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GEOGRAPHIC AND SEASONAL DISTRIBUTION OF RABIES IN SKUNKS, FOXES AND BATS IN TEXAS

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Abstract: The geographic and seasonal distributions of the pathobiocenoses formed by rabies virus, the biotic provinces of Texas, and skunks, foxes and bats were described using synoptic mapping and enumeration by calendar month. Autocorrelation functions with 95% confidence intervals were calculated for the skunk pathobiocenose for lag periods up to 36 mo in length. The geographic distributions were fundamentally different, but all overlapped. The skunk and fox pathobiocenoses were associated with provincial ecotones. The distribution of the bat pathobiocenose was urban. The nature of the autocorrelation functions for the skunk pathobiocenose indicated that this disease association may be spreading throughout the state from an epicenter in the Texan biotic province.

INTRODUCTION

Sylvatic rabies is common in Texas, and is most prevalent in skunks, bats, and foxes, though it has been reported in seven other wild species since 1953 (Texas Department of Health, unpublished). Most efforts to control rabies in Texas are concerned with preventing the spread of the disease from these three species to domestic animals and humans. Prevention and control efforts have been hampered by the lack of a precise description of the geographic and seasonal distribution of reported cases and of factors underlying both. Therefore, we report here a study of the geographic and temporal distribution of rabies in skunks, bats, and foxes in Texas between January 1962 and December 1979. The geographic distributions are analyzed with synoptic maps of the pathobiocenoses formed by rabies virus, the biotic provinces of Texas, and each of the sylvatic hosts — skunk, fox, and bat. Seasonal distributions of the pathobiocenoses are described in each association by summarizing the cases in each by calendar month. Time series analysis is used to describe cyclic components in the temporal distribution of the skunk pathobiocenose.

MATERIALS AND METHODS

Cases of rabies included in this study were those which were confirmed in skunks, foxes, and bats by the Texas Department of Health (TDH) Laboratories between January 1962 and December 1979. These cases were extracted from reports of laboratory confirmed cases of rabies by county and species published monthly by the TDH Laboratory. Cases not diagnosed by the TDH-Austin laboratory or one of the TDH regional laboratories were excluded from the study. The number of cases excluded was less than 1% of the total and consisted of those confirmed by laboratories at various military bases. Submissions to the TDH Laboratory are voluntary, and policy regarding these submissions, where it exists at all, varies among localities. Factors influencing submissions include the local frequency of rabies, the human population, and the bovine population, to name but a few (Lewis, 1972; Smart and Giles, 1972). The effect of such reporting factors was considered in the analysis of these data and is discussed later.

Most specimens submitted for rabies diagnosis lacked expert taxonomic identification, and hence, are identified simply as skunk, fox, or bat. There are six species of skunks, four species of foxes, and 30 species of bats indigenous to Texas. However, the most prevalent skunk is the striped skunk *(Mephitis mephitis)*; the most prevalent fox is the grey fox *(Urocyon cinereoargentius)*, and in most areas of the state, the most prevalent bat is the Mexican free-tailed bat *(Tadarida mexicana)* (Davis, 1974).

Computer generated contour maps were produced using the SYMAP software package developed by the Harvard Computer Graphics Laboratory. SYMAP produces contours by interpolating values for areas between data points based on distance between data points and values at data points (Dougenir and Sheenan, 1975). Contours were calculated from the geographic centers of each county using the number of cases of rabies by sylvatic host species reported from each county during the study period. Contours are presented in deciles of the range of data values. Deciles 6 through 9 are presented as a unit to emphasize the edges and the centers of the geographic distribution.

The county is a political unit and is of little value in describing regional variations in habitat type and ecology. To characterize such regional variations, Blair (1950) partitioned Texas into seven biotic provinces: the Austroriparian, the Texan, the Kansan, the Chihuahuan, the Balconian, the Tamaulipan, and the Navahonian (Fig. 1). Boundaries of these biotic provinces were adjusted to coincide with the nearest county boundary and were superimposed over each contour map. The Navahonian biotic province was excluded since it occupies only a small part of one county, and no cases of rabies were reported from it during the period.

To describe the seasonal variation in rabies prevalence, the number of cases for each species was totaled for each biotic province and month over the 18-yr period of observation. The number of cases of skunk rabies was sufficiently large to allow a time series analysis (Box and Jenkins, 1970), and autocorrelation functions (ACF) were calculated and graphed for each province using the Wisconsin Multiple Time Series Program.

RESULTS

The geographic distribution of the pathobiocenoses formed by the interaction of rabies virus, the biotic provinces of Texas, and the sylvatic host species — skunk, fox, and bat between January 1962 and December 1979 are shown in Figures 2-4. The skunk pathobiocenose (Fig. 2) is principally found in an irregular band that crosses the central area of the state along a north-south axis. This band lies mostly in the Texan biotic province. The fox pathobiocenose (Fig. 3) is found principally in the southwest-central and southwest portions of the state. This pathobiocenose lies mostly in the Balconian biotic province and the eastern part of the Chihuahuan but is also found in portions of adjacent provinces. The bat pathobiocenose (Fig. 4) is principally limited to the major urban centers of the state (Dallas, Houston, San Antonio, Austin, and El Paso) and has a disjunct distribution in several biotic provinces. None of the distributions are discrete; each overlaps the others.

