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Temporal Separation of Activity and Interspecific Dietary Overlap

Raymond B. Huey
and Eric R. Pianka

SYMPATRIC PREDATORS are sometimes active at different times of day (Schoener, 1974). Lizards and raptors (owls and hawks) are conspicuous examples of groups that contain both diurnal and nocturnal species, and many other animal groups contain species that have more subtle differences in times of activity (Pianka, 1969b; Schoener, 1970; Pianka, Huey, and Lawlor, 1979). Interspecific nonsynchrony in activity can be related to the intensity of competition in two fundamental ways. First, if differences in times of activity lower frequencies of direct encounters between predators, interference competition may be reduced (Case and Gilpin, 1974). Second, if such temporal differences lower dietary overlap, exploitation competition for food can also be reduced (MacArthur and Levins, 1967; Levins, 1968).

Because of these direct and indirect effects of temporal separation on competition, time is often treated as a major niche dimension, along with space and food (Pianka, 1969b, 1973, 1974; Cody, 1974; Schoener, 1974). Time has sometimes been viewed as an indicator of dietary or spatial competition. Arguments supporting the use of temporal separation as an indicator of dietary separation rest, however, on the largely unverified assumption (Jaksić, Greene, and Yañez, 1981; Jaksić, 1982) that nonsynchronously active predators should be exposed to differing prey worlds (Lewis and Taylor, 1964) and should therefore encounter and eat different prey (Schoener, 1974). But if prey are rapidly renewed (MacArthur and Levins, 1967) or if differences in activity periods between consumers are major, such as between species active during different seasons, then renewal of prey itself could suffice as an alternative explanation for reduced exploitation competition (Pianka, Huey, and Lawlor, 1979; Jaksić, Greene, and Yañez, 1981).

Despite the intuitive appeal of these arguments, workers have long commented on the similarity of diets of nocturnal and diurnal raptors (Munro, 1929; Baumgartner and Baumgartner, 1944; Lack, 1946; Fitch, 1947; Jaksić, 1982). Indeed, prompted by evidence of a high overlap in diet between great horned owls and red-tailed hawks, Orians and Kuhlman (1956) suggested that a study of the interactions between diurnal and nocturnal predators would be worthwhile.

One indirect test of the assumption that differences in times of activity affect dietary overlap compares dietary overlaps of pairs of synchronous and nonsynchronous predators. If prey worlds are more similar for synchronous than for nonsynchronous pairs, then synchronous predators are more likely to have higher dietary overlaps than are nonsynchronous predators. Conversely, if time has no effect on foods eaten, then both synchronous and nonsynchronous pairs should show similar dietary overlap. Note that this prediction is statistical, not absolute; two synchronous predators that forage in different ways or in different microhabitats might actually be exposed to very different prey worlds (Huey and Pianka, 1981).

Lizards are ideal subjects for examining the influence of time of activity on diet. Here we present data on dietary overlaps among lizards that differ strikingly in short-term activity periods: nocturnal versus diurnal lizards from the Kalahari and Australian deserts. Specifically, we investigate whether pairs of synchronous species (nocturnal × nocturnal, diurnal × diurnal) tend to overlap more in diet than nonsynchronous pairs (nocturnal × diurnal). To determine the generality of our results, we supplement these data with examples from the literature on other diurnal/nocturnal predators (raptors, water snakes). Our analyses and those of Jaksić, Greene, and Yañez (1981) and Jaksić (1982) demonstrate that nonoverlapping activity periods are sometimes but not invariably associated with lower dietary overlaps. In fact, a few nonsynchronous pairs have nearly identical diets. The evolution of more subtle differences in activity periods (within a day or within a night) among closely related species is less likely to be related to reduced exploitation competition than to reductions in interference competition, risk of predation, or other factors.

Our analysis is based primarily on stomach contents of 4,214 lizards (mean ± standard error = 234 ± 45 stomachs/species, range = 19 to 688) of 18 species (12 diurnal, 6 nocturnal) collected in 10 study areas in the Kalahari semidesert of southern Africa (see Pianka, 1971) and from 3,376 lizards ($\bar{x}$ = 80 ± 14 stomachs/species, range = 10 to 511) of 42 species (28 diurnal, 14 nocturnal) collected in the Great Victoria Desert of Western Australia (Pianka, 1969a). We examined 94,915 prey items ($\bar{x}$ = 5,273 ± 1,183 prey/species of lizards, range = 64 to 33,216) from stomachs of Kalahari lizards and 107,820 prey items ($\bar{x}$ = 2,567 ± 1,145 prey/species, range 38 to 60,013) from stomachs of Australian lizards, measured volumes of each prey item, and classified prey into 46 (Kalahari) or 20 (Australia) taxonomic categories (Pianka, Huey, and Lawlor, 1979). After we determined the proportional volumetric representation of each prey category in the diets of all species, we computed dietary overlaps between all species pairs within deserts using a symmetrical formula (Pianka, 1973) that generates values between zero (no overlap) and one (complete overlap). Because certain broad prey categories (beetles, for example) undoubtedly include both nocturnal and diurnal species, we emphasize that these calculated values overestimate true dietary overlap. This bias is less severe in the Kalahari because of the larger number of prey categories and because termites, which constitute nearly half (41.3 percent by volume) of the total diet of all Kalahari lizards (Pianka, 1973), were identified to species and caste.

