AGE AND MOVEMENT OF A HYBRID ZONE: IMPLICATIONS FOR DISPERSAL DISTANCE IN POCKET GOPHERS AND THEIR CHEWING LICE

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Abstract.—Historical flood records for the Rio Grande Valley of New Mexico suggest that a pocket gopher (*Thomomys bottae*) hybrid zone previously thought to be 10,000 years old may actually be closer to 50 years old. Measured zone width (defined genetically) is consistent with the hypothesis of recent contact, if we assume a reasonable dispersal distance of approximately 400 m/year for pocket gophers. A five-year study of movement of the contact zone between the two species of chewing lice that parasitize these pocket gophers also is consistent with the hypothesis of recent origin of the zone.

Key words.—Chewing lice, cline models, dispersal distance, host-parasite coevolution, hybrid zones, pocket gophers.

In this report, we provide evidence to support our contention that a pocket gopher hybrid zone previously thought to be approximately 10,000 years old, may actually be closer to 50 years old. We show that these different estimates for the age of the zone result in dramatically different estimates of dispersal distance for the taxa that meet at this zone (two subspecies of pocket gophers and two species of chewing lice that parasitize the gophers). Our estimates of dispersal distance for chewing lice are the first reported for the order Phthiraptera (= Mallophaga) and suggest that average dispersal distance of these parasites is approximately one-fourth to one-half that of their hosts.

The hybrid zone we studied straddles a narrow constriction of the Rio Grande Valley (known as the San Acacia constriction) located approximately 23 km north of Socorro in central New Mexico (Fig. 1). Two highly differentiated subspecies of pocket gopher, *Thomomys bottae connectens* and *T. b. opulentus*, meet near the San Acacia constriction, as do their respective ectoparasitic chewing lice, *Geomydoecus aurei* and *G. centralis*. Because pocket gophers are largely restricted to the friable soils of the valley floor, their populations are arranged in a narrow, linear band along the south-flowing Rio Grande. Surrounding bajadas, or open deserts, provide limited suitable habitat for pocket gophers (Smith et al. 1983) and, in this portion of their range, gopher populations are rarely found away from permanent water, except on an ephemeral basis (Davis 1940; Smith and Patton 1980).

Smith et al. (1983) conducted a detailed investigation of the pocket gophers at this hybrid zone, including analyses of morphologic, pelage colorometric, karyotypic, and allozymic variation across the zone of contact. They documented presence of limited gene flow between the two gopher subspecies, and they used genetic data to calculate a standardized zone width of approximately 5 km (Hafner et al. 1983; Smith et al. 1983). Smith et al. (1983) used Endler's (1977) neutral diffusion model to show that the observed zone width was reasonably consistent with theoretical expectations under a model of neutral secondary contact. In their model, Smith et

al. used 10,000 years (late Pleistocene) as the estimated age of the zone and 100 m per year as the estimated dispersal distance for pocket gophers. The estimate of dispersal distance was based on studies of *Thomomys* conducted in California by Howard and Childs (1959) and in Colorado by Vaughan (1963).

The Flood of 1929

Since at least late Pleistocene, this region of the Rio Grande Valley has been subject to periodic floods caused by melt-off from heavy snow packs augmented by heavy, late-summer and fall rains (Smith et al. 1983). Prior to the advent of effective flood control measures, these floods were occasionally of immense proportions. The most recent major flood occurred in the summer and fall of 1929 (Patterson 1965). Records of this flood (e.g., Poulson and Fitzpatrick 1929) show that it probably inundated all areas of suitable habitat for gophers in this region. These floodwaters had tremendous erosional impact in the San Acacia region, depositing new sediments up to a meter or more in depth.

Previous studies have shown that pocket gophers either cannot swim (Hamilton 1943; Jackson 1961) or are relatively weak swimmers (test animals swam to exhaustion in less than three minutes; Kennerly 1963), and it is our contention that all pocket gopher populations in the immediate vicinity of the present-day hybrid zone likely were extirpated during the flood of 1929. The few gophers that managed to reach dry land would have faced marginal or unsuitable habitat in the surrounding bajadas and would have been subject to intense predation (tracks of predators indicate that they frequently patrol the perimeter of flooded areas; DJH, pers. obs.). Thus, any genetic structuring that existed in gopher populations in this region prior to 1929 likely was obliterated by this record flood.

