

## MOVEMENT PATTERNS AND SPATIAL EPIDEMIOLOGY OF A PRION DISEASE IN MULE DEER POPULATION UNITS

MARY M. CONNER<sup>1,2,3</sup> AND MICHAEL W. MILLER<sup>1</sup>

<sup>1</sup>Colorado Division of Wildlife, Wildlife Research Center, 317 West Prospect Road,  
Fort Collins, Colorado 80526-2097 USA

<sup>2</sup>Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, Colorado 80523 USA

**Abstract.** Spatial patterns of disease occurrence across a landscape are likely products of both the ecological processes giving rise to underlying epidemics and the physical pathways of disease spread. Spatially explicit epidemic models often rely on assumptions about system boundaries and processes for spread that may not faithfully represent true patterns of host or vector distribution and movements. As a foundation for future modeling and parameter estimation, we evaluated potential influences of distribution and movements of mule deer (*Odocoileus hemionus*) on the spatial epidemiology of chronic wasting disease (CWD) in north-central Colorado. We used cluster techniques to define mule deer population units based on location data, and then used these as the sampling unit for subsequent analyses. We found marked differences in prevalence between population units that appeared at least partially related to deer movements. Migration (mean migration rate = 44%) rather than dispersal movements ( $\leq 2\%$  dispersal rate) appeared the most likely mechanism for disease spread among population units. Analysis of exchange matrices coupled with prevalence differentials between population units indicated that a single source of CWD was unlikely in north-central Colorado. Using anthropogenic boundaries (such as counties or game management units) to define sample units rather than population units could have obscured the potential role of deer movement in the spatial epidemiology of CWD. Using population units or subpopulations as the sample unit and including movements at this scale are broadly applicable approaches for spatial epidemiology.

**Key words:** chronic wasting disease; cluster analysis; Colorado, USA; dispersal; distribution; migration; mule deer; *Odocoileus hemionus*; population home range; prion; prevalence; spatial epidemiology.

### INTRODUCTION

Patterns of wildlife disease across landscapes are rarely homogeneous. Observed spatial variation in prevalence may reflect the ecological processes giving rise to an epidemic, as well as pathways of disease spread. An introduced wildlife disease may appear as a point source with diffusion, as observed in bovine tuberculosis in white-tailed deer (*Odocoileus virginianus*) (Schmitt et al. 1997, Hickling 2002) and raccoon rabies in the northeastern United States (Jenkins and Winkler 1987, Moore 1999). Established epidemics may show a diffusion wave front, as seen in fox rabies in Europe (Kallèn et al. 1985, Smith and Harris 1991), or a patchy distribution, as seen in anthrax epidemics in African ecosystems (Prins and Weyerhauser 1987). Although a broad-scale view of an epidemic may suggest diffusion across a landscape, finer resolution may reveal a more patchy distribution. For example, the pattern of raccoon rabies in Pennsylvania, USA, appeared consistent with simple diffusion when viewed

on a large geographic scale; however, subsequent analyses revealed corridors, high-prevalence areas, and rapid local spread that did not conform to simple diffusion model predictions (Moore 1999). It follows that observed patchiness of a wildlife disease on a landscape could be the product of either environmental factors that enhance the existence or transmission of the disease, or be due to the predominant distribution and movement patterns of hosts or vectors of the disease.

Chronic wasting disease (CWD; Williams and Young 1980), a prion disease of North American cervids, occurs in both captive and free-ranging populations (Williams and Miller 2002). The largest known free-ranging focus of CWD in a natural population is in southeastern Wyoming and north-central Colorado (Miller et al. 2000), where mule deer (*Odocoileus hemionus*) are the most abundant host species. Although only recognized in the wild for about two decades, simple models and field data suggest that CWD has occurred in this area for >30 years, and may be best viewed as an epidemic with a protracted time scale (Miller et al. 2000, Gross and Miller 2001). Surveillance data suggest that CWD prevalence is spatially heterogeneous at both fine ( $\leq 50$  km<sup>2</sup>; Wolfe et al. 2002) and broad (>38 000 km<sup>2</sup>; Miller et al. 2000) scales of resolution (Fig. 1). On a local scale, this observed heterogeneity may be a product of

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<sup>3</sup> Present address: Department of Forest, Range, and Wildlife Sciences, Utah State University, Logan, Utah 84322 USA. E-mail: mconner@cc.usu.edu