To reduce problems associated with species having small samples or unusual microhabitat associations, we do not consider data on 4 other Kalahari species and 19 other Australian species that were represented by fewer than 10 specimens, were fossorial, or had ambiguous activity periods. For the remaining species dietary-niche breadths computed with the diversity index of Simpson (1949) were not significantly correlated with either the number of stomachs per species of lizard (Kalahari $r_s = 0.10$, $P > 0.1$; Australia $r_s = 0.28$, $P > 0.1$) or with the number of prey per species of lizard (Kalahari $r_s = -0.18$, $P > 0.1$; Australia $r_s = 0.25$, $P > 0.1$), suggesting that sample sizes are adequate to characterize the diets of species. Moreover, proportions of species that are ground-dwelling versus arboreal among diurnal and nocturnal lizards do not differ significantly in either desert, suggesting that we have not inadvertently incorporated a habitat effect on dietary overlap.

The basic data contain an inherent statistical bias due to the transitive nature of overlap values (that is, if species A and species B have very high overlap, and if species B and species C also overlap substantially, then species A and species C will probably also have high overlap). The resulting lack of complete independence among overlap values violates assumptions of traditional statistical methods (Meagher and Burdick, 1980; Pimm, appendix to this chapter).

A second potential statistical problem arises when one uses a nearest-neighbor analysis (see below) to determine whether pairs of species that are synchronously active have higher dietary overlap than do nonsynchronous pairs of species. The relative number of synchronous and nonsynchronous pairs is equal only if the numbers of diurnal and nocturnal species are equal; if not, whichever group has the larger number of pairs will tend to have higher overlaps among nearest neighbors because of augmented sample size (R. K. Colwell, personal communication; Pimm, appendix). In our Kalahari and Australian samples synchronous pairs outnumber nonsynchronous pairs. Consequently, the bias favors the hypothesis that nearest neighbors that are synchronous should have higher overlap than do nearest neighbors that are not synchronous in activity.

To circumvent these statistical roadblocks, we exploit Monte Carlo computer simulation techniques (Pimm, appendix) and generate frequency distributions of similarity values obtained from randomly assigning the states "nocturnality" or "diurnality" to each of the observed species in the Kalahari and Australian samples. The resulting distributions allow direct computation of probabilities: thus, if the observed, actual, overlap value (or values more extreme) is encountered only twice in 200 such randomizations, its one-tailed probability of being different is 0.01, if it is encountered less than ten times in 200 runs, then $P < 0.05$, and so on (see Pimm, below).

Desert Lizards

In terms of relative dietary overlap, each species of lizard has a first, second, third, . . . , *n*th nearest neighbor that is synchronous for activity time (nocturnal × nocturnal pairs, diurnal × diurnal pairs) and a second set of neighbors that is not synchronous for activity time (diurnal × nocturnal pairs) (Inger and Colwell, 1977). Because our interest is in the possible effect of time of activity on diet of potentially competing species, we focus on overlaps among closest neighbors. Alternatively, one could compare average or median overlaps among all synchronous versus all nonsynchronous pairs, but this approach, which includes overlap values from many pairs with distinctive diets, obscures potential patterns of dietary differences.

We first compute the percentage of species whose nearest neighbor in diet is synchronous for activity time (Table 13.1). In both deserts significantly more first and second nearest neighbors are active synchronously than is expected using a random null hypothesis (Monte Carlo simulations), but the percentages of both third and fourth nearest neighbors that are synchronous do not differ from the null hypothesis. (We thank J. Felsenstein for helping us with these simulations.) Thus first and second nearest neighbors in diet are usually active at the same general times, but third and fourth nearest neighbors are as likely to be active at different times.

We next examine the magnitude of differences in dietary overlap by computing mean overlap values among all first, second, third, and fourth nearest neighbors for synchronous and nonsynchronous pairs (Table 13.2) and compare these observed averages with expected values that are generated from the Monte Carlo simulations (Fig. 13.1; see Pimm, below). In both deserts nearest neighbors with synchronous activity generally overlap

Table 13.1 Percentages of nearest neighbors (first through fourth) that are synchronously active in 3 independent communities.

