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RECONSTRUCTING THE SPREAD OF *DIROFILARIA IMMITIS* IN CALIFORNIA COYOTES

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ABSTRACT: *Dirofilaria immitis* is a filarial nematode parasite that is currently widely enzootic in dog and coyote (*Canis latrans*) populations of California. Weak historical evidence suggests that the initial focus of *D. immitis* in California occurred 3 decades ago in the Sierra Nevada foothills (SNF) and spread to other parts of California thereafter. However, this hypothesis is difficult to evaluate because of the lack of epidemiological studies on heartworm in California before 1970. We investigated this hypothesis by comparing *D. immitis* prevalence in coyotes between initial (1975–1985) and current (2000–2002) surveys in the SNF and 2 coastal regions. In the SNF, prevalence of heartworm was not significantly different between initial (35%, n = 169) and current (42%, n = 60) surveys ($P = 0.17$), suggesting the existence of a stable enzootic focus in the initial survey period. In contrast, current prevalence was 4 times higher than initial prevalence in the northern Coast Range foothills (44 vs. 10%; n = 119, 107; $P < 0.001$) and in the south San Francisco Bay foothills (32 vs. 8%; n = 31, 59; $P = 0.005$), suggesting that initial surveys were made during the early stages of colonization. *Dirofilaria immitis* prevalence, intensity, and abundance was similar in a coastal location in Mendocino County between 1994–1996 and 1999–2002, suggesting some degree of stability in this enzootic focus. Collectively, these findings support the hypothesis that *D. immitis* established itself initially in California coyotes living in the SNF and subsequently expanded its range of enzootic foci in central California.

Parasite invasions are an increasing threat to public health and ecological systems because of worldwide increases in human movements, which often introduce parasites to nonendemic areas, and changing climates, which can lead to altered environmental conditions that facilitate establishment of novel parasites in previously inhospitable areas (Dobson and Carper, 1992; Vitousek et al., 1997). Effective tools to prevent or mitigate the effects of parasite invasions ultimately depend on our understanding of factors that allow establishment and maintenance of these organisms. Exploring the geographic associations between physiographic variables and the prevalence of parasitic infections can illuminate such factors. However, dynamic aspects of invasions also must be considered. For example, the absence of a particular parasite in a location could indicate either that it lacks the physiographic components necessary for survival or transmission or simply that the parasite has not yet colonized the area. Knowing the course of a parasitic invasion can aid in distinguishing enzootic from preenzootic areas.

Parasite invasions sometimes proceed slowly and gradually across the landscape, making them easy to track (Stromberg et al., 1996), but they often proceed rapidly by leaps and bounds, which confounds efforts to reconstruct the course of spread (McGreevy et al., 1970; Pennsinger, 1977). Here, we use a comparative approach with a wildlife sentinel, the coyote (*Canis latrans*), to reconstruct the spread in central California of the parasite *Dirofilaria immitis*, which seems to have spread rapidly by leaps and bounds. In contrast to other regions, where *D. immitis* spread has occurred over several decades (Stromberg et al., 1996), *D. immitis* in California was recognized as common in dogs from many parts of the state within a decade of the first confirmed autochthonous case of heartworm in the late 1960s (McGreevy et al., 1970; Pennsinger, 1977).