Seasonal distributions of the three pathobiocenoses are summarized in Tables 1-3. The distribution for skunks peaked between March and May depending on location, but the peak in the Texan was in April. That for fox peaked in March in the Balconian, the province in which 65% of all cases in foxes were reported. The peak of the bat cycle occurred between August and October, with most cases being reported statewide in September.

The autocorrelation functions for rabies in skunks are plotted for each biotic province in Figures 5-10. The number of months required for the ACF

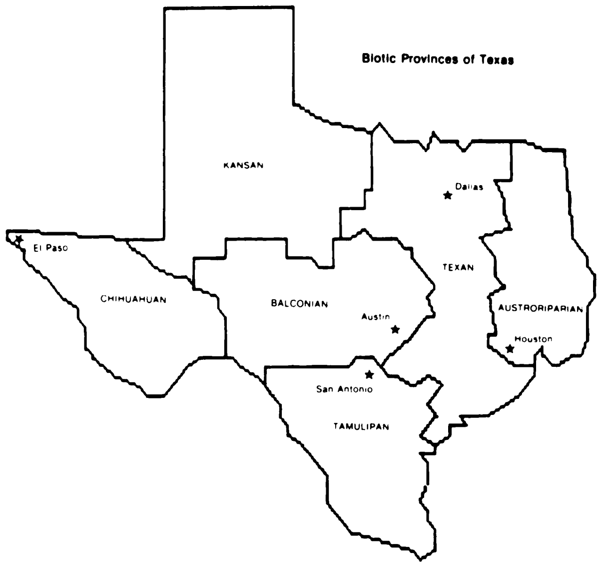

FIGURE 1. The Biotic Provinces of Texas. The Navahonian Biotic Province was not mapped because it occupies only a portion of one county, and no cases were reported from it during the study period.

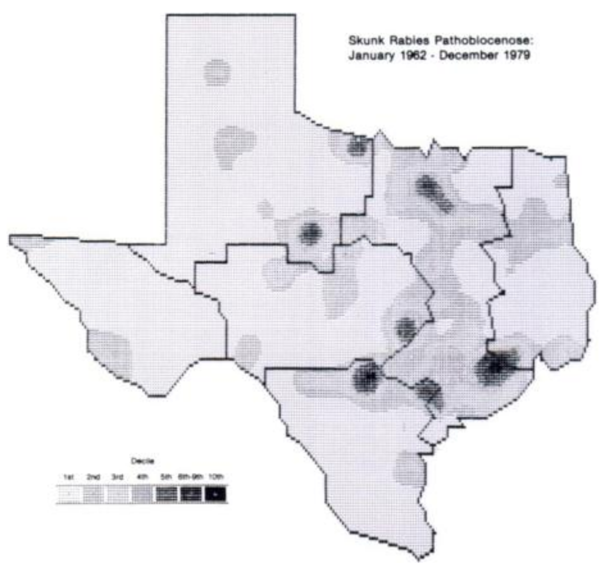

FIGURE 2. The Skunk Rabies Pathobiocenose: January 1962-December 1979. This pathobiocenose lies principally in the Texan biotic province but occupies portions of the other five.

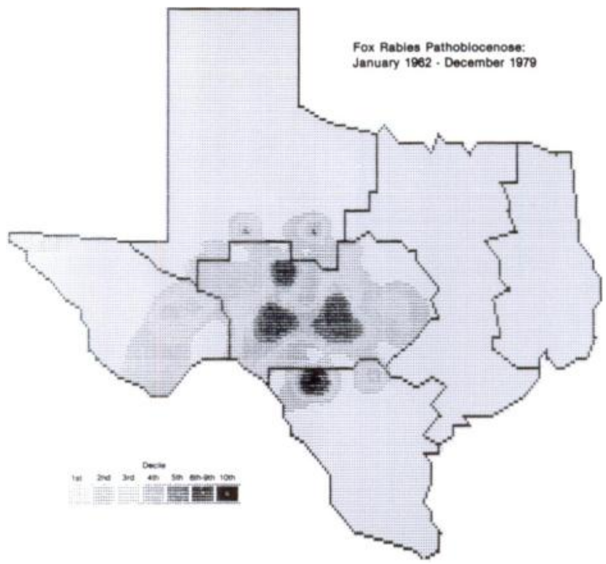

FIGURE 3. The Fox Rabies Pathobiocenose: January 1962-December 1979. This pathobiocenose lies in the Balconian biotic province and the eastern Chihuahuan as well as in adjacent portions of the Kansan, Texan and Tamaulipan provinces.