Implications for Pocket Gopher Dispersal Distance

We contend that the genetic cline described in detail by Smith et al. (1983) was the product of no more than 54
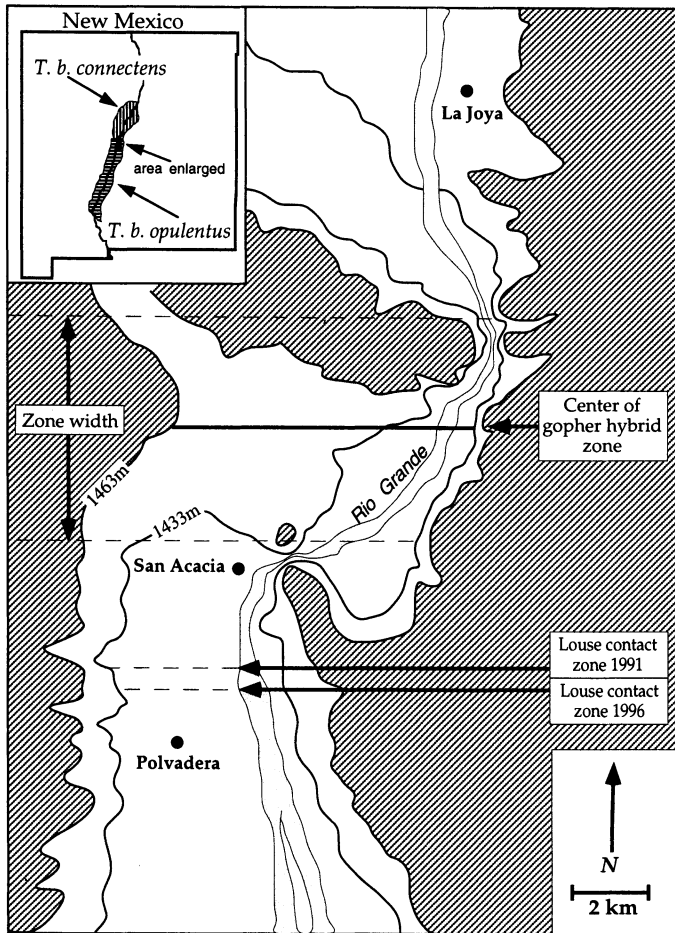
FIG. 1. Map of the Rio Grande Valley in central New Mexico showing the location of the contact zone analyzed in the present study and by Smith et al. (1983). Elevational contours (in meters above sea level) are shown to emphasize the narrowness of the San Acacia constriction. The midpoint of the hybrid zone between the pocket gopher subspecies *Thomomys bottae connectens* and *T. b. opulentus* is located within the San Acacia constriction. The width of the zone (5 km) was estimated using conventional boundary criteria (Endler 1977; Hafner et al. 1983). The narrow zone of overlap between the louse species *Geomydoecus aurei* (hosted by *T. b. connectens*) and *G. centralis* (hosted by *T. b. opulentus*) is located approximately 6 km south of the center of the gopher hybrid zone.

years—rather than 10,000 years—of contact between the two subspecies of gophers. Further, we suggest that this hybrid zone probably has formed and reformed many times in the past, each time destroyed by a catastrophic flood (the most recent major flood prior to 1929 occurred in 1905). Although it is possible that gene flow during one interflood period would have residual effects (i.e., introgressed alleles) that persist into the next interflood period, we consider this unlikely given the fact that the narrow constriction at San Acacia constrains dispersal and resultant genetic introgression to extremely low levels during periods of contact (Smith et al. 1983). Considering the overall physiography and geologic history of this region, it seems more reasonable to assume that each flood has obliterated the entire hybrid zone, leaving predominantly (or exclusively) parental forms of *T. b. con-*

nectens north of the San Acacia constriction and predominantly parental forms of *T. b. opulentus* to the south. Once the floodwaters recede, these parental forms reinvade the region, where they interbreed to a limited extent and reestablish the genetic cline much as we see it today.