At present, *D. immitis* occurs in both domestic dog and coyote populations in 3 foothill regions of central California: the Sierra Nevada foothills (SNF), the North Coast Range foothills (NCRF), and the south San Francisco Bay foothills (SBF; Fig. 1). The evidence suggests that the SNF was the initial focus of *D. immitis* in California (Garcia and Voigt, 1990). Of the first 12 documented autochthonous cases of *D. immitis* in California dogs (1957–1968), 4 were localized in Placer County in the SNF and the others were widely scattered throughout the SNF (McGreevy et al., 1970). In the early 1970s, veterinary practitioners routinely diagnosed *D. immitis* in dogs from the SNF (Weinmann and Garcia, 1974, 1980; Pennsinger, 1977). *Dirofilaria immitis* was apparently absent in the SBF until 1977, when many dogs were suddenly diagnosed with *D. immitis* infections (Hansen, 1978; Acevedo and Theis, 1982a). It is not known whether *D. immitis* occurred in the NCRF before the late 1970s, after which time *D. immitis* was found in all 3 regions (Acevedo and Theis, 1980, 1981, 1982a, 1982b; Leftwich and Carey, 1981; Walters et al., 1981; Hansen, 1982). Veterinary records provide little help in inferring the arrival of *D. immitis* in the NCRF because the lack of reports could reflect an absence of testing by veterinarians. Veterinary records also are unreliable for estimating the prevalence of *D. immitis* because of confounding factors such as differential prophylaxis, veterinary criteria for testing, and travel by dogs (Acevedo and Theis, 1982a). Geographic patterns of prevalence in coyotes, which are not subject to these biases, at least grossly parallel, but are generally higher than, the patterns of prevalence in dogs (Theis et al., 1995; Sacks, 1998). Therefore, coyotes make excellent sentinels for *D. immitis*, enabling relatively accurate inferences about the geographic distribution and abundance of heartworm (Acevedo and Theis, 1982b).

During the late 1970s and the early 1980s, several surveys of coyotes indicated that prevalence was greater in the SNF than in the NCRF or SBF regions (Weinmann and Garcia, 1980; Acevedo and Theis, 1982b Hansen, 1982), possibly because *D. immitis* was comparatively newer to the coastal regions. Alternatively, the pattern could have reflected inherent differences in transmission intensity among these regions (Garcia and Voigt, 1990). One way to determine the most likely explanation is to compare prevalence at 2 different times. In contrast to microparasites, for which prevalence often fluctuates greatly over time, prevalence of macroparasites usually increases to a stable level (Anderson and May, 1978; May and Anderson, 1978). Such stable equilibria are especially likely in macroparasites that do not strongly impair host reproduction. This ap-

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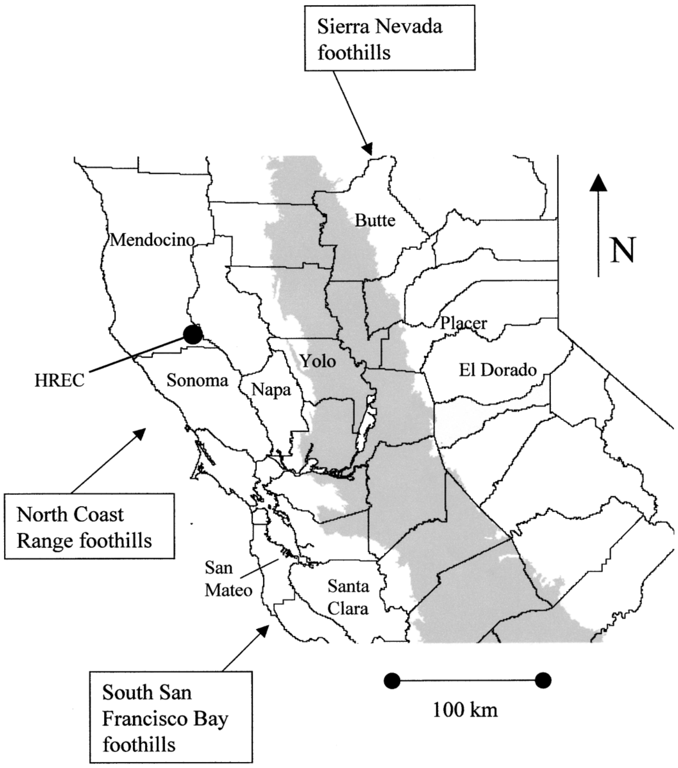

FIGURE 1. Central California foothill regions and counties. Labeled counties were surveyed for heartworm in coyotes in 1975–1985 (initial) and 1999–2002 (current), except for Santa Clara County, which was not initially surveyed. The Sierra Nevada foothill (SNF) region is separated from the northern Coast Range foothill (NCRF) region (north of the San Francisco/San Pablo Bay) and the south San Francisco Bay foothill (SBF) region by the Great Central Valley (gray). The HREC is a 21-km^2 research facility located in southeastern Mendocino County.

