

# 5

## THE TEMPORAL NICHE

Time represents an important resource axis that may be partitioned by an assemblage of competing species. Diel differences in activity times of vertebrate predators and seasonal differences in flowering times of animal-pollinated plants constitute the primary evidence for temporal partitioning. For example, owls and hawks that forage at different times of day may reduce competition for limited food resources (e.g., Craighead and Craighead 1956), and co-occurring plant species that flower at different times of the year may reduce competition for animal pollinators (e.g., Heinrich 1976; Stiles 1977).

Because it is both ordered and circular, the temporal niche axis has a unique geometric representation, with the two orthogonal components of season and time of day forming a three-dimensional ring (Figure 5.1). The temporal niche of a species represents a subset of the surface area of this ring. At the community level, we may ask if there are nonrandom patterns of overlap in the set of surfaces that represent a local assemblage. Because the temporal niche is both ordered and circular, it may need to be analyzed in null models differently than dietary or microhabitat data.

Temporal partitioning is also likely to reflect different selective forces in assemblages of animals and plants. For animals that can pick up and move, migration is always a potential response to local resource competition. In contrast, plants and sessile animals must cope with persistent competition from close neighbors. On the other hand, many vertebrates must forage more or less continuously, whereas most plants and invertebrates can afford to wait out periods of resource scarcity.

Under traditional models of exploitation competition (MacArthur and Levins 1967), time is not a truly independent (orthogonal) niche axis (Carothers and Jaksić 1984). However, differences in activity time may allow species to directly partition food resources in two ways. First, seasonal differences in activity may allow predators to coexist by exposing them to different prey

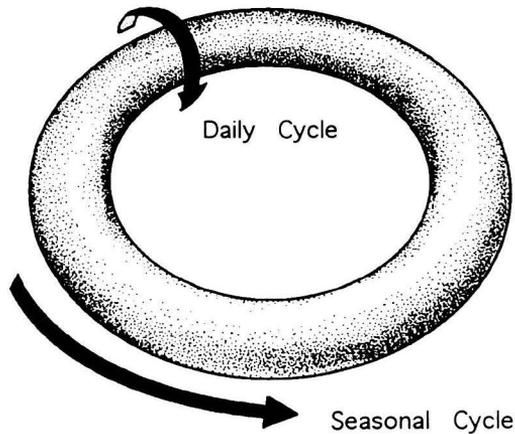


Figure 5.1. A three-dimensional representation of the temporal niche, showing both seasonal and diel axes. Temporal activity patterns can be represented as a subset of the surface of this ring. Null models predict overlap patterns on this surface in the absence of competitive interactions.

assemblages. Second, diel differences in activity may allow predators to partition a rapidly renewing resource. But in many animal communities, the second mechanism is unlikely, because a predator that consumes prey at night would still be competing with predators that hunt during the day. For vertebrate predators such as raptors or lizards, it seems especially unlikely that prey populations can renew fast enough to permit diel food partitioning (Schoener 1974c; Huey and Pianka 1983). A more reasonable scenario is that diel differences in activity evolved to minimize interference competition among foragers (Carothers and Jaksić 1984). For example, some ant assemblages are characterized by strong interference competition and dramatic diel shifts in the dominant foraging species (e.g., Klotz 1984; Hölldobler 1986). Diel foraging differences may also reduce overlap if prey activity schedules are nonoverlapping.

Nevertheless, temporal partitioning may be relatively uncommon in animal communities. Schoener (1974a) reviewed the early literature and concluded that animals often segregate food and habitat dimensions but rarely segregate along temporal niche axes. However, he did suggest that predators separated more often by diel activity time of day than did other trophic groups. Given this background, we now review null model studies of temporal partitioning in animal and plant communities.

## TEMPORAL PARTITIONING IN ANIMAL COMMUNITIES

One way to analyze temporal partitioning is to treat activity time as any other niche axis. As described in Chapter 4, Lawlor's (1980b) randomization algorithms RA1 through RA4 could be used to reshuffle observed activity data, which could then be compared with conventional metrics for niche overlap. For example, Pianka et al. (1979) used RA2 to analyze extensive data on the seasonal and daily activity of desert lizards. In this algorithm, the percentage of time that an animal was active during a particular season (or time of day) was replaced by a random uniform number. The only restriction on this randomization is that "zeros" were retained. In other words, simulated activity could not occur at times of the year or day when an animal was inactive in nature. Temporal overlaps in lizard assemblages did not differ from the predictions of this null model, or they showed significant aggregation (high overlap). In contrast, overlap in measures of habitat and food was often less than that predicted by the null model (see Table 4.4).

Field (1992) used RA1 as a null model and found a significant reduction in seasonal overlap of spider-hunting pompilid wasps of Britain. However, RA1 does not retain the placement of zeros in the data and consistently produces a random community with a high mean and a low variance in overlap (Pianka et al. 1979; Winemiller and Pianka 1990). Consequently, Field's (1992) result does not necessarily suggest temporal resource partitioning.