If we are correct that the flood of 1929 erased most or all traces of the previous hybrid zone between these pocket gopher taxa, then we have the rare opportunity to know with some precision the time of formation of the present zone. This provides us with empirical estimates for two of the three variables in Endler's (1977) neutral diffusion model—namely, zone width and age of the zone—allowing us to solve for the third variable, dispersal distance. We should note that Endler's (1977) equation depends on the meeting of uniform fronts of the two forms, which is probably unrealistic for organisms that colonize new territory in a patchy fashion that involves a small number of long-distance migrants. Nichols and Hewitt (1994) and Ibrahim et al. (1996) have modeled this mode of dispersal and shown that it can generate a hybrid zone that is initially wide, but may become narrower with time if there is selection against hybrids. Unfortunately, little is known about the frequency of long-distance dispersal in pocket gophers, but this behavior probably is less common in fossorial mammals than in more vagile organisms. We also lack multiple point-in-time estimates of the width of the San Acacia hybrid zone. However, the analysis of the zone by Smith et al. (1983) showed steep, narrow, and coincident clines for several independent datasets (allozymes, chromosomes, and cranial morphology), which is consistent with expectations of neutral secondary contact (Barrowclough 1980; Hafner 1982). Additional genetic evidence in the form of multiple filial and backcross individuals argues against hybrid disadvantage at this contact zone (Smith et al. 1983).

In Endler's (1977) model, width of a cline (w) is expressed as a function of time since neutral secondary contact, as follows:

$$w = 1.68l\sqrt{T} \qquad (1)$$

where l is dispersal distance per generation and T is time measured in generations. Because generation time in *Thomomys* is approximately one year (Howard and Childs 1959; Vaughan 1963), T is roughly equivalent to years in our model. Substituting into equation (1) the measured zone width (5 km; see Hafner et al. 1983) and probable age of the zone (54 years elapsed between the 1929 flood and Smith et al.'s measurement of zone width), we obtain an estimated dispersal distance of $l = 0.405$ km per generation (or roughly 400 m/yr) for pocket gophers in this region. Although this estimate of dispersal distance is four times larger than the value of 100 m/yr used by Smith et al. (1983), it is not unrealistic. For example, Hafner et al. (1983) analyzed several pocket gopher contact zones and concluded that published estimates of gopher dispersal distance likely are too low; they suggested that a value of 500 m/yr may be more realistic under certain conditions. Daly and Patton (1990) measured dispersal distance in *Thomomys bottae* in the coastal ranges of California and found that four of 10 dispersing individuals traveled distances > 100 m to as much as 300 m. These results suggest that dispersal distances probably vary throughout a species' range, depending on physiographic, demographic, historical,

and stochastic factors (Patton and Yang 1977; Hewett, 1988), such that extrapolation of dispersal distance estimates from one study to another (or from one time period to another) must be done with caution. The important point here is that the assumption of a very young (54-year-old) contact zone is consistent with historical accounts of flooding in the region (e.g., Poulson and Fitzpatrick 1929) and does not require an unrealistically high estimate of dispersal distance for *T. bottae*.

Implications for Chewing Louse Dispersal Distance

Chewing lice of the genus *Geomydoecus* are wingless insects that are found only on pocket gophers. The entire life cycle of chewing lice occurs on the host (Marshall 1981), and transmission of lice among hosts appears to require host-to-host contact (Timm 1983). Thus, it seems axiomatic that louse dispersal cannot occur independent of gopher dispersal (Hafner and Nadler 1990), hence louse dispersal distance cannot exceed gopher dispersal distance.

Unlike the gophers, the two species of chewing lice that meet at this zone show fixed allelic differences, and there is no evidence of interbreeding (Demastes 1990). Away from the zone, *G. aurei* is widespread on the northern subspecies of gopher (*T. b. connectens*), and *G. centralis* occurs only on the southern gopher (*T. b. opulentus*). Because contact between the lice is dependent upon contact between their hosts, it is reasonable to assume that the present-day contact between *G. aurei* and *G. centralis* began when their hosts reestablished contact after the flood of 1929.

In 1991, we discovered that the contact zone between the louse species was located approximately 6 km south of the midpoint of the pocket gopher hybrid zone (Fig. 1). At the louse contact zone, we captured pocket gophers with pure populations of northern lice (*G. aurei*), others with pure populations of southern lice (*G. centralis*), and a few with mixed louse populations. The louse zone was actually a narrow zone of overlap between the two species of lice, with the transition from hosts with 100% northern lice to hosts with 100% southern lice occurring over a relatively short distance of 1600 m.

The 6-km distance between the midpoints of the gopher and louse contact zones indicates that they have moved relative to one another since time of initial contact. The simplest way to explain this 6-km offset between the gopher and louse zones is to suggest that the northern species of louse (*G. aurei*) has expanded its range 6 km southward during the past 62 years (the time period between the 1929 flood and our 1991 field season). This would translate into an average rate of southward movement of 0.097 km (or approximately 100 m) per year for the louse, *G. aurei*.

