 1990) are both affected directly by the other species' density. This competitive relationship stimulated an extensive study on the two species' coexistence mechanisms and the spatial and temporal niche partitioning between them (e.g., Abramsky et al. 1990, 1991, Kotler et al. 1993, Brown et al. 1994).

Two distinct activity patterns have been demonstrated experimentally for these species - the first relates to spatial partitioning and the second relates to temporal partitioning. Abramsky and co-authors (Abramsky et al. 1990, 1991, 1992, 1994) have studied the habitat preference of the two gerbil species in an area with two habitat types: semistabilized dunes and stabilized sands. Both species primarily prefer the semistabilized dunes because each species enjoys a foraging advantage in this habitat type (Ziv et al. 1995). Hence, the two species reveal what is called "shared-preferences habitat selection" (e.g., Pimm et al. 1985). However, habitat preference is both intra- and interspecifically density dependent. In the presence of a relatively low density of *G. pyramidum*, *G. allenbyi* uses both habitat types equally. In the presence of relatively moderate or high density of *G. pyramidum*, *G. allenbyi* shifts its habitat preference to the stabilized sands. In contrast, the preference of *G. pyramidum* for the semistabilized dunes increases in the presence of high densities of *G. allenbyi*. At natural densities (see Abramsky et al. 1991, 1992, 1994 for isocline analysis) *G. pyramidum* uses the semistabilized dunes while *G. allenbyi* mainly uses the stabilized sands ("apparent preference"; Rosenzweig 1991).

Regarding time, Kotler et al. (1993) showed, observationally, that each species is active during a different part of the night, thus suggesting a temporal-partitioning pattern. Additional studies showed that *G. allenbyi* is the more efficient forager at low resource abundances (Kotler and Brown 1990, Ziv 1991, Brown et al. 1994). That is, at resource densities when *G. pyramidum* cannot profit from foraging any further, *G. allenbyi* can still profit (for more details on optimal patch use see Brown 1986, 1988, 1989a, Kotler and Brown 1988, 1990, Kotler et al. 1993, Brown et al. 1994).

However, the main question regarding the two-species system remained unsolved: How do these two sympatric species coexist? Brown et al. (1994) found evidence against five mechanisms of coexistence that depend on habitat partitioning and annual temporal partitioning in resource abundance (see Kotler and Brown 1988 for "mechanisms of coexistence" and Brown 1989b for testing some of these mechanisms). However, evidence on daily renewal of resource patches suggested that coexistence should depend on this scale of habitat heterogeneity (see Kotler et al. 1993 for detailed evidence of the daily renewal).

Following this information, Ziv et al. (1993) hypothesized that coexistence between *G. allenbyi* and *G. pyramidum* depends on one of two trade-offs: 1) Interference (*G. pyramidum*) vs. foraging efficiency (*G. allenbyi*), or 2) Foraging efficiency in the early part of the night (*G. pyramidum*) vs. foraging efficiency in the late part of the night (*G. allenbyi*; see Brown 1989a for similar hypothesis on a seasonal scale). Interference versus foraging efficiency means that *G. pyramidum* monopolizes rich resource patches at the beginning of the night. But, due to its higher foraging efficiency, *G. allenbyi* can and does exploit poorer resource patches available later at night after *G. pyramidum* quits foraging (Ziv et al. 1993). Foraging efficiency in different parts of the night means that each species can and does profit more from resource patches available at different times (Ziv et al. 1993; see also Kotler and Brown 1988 for a general review). If interference vs. foraging efficiency is correct, then in the absence of its competitor, *G. allenbyi* will increase its activity in the first part of the night. However, if time of activity is determined only by foraging preferences without interference, then we should not expect any qualitative shift in *G. allenbyi*'s activity behavior.