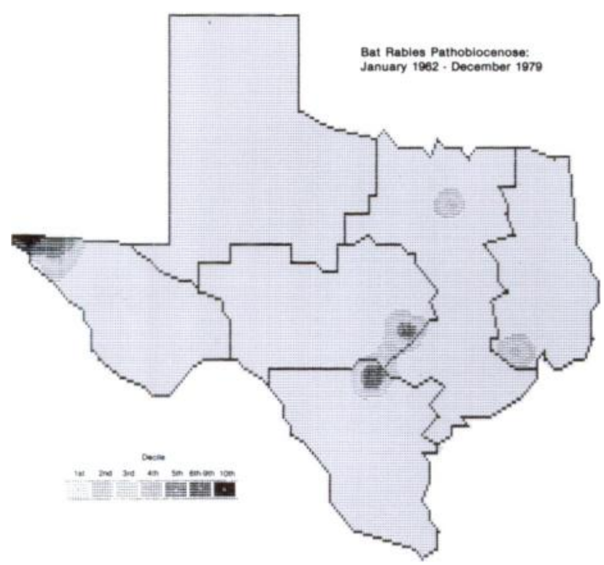

FIGURE 4. The Bat Rabies Pathobiocenose: January 1962-December 1979. This pathobiocenose is urban in nature and is centered in Dallas, Houston, Austin, San Antonio and El Paso.

TABLE 1. Total cases of rabies in skunks by province by calendar month, January 1962-December 1979.

Biotic Province	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Total
Austroriparian	39	40	36	50	71	62	42	37	33	49	39	46	544
Texan	80	118	179	269	207	136	131	107	105	103	102	101	1,638
Kansan	33	21	89	81	97	70	26	32	31	25	27	26	558
Chihuahuan	9	13	16	28	12	17	13	9	12	11	8	8	156
Balconian	40	50	116	91	64	55	51	53	32	27	37	33	649
Tamaulipan	24	37	94	60	58	46	39	37	32	32	28	20	507
Total	225	279	530	579	509	386	302	275	245	247	241	234	4,052

TABLE 2. Total cases of rabies in foxes by province by calendar month, January 1962-December 1979.

Biotic Province	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Total
Austroriparian	2	2	2	1	0	0	0	0	0	0	1	0	8
Texan	2	1	2	5	1	2	1	2	0	3	3	0	22
Kansan	1	0	1	2	1	2	4	0	0	1	1	1	14
Chihuahuan	4	11	7	5	1	3	2	2	5	12	3	5	60
Balconian	42	36	46	39	17	17	10	12	14	21	24	38	316
Tamaulipan	9	8	4	3	9	4	3	4	5	7	4	6	66
Total	60	58	62	55	29	28	20	20	24	44	36	50	486

TABLE 3. Total cases of rabies in bats in province by calendar month, January 1962-December 1979.

Biotic Province	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Total
Austroriparian	1	1	3	5	7	6	15	24	14	6	4	1	87
Texan	0	0	0	3	8	7	12	26	34	24	6	0	120
Kansan	1	0	0	1	7	4	2	1	4	8	1	0	29
Chihuahuan	0	0	1	11	22	16	26	17	55	33	5	0	186
Balconian	3	1	7	17	10	11	14	30	33	28	3	0	157
Tamaulipan	2	1	11	17	17	9	18	32	23	29	7	0	166
Total	7	3	22	54	71	53	87	130	163	128	26	1	745