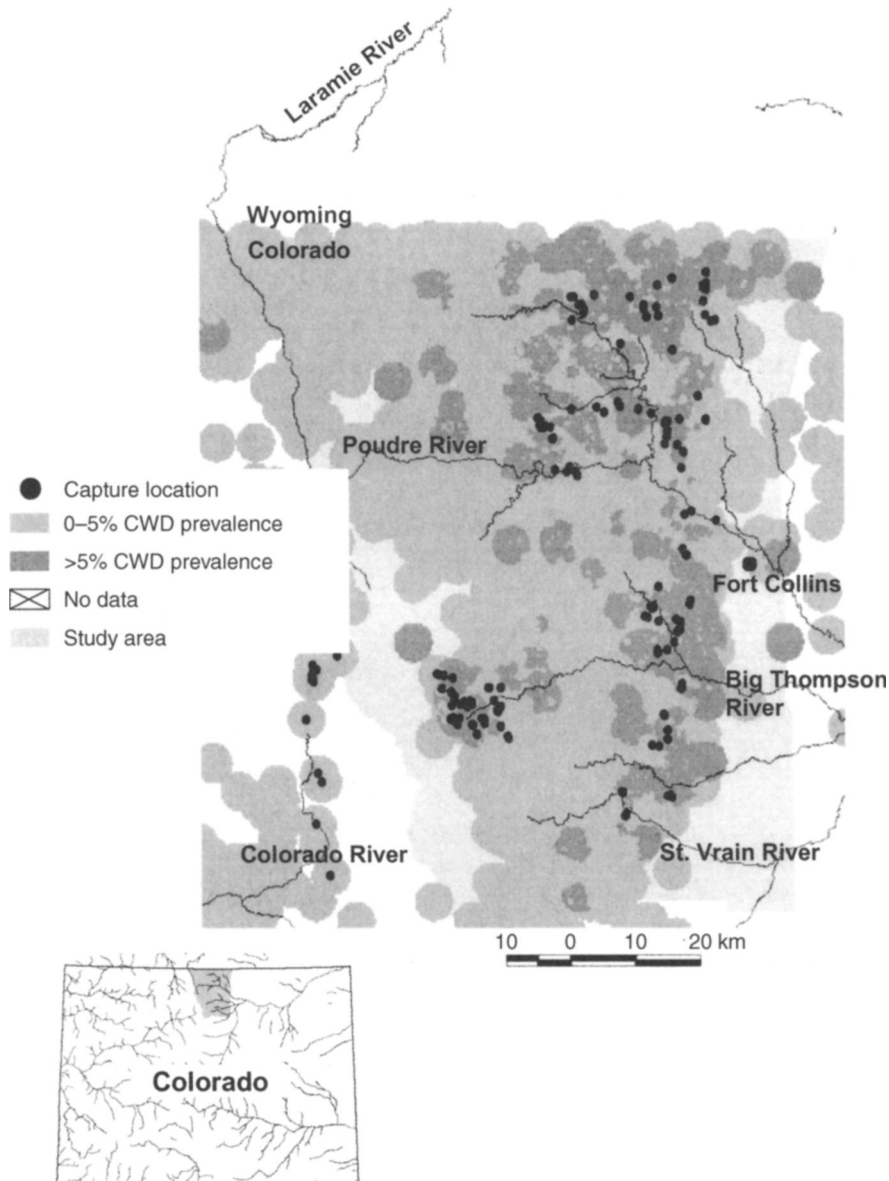


FIG. 1. Chronic wasting disease endemic area, background prevalence, and capture locations for 363 mule deer instrumented with VHF radiocollars in north-central Colorado, USA, December 1996–March 2002. One circle may represent the general capture location of several deer.

processes affecting transmission or persistence of the CWD agent. At larger geographic scales, however, heterogeneity of CWD prevalence seems more likely a product of mule deer movements and the duration of local epidemics.