Although RA1–RA4 are valid null models for looking at unordered dietary or microhabitat categories, we think they are usually inappropriate for the analysis of temporal overlap. On both daily and seasonal time scales, temporal activity patterns show strong modalities, with peak activity in certain months or hours of the day. Activity curves are often not simple bell-shaped distributions and may exhibit considerable skewness or multiple modes (e.g., Riechert and Tracy 1975). For ectotherms, in particular, these modes may reflect a temperature-humidity envelope that physiologically constrains animal activity (Tracy and Christian 1986). The RA1–RA4 algorithms destroy the shape of activity curves, so that patterns revealed by them do not necessarily reflect temporal resource partitioning.

A better approach is to retain the shape of the activity curve and randomize the placement of its peak. Tokeshi (1986) followed this procedure in an analysis of nine species of chironomid larvae co-occurring in a river in eastern England. Two null models were used. In the first, activity peaks for each species were located randomly through the year, with the distributions overlapping circularly (across the year) if necessary. In the second, peaks were placed randomly during nonwinter months, to reflect an obvious temperature constraint on

activity that was unrelated to interspecific competition. Compared to both null distributions, overlap in the observed chironomid assemblage was significantly greater than expected. These null models are similar to those used in the analysis of flowering phenology (Poole and Rathcke 1979; Cole 1981), which we discuss later in this chapter.

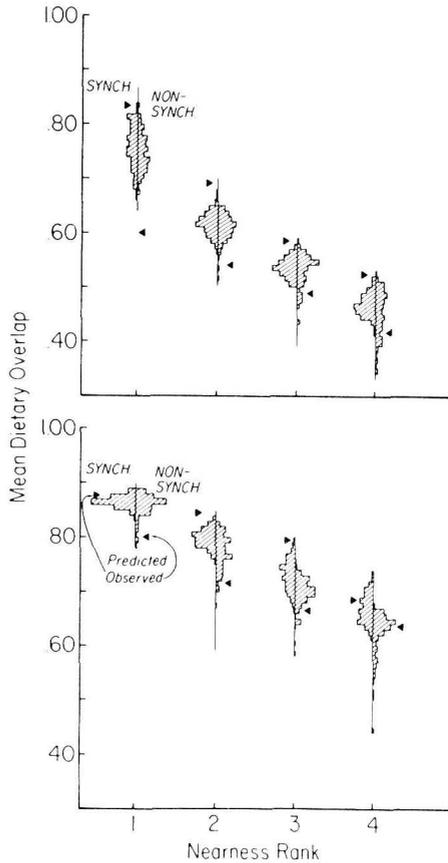
An important assumption underlying the analysis of temporal activity patterns is that animals that feed at different times have different diets. This assumption can be tested by examining the correlation between activity patterns and diet (Jaksić 1982). For example, diurnal and nocturnal predators may differ in their diets and thereby face less competition for food than predators with identical activity profiles. The null hypothesis here is that dietary overlap between “matched” species pairs that forage at the same time (diurnal-diurnal or nocturnal-nocturnal) is no different than that for “mixed” species pairs that forage at different times (diurnal-nocturnal). The alternative hypothesis is that competition has promoted temporal segregation, so that matched species pairs overlap less in diet than mixed species pairs (Huey and Pianka 1983).

Jaksić (1982) tested these hypotheses for dietary overlaps of diurnal falconiform and nocturnal strigiform raptors. Overlaps of all possible species pairs were compared using standard nonparametric statistics. In no case was there a significant difference in dietary overlap of mixed versus matched species pairs. Thus, temporal partitioning did not reduce exploitative competition for food resources, although it may have alleviated interference competition (Jaksić et al. 1981).

However, conventional statistics may be unsuitable for testing the mixed-matched dietary overlap hypothesis (Pimm 1983). First, none of the pairwise dietary overlaps are independent—the overlap between species A and B is not independent of the overlap between A and C and between B and C. Second, the overlap distances are geometrically constrained so that the maximum distance between any pair of species is 1.0. Finally, the analysis is likely to be sample-size dependent: the more species there are in the comparison, the closer, on average, are the nearest neighbor distances in dietary niche space. For all these reasons, a null model is necessary to properly test the mixed-matched dietary hypothesis.

Suppose there are  $n$  nocturnal and  $m$  diurnal species. Then there are  $mn$  mixed comparisons and  $0.5[n(n-1) + m(m-1)]$  matched comparisons of species pairs. Pimm (1983) suggested randomly assigning the  $m+n$  labels of nocturnal or diurnal to each species and then calculating dietary overlaps of mixed and matched pairs for this random assemblage. Repeating the procedure many times gives the mean and sample variance of the distribution of dietary overlap for each nearest neighbor, which can then be compared to the actual

Figure 5.2. Dietary overlaps for synchronous and asynchronous lizard predators in the deserts of Africa (upper panel) and Australia (lower panel). Synchronous species pairs forage at the same time of day. The histograms are the results of 200 randomizations, and the triangles show the observed values. Analyses are given for the first four nearest neighbors in niche space. Note that synchronous predators show more overlap and asynchronous predators less overlap than expected. These patterns are opposite to what one would expect if temporal partitioning of food resources were important. From Huey and Pianka (1983). Reprinted by permission of the publisher from *Lizard Ecology: Studies on a Model Organism*. R. B. Huey, E. R. Pianka, and T. W. Schoener (eds). Cambridge, Mass.: Harvard University Press. Copyright © 1983 by the President and Fellows of Harvard College.



values. If the mixed-matched dietary hypothesis is correct, matched species pairs should overlap in diet less than expected, and mixed species pairs should overlap more than expected. Moreover, the percentage of first nearest neighbors in niche space that are matched should be less than that predicted by the null model.