To test their hypotheses, Ziv et al. studied the two species in a sandy part of the Negev Desert, Israel. The area provides two main habitats: semistabilized dunes and stabilized sands (Danin 1978). Strong afternoon winds occur almost daily, and the average annual precipitation at the site is 108 mm. Ziv et al. used one-hectare enclosed and unenclosed grids to test the behavior of *G. allenbyi* with and without *G. pyramidum* (see Abramsky et al. 1990, 1991 for detailed description of the enclosures). Each enclosure contained similar proportions of both habitats, and all fences were perforated with adjustable gates with small openings that only *G. allenbyi* could traverse to control the preferred densities (see Ziv et al. 1993). Forty "sand-tracking" plots (0.4 X 0.4 m) in each enclosure (20 plots in each habitat) allowed scoring of plots for rodent acticity by estimating % coverage by tracks on a scale of 0 (no footprints at all) to 4 (100% coverage). Scores could be assigned to species on the basis of species-specific toe clips. The sum of scores of a species in a habitat in a grid divided by the number of individuals of that species in that grid gave the "per-capita activity density" which represents an accurate measure of the species activity (e.g., Abramsky et al. 1990, 1991).

In the presence of both species, a temporal partitioning pattern exists (Figure 1). *G. pyramidum* is active in the beginning of the night immediately after sunset with a sharp decrease in its activity towards midnight. From then on, almost no individuals of *G. pyramidum* are active. In contrast, *G. allenbyi* is hardly active until midnight. However, from midnight it increases its activity approximately three fold. Similar activity patterns were found in control grids, suggesting that the enclosures represent the natural situation accurately. This temporal-partitioning pattern is consistent with what has been shown by Kotler et al. 1993.

However, the activity pattern of *G. allenbyi* does depend on the density of *G. pyramidum*. In the absence of *G. pyramidum* (open-dot line in Figure 1), the activity of *G. allenbyi* was highest immediately after sunset and declined moderately until the end of the night. During the earlier part of the night *G. allenbyi* was more active in the enclosed grids without *G. pyramidum* than on either the control grids or the enclosures where both species were present (Ziv et al. 1993).

The temporal niche shift of *G. allenbyi* as a result of *G. pyramidum*'s presence supports the hypothesis that the two species coexist due to a trade-off between interference competition and foraging efficiency (see also Ziv et al. 1993). This finding is consistent with previous studies regarding the relationship between ecologically-related species that differ slightly in body size (Vance 1984, Brown 1986). The bigger species should be dominant (e.g., Fyre 1983, Bowers et al. 1987) while the smaller species should forage more efficiently (Rosenzweig and Sterner 1970, Kotler and Brown 1990). This relationship leads to a dominant-subordinate community organization (Rosenzweig 1991).

The temporal-partitioning pattern is only one pattern in the complex relationship between the species. Can we incorporate the spatial-partitioning pattern of the species to get a spatio-temporal understanding of their actvity? To do that, Ziv et al. (1993) further asked what proportion of *G. allenbyi*'s activity density in the semistabilized dunes occurs during different times of the night when *G. pyramidum* is present and absent. A proportion of 0.5 indicates no preference, while values above or below 0.5 indicate preference for the semistabilized dunes or for the stabilized sands, respectively. Figure 2 shows that in the presence of *G. pyramidum* during the first two time periods, *G. allenbyi* used mostly the stabilized sands. During later time periods when *G. pyramidum*'s activity ceased, *G. allenbyi* used both habitats equally. In the absence of *G. pyramidum*, *G. allenbyi* used both habitat types equally all night. The use of both habitats by *G. allenbyi* in the absence of *G. pyramidum* is expected from "ideal free distribution" intraspecific habitat selection (see Abramsky et al. 1990, their Figure 1b).

With regard to space, Ziv et al. (1995) show two ways that foraging advantages contribute to the preference of both species for the semistabilized dunes. First, both species have a higher foraging efficiency (Brown 1988) when foraging on the sandy substrate in the semistabilized dunes relative to that on the loess-based substrate of the stabilized sands. Second, the semistabilized dunes provide a better substrate for escape from predators than the stabilized sands, probably in part because a higher number of burrows exist in the semistablized dunes. Overall, foragers of both species should experience a higher net energy gain in the semistabilized dunes (see Ziv et al. 1995 for more details).