Few data have been published on the effects of larger neighborhoods and long-distance movements and contacts on the spatial epidemiology of wildlife diseases (Mollison and Levin 1995, Hess et al. 2002). Recently, cluster analysis, in conjunction with home range estimators, has been applied to animal location data to delineate subpopulations or population units (Bethke et al. 1996, Schaefer et al. 2001, Taylor et al. 2001,

Mauritzen et al. 2002). We had the unique opportunity to apply these methods, but not with the primary goal of delineating population units. Rather, we sought to explicitly define mule deer population units as sample units (i.e., to draw inference from deer population units rather than from individual deer), and then to assess how the distribution and movements of these population units may have contributed to observed large-scale spatial patterns of CWD occurrence. We viewed this as a first step toward developing an empirical basis for generating hypotheses about spatial epidemiology of CWD for future experimental and modeling efforts. Here, we used radiotelemetry location data and cluster

analysis to define mule deer population units and their spatial relationships, and georeferenced surveillance data to estimate CWD prevalence. Specifically, our objectives were to use these independent data sets to examine: (1) general dispersal and migration movement patterns of the population units, (2) variation in CWD prevalence between population units on winter and summer ranges, (3) potential exchange rates between population units on winter and summer ranges, and (4) likely paths of disease flow based on prevalence and potential exchange rates.

## METHODS

### *Study area*

Our study area was a 7100-km<sup>2</sup> area in north-central Colorado, USA, (Fig. 1) where CWD is endemic in free-ranging cervids (Miller et al. 2000). Elevation ranged from 1400 m in eastern portions to 4300 m in western portions of this area. The northeastern quarter of the study area, from Fort Collins north, was rolling foothills and high prairie where livestock grazing was the main land use. Vegetation was primarily sagebrush-steppe habitat with big sagebrush (*Artemisia tridentata*), antelope bitterbrush (*Purshia tridentata*), mountain mahogany (*Cercocarpus montanus*), and mixed grasses. The southeastern quarter of the study area, from Fort Collins south, consisted of urban centers separated by rural areas with numerous small ranches and agricultural fields, as well as some suburban areas. The higher elevation areas in the western half of the study area were a gradation from mainly dense stands of mountain mahogany interspersed with grassland openings and small timbered patches of ponderosa pine (*Pinus ponderosa*), to mountain shrub habitat with a ponderosa pine and Douglas-fir (*Pseudotsuga menziesii*) overstory that gave way at the highest elevations to alpine tundra. Mule deer resided throughout the study area, at least seasonally.

### *Data collection and sample size*

Deer were captured by helicopter netgunning (Barrett et al. 1982), clover trapping (Clover 1956), and chemical immobilization, primarily during December–March. We used expandable, very high frequency (VHF) radiocollars (Telonics, Incorporated, Mesa, Arizona, USA; Smith et al. 1998) to allow for neck growth in fawns and neck swelling in male deer during the breeding season. We used data from deer captured for two different projects. For the first project, conducted from December 1996 to December 1998, deer were collared as part of an investigation of fawn and doe survival and basic distribution (i.e., enough locations were collected to describe summer and winter range); for the second, conducted between December 1999 and March 2002, deer were collared explicitly to study spatial epidemiology of CWD. During the first project, many of the fawns were marked with drop-off collars

that lasted 5–8 mo, and animals were not located as frequently as during the second project. Thus, animals marked for the first project could not be used to describe dispersal or migration movements (the collars were not on long enough), but data from these could be used to help define population units and their respective summer and winter ranges. From both projects, there were usable data from a total of 363 deer that were radiocollared between 4 December 1996 and 12 March 2002. We captured deer on winter ranges throughout the study area to obtain a representative sample of deer distribution and established population units (Fig. 1).

Radiocollared deer were located using aerial telemetry every 6 wk to 3 mo from December 1996 to December 1999 and every 4–6 wk from December 1999 to January 2003. Deer were located between 0700–1500 hours using a Cessna 185 fixed-wing aircraft with a two-element Yagi antenna mounted to each strut of the airplane. For each deer relocation, universal transverse mercator (UTM) coordinates were recorded with a global positioning system (GPS). A total of 1698 winter and summer locations collected from the 363 radiocollared deer were used in our analyses.

In addition to defining population units, dispersal and migration movements were also of interest. Because mule deer typically disperse when 12–30 months of age (Robinette 1966, Bunnell and Harestad 1983), during the winter of 1999 we focused capture efforts on fawns and yearlings (i.e., deer 6–18 months of age). Of 111 deer radiocollared and tracked during winter 1999, 88 were fawns or yearlings. During the study period, 187 fawns or yearlings and 176 adults were radiocollared.