pears to be the case for *D. immitis* in coyotes (B. N. Sacks, unpubl. data). Therefore, the higher *D. immitis* prevalence in the coastal regions during the latter period, but not (or less so) in the SNF regions, would suggest an earlier establishment of *D. immitis* in the SNF. If, however, prevalence has remained low in the coastal regions, this would support the hypothesis that initial patterns of prevalence among regions reflected differences in factors affecting transmission such as vector density or abundance of noncanid hosts for vector mosquitoes (Garcia and Voigt, 1990). Recently, the prevalence in a Mendocino County NCRF coyote population was found to be higher than the prevalence estimated from earlier NCRF surveys (and higher than in SNF surveys; Sacks, 1998). However, the specific location had not been previously surveyed, and the difference could have been due to the heterogeneous distribution of heartworm (Acevedo and Theis, 1982b). Thus, the high prevalence that was found recently could have reflected a focus of unusually high heartworm infection and not necessarily a general increase in prevalence in the NCRF.

This study was undertaken to determine if *D. immitis* prevalence has increased since the initial surveys in the 2 coastal regions relative to the SNF and also to determine if the high prevalence in Mendocino County (Sacks, 1998) was spatially or temporally anomalous. Coyote carcasses were obtained from previously surveyed locations and examined for heartworm infection. Estimates of *D. immitis* prevalence from past and present surveys were compared to test the hypothesis that prevalence has increased more in the SNF than in the NCRF and the SBF. This approach assumed that heartworm prevalence was relatively stable over time once it reached equilibrium for a particular location. To assess stability, we compared heartworm prevalence, intensity, and abundance in coyotes from the recent Mendocino County location (1999–2002) with results from the earlier survey (1994–1996; Sacks, 1998). We also compared prevalence, intensity, and abundance of heartworm in coyotes among Mendocino and 2 other NCRF counties to determine whether the high prevalence found in Mendocino County was specific to that county or was representative of overall prevalence in the NCRF.

MATERIALS AND METHODS

Carcass collection and necropsy

We obtained coyote carcasses from the United States Department of Agriculture, Wildlife Services and the Santa Clara County Vector Control District. Coyotes were obtained by wildlife specialists as part of livestock depredation control and public health programs, and no coyote was killed expressly for this study. Obvious pups (through August) were not collected. The age of each coyote was assessed by enumeration of root cementum annuli of a lower canine or premolar (Linhart and Knowlton, 1967; Matsons Laboratory, Milltown, Montana). We determined infection status and number of adult heartworms in each coyote by inspection of the right ventricle through both branches of the pulmonary artery, the right atrium, and the thoracic vena cavae. Heartworms were sorted by sex, measured, and frozen in physiological saline for future genetic analyses.

Study design

We compared current prevalence with previous prevalence in the 3 regions, SNF, NCRF, and SBF, which included foothills and adjacent portions of valleys. Within these regions, we selected spatial sample units that were as similar as possible to those from previous surveys (Fig. 1). Because wildlife specialists serviced particular counties, initial surveys presented data by county. Therefore, counties were the basis for spatial units in this study. In 3 counties where the locations of initial survey samples were known, we restricted our sampling to the same parts of those counties, specifically western portions of El Dorado, Placer, and Yolo counties (as divided by longitudes 120.70°W, 121.19°W, and 121.90°W, respectively). We were unable to collect enough specimens from San Mateo County, where earlier surveys had been conducted in the SBF (Acevedo and Theis, 1982b), so we also used coyotes from the adjacent Santa Clara County. To assess whether this comparison was confounded by spatial differences between initial and current surveys, we compared subsets of coyotes that came from a 20-km length of a northeast-facing slope of the Santa Cruz Mountains that spanned the 2 counties and included Los Trancos Woods, the site of the putative initial SBF focus (e.g., Hansen, 1978). This 20-km area was sufficiently small and continuous so as to represent the same coyote population. Although 2 initial surveys were conducted in San Mateo County, an unspecified portion of Hansen's (1982) data for San Mateo County (but not other counties in his survey) was based on inspection of lungs only; so for San Mateo County, we used only the data from Acevedo and Theis (1982b), which (like the other surveys) consistently incorporated data from the examination of hearts.