With regard to time, the preference for the early part of the night by both species is consistent with the availability of resources in the area. The strong afternoon winds that occur almost daily are probably responsible for the daily renewal of seeds by uncovering seeds buried in the ground (Kotler et al. 1993). It is therefore advantageous to forage early in the night to get the newly exposed seeds before they are picked up by another forager. (Seed disinterment should be greatest in the semistabilized dunes because of their less stabilized substrate (Danin 1978).) Additionally, harsher environmental conditions later at night, such as low temperature and high humidity, might increase foraging costs for gerbils.

We have other indirect evidence that competition for food resources may play a major role in the temporal-partitioning pattern. We conducted our experiment in October after a hot summer when resources should have been limited. However, a study conducted a few months later in late winter, when resources were abundant, revealed no temporal partitioning; both species were active from the beginning of the night (O. Ovadia and E. Vaginsky, pers. comm.). This suggests that resource availability is important in determining the temporal-partitioning pattern.

G. pyramidum prefers a particular habitat which is defined in both space and time, i.e. semistabilized dunes soon after sunset. It exploits this spatio-temporal habitat due to its dominance, while *G. allenbyi* gets the rest. So, the temporal and the spatial partitioning patterns exhibited by the species are not independent. Yet, the distribution of the seed resources in space and time provides more opportunities in the semistabilized dunes during the beginning of the night for foragers of both species. *G. allenbyi*'s restriction depends on *G. pyramidum*'s presence. Thus, the species demonstrate shared-preference spatio-temporal selection (Rosenzweig and Abramsky 1986, Abramsky et al. 1990, Kotler et al. 1993, Ziv et al. 1993).

G. allenbyi and *G. pyramidum* compete for food resources, mainly seeds (e.g., Bar et al. 1984, Abramsky 1988). Bar et al. (1984) showed that the two species have a high diet overlap and concluded that resource partitioning (i.e., food) cannot explain their coexistence. This conclusion is consistent with the known ecology of granivorous desert rodents in North America (see Kotler and Brown 1988 for review). In particular, the high temporal and spatial variance in desert ecosystems requires competing species to share diets (e.g., Reichman 1975, 1984, M'Closkey 1983, Price 1986). This precludes coexistence on the basis of resource partitioning. As a result, spatial and temporal habitat axes play major roles in species coexistence (Kotler and Brown 1988). Among the two species, *G. allenbyi* is the more efficient forager, partly due to its basal metabolic rate and thermoregulation (Linder 1988). However, *G. pyramidum*, the bigger species, dominates the shared-preferred parts of the temporal and spatial axes. Only after *G. pyramidum* stops foraging can *G. allenbyi* forage freely with no foraging costs of interference. Hence, the nature of the available resources, together with the differential abilities of the species, promote the existence of a dominant-subordinate community organization. In turn, the community organization affects the spatial and temporal partitioning patterns we observe.

3. HETEROMYIDS AND SEASONAL TEMPORAL PARTITIONING

The temporal also shows extensive variation on a seasonal or annual scale as well as the daily scale seen in the gerbil niche partitioning example. We therefore find it useful to review an example of a niche shift which occurs at a seasonal scale. As with gerbilline systems, competition has been demonstrated in many heteromyid systems and resource partitioning is common (see Brown and Harney 1993, and Reichman and Price 1993 for recent reviews). Much research has shown partitioning of resources to occur by means of microhabitat specialization, especially partitioning among the genera (Rosenzweig 1973, Price 1978, Kotler and Brown 1988, Brown and Harney 1993, Reichman and Price 1993). Despite extensive knowledge of activity patterns (Daly et al. this volume), very little work has been done which demonstrates temporal partitioning of resources by heteromyids (Brown 1989b). Brown (1989b) found that the two heteromyids which co-occur on his southeast Arizona study site (*Dipodomys merriami* and *Perognathus amplus*) partition resources by means of seasonal variation in foraging costs; trade-offs between foraging efficiencies in different times of the year allows coexistence in that system.