Another possible explanation for the 6-km offset between the gopher and louse zones is that the current louse zone is more-or-less stationary and marks the original site of contact between the northern and southern gophers. According to this hypothesis, the midpoint of the gopher cline has moved 6 km northward between 1929 and 1991 to arrive at its present position straddling the San Acacia constriction. The attraction of clines toward partial barriers located within approximately one zone width of the cline (as in this case) is a well-known feature of contact zones (Endler 1977; Kohlmann and Shaw

1991). Zone movement is usually thought to result from numerical superiority of one form resulting in genetic swamping of the other (Kohlmann and Shaw 1991). Because this hypothesis predicts that the zone of overlap between the louse species has remained relatively stationary since time of initial contact, we might expect to see a habitat shift or other discontinuity in this region to which the two louse species respond differentially. Visual inspection of habitat composition and quality at the zone of overlap reveals no such discontinuity, although it is also possible that a simple density trough caused by frequency-dependent selection against colonizing lice of one or both species has trapped the zone at its present location.

A third hypothesis to explain the 6-km offset of the gopher and louse zones suggests that the site of initial contact between the gophers (hence, the lice) occurred well south of the San Acacia constriction. According to this hypothesis, both zones (i.e., the gopher zone and the louse zone) subsequently have moved northward, but at different rates and, perhaps, for different reasons. As discussed earlier, the most likely mechanism to explain northward movement of the gopher zone is attraction of the genetic cline toward the partial geographic barrier. Similarly, northward movement of the louse zone may result simply from numerical dominance of southern lice south of the geographic constriction, or it could result from competitive superiority of the southern louse species, or a combination of these causes. Regardless of its cause, this hypothesis predicts northward movement of the louse zone.

A Test of the Three Hypotheses of Zone Movement

Each of the three hypotheses to account for the 6-km displacement of the gopher and louse contact zones entails very different predictions about zone movement: the first hypothesis predicts southward movement of the louse zone, the second predicts a stationary louse zone, and the third predicts northward movement of the zone. In spring of 1996, five years after our initial location and characterization of the louse zone, we returned to the study site to relocate the zone of overlap between the louse species. We discovered that the center of the zone had moved approximately 700–900 m south of its 1991 position (Fig. 2), which translates into an observed rate of southward movement of approximately 140–190 m/yr for the northern louse, *G. aurei*. Considering the multitude of factors that potentially could affect rate of zone movement (including host density over space and time, relative and absolute density of the two louse species, and competitive interactions between the louse species), this measured rate of southward movement (140–190 m/yr) is not far from the hypothesized average rate of movement (100 m/yr) necessary to move the zone a total of 6 km in 62 years (between 1929 and 1991).