Specific locations of samples for the initial surveys in Napa and Sonoma counties were unavailable (Hansen, 1982). However, coyotes are currently taken from the same areas of the county as for the initial surveys so that samples used in the current survey are distributed similarly as those in the initial surveys (E. Goymerac, pers. comm.). Nevertheless, for the present survey, we assessed the heterogeneity of prevalence in these counties to gauge the potential for bias in comparisons. We compared prevalence between the northern and southern halves of the 2 counties (divided by latitude 38.4°N) by using the current survey data (1999–2002). The northern halves of these counties are character-

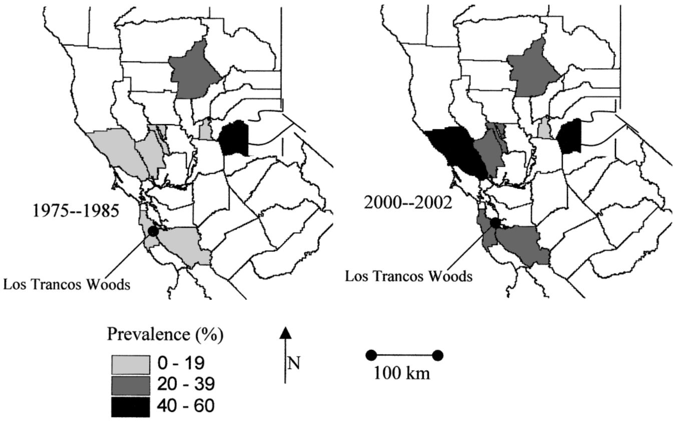

FIGURE 2. Prevalence of heartworm in 9 counties observed during initial surveys (1975–1985) and current surveys (1999–2002).

ized by wooded foothills, which are especially suitable for the western tree hole mosquito (*Ochlerotatus sierrensis*), considered the primary *D. immitis* vector in California (Weinmann and Garcia, 1974). The southern halves are composed primarily of grassland foothills and agricultural valley, which are poor habitats for the western tree hole mosquito.

Although coyote age influences probability of infection, to be consistent, we pooled coyotes of all ages for comparisons involving data from initial surveys. Two of the initial surveys did not report coyote ages (Acevedo and Theis, 1982b; Hansen, 1982), and 1 that did (Weinmann and Garcia, 1980) used tooth wear to indicate age, which is a subjective, less reliable method (Linhart and Knowlton, 1967). Chance variability in the proportions of subadult coyotes (less likely to have heartworm) in samples was a source of random error that could weaken the statistical power to detect regional differences between past and present prevalence. However, a systematic bias in age representation within regions was not expected.

In comparisons between time periods in the Mendocino County site, Hopland Research and Extension Center (HREC; Fig. 1), and between Mendocino County (broader than the site) and 2 other NCRF counties (Sonoma, Napa), we used only adult coyotes (>1 yr), and comparisons were made with respect to prevalence (proportion of individuals infected), intensity (number of heartworms per infected individual), and abundance (prevalence × intensity) (sensu Bush et al., 1997). Additionally, adult coyote ages, in months (assuming birth on 1 April; Sacks and Neale, 2001), were compared among time periods or locations to test for the possibility that age distributions differed, which could have confounded the comparisons.

Statistical analyses

For each region, chi-square values and their degrees of freedom were summed across spatial units and used to test for significance of the entire region (Zar, 1984). This procedure effectively controlled for unequal sampling among spatial units. Because the SBF was represented by a single spatial unit, Fisher's exact test was used for that region (Zar, 1984). Otherwise, prevalence was compared using Fisher's exact tests (2 groups) or log-likelihood *G*-tests (3 groups; Zar, 1984). Heartworms were overdispersed among coyote hosts (Sacks and Blejwas, 2000), and coyote age also was nonnormally distributed (Sacks et al., 1999). Therefore, nonparametric Kruskal–Wallis analysis of variance and Mann–Whitney *U*-tests were used to test for differences in median heartworm intensity, abundance, and coyote age (Zar, 1984).