The three most common species throughout the Sonoran Desert habitats of southwest Arizona are *Dipodomys merriami* (Merriam's kangaroo rat; 36 g), *Chaetodipus penicillatus* (Desert pocket mouse; 20 g) and *C. intermedius* (Rock pocket mouse; 13 g) where they co-occur in two adjacent habitats, rocky slope and sandy flat (Schmidly et al. 1993). An extensive review of activity patterns and general ecology of kangaroo rats appears in Daly et al. (this volume). The physiological differences (Hoover et al. 1977, French 1993) and size sequence represented by these three species provide an excellent opportunity to investigate competitive coexistence with respect to habitat use and habitat partitioning. In order to understand their coexistence, Smallwood and Swift (In review) studied the effects of interspecific interactions on habitat use by utilizing the differences in temporal activity patterns and their relationship to ambient temperatures and resource availability in a typical environment.

Variations in occurrence of important seed producing plants within these two habitats results in a generally more dense and continuous seed bank (richer resource for heteromyids) on the sandy flat as compared to the rocky slope (Smallwood and Swift In review). Thus, resource availability is both spatially and temporally heterogenous in this location as has been demonstrated in other desert seed resource studies (Nelson and Chew 1977, Reichman 1984, Price and Reichman 1987). The sandy flat also apparently provides more favorable burrow locations with increased buffering of ambient temperatures (Hoover et al. 1977).

In the combined habitats, peak frequencies of *Dipodomys* and *Chaetodipus* occur at different times of the year (relationship between frequencies of the two genera: $R = -0.896$, $P < 0.001$, $n = 12$). Thus, the two genera partition the seed resource by varying the time of year when each genus is the numerically dominant forager. The out-of-phase pattern of the generic densities supports the idea that potentially competing heteromyid genera have seasonally distinct density peaks, like has been found to be the main mechanism of coexistence between the two co-occurring heteromyids in the study by Brown (1989b; see above).

Peak frequencies of the two *Chaetodipus* species in combined habitats are occasionally in phase (relationship between the two congeners: R = -0.274, NS, n = 12). In separate habitats, the relationships in either habitat between a *Chaetodipus* species and either of the other two common heteromyids are negative and significant where that particular *Chaetodipus* is the numerically dominant species through most of the year (Table 1; *C. penicillatus* most common on the sandy flat, *C. intermedius* most common on the rocky slope). The relationships between *D. merriami* and the *Chaetodipus* species that is not numerically dominant in either habitat are positive and either non-significant or weakly significant (Table 1; e.g., *D. merriami* with *C. penicillatus* on the slope, and with *C. intermedius* on the flat).

In addition to these general patterns, individuals move between habitats (Smallwood and Swift In review); the rare *C. intermedius* marked on the flat frequently move to the slope, particularly when *C. penicillatus* are increasing in density on the flat (i.e. in spring). The reverse movement by *C. penicillatus* is far less frequent, and most of those on the slope appear to be permanent residents there. Thus, while *C. intermedius* is usually more common on the rocky slope, their numbers of individuals using the sandy flat increases in the absence of C. penicillatus. *Chaetodipus penicillatus* prefers the sandy flat and is numerically and behaviorally dominant there most of the year; it seems able to preclude extensive use of the sandy flat habitat by *C. intermedius* during all times when the former is active (Smallwood and Swift In review). *Chaetodipus penicillatus* can use the slope at will, but never in very high densities even if *C. intermedius* is absent (Figure 3b: Dec 1994). Thus, *C. intermedius* can utilize the flat habitat only when *C. penicillatus* is at low densities there (Figure 3a). Low densities are probably due to hibernation in cold weather (Hoover et al. 1977). The increase in the proportional presence of *C. penicillatus* on the slope at times of low *C. intermedius* densities is not the result of increased capture rates, rather it is an artifact of the use of proportions and the decrease of *C. intermedius* density. Alternatively, the increase of *C. intermedius* on the flat at low *C. penicillatus* densities is the direct result of increased trapping frequencies of both marked and unmarked individuals.

Movements and changing densities among habitats show that *C. intermedius* is able to expand its niche at times when *C. penicillatus* is absent. Trappings and markings show that individuals of *C. intermedius* are shifting their niche in a temporal fashion in order to take advantage of the open niche in the flat habitat that is left by *C. penicillatus*' absence during periods of apparent inactivity or hibernation. The reverse is not true: *C. penicillatus* does not shift niches to utilize the slope habitat; certain individuals are permanent residents there, but additional individuals do not appear from the sandy flat marked population when *C. intermedius* is in low density on the slope. The use of both habitats by both species is evidence of extensively overlapping niches, therefore the use of habitats by these two species appears to fit a shared-preference model of habitat selection (Pimm et al. 1985, Rosenzweig 1991) as do the aforementioned gerbils.