	Nearest neighbor			
Population (diurnal, nocturnal)	First	Second	Third	Fourth
Kalahari lizards (12,6)				
Observed synchronous pairs	88.9	83.3	61.1	61.1
Predicted synchronous pairs	52.9	52.9	52.9	52.9
P	< 0.01	< 0.01	> 0.30	> 0.30
Australian lizards (28,14)				
Observed synchronous pairs	83.3	81.0	57.1	57.1
Predicted synchronous pairs	54.5	54.5	54.5	54.5
P	< 0.001	< 0.001	> 0.40	> 0.40
Michigan raptors (5,4)				
Observed synchronous pairs	66.7	55.6	55.6	55.6
Predicted synchronous pairs	44.4	44.4	44.4	44.4
P	> 0.25	> 0.35	> 0.35	> 0.35

NOTE: Observed values are derived from dietary comparisons. Probability levels (P) are derived from the results of 1,000 simulations (Monte Carlo) assuming a null hypothesis that the similarity of diet is independent of time of activity. The predicted percentages of synchronous pairs under a null hypothesis are calculated from a formula: $[D(D-1) + N(N-1)]/[(N+D)(N+D-1)]$, which is the probability that 2 species chosen at random without replacement will have the same activity time (J. Felsenstein, personal communication).

$P < 0.005$) when first through fourth nearest neighbors are examined together using Fisher combined probability tests. In these comparisons, dietary overlaps tend to be lower than expected among pairs with nonsynchronous activity (Table 13.2, Fig. 13.1), and overall trends are also significant nevertheless (Fisher combined probability tests: $P < 0.005$ in Kalahari, $P < 0.05$ in Australia). Clearly, time of activity significantly affects average dietary overlap among nearest neighbors of these lizards.

Both the above methods emphasize that time of activity influences dietary overlap. Nevertheless, the magnitude of this effect tends to decrease as nearness rank increases (Tables 13.1 and 13.2, Fig. 13.1). Average overlap values among first nearest neighbors that are nonsynchronous in activity times are comparable or even higher than the average overlap values for third and fourth nearest neighbors that are active synchronously (Fig. 13.1, Table 13.2). In other words, whereas the first and second most similar species are normally active at the same times, the third and fourth nearest neighbors

Table 13.2 Average (± S.E.) dietary overlaps among first, second, third, fourth nearest neighbors that are synchronously or nonsynchronously active.

Population (number of species)	Average dietary overlap			
	First	Second	Third	Fourth
Kalahari lizards (18)				
Synchronous	0.84 ± 0.04	0.69 ± 0.04	0.58 ± 0.04	0.53 ± 0.4
Significance	< 0.001	0.010	< 0.001	< 0.001
Nonsynchronous	0.60 ± 0.05	0.54 ± 0.05	0.49 ± 0.05	0.41 ± 0.04
Significance	< 0.001	0.042	0.208	0.286
Australian lizards (42)				
Synchronous	0.87 ± 0.02	0.84 ± 0.02	0.79 ± 0.02	0.68 ± 0.03
Significance	0.070	< 0.001	0.005	0.231
Nonsynchronous	0.80 ± 0.03	0.71 ± 0.03	0.67 ± 0.04	0.64 ± 0.04
Significance	0.065	0.055	0.141	0.578
Michigan raptors (9)				
Synchronous	0.99 ± 0.01	0.88 ± 0.05	0.86 ± 0.05	
Nonsynchronous	0.95 ± 0.03	0.93 ± 0.04	0.78 ± 0.04	

NOTE: Significance levels for synchronous pairs indicate whether overlap is greater than expected on a random null hypothesis, whereas those for nonsynchronous pairs indicate whether observed overlap is less than expected.

Water Snakes and Raptors

Although our primary results concern the above analysis of our original Kalahari and Australian lizard data, we made a cursory search of the literature to determine whether the observed pattern has general application. Certain water snakes (*Nerodia* = *Natrix*) and raptors (hawks and owls), which differ in activity times and have well-studied diets, are suitable subjects from very different ecosystems.

Mushinsky and Hebrard (1977a,b) studied activity periods and diets of 4 species of *Nerodia* in Louisiana. Most important, they identified prey at least to genus, thereby minimizing the problem of overestimating dietary overlap. Mushinsky and Hebrard (1977a) observed some differences in diet between nocturnal and diurnal species (for example, the nocturnal *Nerodia rhombifera* ate more frogs and catfish, which are nocturnal, than comparable diurnal species). Although numbers of species are too few for meaningful statistical analysis (Pimm, below), average overlap between nonsynchronous pairs ($\bar{x}$ = 0.85, N = 4, range = 0.78–0.96) is actually slightly higher than that between synchronous pairs ($\bar{x}$ = 0.79, N = 2, range = 0.74–0.83). In particular, the nocturnal *N. rhombifera* and the diurnal *N. cyclopion* have nearly identical diets (0.96). Differences in times of activity certainly do not guarantee low dietary overlap.