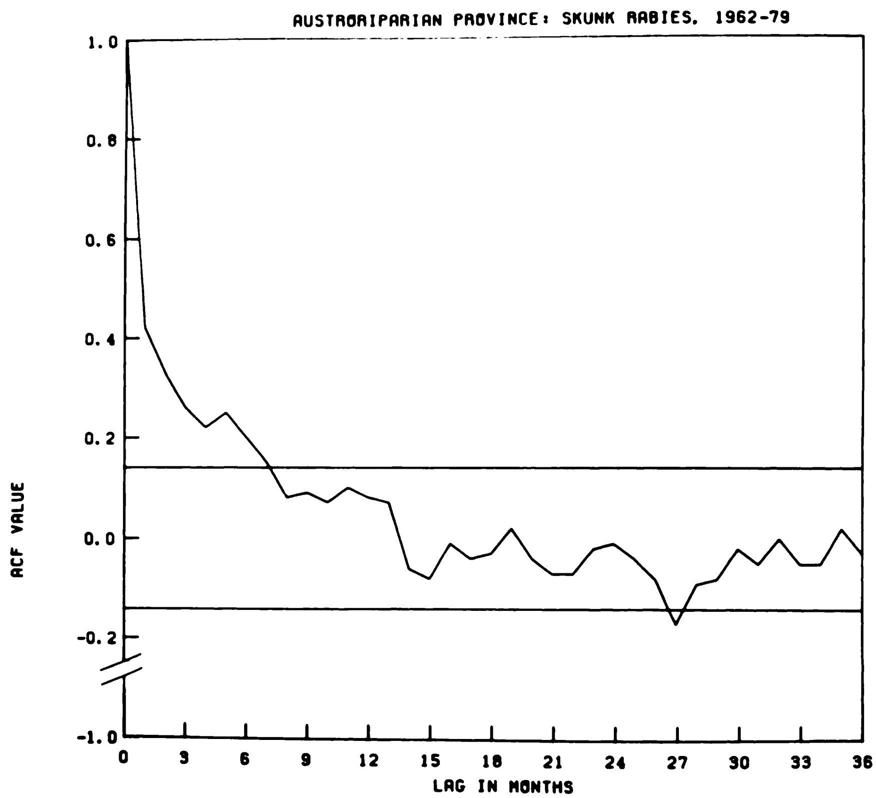

FIGURE 5. ACF Plot — Austroriparian Province; Skunk Rabies, 1962-79. Skunk rabies exhibits some persistence but no defined periodicity in this province.

to decline to the upper 95% confidence inteval is directly related to the stability or persistence of the pathobiocenose in each area. Additionally, the presence of a periodicity in these time series can be detected readily from the ACF plots, and the length of these periods can be estimated by averaging the number of months between peaks in ACF values. The number of months for the ACF to decline to upper 95% confidence interval and the mean length of the periodicity are summarized for each province in Table 4. The skunk pathobiocenose was very stable in the Tamaulipan and Texan provinces and exhibited an annual periodicity. In the Kansan and Balconian provinces the pathobiocenose showed little persistence but had a definite annual periodicity. In these provinces the annual peaks were preceded by much smaller and less distinct peaks. In the Chihuahuan province neither persistence nor periodicity was apparent.

DISCUSSION

Synoptic mapping and time series analysis have been used to describe geographic and temporal variations of rabies in three wildlife populations in Texas. The reporting of a rabies case in this study was voluntary and could be

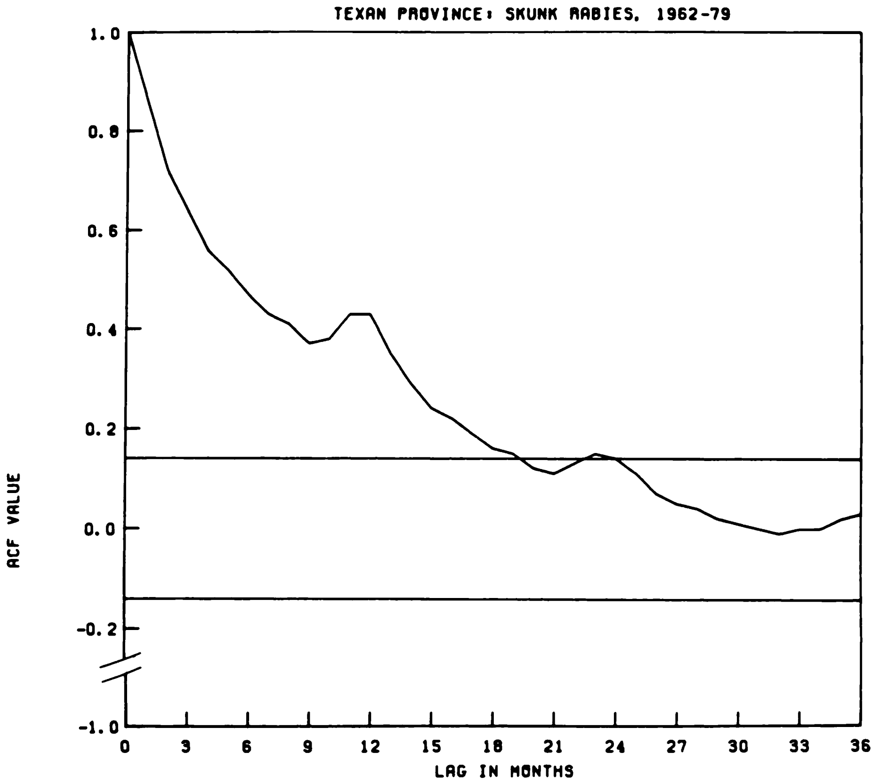

FIGURE 6. ACF Plot — Texan Province: Skunk Rabies, 1962-79. Skunk rabies exhibits both persistence and an annual periodicity in this province.

influenced by factors that are beyond experimental control. Furthermore, no estimate of the size of the wildlife population at risk of contracting rabies could be obtained. These limitations are inherent in any retrospective analysis of a disease. Even so, data such as these are useful. Elton and Nicholson (1942), for example, analysed the lynx-hare cycle using fur harvest records kept by the Hudson's Bay Company. By assuming that the number of pelts in a reporting district was related to the total number of animals in that area by a unique and constant factor, they were able to detect a 10-yr cycle throughout a 200-yr span of harvest records in spite of changes in administrative policy, changes in personnel and collecting methods, fluctuations in the fur market, wars and other major economic upsets, and epidemics.