Some evidence exists to suggest that closely related species differ in their foraging efficiencies (Kotler and Brown 1988), generally with the smaller species being more efficient foragers (Rosenzweig and Sterner 1970, Kotler and Brown 1990) , and that larger species being behaviorally dominant (Frye 1983, Bowers et al. 1987). Perhaps then, each *Chaetodipus* species has a range along the resource axis where resource availability is appropriate to enable each to tolerate the presence of competitors, and a range where each cannot tolerate the presence of competitors. Under this scenario, it may be possible that only one *Chaetodipus* species is able to compete for a specific resource density under certain cold conditions. Since larger species tend to be the less efficient foragers, *C. penicillatus* might be expected to require higher resource densities in order to out compete *C. intermedius* in cold weather. At lower resource densities, *C. intermedius* may be able to persist while *C. penicillatus* cannot locate enough seeds to remain active. Thus, as with the gerbils, the temporal and spatial patterns exhibited by these two *Chaetodipus* species are not independent and they demonstrate shared-preferences habitat selection. The two pairs of congeners partition resources along a temporal axis, the scale being daily for the gerbils, and annual for the pocket mice.

Certainly other factors may influence these relationships such as finer scale dynamics of resource availability. Further analysis of the resource base is required to determine if this is the mechanism by which these two species partition the resource under stressful conditions, but this hypothesis of partitioning fits well with a shared-preference habitat selection model. While the occurrence of this phenomenon is observable without manipulation, the mechanism would appear to be highly complex, but at least involves variability in physiological tolerances, resource heterogeneity, differing foraging efficiencies, and competition.

4. CONCLUDING REMARKS

The concept of resource partitioning between sympatric species dominated studies of rodent communities (Rosenzweig and Winakur 1969, Grant 1972, Brown 1975, Rosenzweig 1977, Brown et al. 1979, Price 1986, Kotler and Brown 1988, Brown and Harney 1993) that tried to explain how ecologically-related species partitioned their food, habitat or time of activity to allow coexistence (Schoener 1974a, 1986a). Here, we provide evidence for and discuss the contribution of temporal partitioning to the concept of resource-partitioning dimensions and species coexistence.

4.1. Tempoal partitioning and its relation to species coexistence

Both gerbils and pocket mice rely on the time axis to coexist. Gerbils partition the time of activity on a daily scale while pocket mice coexist due to environmental differences between different seasons on an annual scale. Between-year variability may also provide a temporal-partitioning dimension to allow the existence of competing species on a much larger scale. Although they represent different temporal scales, we can still attempt to generalize the contribution of time to coexistence and species diversity. In particular, we would like to emphasize three points emerging from our study systems that connect the time dimension to competition theory and community organization.

The first point deals with the relationship between the competitively-limiting factor and the resource-partitioning dimensions. The temporal axis does not necessarily represent the limited factor on which species compete, but a dimension along which species can partition the limited factor and thereby coexist. For example, suppose a particular food type is a shared limiting factor for species. Competitive coexistence may occur when each species utilizes a similar food type in different habitats or a similar food type at different times (as in cases 1 and 2 of Schoener 1974a, respectively). As a result, we may observe spatial or temporal partitioning between the species. However, in this case, food type is still the competitively-limiting factor that enhances interspecific competition; time or space are the dimensions along which species can partition it and thereby coexist. Hence, we should distinguish between the limiting factor on which species compete and the environmental axes on which each species can gain an advantage over the other. This may happen by consuming that limiting factor differently, and, thereby, generating the required niche differentiation for coexistence (e.g., Levins 1979, Chesson and Warner 1981; and see Kotler and Brown 1988, Cornell and Lawton 1992 for reviews). It is important to recognize that for a given limiting factor, several "solutions" (i.e., mechanisms of coexistence) may be available. This is why we can group the above different temporal scales together to discuss the "temporal-partitioning dimension". The specific temporal scale may depend on the similarity between the species, on the range of the environmental axes in the particular environment, or even on the evolutionary scenario by which speciation events led to the evolution of the related species or groups of species. This also leads us to the conclusion that observing a given partitioning pattern between species does not necessarily tell us by what mechanism the species coexist.