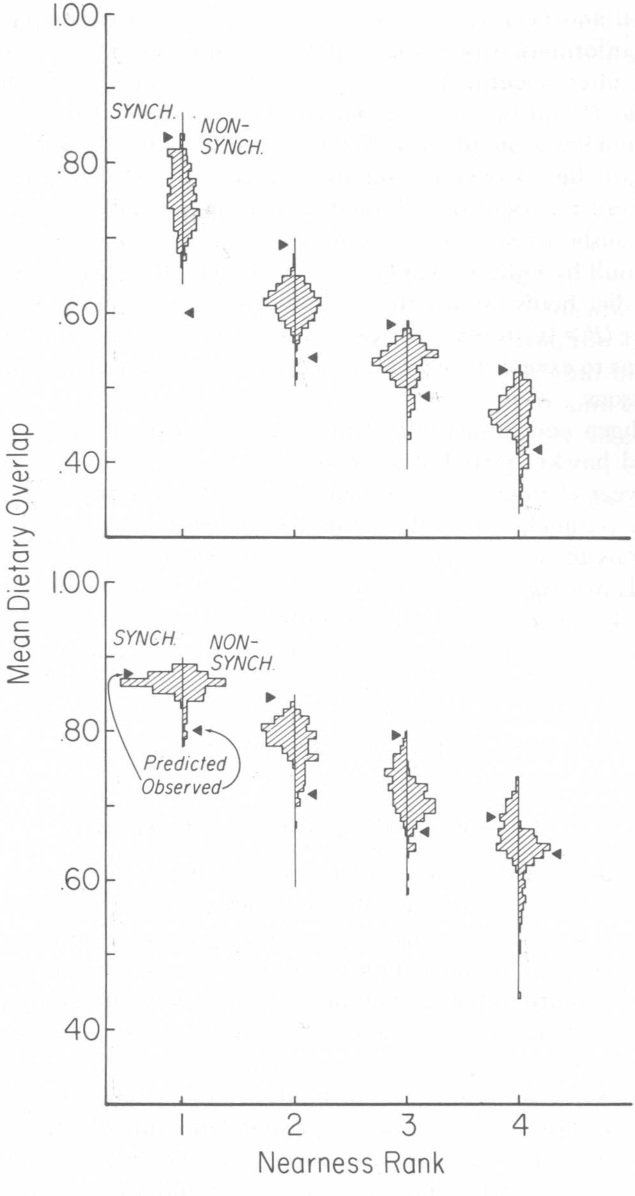

Figure 13.1 Frequency distributions of dietary overlap values generated by Monte Carlo simulations for the first 4 nearness ranks in niche space for lizards in the Kalahari semidesert (*upper panel*) and for lizards from the Great Victoria Desert in Western Australia (*lower panel*). Monte Carlo histograms are cross-hatched: those on the left side of the vertical line represent synchronous pairs (N = 200), whereas those to the right represent nonsynchronous pairs (N = 200). Observed average overlap values are depicted by solid triangles outside the histograms.

Diurnal and nocturnal raptors are an especially rich source of comparative information (see Jaksić, 1982). Samples are usually large, and prey are often identified as to species. For example, Craighead and Craighead (1956) presented extensive data on diets of nocturnal owls and diurnal hawks in Superior Township, Michigan. We used these data to calculate dietary overlaps among all species pairs during the fall and winter. Percentages of first through fourth nearest neighbors that were synchronously active were not significantly higher than expected on a random null hypothesis (Table 13.1). Moreover, this lack of an effect of time on diet holds even if the probabilities are combined by a Fisher exact text ($P > 0.10$). As is the case for the water snakes, time of activity thus seems to exert little effect on dietary overlap among raptors during these seasons.

Korschgen and Stuart (1972) presented 20 years of data on diets of red-tailed hawks, great horned owls, and barred owls from Missouri. Year-to-year changes in the proportional utilization of prey species are generally parallel among these raptors. Between-year Spearman rank correlations in percentage (by volume) of *Sigmodon hispidus,* of rabbits (primarily *Sylvilagus*), and of *Microtus* in the diets are 0.77, 0.56, and 0.42, respectively (all $P < 0.05$), for red-tails versus great horned owls; 0.82, 0.50, and 0.58, respectively (all $P < 0.05$), for red-tails versus barred owls; and 0.88, 0.48, and 0.67, respectively (all $P < 0.05$) for great horned owls versus barred owls. Thus yearly shifts in diet are similar between raptors with different activity periods (Korschgen and Stuart, 1972).