Our perspective in this study goes beyond looking at rabies simply as a host-pathogen interaction; instead, we include the environment in which these organisms occur. Audy (1958) termed this community of host-pathogen-environment a pathobiocenosis and argued that this assemblage could be considered an integrated biological unit with properties not found in the individual components (see also, Odum, 1959; Read, 1970). The ecological community component of the rabies pathobiocenoses consists of the biotic

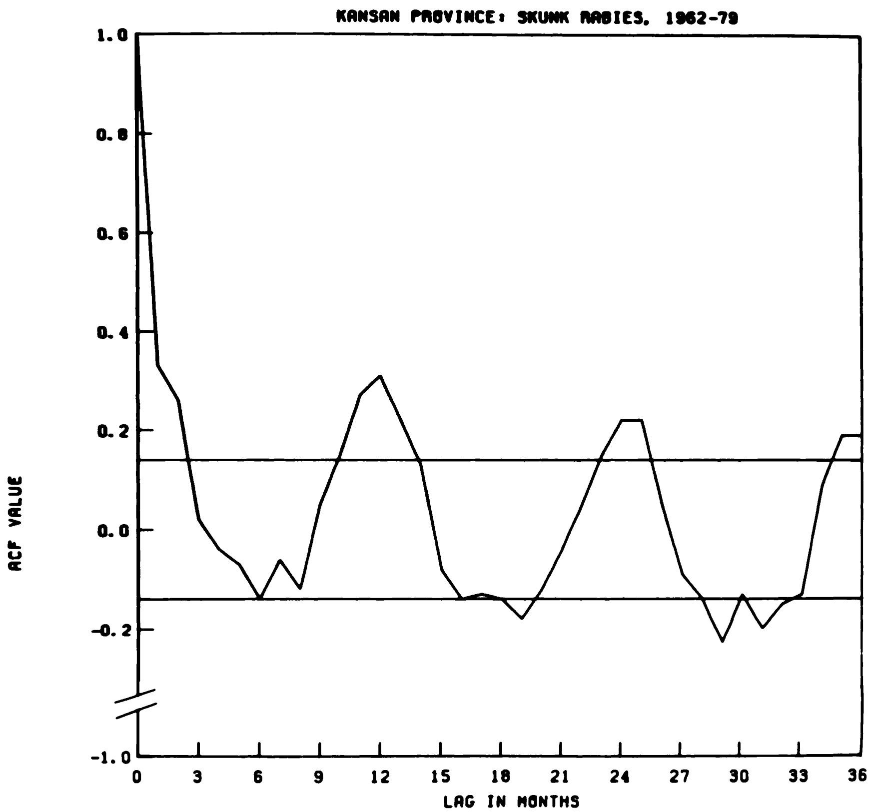

FIGURE 7. ACF Plot — Kansan Province: Skunk Rabies, 1962-79. Skunk rabies exhibits little persistence but regular annual periodicity in this province.

provinces of Texas. Blair (1950) defined a biotic province as a large, continuous area with one or more characteristic ecological associations differing at least in proportional area covered from those in adjacent provinces. He characterized seven provinces in Texas on the basis of vegetation, topography, climate, and terrestrial vertebrates excluding birds. A literal interpretation of this definition includes the human population of each area as a terrestrial vertebrate species whose distribution and activities are integrally involved in the character of the ecological associations in each province. Since a laboratory-confirmed case of rabies ultimately results from an interaction between a rabid animal, a human, and several environmental factors (Lewis, 1972; Smart and Giles, 1972), the assumption of a "reporting factor" unique to each pathobiocenose is further supported. The use of the biotic province as the ecological community of the pathobiocenoses rather than a smaller, more precisely defined ecological unit allows the aggregation of enough cases in each geographic area by species and month to permit quantitative analysis. Division of the state into six biotic provinces, the Navahonian being excluded due to its small size and lack of