The second point deals with the difference between a species' realized and fundamental niches. Very often, the resource-partitioning dimension (and in our case temporal partitioning) represents the species' realized niche, i.e., the observed resource use of species given the presence of other species in the community. However, to understand the contribution of resource partitioning, and more specifically temporal partitiong, to species coexistence, we should know the primary preference of each species (i.e., its resource preference in the absence of the competitor) for the competitively limiting factor as well as the primary preferences to other resource-partitioning dimensions. Although species' realized niches reflect the way species actually use resources, differences or similarities in species fundamental niches provide the basic understanding for the potential mechanisms that may allow for coexistence. Hence, the community organization of the species play an imporatnt role in understanding the contribution of temporal partitioning to coexistence. For example, in the case of the gerbil species, both species prefer the first part of the night for their activity due to the better conditions available then. Temporal partitioning here is a product of the exclusion of *G. allenbyi* by *G. pyramidum* from the preferred part of the night. This emphasizes the crucial effect of interference for the produced temporal-partitioning pattern and coexistence. It does not diminish the contribution of the temporal dimension for coexistence; without the differential ability of the species to consume resources during different parts of the night, coexistence might not have existed! Therefore, community organization, through the fundamental niches of the species, is impoartant for understanding how temporal partitioning mediates and allows niche differentiation to promote coexistence.

The third point recognizes the dependency between the different resource-partitioning dimensions. Temporal partitioning is not necessarily independent of spatial partitioning. (For a general view of the tie between spatial and temporal scales see Holling 1992.) For example, imagine that particular food types are available during specific times of the day in particuar habitats (e.g., competitors specializing on prey types that are active during different hours of the day in different habitats will show an “apparent spatio-temporal partitioning"). When interference competition occurs, the dominant species may be capable of monopolizing a few preferred parts of different niche dimensions. This is true especially if these dimensions link together to provide the best resource gain. The subordinate species may be simultaneously excluded from preferred parts of the niche dimensions. Without looking carefully at the dependency between the different dimensions we could easily misinterpret the niche relationship of the species. Recognizing one resource partitioning dimension should not suggest that we stop studying other potential resource-partitioning dimensions. Other resource-partitioning dimensions may also be part of the picture.

We emphasize interference competition because it may be more likely to produce this dependency between temporal and other resource-partitioning dimensions. This is because a monopolizable limiting factor may be distributed in a specific habitat during a specific part of the day (or season). Given the likelihood of community organization based on shared preferences of closely-related species, one, and maybe the most parsimonious outcome is a mechanism of coexistence based on a trade-off between dominance and foraging advantage on a linked spatio-temporal dimension. Therefore, temporal partitioning should at least be considered to promote coexistence.

4.2. Synthesis

We treated the three points above independently in order to focus on different important points regarding temporal partitioning and competition theory. However, the three of them represent a closely related sequence of processes and patterns. This does not mean that the sequence we found is the only general sequence expected from any two-species competitive system. Rather, different sequences may emerge depending on the relationship between the species, their primary resource utilizations, and the heterogeneity of the environment which they occupy. Temporal partitioning may provide a potential axis along which species can partition the limited factor and thereby coexist in many other sequences as well.