Time of Activity and Dietary Overlap

Our analysis of diets of nocturnal versus diurnal predators demonstrates that differences in time of activity are sometimes associated with significantly lower dietary overlaps, but only among species with very similar diets. Even so, the magnitude of this effect is not great: moreover, nocturnal × diurnal pairs sometimes have nearly identical diets. Therefore, degree of synchrony in activity periods is evidently an unreliable index of dietary overlap.

These results, which refute expectations of a strong relationship between activity time and diet, are surprising. Undoubtedly, the crudeness of many prey taxa categories obscures some real dietary differences. Nevertheless, even with the data on raptors and water snakes, where prey were identified as to genus or species, time of activity has no dramatic effect on diet. If these patterns are real, we need to question our initial assumptions rather than the data base.

The first assumption is that prey are either nocturnal or diurnal. However, some prey species are probably crepuscular (Lewis and Taylor, 1964) and might be eaten by both diurnal and nocturnal predators (Jaksić, Greene, and Yañez, 1981). Some predators, including certain owls, are also crepuscular. Moreover, other prey (and some predators) may switch from diurnality to nocturnality on a daily (Wilson and Clark 1977) or a seasonal basis (Jaksić, Greene, and Yañez, 1981) and thus be eaten by both types of predators.

A second implicit assumption, that prey are vulnerable to predation only while active, is certainly not universally true. In particular, few inactive arthropods enjoy inviolate sanctuaries. In the Kalahari, for example, nocturnal scorpions spend daylight hours in underground burrows, but are nevertheless the dominant prey of *Nucras tessellata*, a strictly diurnal lizard which searches for inactive scorpions in burrows (Pianka, Huey, and Lawlor, 1979). An Australian lizard species, the legless and snake-like *Pygopus nigriceps*, is also a scorpion specialist, but in this case the predator is nocturnal and captures its prey above ground during the latter's period of activity at night. Interestingly, no North American desert lizard species is a scorpion specialist, even though these large arachnids are abundant. Perhaps the small snake *Chionactis occipitalis* has usurped this ecological role (Norris and Kavanau, 1966).

Similarly, predators such as the diurnal lizard *Cnemidophorus tigris* that dig or search for inactive prey (termites) can have high dietary overlap with other predators like the sympatric nocturnal gecko *Coleonyx variegatus* which eats the same prey but captures them when they are active (dietary overlap between this species pair is 0.897 compared with an overall community-wide average overlap in diet of only 0.43). In short, diurnal predators can often find nocturnal prey in their diurnal retreats, whereas nocturnal predators may frequently be able to do the equivalent with diurnally active prey. For these reasons, time of activity may be of limited significance in reducing dietary overlap; attempts to analyze predator-prey interactions from measured or predicted overlaps in activity times (for example, Porter et al., 1973) are potentially risky.

In an analysis of vertebrate predators in Chile (hawks, falcons, owls, foxes, and snakes), Jaksić, Greene, and Yañez (1981) found only subtle differences in diet between diurnal and nocturnal predators. They argue that temporal separation of activity is an inefficient mechanism for reducing dietary overlap and propose that predatory guilds should be recognized "solely on food-niche overlap patterns, because activity times and habitat selection of both predators and prey are thereby implicitly included."

Evolution of Thermal Preferences

The times that a lizard can be active depend primarily on interactions among the physical environment thermoregulatory resent one potential mechanism by which temporal overlap can be adjusted.

Nevertheless, for several reasons we doubt that the evolution of thermal preferences is often related to exploitation competition for food. Thermal preferences seem to evolve very slowly in most ectotherms (Bogert, 1949; Huey and Slatkin, 1976; but see Hirshfield, Feldmeth, and Soltz, 1980; Huey, 1982): thus a particular competitive interaction would probably have to persist for a long period of time to influence thermal preferences. Also, in thermally heterogeneous habitats, even species with nonoverlapping thermal preferences can still overlap extensively in times of activity (see Huey, 1982).

These arguments suggest that the evolution of thermal preferences in lizards should be weakly related to exploitation competition for food. However, a divergence in thermal preference could be influenced by interference competition (Case and Gilpin, 1974), by divergence in habitat associations, or even by risks of predation. Indeed, perhaps reductions in temporal overlap with predators were the major reason for evolution of activity at low body temperatures among nocturnal lizards such as geckos and some skinks, as well as at very high body temperatures (for example, *Dipsosaurus dorsalis, Nucras tessellata,* and *Ctenotus leae*).

Our results and those of Jaksić, Greene, and Yañez (1981) and Jaksić (1982) demonstrate that major differences in time of activity, such as those between diurnal and nocturnal predators, do not invariably result in low dietary overlap. These findings challenge the widely accepted assumption that temporal separation of activity is invariably effective in lowering dietary overlap and invite caution in using time as a niche dimension. Minor differences in activity periods (within a day), which occur commonly in lizards (Pianka, 1971; Schoener, 1977), would appear to be even less effective in reducing dietary overlap. We encourage more empirical studies on this general problem as well as additional theoretical analyses (Case and Gilpin, 1974) on time of activity as a mechanism of coexistence of species. Both would be timely.