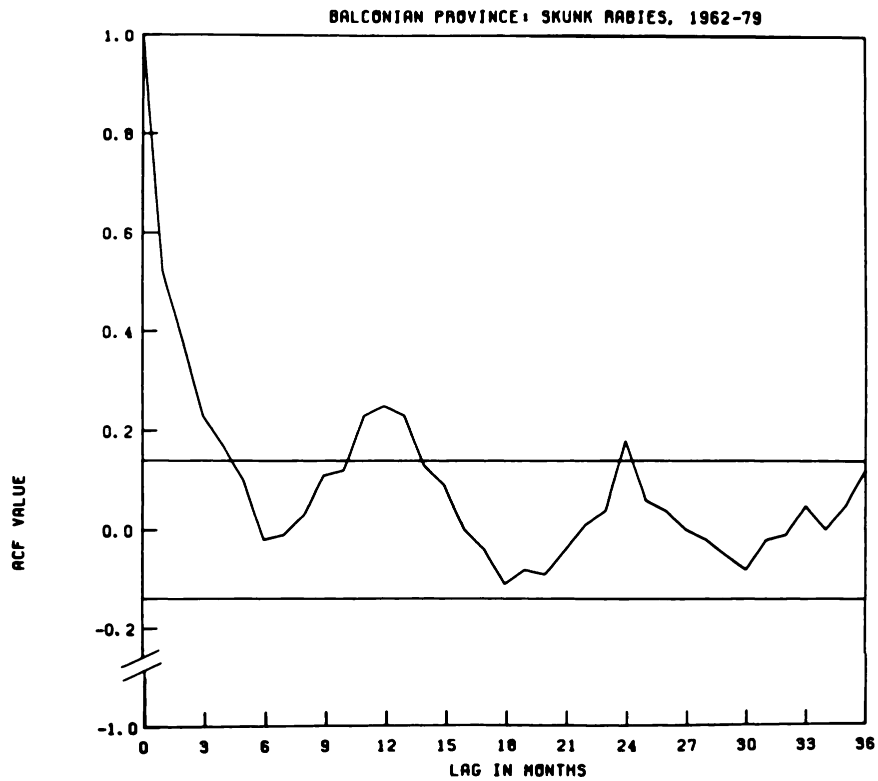

FIGURE 8. ACF Plot — Balconian Province: Skunk Rabies, 1962-79. Skunk rabies exhibits little persistence but an annual periodicity in this province.

reported cases, allows a description of the variation in rabies activity which can be associated with the ecology of each region.

The skunk pathobiocenose is located principally in the Texan biotic province (Fig. 2), a broad ecotone between Austroriparian forests to the east and semiarid grasslands to the west, with the distinctive characteristic of the area being the interdigitation of grassland and forest. Major portions of the prairie areas are under cultivation. Rainfall barely meets the needs of the ecosystem for water. Periods of surplus rainfall alternate with periods of rainfall insufficiency. The dominant species of skunk in the area is the striped skunk. This skunk, though found in a great variety of habitats, is most frequently found on agricultural lands used for pasturage, row crops, wooded acreage, and combinations of all three, but is seldom found in areas prone to flooding (Verts, 1967). They frequently build dens directly under fences. Epizootic rabies in skunks has been associated with periods of high population density and with periods of physiologic stress (Smart and Giles, 1972; Verts, 1967). Stressful periods such as breeding season and times of water shortage often bring individual animals together during competition for resources in short supply. The marginal

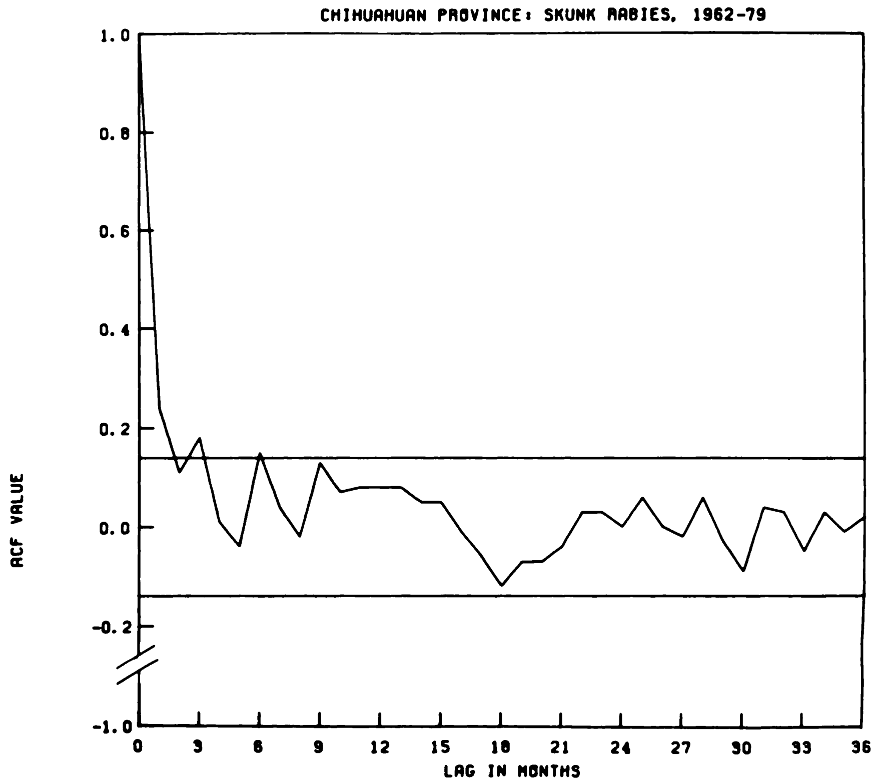

FIGURE 9. ACF Plot — Chihuahuan Province: Skunk Rabies, 1962-79. Skunk rabies exhibits neither persistence nor periodicity in this province.

rainfall conditions characteristic of the Texan biotic province frequently produce periods of intense intraspecific competition for essential resources which become scarce due to rainfall insufficiency. Such periods of scarcity seem to favor the appearance of rabies.