Closely-related species may have similar resource-utilization curves due to their physiological, morphological or behavioral constraints. These, in turn, are likely to produce similar primary preferences (fundamental niches) for many resources and environmental dimensions. At this point we have to introduce another set of conditions: Are the species' fundamental niches "included" or "reciprocal" (Colwell and Fuentes 1975)? Included niches mean that one species niche is included within the other species' niche. Reciprocal niches means that although species' niches greatly overlap, each species can use some resources that are not available to the other. Given included niches, the species with the smaller niche must better utilize the limiting resource, or must monopolize the limited resource by interference. As a result, one of the two following trade-offs may allow for coexistence: foraging advantage (e.g., higher consumption rate) vs. tolerance (higher ratio of the variance of the fundamental niche to the best fitness possible), and interference (i.e., dominance) vs. tolerance. A more tolerant species can exploit varied resources that cannot be used with the same efficiency by an intolerant species. However, in the case of reciprocal niches, an additional trade-off may exist: tolerance on one part of the niche dimension vs. tolerance on the other part of the niche dimension. A specific example is the habitat selection of the gerbils in the presence of three habitat types (Rosenzweig and Abramsky 1986). The community organization and the produced trade-off for coexistence determine whether species partition the limiting factor directly. Whenever this is impossible, other dimensions may help indirectly to partition the limiting factor. In the two studied systems presented in this chapter, both the spatial and the temporal dimensions allowed each species to have some advantage over the other by consuming the limiting factor better in different parts of those dimensions. The dependency between the spatial and temporal dimensions through the mechanism of coexistence suggests that we should examine them together and not necessarily separately.

The purpose of this chapter is not to dismiss or diminish the contribution of the concept of resource-partitioning dimensions. Rather, we wish to point out that the observation of such resource-partitioning dimensions is the first step on a journey whose roots are the primary preferences of the competing species and the trade-off(s) that allow for coexistence. We must distinguish between the processes and their products; in most cases we observe the products, but we really want to understand the processes. We need to order the ecological processes and patterns correctly. To do so, we should adopt mechanistic approaches to the study of species coexistence and community structure (e.g., Price 1986, Schoener 1986b). These should take into consideration the complexities mentioned above. For our studies we used two such approaches: "A theory of habitat selection" (Rosenzweig 1981) and "mechanisms of coexistence on a single resource" (Brown 1986, 1989a). By using these approaches we were able to distinguish between the processes emerging from the primary ecological needs of the species and the products, i.e. the resource-partitioning. We hope we were able to convince you that understanding competitive coexistence is more complex than has been previously thought, BUT that this complexity is not hopeless. We have the scientific tools to understand it.

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Table 1. Matrices of Pearson correlation coefficients (R) for the relationships of frequencies of all possible heteromyid species pairs in the rocky slope and sandy flat habitats. Correlations of frequencies on the slope are in the upper right, and those for the flat are in the lower left. Frequencies are proportions of capture rates averaged over the number of trap nights for each sampling date. Species abbreviations are as follows: Dm = *Dipodomys merriami*; Cp = *Chaetodipus penicillatus*; Ci = *C. intermedius*. In all cases n = 12 sampling dates. Significance levels: NS = not significant; * = P < 0.05; ** = P < 0.01; *** = P < 0.001.

	Dm	Cp	Ci
			Rocky Slope
Dm	—	0.583*	-0.816***
Cp	-0.872***	—	-0.742**
Ci	0.553NS	-0.773**	—
		Sandy Flat	

FIGURE CAPTIONS

Figure 1. Per capita activity density values (±SE) of *G. allenbyi* (Ga; solid lines) and *G. pyramidum* (Gp; broken line) during different hours of the night. Closed and open circles represent the per capita activity density of *G. allenbyi* in the presence and absence of *G. pyramidum*, respectively. Per capita activity density is the sum of scores of a species' sand tracking in a habitat in a grid divided by the number of individuals of that species in that grid (see text).

Figure 2. The preference (±SE) of *G. allenbyi* (Ga) for the semistabilized dunes during different hours of the night in the presence (closed circles) and absence (open circles) of *G. pyramidum* (Gp). Preference of *G. allenbyi* means the proportion of *G. allenbyi*'s per capita activity density in the semistabilized dunes compared with its per capita activity density in both habitats. Preferences of *G. allenbyi* in the absence of *G. pyramidum* are significantly different than preferences of *G. allenbyi* in the presence of *G. pyramidum* at 20:00 and 22:00. Data were arcsine transformed for the analysis.

Figure 3. Frequencies of Chaetodipus species in each habitat. a. Frequency of each Chaetodipus species using the sandy flat (FLAT) habitat on each sampling date. b. Frequency of each Chaetodipus species using the rocky slope (SLOPE) habitat on each sampling date. Frequencies are proportions of capture rates averaged over the number of trap nights for each sampling date.