Appendix: Monte Carlo Analyses in Ecology

Stuart L. Pimm

The central feature of a statistical test is conceptually simple. We measure a quantity and then determine the probability of the appearance of a value as extreme as or more extreme than the one measured. This probability is stated in terms of a mathematically formulated hypothesis (the null hypothesis). If this probability is sufficiently small (usually < 0.05), then we reject the null hypothesis and the biological hypothesis that it implies. We usually obtain the probability from a well-known model of how the values of the quantity should be distributed and more directly, from a set of tables (F, t, χ^2, etc). Although the majority of distributions we encounter fit or can be made to fit one of a very limited number of simple distributions, not all do. In these exceptional cases we must resort to other techniques to find distributions and, from these, the required probabilities. Sometimes these special distributions can be derived analytically. More often, this is difficult or impossible due to the special constraints biology places on the distributions. But we can often approximate the distributions using numerical methods on a computer. Such is the case with the problem posed above by Huey and Pianka's study of the influence time of activity has on dietary overlap.

Their data involve the similarity in diet between lizard species that are either nocturnal or diurnal. To simplify discussion of the problems the data pose, I shall consider the dissimilarity between species' diets. These values can be obtained simply by subtracting the similarity values from unity. And the dissimilarity values can be represented graphically by the distances between points (which represent species). Though the dimensionality of the data is large—it requires up to $n - 1$ dimensions to represent all the distances between n species—a two-dimensional representation (Fig. 13.2) of the problem is adequate for my purposes.

The figure shows a hypothetical array of 3 nocturnal and 3 diurnal species. We need to ask: how should the distances between these 6 points be distributed? The answer is "not simply" for several reasons:

Suppose the nearest diurnal species to diurnal species D_1 is D_2; the distance between them is x. And further suppose that the nearest nocturnal species to D_1 is N_1, the distance between them being y. Now, a requirement of all simple statistical tests is that each quantity involved (say the individual observations that contribute to a mean) be independent of all the other quantities in the test. This requirement is clearly violated in our example. The distance between D_2 and N_I—call it z—is limited by simple geometry thus: $z < x + y$, and $z > y - x$. These and similar conditions mean that distances between species that are active at similar times of day (either both nocturnal or both diurnal) and those distances between species active at different times of day will be interrelated. (For convenience, I shall call the first set of distances nocturnal-nocturnal or diurnal-diurnal distances, matched, and the other dis-