Huey and Pianka (1983) used Pimm's (1983) recipe to examine dietary differences between nocturnal and diurnal predators in assemblages of lizards, raptors, and water snakes. For both African (Kalahari) and Australian lizards, significantly more first- and second-nearest neighbors in dietary similarity were synchronous than were asynchronous in their activity times. Similarly, synchronous pairs of species tended to overlap in diet more often than predicted, and asynchronous pairs less often than predicted, by the Monte Carlo simulation (Figure 5.2). These patterns are opposite to the predictions of the mixed-matched dietary hypothesis, suggesting that lizard food resources are

not being partitioned by species that are active at different times of day. For a large data set on raptor diets (Craighead and Craighead 1956), Huey and Pianka (1983) found that overlaps of synchronous versus nonsynchronous predators did not differ significantly from predictions of the null model. Finally, for dietary data on four species of water snakes (Mushinsky and Hebrard 1977a,b), dietary overlaps of synchronous species were higher than expected, although there were too few species in the assemblage for a statistical test.

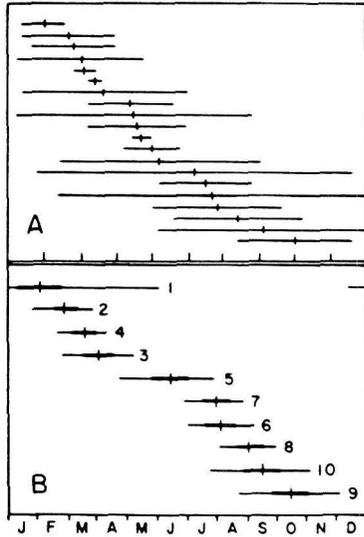
These analyses indicate that the degree of synchrony in activity periods is unreliable as an indicator of dietary overlap. The null model simulations contradict widely held beliefs that activity times allow vertebrate predators to partition food resources, and caution against the use of time as a niche dimension in competition analyses. Alternative explanations for the evolution of nocturnal and diurnal feeding strategies include predator avoidance (Lima and Dill 1990), alleviation of interference competition (Carothers and Jaksić 1984), and physiological thermal constraints (Porter et al. 1973).

Although there is little evidence for temporal partitioning by predators on a daily time scale, partitioning of food resources on a seasonal basis may be slightly more plausible. For example, Vannote and Sweeney (1980) hypothesized that competition for food within functional feeding guilds of stream insects will lead to a temporally staggered sequence of maximum resource use by species. Georgian and Wallace (1983) tested the prediction by measuring seasonal production of six species of periphyton-grazing insects in an Appalachian stream. Peak production for each species followed an orderly sequence, with very little overlap between species. Based on the Poole and Rathcke (1979) test (described later in this chapter), production peaks for each species showed an unusually large degree of separation ( $p < 0.1$ ). Overlaps based on density and biomass were generally higher than those based on production.

## PHENOLOGICAL OVERLAP IN PLANT COMMUNITIES

Robertson (1895) first proposed that pollen transfer by animals was a potentially limiting resource that could lead to staggered phenologies of flowering plants. However, at least three hypotheses may explain a staggered sequence of flowering times in a community (Waser 1983): (1) pollinator preference, in which one plant species attracts pollinators away from other species, leading to reduced reproductive success (Mosquin 1971; A. Lack 1976); (2) interspecific pollen transfer, in which pollen is exchanged between simultaneously flowering species, causing pollen loss, reduction of receptive stigma surfaces, and reduced reproductive success (Thomson et al. 1981); (3) formation of mal-

Figure 5.3. A randomly generated 20-species flowering phenology (A). Overlap patterns in this assemblage can be used as a null expectation for overlaps in the absence of competitive interactions. Phenology in a real assemblage is shown in (B) (see Figure 5.4). From Gleeson, S. K. 1981. Character displacement in flowering phenologies. *Oecologia* 51:294–295, Figure 1. Copyright © 1981 by Springer-Verlag GmbH & Co. KG.



adapted hybrids, in which pollen exchange between related species reduces fitness (Levin 1971). Mechanism (1) is implicit in most ecological studies of phenological overlap. Mechanism (2) is a form of interference competition that can lead to segregation in flowering times even when pollinators are not a limiting resource, and can affect wind-pollinated species as well. All three mechanisms assume that an increase in the abundance of one plant species reduces pollination of other species that share common pollinators. This assumption notwithstanding, rare plant species may sometimes benefit from the presence of other, common species acting as “magnets” for pollinators (Thomson 1978; Schemske 1981).