Throughout its range in Texas the skunk pathobiocenose is distributed in ecological transition zones, such as boundaries between two or more biotic provinces, boundaries between biotic districts, boundaries between vegetational areas, and in the Texan biotic province. The pathobiocenose is present in the Austroriparian biotic province in two bands crossing the province in east-west axes. These incursions are associated with the boundaries of three vegetational regions. In the south the coastal prairie bounds the long-leaf pine forest, and farther north, the long-leaf pine forest bounds the pine oak forest. These areas have repeatedly been subject to logging and burning. The two disjunct areas of the pathobiocenose lying in the central area of the Kansan biotic province lie on the eastern boundary of the Short-grass Plains biotic district which bounds the two other biotic districts of the province. This province is moisture deficient, which would cause some aggregation of individual skunks where moisture is available. The entire geographic distribution of the pathobiocenose can be associated with high habitat diversity

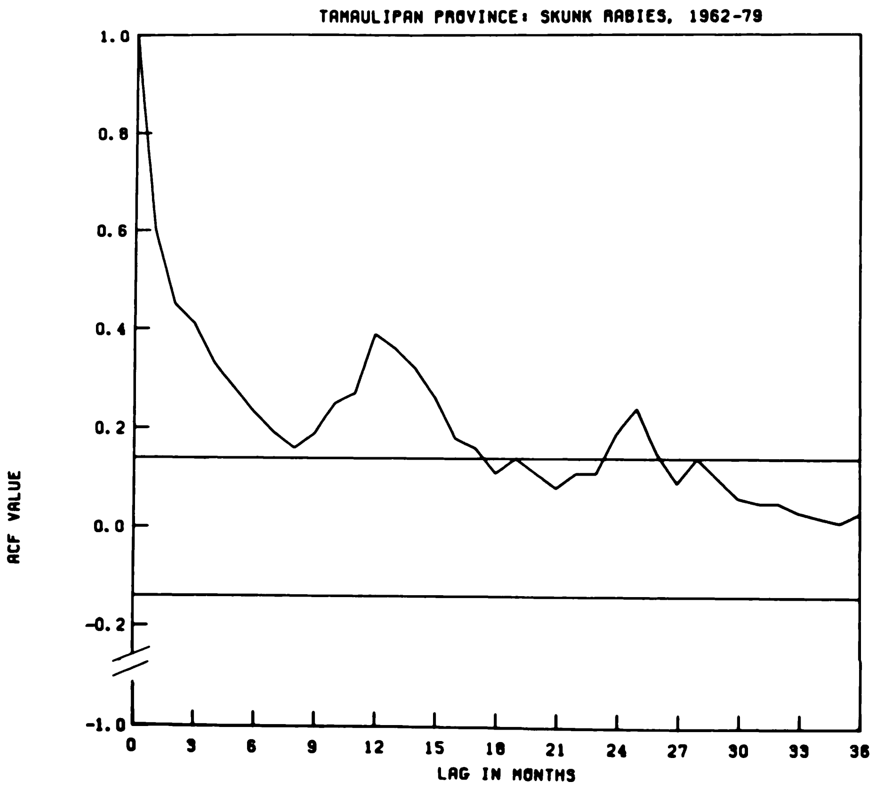

FIGURE 10. ACF Plot — Tamaulipan Province: Skunk Rabies, 1962-79. Skunk rabies exhibits both persistence and an annual periodicity in this province.

TABLE 4. ACF for skunks by province: months to decline to upper 95% confidence interval and mean length of periodicity in months.

Biotic Province	Months to Upper 95% C.I.	Mean Length of Period in Months	Number of Skunk Cases
Austroriparian	7	0	544
Texan	19	12.0	1,638
Kansan	3	12.0	558
Chihuahuan	5	0	156
Balconian	2	12.0	649
Tamaulipan	18	12.5	507

and ecotone length, marginal or deficient moisture from rainfall, and disturbance of habitat due to agriculture or other human activities.

The fox pathobiocenose is limited almost entirely to the Balconian biotic province as well as adjacent areas of the Kansan and Tamaulipan (Fig. 3). It is present in the Chihuahuan in the vicinity of El Paso and extends from the Big Bend region northeast into the Balconian. The Balconian biotic province is a region of intermediate ecologic conditions between the western deserts and the eastern forests. Its climate shows a decrease in rainfall from the east to west with that in the eastern half being similar to that in the Texan. Its topography is characterized by massive limestone and granite outcrops dissected into canyons by rivers and streams. Springs and limestone caverns are common.

The predominant species of fox indigenous to the area is the grey fox (Davis, 1974). Preferred habitat for the grey fox is agricultural land used for pasturage, particularly pasturage bounded by wooded plots (Carey et al., 1978). Because the Balconian biotic province is covered with scrub forest and savannah with more mesic forest growth limited to the floodplains of streams, and because the predominant agricultural utilization of most of the land in the province is pasturage, this province provides a considerable area suitable for the grey fox. Much of the pasturage in this province has been severely overgrazed (Blair, 1950). The maintenance of endemic foci of fox rabies and its epidemic spread has long been associated with a ridge and valley topography similar to that common in this province. These processes have more recently been associated with limestone caverns, such as those common in this area (Fischman, 1976). The areas of the Kansan, Tamaulipan and Chihuahuan biotic provinces in which this pathobiocenose is distributed are similar to the Balconian relative to topography, land use, and availability of water.