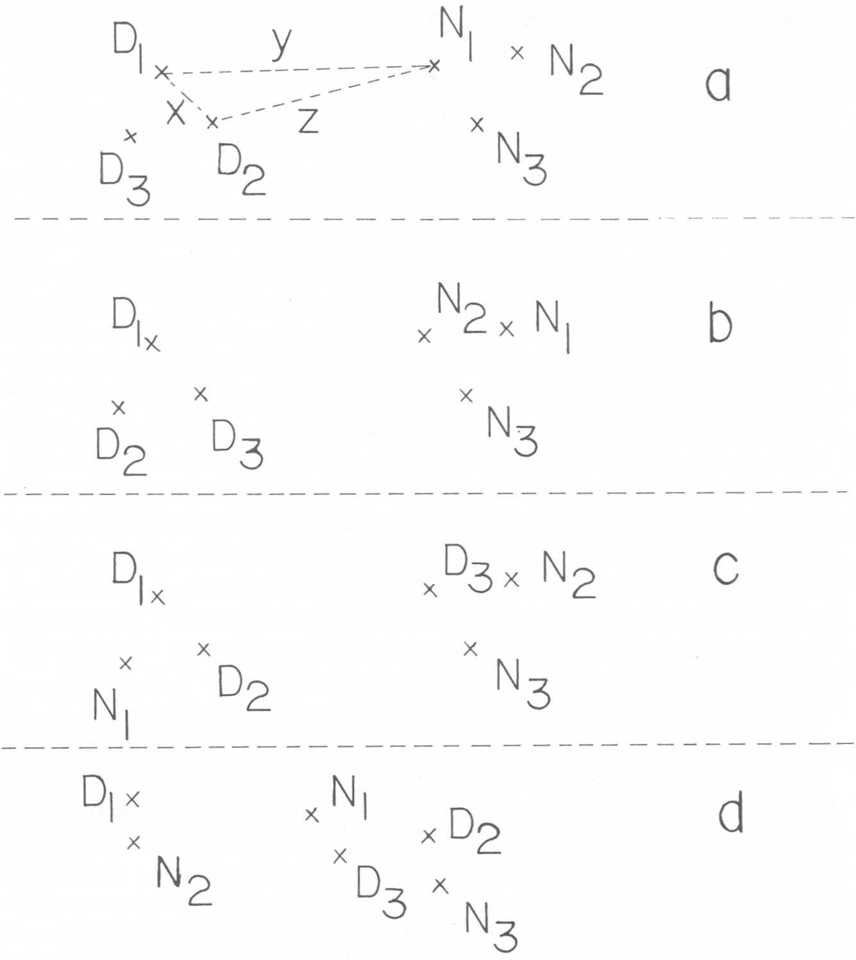

Figure 13.2 Four examples to illustrate the methods used to calculate statistics on dietary similarities. There are 6 species: 3 diurnal (D_1,D_2,D_3) and 3 nocturnal (N_1,N_2,N_3). The arrangement of their positions reflects their dietary similarities such that the dietary dissimilarities are represented by distances. Thus, the dietary dissimilarity between D_1 and D_2 is *x;* alternatively the dietary similarity between D_1 and D_2 would be $1 - x$. (*a*) The hypothetical observed data. (*b*) A randomization of names that preserves the same arrangement of diurnal and nocturnal species. (*c*) A randomization that does not

Another reason to use numerical techniques with this particular problem is a common one in many ecological applications: the statistics are strongly sample-size dependent. In this case, the nearest species distances depend on the proportions of species that are diurnal and nocturnal. Because the distances between species must all fall within a hypersphere of unit diameter there will be a tendency for species to be, on average, closer to other species the more species there are involved in the comparison. Suppose there are n nocturnal and m diurnal species. There are $\frac{1}{2}[n(n-1) + m(m-1)]$ matched comparisons and mn mixed comparisons. Unless the numbers of comparisons in each set (mixed, matched) are equal, we should expect, by chance alone, for the smallest distance to be usually in the set that involves the greater number of comparisons.

In sum, the distances between species and hence the similarities between species are interrelated and have properties that prevent them from being the normally and independently distributed variables required for most statistical tests. But this need not prevent our developing and testing hypotheses using them.

Huey and Pianka are interested in such questions as: are diets of species that are matched for time of activity more or less similar than those that are mixed? The question "more or less similar" can be addressed in terms of a null hypothesis. Consider this null hypothesis: suppose each species takes its array of prey species without regard to whether it is diurnal or nocturnal. Then this hypothesis would imply, for the data in Figure 13.2, that the 6 points (whose relative positions reflect diets) would have arbitrary designations (D_1, D_2, . . . , N_3). In the example, there are 6 species and thus 6! (equals 720) ways of arranging the names to the points. Some of these, however, involve the same arrangement of diurnal and nocturnal species—Figure 13.2b is an example. Others represent distinct arrangements (Fig. 13.2c). There are 36 ways of arranging the names that maintain each particular configuration of nocturnal and diurnal species. So, if we were interested in the distribution of mixed and matched distances there would be 20 different configurations (720/36). Each one of these 20 possibilities would occur equally probably under the null hypothesis that time of activity did not influence diet.

Finally, we ask the crucial question: how unusual is the observed arrangement of diets shown in Figure 13.2a? It is clear from the figure that each diurnal species is always more similar in diet to a diurnal species than to any nocturnal species and each nocturnal species is always more similar to a nocturnal species than to a diurnal species. In short, matched distances are smaller than mixed distances arrangements, one or more mixed distances would be smaller than a matched distance. Thus, the chance of finding an arrangement this extreme is 0.1 (2 out of 20).

Finally, consider the arrangement of Figure 13.2d. Here each mixed distance is always smaller than a matched distance. In biological terms, each diurnal species has a nocturnal replacement with very similar diet. This also is an extreme arrangement and has an identical probability of occurrence of 0.1.

Depending on our prior biological knowledge we may wish to formulate 1 of 3 pairs of hypotheses. The first pair involves a null hypothesis and an alternative that supposes that matched distances will be less than mixed distances. In the second pair the alternative supposes that matched distances will be greater than mixed differences, and the alternative for the third pair supposes only that matched and mixed differences will differ. The structure of these hypotheses should be familiar. The first two pairs are considered one-sided: of the two possible kinds of extreme arrangements only one kind will reject the null hypothesis in each case. The third pair of hypotheses is two-sided: either of the two extreme arrangements would reject the null hypotheses. For the first pair, we ask how likely is it that the arrangement we observe (Fig. 13.2a) or some more extreme arrangement will occur, given the null hypothesis. In this case there are no more extreme arrangements (matched distances are less than mixed in each case). The chance of obtaining this arrangement is 0.1, as I have already discussed. If the data were as in Figure 13.2d and we were testing the second pair of hypotheses, then the chances of this arrangement would be 0.1 yet again. Of course, if we were testing the third pair of hypotheses (with either the data of Fig. 13.2a or 13.2d), then either extreme arrangement would satisfy us and the chance of getting one of them would be 0.2 (4 out of 20).