Whereas temporal segregation of animal foragers does not necessarily reduce dietary overlap, segregation of plant flowering times will reduce overlap in shared pollinators. However, the converse is not necessarily true—high overlap in flowering times need not imply strong competition for pollinator visits. For example, Thomson (1982) found that overlaps in flowering times of subalpine meadow plants were unrelated to relative visitation rates by pollinators. Thus, phenological overlap was not a good indicator of competition for pollinator visits.

In spite of an extensive catalog of flowering phenology studies, the evidence for staggered flowering times in most plant communities is weak (Waser 1983; Rathcke and Lacey 1985; Wheelright 1985). Before the advent of null models, staggered flowering patterns were evaluated visually, not statistically (e.g., Heinrich 1976; Stiles 1977). But appearances can be deceiving. For example, Figure 5.3a looks, to our eyes, like a staggered flowering sequence that might

be the result of interspecific competition. But this sequence of flowering times was generated by a random draw of numbers from a uniform distribution and represents a pattern that might be expected in the absence of competition for pollinators (Gleeson 1981).

When flowering phenologies are compared to appropriate null models, the results may be surprising and controversial (Rathcke 1984). Poole and Rathcke (1979) proposed the first statistical test of flowering overlap patterns. Their test considered the spacing of peak flowering time for each species and therefore did not directly test for overlap. Analyses of the spacing of flowering peaks in plant communities are identical to analyses of the spacing of body sizes in an animal community (Pleasants 1980), which we discuss in Chapter 6.

The Poole and Rathcke (1979) test summarized overlap as a single index, the sample variance of the distance between adjacent flowering peaks. For the first and last flowering species in the assemblage, distance is measured from the peak to the boundary of the growing season. The null hypothesis is the equivalent of assigning each species a random uniform value, ranging from 0.0 to 1.0, for its flowering peak within the growing season. If competition has led to a regular spacing of peak flowering times, the observed (population) variance in the position of the flowering peaks,  $P$ , should be significantly smaller than expected. Under the null hypothesis, the expectation of  $P$  for a set of  $k$  species is

$$E(P) = \frac{k}{(k+1)^2(k+2)} \quad (5.1)$$

The ratio of observed to expected variance ( $P/E(P)$ ) is an index that corresponds to flowering peaks that are aggregated ( $P/E(P) > 1$ ), random ( $P/E(P) = 1$ ), or staggered ( $P/E(P) < 1$ ) within the growing season. Although Poole and Rathcke (1979) compared the quantity  $kP$  to a chi-squared distribution, it is more appropriate to compare the results to a randomization test (Williams 1995). De Vita (1979) developed a similar null model for analyzing resource utilization peaks of species (see Chapter 4). These tests ultimately derive from MacArthur's (1957) broken-stick model, in which points are randomly placed on a unit interval to simulate the relative abundance of species in an assemblage (see Chapter 3).

A case history illustrates the use of the Poole and Rathcke (1979) test and a typical cycle of reanalysis that has accompanied many null model investigations. Poole and Rathcke (1979) applied their test to Stiles's (1977) data on flowering times of 11 hummingbird-pollinated plant species in a Costa Rican rain forest (Figure 5.4). Stiles (1977) had claimed that flowering peaks exhibited an orderly, staggered sequence, but the Poole and Rathcke (1979) test