RESULTS

During 1999–2002, 268 coyotes from 9 counties were examined for *D. immitis*; 129 (48%) coyotes were infected, each with 1–158 adult heartworms. Compared with the initial surveys during 1975–1985, which indicated a higher prevalence in the SNF than in the 2 coastal foothill regions, the current surveys indicated similar high prevalence in all 3 regions (Fig. 2). In the SNF, prevalence of heartworm was not significantly different between initial and current surveys (Table I). In contrast, prevalence was higher in current than in initial surveys, both in the SBF and in the NCRF regions. In the SBF, when the subset of locations occurring on the northeast-facing slope of the Santa Cruz Mountains was compared, prevalence was higher in the current (8/16, 50%) than in the initial (3/22, 14%) samples (Fisher exact $P = 0.01$).

In the current NCRF surveys, prevalence was higher in northern (25/32, 78%) than in southern (4/19, 21%) Sonoma County (Fisher's exact $P < 0.001$), but it was not significantly different between northern (12/28, 43%) and southern (6/25, 24%) Napa County (Fisher's exact $P = 0.08$).

The prevalence, intensity, and abundance of *D. immitis* in adult coyotes at HREC were similar in 1994–1996 and in the current survey, as was median adult coyote age (Table II).

TABLE I. Comparison of heartworm prevalence in coyotes between initial surveys (1975–1985) and current surveys (2000–2002) for the Sierra Nevada foothill (SNF), North Coast Range foothill (NCRF), and south San Francisco Bay foothill (SBF) regions.

County	No. positive/no. examined (%) Initial surveys*	Current surveys	χ^2	df	*P*
SNF total			3.54	2	0.17
Placer	2/26 (8)	0/4 (0)	—	—	—†
Butte	15/38 (39)	4/17 (24)	1.32	1	0.25
El Dorado	42/105 (40)	21/39 (54)	2.22	1	0.14
NCRF total			33.20	3	<0.001
Sonoma	3/41 (7)	29/51 (57)	24.60	1	<0.001
Napa	5/41 (12)	18/53 (34)	5.93	1	0.01
Yolo	3/25 (12)	5/15 (33)	2.67	1	0.10
SBF					
San Mateo, Santa Clara	5/59 (8)	10/31 (32)			0.005‡

* Initial data from Theis et al. (1995) (Placer and Butte counties, 1980–1985), Weinmann and Garcia (1980) (El Dorado County, 1975–1977), Hansen (1982) (Sonoma and Napa counties, 1980–1981), and Acevedo and Theis (1982b) (Yolo and San Mateo counties, 1980–1981).
† Insufficient data for statistical comparison.
‡ Fisher's exact test.

TABLE II. Comparison of heartworm prevalence, intensity, and abundance in adult coyotes and age of adult coyotes between 1994–1996 and 1999–2002 at the (Hopland Research and Extension Center) HREC site in Mendocino County.

Variable	1994–1996*	1999–2002	Test	*P*
No. positive/no. examined (%)	21/23 (91)	24/30 (80)	†	0.17
Intensity (median)	15	20.5	184‡	0.18
Abundance (median)	12	15	313‡	0.56
Age (median, yr)	2.4	1.7	426‡	0.15

* Data from Sacks (1998).
† Fisher's exact test.
‡ Mann–Whitney *U*-test.

The current prevalence and abundance of *D. immitis* in adult coyotes were higher in Mendocino County than in Sonoma and Napa counties (Table III). Median heartworm intensity and coyote age did not differ significantly among the 3 counties.