Because we usually choose to reject hypotheses if their probabilities fall below 0.05, we would not reject the null hypothesis in any of these cases even though the data may be the most extreme arrangement possible. Simply, for the data shown in the figure, rejecting the null hypothesis is not possible. The probability of accepting the null hypothesis, when the truth is that the alternative hypothesis is correct, is assigned a value, β; we call $1 - \beta$ the *power* of a statistical test and hope our tests will be powerful. In this example, the test is not and the lack of power is one problem inherent to analyses of this kind when data are few. I shall return to this problem later, but it does not cause any difficulties in the case of Huey and Pianka's data.

cies most similar in diet identified for species active at the same time of day (matched values) and for species active at a different time of day (mixed values). I then calculated the mean of the differences between matched and mixed values: I call this mean value $D_{1,\mathrm{obs}}$ (the observed difference between the dietary similarities of species active at the same and different times of day averaged over all the $n + m$ species).

In the above example, the number of possible arrangements was only 20. Each arrangement could be explored. With the real data, the number of possible arrangements is often vast. Some authors, notably Schoener (1982), using their own minicomputers and having adequate time, have chosen in these circumstances to investigate all possibilities. For those of us with limited computer time, a satisfactory alternative is to select randomly a sufficient number of arrangements (200 in this case) from the total array of possibilities. For each random arrangement I used a program that assigned $m + n$ labels randomly to the $m + n$ species: n of the labels implied a species was nocturnal, m, diurnal. From this point the calculations were identical to those performed on the actual data and yielded means I call $D_{1,i}$ ($i = 1$ to 200). The final stage was to compare $D_{1,\mathrm{obs}}$ with the statistical distribution of values of D_1 under the null hypothesis, the $D_{1,i}$. If, for a one-sided test, less than 10 (5 percent) of the simulated means, $D_{1,i}$, were greater than the observed mean $D_{1,\mathrm{obs}}$, then one would conclude that dietary similarities were greater between species active at the same time of day than one would expect by chance.

The extension of these analyses to the other tests follows directly. I calculated the dietary similarities not only of the nearest but also of the second, third, and fourth nearest species both for matched (call these S_1, S_2, S_3, and S_4) and mixed (call these M_1, M_2, M_3, M_4) for time of activity. From the mean of $S_1 - M_1$ I calculated D_1 as described above and also D_2 (the mean of $S_2 - M_2$; that is, the mean of the differences between the second most similar species active at the same time of day and the second most similar species active at a different time of day), D_3, and D_4 defined analogously. Also calculated were cross comparisons; for example $M_3 - D_1$—the mean difference between the third nearest species active at a different time of day and the nearest species active at the same time of day. In each case, calculations were performed on the actual data and then repeated 200 times on randomized data to generate distributions of these means under the null hypotheses.

Several comments need to be made. First, the sample size of 200 is chosen as a compromise between accuracy and computer time. The values of interest are proportions and, therefore, are binomially distributed. The critical value is 0.05 and the standard error for such a proportion is $[(0.05)(0.95)/\mathrm{N}]^{1/2}$, where N is the sample size. For $\mathrm{N} = 200$, the standard error is 0.015. For small proportions confidence intervals are F-distributed and the upper-95-percent confidence interval approaches

3/N for large N. Simply, with a sample size of 200 we can be certain that the true level of significance will not be more than a few percentage points from our assertion.

Second, these methods can often lack power because the number of distinct arrangements under the null hypothesis is small. In such cases it still may be possible to obtain biologically useful results by repeating the analyses on many different sets of data. Proportions from each of these analyses can be combined to give an overall test of the null hypotheses. Examples of this are given in Pimm (1980).

Finally, we note that Monte Carlo methods, of which this paper describes a special case, are becoming popular in ecology. (Some examples are Connor and Simberloff, 1979; Pimm, 1980; Pimm and Lawton, 1980; Schoener, 1982). Yet it is my impression that they are underused. If this impression is correct, it may be because the problems that require one to resort to such methods—interdependence of data, sample-size-dependent biases, etc.—are common in ecological problems but are usually overlooked. This may reflect an antipathy toward statistics or a reluctance to compute. Such a reluctance would have been unfortunate in this case. Over 80 percent of the computer code required by this analysis involved the calculations of dietary similarities between species and the extraction from these data of the first through fourth mixed and matched values. These calculations were required for analysis of the observed data; performing the simulations required only the addition of a small subroutine which randomly assigned diurnal or nocturnal status and a loop to repeat the process. Such minor modification of data analysis routines to permit statistical inferences to be drawn is, in my experience, quite typical.