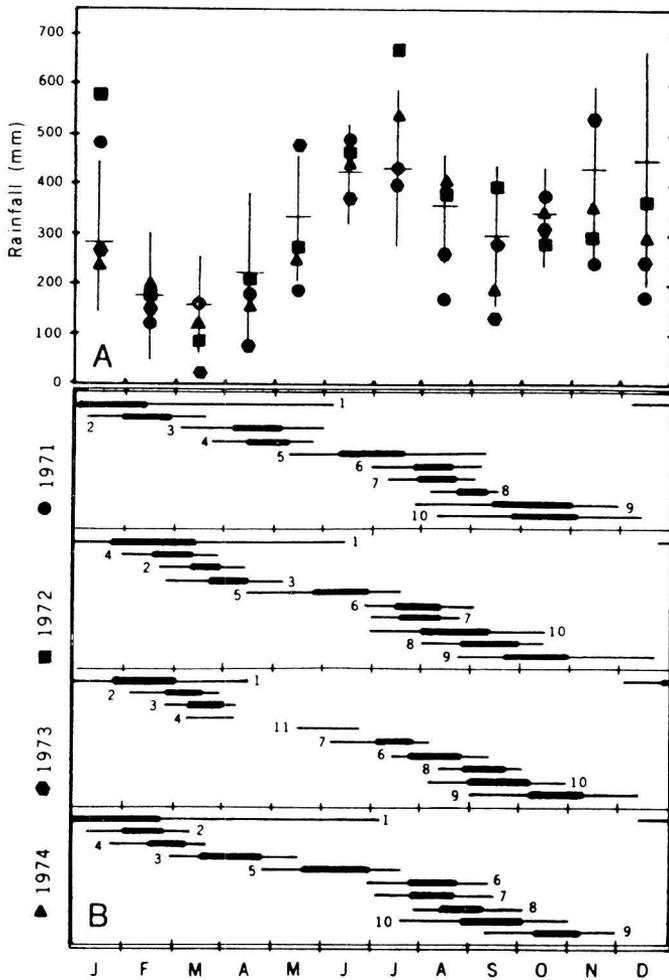


Figure 5.4. Flowering times of 11 species of hummingbird-pollinated plants (lower panel). Numbers denote individual plant species: (1) *Heliconia pogonatha*; (2) *Passiflora vitifolia*; (3) *Heliconia wagneriana*; (4) *Jacobinia aurea*; (5) *Costus ruber*; (6) *Heliconia* sp. 18; (7) *Heliconia* sp. 16; (8) *Aphelandra sinclairiana*; (9) *Costus malortieanus*; (10) *Heliconia* sp. 3; (11) *Malvaviscus arborea*. The upper panel gives the mean and standard deviation of monthly rainfall, with symbols for each of the 4 years of the study. The rainfall data were used to divide the data into wet- and dry-season plants. Depending on the data partition and the null model used, this flowering sequence has been described as aggregated (Poole and Rathcke 1979), random (Gleason 1981), or segregated (Cole 1981). From Stiles, F. G. 1977. Coadapted competitors: the flowering seasons of hummingbird-pollinated plants in a tropical forest. *Science* 198: 1177–1178. Copyright © 1977 American Association for the Advancement of Science. Reprinted with permission.

revealed that flowering peaks in four consecutive years were significantly aggregated, not staggered. However, these results appear to have been inaccurate due to a computational error (Robert W. Poole, personal communication, cited in Gleeson 1981). Gleeson (1981) recalculated the test and found that the pattern actually was staggered ( $P/E(P) < 1$ ), but not significantly so. In any case, the results did not strongly support the original claim of staggered flowering times.

Both Stiles (1979) and Cole (1981) argued that Poole and Rathcke's (1979) analysis was invalid because different groups of species flowered during distinct wet and dry seasons in the Costa Rican rain forest. Cole (1981) reanalyzed flowering times separately for wet- and dry-season species and found significant staggering with the Poole and Rathcke (1979) test.

Cole (1981) argued that the Poole and Rathcke (1979) test was problematic for two reasons: (1) boundaries of the growing season are incorporated into the distance measure for the two terminal species of an assemblage; (2) the test measures not overlap in flowering times, but regularity in the spacing of peak flowering times. Species could have a regular spacing of flowering peaks but still overlap highly in flowering times. Alternatively, species could have clumped flowering peaks but still have little overlap in flowering times. Neither pattern would be revealed by the Poole and Rathcke (1979) test.

Cole (1981) proposed a different metric, which represents the flowering period as a line segment rather than representing the flowering peak as a single point. For the null hypothesis that the flowering period of each species occurs randomly and independently within the growing season, the expected amount of overlap between any given pair of species ( $E(d)$ ) is

$$E(d) = L_2 \frac{LL_1 - L_1^2 - L_2^2}{(L - L_1)(L - L_2)} \quad (5.2)$$

$$L > (L_1 + L_2)$$

$$L_1 > L_2$$

where  $L$  is the length of the growing season,  $L_1$  is the length of the first segment, and  $L_2$  is the length of the second segment. This same model has been developed in the context of niche overlap (Sugihara 1986; see Chapter 4) and the overlap of species spatial ranges (Pielou 1977; Dale 1986; see Chapter 9).

Statistical analysis is problematic. Cole (1981) suggested comparing observed and expected overlaps of all possible species pairs and using a binomial test to evaluate the number of species pairs above and below the expectation. By this test, overlap for Stiles's (1977) data was unusually low ( $p = 0.02$ ). The binomial test assumes that the probability distributions are symmetric and that the species pairs are independent of one another. Cole (1981) showed by

simulation that the symmetry assumption was not critical, but nonindependence of species pairs is a serious problem. Similar comments apply to tests of body size ratios (Case and Sidell 1983; Schoener 1984) and co-occurrence data (Wright and Biehl 1982) that compare all possible species pairs. In contrast to Cole's (1981) test, the Poole and Rathcke (1979) test has relatively weak statistical power (Simberloff and Boecklen 1981), but it summarizes the pattern of peak spacing for an entire assemblage in a single number, so it is not burdened by nonindependent comparisons of individual species pairs.

Fleming and Partridge (1984) investigated phenological overlap with a simulation of Cole's (1981) model. They assumed that the flowering period for each species was fixed in length, and then randomly placed each interval on a line segment. The end points of this line segment corresponded to the observed beginning and end of the flowering season. In addition to pairwise overlap, Fleming and Partridge (1984) measured the  $n$ -wise overlap of each species with the aggregate phenology of the remaining  $n - 1$  species. The  $n$ -wise overlap might provide a better measure of the effects of diffuse competition (Pianka 1974) than the pairwise overlap. Both measures gave similar results, although the null hypothesis was rejected more often with pairwise overlap. Using these methods, Fleming and Partridge (1984) analyzed a variety of published phenologies and found that random or aggregated patterns were the rule. Their test has subsequently been used to assess phenological overlap of other tropical plant assemblages (Fleming 1985; Murray et al. 1987), the timing of seedfall in a guild of ant-dispersed herbs (Kjellsson 1985), and the spatial distribution of parasitic helminths along bat guts (Lotz and Font 1985), all of which were random or aggregated.