DISCUSSION

The current survey indicated that *D. immitis* prevalence in coyotes was similarly high in the coastal and SNF regions of central California, in contrast to the surveys conducted 2 decades earlier indicating lower prevalence in the coastal regions. Although the spatial similarity of sampling between the current and initial surveys was difficult to evaluate in some counties, there was no reason to expect systematic bias relative to prevalence. Therefore, spatial variation among sample sites in the 2 surveys likely would not account for the observed higher prevalence in current surveys in almost all the coastal spatial units. Further, when comparisons were made using data from a small area of SBF, the qualitative result was the same as that for the entire region. Although Sonoma County had higher prevalence in the northern than in the southern half, prevalence in the southern half was still >3 times that estimated for the entire county during the initial survey. Prevalence was not detectably heterogeneous in Napa County.

The fact that prevalence increased in the coastal regions between the initial and the current surveys suggests that the initially lower prevalence reflected a pre-equilibrium state. It seems unlikely that the initially lower prevalence was due to a transient fluctuation in prevalence. First, the similarity in prevalence (as well as intensity and abundance) of heartworm at HREC observed between 2 periods spanning 9 yr suggests a relatively stable enzootic in the northern Coast Range foothills. Indeed, heartworms do not strongly reduce coyote fecundity (B. N. Sacks, unpubl. data), and stable abundance is a pattern typical of such macroparasites (Anderson and May, 1978; May and Anderson, 1978). Although incidence (i.e., rate of newly infected coyotes) and transmission intensity (rate of third-stage larval heartworms infecting coyotes) vary somewhat from 1 yr to the next depending on annual rainfall and, therefore, vector density, prevalence in the entire coyote population is relatively insensitive to such fluctuations unless several consecutive drought years accumulate (B. N. Sacks, unpubl. data). There is evidence that heartworm prevalence was reduced by an unusually long statewide drought during 1987–1992 (Sacks, 1998; Theis et al., 1999). However, drought was not a factor in the comparisons here because average rainfall was similar between periods of initial (HREC $\bar{x}$ = 102 cm, SE = 13 cm) and current (HREC $\bar{x}$ = 109 cm, SE = 23 cm) surveys. The inclusion of SNF in the comparison provided a control for such transient fluctuations because all 3 regions are likely to experience similar precipitation levels in a given year (relative to the norm for the particular region). The fact that we found higher prevalence in current than in initial studies in coastal but not in Sierra regions argues against transient fluctuations as an explanation. We cannot rule out the possibility that transmission potential, e.g., vector density, increased systematically in coastal regions between initial and current surveys, e.g., because of landscape changes, causing the observed increases in prevalence. However, this seems unlikely given the similarity in current prevalence among all 3 regions.

In conclusion, findings suggest that *D. immitis* prevalence in coyotes has increased in coastal foothills since the initial surveys and support the hypothesis that heartworm endemism occurred in the SNF before the SBF and the NCRF. The unusually high abundance of heartworm found at HREC (Sacks, 1998), although stable, was not representative of the coastal foothills generally but rather was an intense infection focus. The prevalence in northern Sonoma County, just south of Mendocino County (and HREC), was similarly high, indicating that the focus likely extended to a substantial part of the coastal mountains, probably related to physiographic similarities between the

TABLE III. Comparison among Mendocino, Sonoma, and Napa counties of current (1999–2002) heartworm prevalence, intensity, and abundance in adult coyotes and age of adult coyotes.

Variable	Mendocino	Sonoma	Napa	Test	*P*
No. positive/no. examined (%)	42/58 (72)	23/41 (56)	15/34 (44)	7.64*	0.02
Intensity (median)	19	9	10	2.98†	0.23
Abundance (median)	8	2	0	10.06†	0.007
Age (median, yr)	1.8	2.1	1.8	2.26†	0.32

* Log-likelihood *G*-test.
† Kruskal–Wallis test (*H*).

areas. Because heartworm appears to have reached a stable enzootic level in central California, a logical next step is to quantify relationships between physiographic variables affecting transmission, e.g., precipitation, temperature, vector species and habitat, and heartworm abundance in coyote populations in these areas, and then to build spatial models that can be used to predict heartworm abundance, and therefore transmission risk, over a wider area.

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