Zone movement is expected in cases where populations coming into secondary contact compete for a common limiting resource (Endler 1977). Considering that stable coexistence of two species of *Geomydoecus* on a single host is virtually unknown (Price and Emerson 1971), competitive superiority of the northern louse (*G. aurei*) would seem to be the driving force moving the louse contact zone southward.
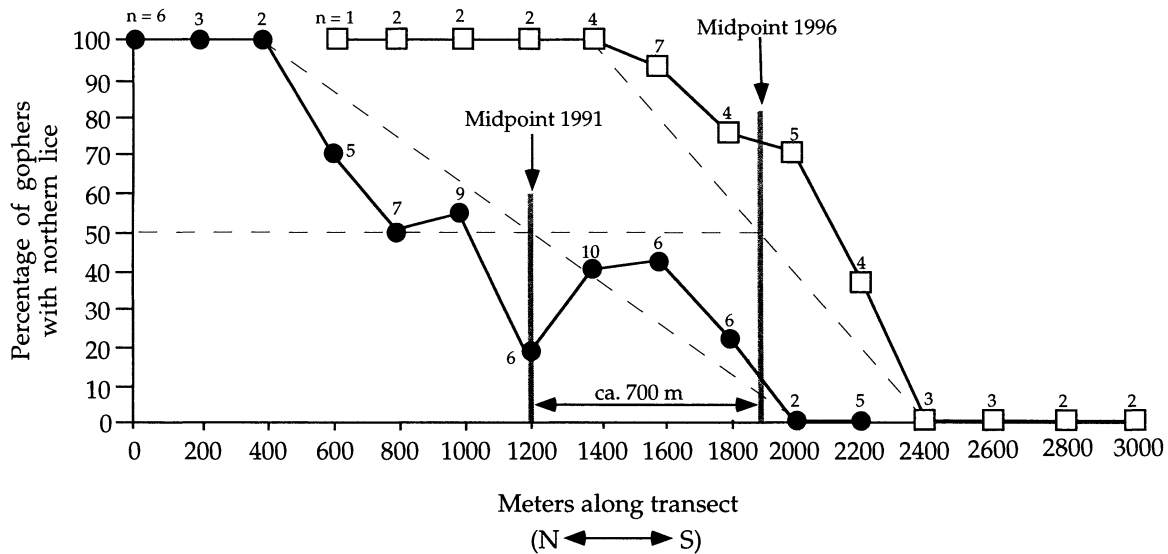
FIG. 2. Transects (sampled in 1991 and 1996) through the zone of overlap between the northern species of louse (*Geomydoecus aurei*) and the southern species of louse (*G. centralis*) in the Rio Grande Valley of central New Mexico (see Fig. 1). For each transect, the zone was divided into 200-m intervals, and the percentage of pocket gophers in each interval hosting the northern species of louse was recorded (number of gophers sampled per interval is indicated on the plots). Gophers hosting both species of lice were scored as one-half north, one-half south (e.g., three of the seven gophers at the 800-m interval hosted only northern lice, three hosted only southern lice, and one hosted both species of lice). The midpoint of each zone was calculated in two ways. In the first method, the midpoint was simply one-half of the distance between the northernmost occurrence of a southern louse and the southernmost occurrence of a northern louse on the pocket gophers sampled (indicated by dashed lines on the plot). According to this method, the midpoint of the louse contact zone moved approximately 700 m southward between 1991 and 1996. The second method calculated the midpoint of the zone as the midpoint of a least-squares regression line (not shown) fit to the data points for each of the two samples. The regression analysis of the 1991 sample included only the data points between the 400-m and 2000-m transect intervals, and the analysis of the 1996 sample included only the data points between the 1400-m and 2400-m intervals. The regression line for the 1991 sample was $y = 82.333 - 0.0467x$, and the midpoint (where $y = 50$) was located at 692 m. The regression line for the 1996 sample was $y = 209.29 - 0.0979x$, and the midpoint was located at 1627 m. According to this method of midpoint calculation, the louse contact zone moved 935 m southward between 1991 and 1996.

Competition between the two louse species also may account for the discrepancy between estimated dispersal distances for gophers (400 m/yr) and lice (140–190 m/yr) in this region. Although the lice are dependent on pocket gophers for dispersal, successful establishment of a new louse colony following gopher dispersal will be impeded by competition from resident louse populations. Although the northern species of louse may be competitively superior, the southern species of louse will be numerically dominant south of the zone, which will retard southward movement of northern lice. Future studies of louse distribution and movement in the zone of overlap and laboratory studies of competition between the two louse species should elucidate the role that competition plays, if any, in zone movement.

In conclusion, our reassessment of this contact zone leads us to argue that the zone was formed sometime after the 1929 flood, rather than 10,000 years ago in the Pleistocene. Importantly, the evidence we provide is an alternative to, but not a falsification of, the hypothesis of a Pleistocene origin of the zone (Smith et al. 1983). The gopher dispersal distance (400 m/yr) required to generate a 5-km-wide cline in only 54 years is biologically tenable and fits within the range of both estimated and measured dispersal distances for pocket gophers (100–500 m/yr). Similarly, our hypothesized rate of southward movement of the louse contact zone (average of 100 m/yr since 1929) fits reasonably well with our measured rate of zone movement between 1991 and 1996 (140–190 m/yr).

Because it is well established that the Pleistocene epoch was a period of intense climatic fluctuation, there is a widespread tendency among biologists to assume that the current geographic distribution of most terrestrial organisms has been determined primarily by Pleistocene events (e.g., Orr 1960; Savage 1960; Findley 1969; Hubbard 1973; Morafka 1974; Schmidly et al. 1993). Although this supposition may be correct on a global or even continental scale, the current study illustrates that preoccupation with Pleistocene events and their attendant effects on plant and animal distributions may cause researchers to overlook more recent events that may have had profound influence on organismal distributions on smaller, or local, geographic scales (Hewitt 1988). Considering the dramatic distributional changes recorded for several species of mammals over relatively short periods of time (Frey [1992] reported shifts of up to 450 km during the past 30 years), it may be tenuous to assume—in the absence of actual evidence—that a present-day zone of contact between two mammalian taxa is of Pleistocene origin.

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