However, these measures of phenological overlap may be misleading. Pleasants (1990) tested the statistical power of the pairwise and  $n$ -wise overlap measures against a hypothetical phenology that was strongly segregated. These indices did not reveal significance for assemblages that were obviously structured by competition (Type II error), whereas low overlap was revealed for a hypothetical assemblage that was not ordered by competition (Type I error). Rather than comparing individual species pairs, Pleasants (1990) recommended calculating the average pairwise overlap for the entire assemblage and comparing this single number to the values emerging from the simulation. This is the same metric used in niche overlap studies (Inger and Colwell 1977; Pianka 1980), and it did not suffer from Type I and Type II errors. As we noted for the Poole and Rathcke (1979) test, mean pairwise overlap avoids nonindependent comparisons. Mean pairwise overlap may not reveal some low-overlap patterns (Thomson and Rusterholz 1982), but if both the mean and the variance of overlap are calculated, comparisons with null models will usually be valid (Winemiller and Pianka 1990).

Ashton et al. (1988) pointed out a more serious problem with Monte Carlo simulations of Cole's (1981) model. If the boundaries of the flowering season are determined by the observed first and last flowering species (which is usually the case), the simulated flowering season will always be too short because the segments are thrown randomly between these two boundaries. This "edge effect" (Haefner et al. 1991) biases the test toward finding staggered (low-overlap) patterns. It is therefore noteworthy, and worth repeating, that most simulation studies have detected random or aggregated patterns, which are in the opposite direction of this inherent bias.

Ashton et al. (1988) suggested a simple scaling procedure that adjusts the simulated flowering phenologies to the correct growing season. First, randomize the placement of the flowering *peaks* within the line segment, as in the Poole and Rathcke (1979) test. Then expand the scale of the segment to encompass the starting time of the first species and the ending time of the last. This scaling ensures that the simulated flowering times are randomly placed within the growing season. Overlap in the null assemblage can then be compared to the real data. Using this procedure, Ashton et al. (1988) detected a significant staggering of flowering times in tropical dipterocarps. An additional null model showed that mass flowering years were associated with droughts and the occurrence of El Niño events.

Staggered flowering times have also been detected in meadow plant communities of the Rocky Mountains. Pleasants (1980) divided the assemblage into guilds based on the identity of the dominant species of bumblebee pollinator. Of 11 guild comparisons, mean pairwise overlaps were significantly less than expected in five, and marginally less than expected ( $0.05 < p < 0.15$ ) in five others. However, these simulations followed Cole's (1981) procedure, so they were biased against the null hypothesis (Ashton et al. 1988). In addition, previous null model tests of flowering times in a different set of sites in the Rocky Mountains did not reveal a significant reduction in temporal overlap (Thomson 1982).

Phenological studies indirectly assess competition for pollinators by assuming it is more severe with increasing temporal overlap. Armbruster (1986) addressed competition more directly by examining species co-occurrence and shared pollinators in assemblages of the euphorb *Dalechampia*. His study is a botanical analog to the mixed-matched dietary hypothesis for predator assemblages. Armbruster's (1986) analysis is noteworthy for its use of both "ecological" and "evolutionary" null hypotheses. These null hypotheses are similar in spirit to tests for mechanisms of ecological assortment and evolutionary divergence (Case and Sidell 1983) in producing patterns of character displacement (see Chapter 6). The ecological null hypothesis was that sympatric species

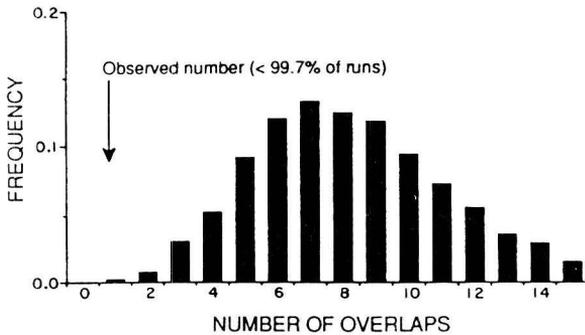


Figure 5.5. Frequency distribution of pollinator niche overlaps generated by a null model for Australian triggerplants (*Stylidium*). From Armbruster et al. (1994), with permission.

were assembled at random with respect to the pollinator species utilized. The evolutionary null hypothesis was that each population evolved pollinator associations at random with respect to those of sympatric congeners. A mixed model contained elements of both ecological and evolutionary models. Overall, there was a marginal tendency toward reduced overlap in shared pollinators, although the results depended on the type of null model used, whether source pool species were equiprobable colonists or not, and how local sympatry was operationally defined.