The geographic distribution of the bat pathobiocenose is in sharp contrast to that of the skunk and fox. It is distributed in four disjunct foci at Dallas, Houston, El Paso, and one lying between San Antonio and Austin (Fig. 4). Reports of rabid bats attacking humans or other animals are relatively rare. Rabid bats are typically found dead or in a morbid condition before being submitted for rabies diagnosis. Individual bats and bat colonies are frequently found in buildings, and cities located in areas with large bat populations may have large numbers of buildings inhabited by bats. All of the cities at the foci of the bat pathobiocenose have animal control programs and large, well-developed city and county health departments. This greatly simplifies submission of morbid bats for rabies diagnosis. It is, therefore, possible that the distribution of reported bat cases is an artifact of reporting.

In order to describe seasonal peaks in numbers of reported cases, total cases were enumerated by species, calendar month, and biotic province. The peak of the cycles in skunks varied between March and May statewide but in the Texan occurred in April (Table 1). This is consistent with the second calendar quarter peak reported by other authors, and suggests that most rabid skunks in Texas become infected during the breeding season in the late winter and early spring (Davis, 1974; Verts, 1967). The peak of the annual fox cycle in the Balconian biotic province is in March, and is the culmination of a rising trend beginning in October (Table 2). The initiation of the cycle in October may be associated with the "fall shuffle" in which juvenile foxes begin their fall dispersal (Carey et al., 1978; Smart and Giles, 1972). The March peak can be associated with the climax of the breeding season. The peak of the annual bat cycle is between August and October with most cases being reported in September (Table 3). This corresponds with the fall migration in migratory species (Smart and Giles, 1972). Between November and March, reported rabies is at a minimum in bats statewide. Seasonal peaks in case reporting of all three pathobiocenoses are associated with periods of high intraspecies contact between susceptibles, with periods of dislocation from normal territory and home range, or with intense physiological stress. Such conditions normally occur during breeding, during the displacement of mature juveniles from family groups, and during migration in migratory species. Association of temporal fluctuations in case numbers with territorial dislocation of individuals is consistent with a hypothesized case for competition between pathobiocenoses in areas of geographic overlap.

The number of cases of skunk rabies was sufficiently large to allow the application of time series analysis. This statistical technique can be used to quantify the persistence of a population and to detect the occurrence of cyclic variation in population density. A slowly decaying autocorrelation function implies that the density of a population at a given time interval is strongly related to the densities of the population at previous time intervals. Often a cyclic wave can be seen superimposed on this function. The average length of the period between the peaks of this wave is a measure of the cyclic periodicity of this time series (cf. Fig. 6 and 7).

Time series analysis of the skunk pathobiocenose indicated marked regional variation in both its persistence and periodicity. It is clearly most persistent in the Texan and Tamaulipan biotic provinces. These areas contain the epicenter of its geographic distribution in Texas. This temporal persistence is consistent with that for an organism or super-organism in the niche in which it is most firmly established. The periodic peaks in the Texan are small, and are characteristic of relatively minor fluctuations about an equilibrium. This pattern is, again, consistent with that for an organism in a niche in which it is well established. The persistence of the pathobiocenose in the Austroriparian indicates that as a super-organism, it is definitely established in the niche and its lack of clear periodicity indicates that it may be very near equilibrium with the environment. In the Kansan and Balconian the lack of persistence and the clear regular periodicity implies that the skunk pathobiocenose is not very well established. The ill-defined leading waves of the annual cycles may be associated with the index cases to following epizootic waves (Smart and Giles, 1972). This pattern suggests explosive, annual outbreaks of rabies in skunks in these areas. The number of cases of rabies in skunks in the Chihuahuan province is too small to lend itself to time series analysis. The small number of cases implies that the pathobiocenose is not well established in this area.

Much research and speculation have been directed at relationships between rabies in the species discussed, since transmission of rabies between these species is known to be possible. Description of possible interrelationships between species is beyond the limits of this study, but similarities between the three pathobiocenoses should be noted: (1) all lie in ecological transition zones; (2) all lie in areas subject to periods of moisture insufficiency which may lead to aggregation of susceptible individuals during periods of physiological stress; (3) all include extensive areas of disturbed and abused land. In the case of foxes and skunks, preferred habitat includes an interface between agricultural and nonagricultural lands. Compartmentalization, the frequent failure of sylvatic hosts to transmit rabies to other susceptible species in the same area, is known to give rise to "skunk rabies areas" and "fox rabies areas" (Smart and Giles, 1972). If similarities in niche implied by the similarities in associated habitat listed above are examined in light of Audy's characterization of a pathobiocenose as a super-organism, it can be hypothesized that changes in relative frequencies of cases of rabies in sympatric populations are related to competition between two super-organisms for control of a niche.

Changes in the niche due to land use and abuse, and due to fluctuations in critical climatic factors could not only allow penetration of the niche by a new super-organism but could also cause slow oscillations about an equilibrium between populations of the two super-organisms in the contested areas.

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