A similar analysis revealed much more striking patterns in an assemblage of 31 species of triggerplants (*Stylidium* spp.). At 25 sites in western Australia, there was only one overlap of discretely defined pollinator niches for 86 comparisons of sympatric species pairs (Armbruster et al. 1994). In contrast, the ecological, evolutionary, and mixed null models generated an expectation of approximately four to seven pollinator niche overlaps (Figure 5.5). Nine species of *Stylidium* in this assemblage exhibited intraspecific variation in column reach, which determines pollen placement. A significant pattern of character displacement in the presence of sympatric congeners also suggested that competition for shared pollinators structured this assemblage.

These examples of reduced overlap in pollinators or flowering times are exceptional. Most tests have revealed aggregated or random phenological overlap, compared to the null hypothesis of equiprobable flowering periods within a uniform growing season. Detailed studies of phenology in temperate (Parrish and Bazzaz 1979; Anderson and Schelfhout 1980; Rabinowitz et al. 1981) and tropical (Wheelright 1985) plant communities have not revealed unusually low temporal overlap. For example, Rathcke (1988a) measured the flowering periods of 14 species of temperate shrubs over five years. Flowering

phenologies were significantly aggregated within a season and consistent across years. Although aggregation might increase competition for pollinators, field experiments showed that seed production of only four of the 14 species was limited by pollination, and of these, only one was likely to have suffered competitive effects (Rathcke 1988b).

## CONSTRAINTS

The independent placement of species flowering times within a uniform growing season is the appropriate null hypothesis for tests of phenological overlap. However, even within an appropriately defined growing season, there may be other types of constraints on flowering phenology. For example, the flowering interval for a species may be correlated with the time of the flowering peak in the growing season (Ashton et al. 1988), and null models might be made more sophisticated by incorporating such constraints. Divergence in flowering times may also be constrained by plant mating systems (Lindsey 1982; Flanagan and Moser 1985), seed predators (Augsburger 1981), seed production (Roach 1986), and pollinator attraction (Augsburger 1980). Some of these forces may promote convergence rather than divergence of flowering times.

A more fundamental limitation to flowering phenology may be inherent phylogenetic constraints on flowering time. Independent of ecological forces, the flowering time of a species may fall within certain limits that are characteristic of its clade. Kochmer and Handel (1986) used phylogeny as a “null hypothesis” in a comparative study of flowering times of animal-pollinated angiosperms of North and South Carolina and temperate Japan. Flowering times were similar on the two continents but differed significantly for species in different plant families. Each plant family had a characteristic flowering time and skewness, and there were negative correlations between skewness and mean family flowering times. These phylogenetic “fingerprints” were more pronounced than differences in flowering times among plant life forms (e.g., trees versus shrubs). The results suggest that, regardless of local competitive pressures, the flowering times of plant species were limited by phylogeny. Within these limits, phenology may still be shaped by competition, mutualism, and other ecological interactions, although Kochmer and Handel’s (1986) analyses were too coarse to evaluate such effects. In any case, the use of phylogeny as a null hypothesis is a promising avenue for future studies of phenology and other community-level patterns (Harvey and Pagel 1991).

## NONEQUILIBRIUM ANALYSES

The preceding analyses all make the implicit assumption that flowering times or activity periods of species have reached an ecological or evolutionary equilibrium. The equilibrium assumption underlies much of the deterministic mathematics of community ecology theory (e.g., MacArthur 1972), but its relevance to many real communities is questionable (e.g., Boecklen and Price 1991). Equilibrium and nonequilibrium communities may be structured by different mechanisms (Wiens 1984). For example, predictable patterns of resource availability may lead to specialization and resource partitioning by competitors in an equilibrium community (Schoener 1974a). In phenological studies, equilibrium communities would exhibit the same patterns of temporal overlap from one year to the next (e.g., Stiles 1977; Rathcke 1988a). In contrast, if the availability of resources fluctuates through time, competitive effects may be intermittent and may only be important during occasional “resource crunches” (Wiens 1977). For phenological studies, nonequilibrium communities would be characterized by variable patterns of temporal overlap and sets of shared pollinators.

What would constitute a valid null model for assessing the equilibrium status of a community? In Chapter 10, we consider this problem in the context of community stability and food web models. Here, we address a more restricted question: Do co-occurring species exhibit compensatory fluctuations in abundance, activity, or phenology? Compensatory change might suggest competitive interactions as species covary negatively in abundance. Alternatively, positive covariation might result if species tracked shared resources that fluctuate in abundance (Schluter 1984).

The data for such an analysis would consist of a matrix with rows representing species and columns representing census dates. The entries in the matrix are the abundance (or activity) of each species at each census. Patterns of covariation in this matrix can be quantified by comparing the sum of the individual species variances to the variance of their sums (Pielou 1972a; Robson 1972). The latter variance includes the average covariation between species pairs, which is a good measure of compensatory fluctuations. The ratio of the second variance to the first,  $V$ , reveals whether species are fluctuating independently ( $V = 1$ ), concordantly ( $V > 1$ ) or compensatorily ( $V < 1$ ). Järvinen (1979) calculated the reciprocal of  $V$  for censuses of avian communities at different latitudes. This index was not consistently different for northern versus southern assemblages, contradicting the hypothesis that compensatory fluctuations stabilize species-rich tropical communities (McNaughton 1977).

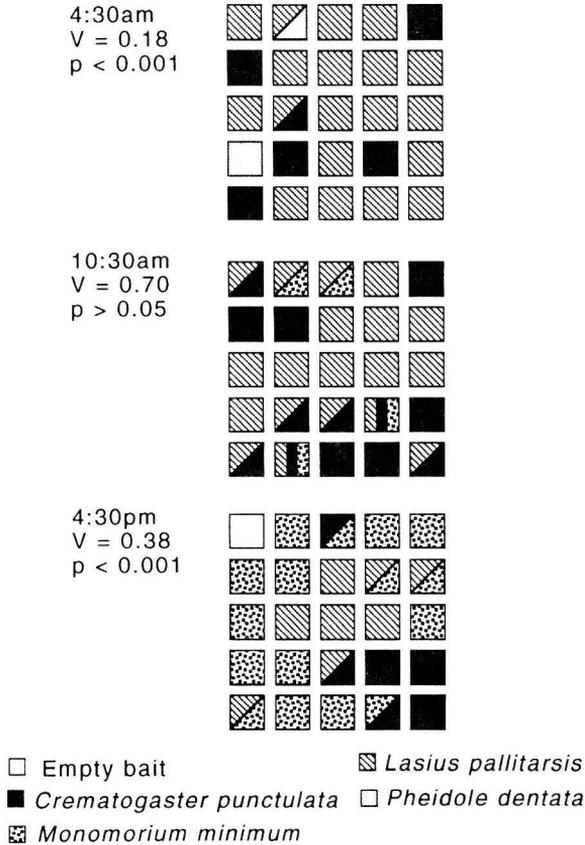


Figure 5.6. Spatial and temporal segregation of common grassland ants as measured by the variance ratio (Schluter 1984). Each matrix shows the species occurrences at 25 tuna-fish baits placed in a  $5 \times 5$ -m grid that were censused for 24 consecutive hours in Caddo County, Oklahoma, July 1992. The variance ratio indicates significant spatial partitioning at certain times of the day. Symbols indicate the presence of particular species at individual baits. Unpublished data from Marc C. Albrecht.

James and Boecklen (1984) refined this approach in an analysis of seven years of breeding bird census data from Maryland woodlands. To estimate the variance components, they assumed that individual birds were distributed according to a Poisson process.  $V$  for this assemblage was 0.65, which was in the direction of negative covariation, although still within the limits expected by chance ( $p \approx 0.28$ ). The covariance matrix revealed one pair of species (Cardinal–Red-eyed Vireo) with a large positive covariation, followed in order of decreasing magnitude by pairs with positive or negative covariation. Al-

though the abundances of particular pairs of species were correlated, there was no evidence over the 7-year study for strong compensatory fluctuations in the assemblage as a whole.

Schluter (1984) developed significance tests for the variance ratio. The product of the variance ratio and the number of censuses ( $VT$ ) has an approximate chi-squared distribution with  $T$  degrees of freedom. Simulated data showed an acceptable fit to the chi-squared distribution, so the variance ratio can be evaluated without the use of a simulation. McCulloch (1985) showed that, for presence-absence data, the variance ratio is a multiple of Cochran's  $Q$  statistic (Cochran 1950), which has been used as a null hypothesis to test equiprobable colonization of aquatic taxa in experimental ponds (Wilbur and Travis 1984). Hastings (1987) found that the variance ratio did not always reveal significant patterns for a simple competition model in which the probability of extinction was proportional to species richness. The variance ratio will reveal cases where the average pairwise correlation between species is negative (McCulloch 1985), although, like all statistical tests, the variance ratio is sensitive to sample size and sampling error. Perhaps for this reason, a literature survey of species co-occurrence matrices revealed mostly random or aggregated spatial patterns as measured by the variance ratio (Schluter 1984).

An interesting exception can be found in the co-occurrence pattern of ant species at tuna-fish baits in an Oklahoma grassland (Marc C. Albrecht, unpublished data). Spatial occurrence, as measured by the variance ratio, was strongly negative. However, the spatial pattern changed on an hourly basis, as different associations of species emerged because of diel foraging patterns (Figure 5.6). Most authors have used the variance ratio as an index of spatial co-occurrence (see Chapter 6), and more long-term community studies such as James and Boecklen's (1984) are needed to evaluate the compensatory fluctuations hypothesis.

## RECOMMENDATIONS

To compare the diets of synchronous and asynchronous predators, we recommend Pimm's (1983) Monte Carlo simulation of the mixed-matched dietary hypothesis. The Poole and Rathcke (1979) test, with modifications by Williams (1995), is acceptable for simple analyses of flowering peaks, although some of the character displacement tests described in Chapter 6 may be more powerful. If the data consist of flowering intervals for each species, we recommend the modification of Cole's (1981) test by Ashton et al. (1988). The variance ratio (Schluter 1984) is appropriate for testing the hypothesis of compensatory fluctuations of abundance or activity through time.