To estimate local CWD prevalence throughout the study area, we used georeferenced data from ongoing CWD surveillance, management, and research programs. Sampled mule deer were classified as CWD-positive (infected) or CWD-negative (uninfected) based on immunohistochemical exam of retropharyngeal lymph node or tonsil tissue (Miller and Williams 2002); CWD surveillance and diagnostic methods were as described elsewhere (Miller et al. 2000, Miller and Williams 2002, Wolfe et al. 2002, Hibler et al. 2003). Because CWD prevalence did not differ dramatically within the study area between 1996 and 2001 (Conner et al. 2000; M. W. Miller, *unpublished data*), we used all available surveillance data to estimate local CWD prevalence. Sources of tissue samples included mule deer killed by hunters during September 1996–January 2003 (Miller et al. 2000; M. W. Miller, *unpublished data*), mule deer killed by wildlife managers during December 2001–January 2003 (M. W. Miller, *unpublished data*), and mule deer captured and tonsil biopsied during March 2001–January 2003 (Wolfe et al. 2002, 2004; L. L. Wolfe, *unpublished data*). Only data from adult mule deer ( $\geq 1.3$  yr old) were used to estimate

CWD prevalence (Miller et al. 2000, Miller and Williams 2003).

For all analyses, "winter" was defined as 1 December–28 February, and "summer" was defined as 15 June–30 September. We used these definitions because 93% of radiocollared deer were on their winter range by 1 December and 92% were on summer range by 15 June; they then remained on respective seasonal ranges during these timeframes.

#### *Population units*

We focused our analyses on population units of deer that were in close spatial proximity during the winter, using cluster analysis to assign individual deer membership to population units. We defined a "population unit" as a group of mule deer that used a common winter range. Following Mauritzen et al. (2002), we used the term "population unit" rather than "population" or "subpopulation," because both of the latter assume segregation between units that is not readily demonstrated by cluster analysis (Wells and Richmond 1995). Only winter locations were used in cluster analysis to define deer population units because mule deer occur in larger groups and at higher densities on winter ranges than at other times of year (Russell 1932, Richens 1967, Mackie 1994a), making these groupings the logical focus of spatial epidemiology questions.

For each deer, we used median winter location for each deer, weighted on number of locations (Romesburg 1984, Bethke et al. 1996), to represent winter locations used in cluster analysis. Because only UTM  $x$ - and  $y$ -coordinates were used in the cluster analysis, we did not standardize location data (Romesburg 1984, SAS Institute 1990). The robustness of a cluster can be assured by independence between the cluster and the method used to demonstrate it. We used three hierarchical methods to identify clusters, including average (unweighted pair-group method using arithmetic averages; UPGMA), centroid, and equal variance maximum likelihood (EML) methods; all cluster analyses were performed by PROC CLUSTER (SAS Institute 1990). We chose these established methods for analyzing location data (Bethke et al. 1996, Schaefer et al. 2001, Taylor et al. 2001, Mauritzen et al. 2002) primarily for their robustness to outliers and for our data set's ability to meet their assumptions (Romesburg 1984, SAS Institute 1990). Clusters were identified using four criteria: (1) minimum cubic clustering criterion (CCC)  $\geq 2$  (CCC  $\geq 2$  indicates good cluster resolution, while large negative numbers indicate outliers and poor fit; SAS Institute 1990); (2) relatively large pseudo  $F$  statistic (PSF; SAS Institute 1990, Bethke et al. 1996, Mauritzen et al. 2002); (3) expected  $R^2$  of  $\geq 0.9$  (ERS; Mauritzen et al. 2002); and (4) minimum Akaike's Information Criterion corrected for small sample sizes (AIC<sub>c</sub>) for the EML method (SAS Institute 1990, Burnham and Anderson 2002).

Once we defined clusters, we then used the UPGMA method to define population units. Although all three methods yielded similar group membership, we selected UPGMA because our data met all assumptions and UPGMA performs slightly better than centroid linkage (SAS Institute 1990). Also, UPGMA has been used in similar studies of population delineation based on location data (Bethke et al. 1996, Taylor et al. 2001, Mauritzen et al. 2002).

Based on the results of cluster analysis, individual deer were assigned to a population unit. We then used all summer or winter locations for all deer in a given population unit in seasonal-range analysis. Winter and summer ranges were delineated using a kernel home range estimator using a least-squares cross-validation procedure to estimate the smoothing parameter (Worton 1989). Following previous work on delineating seasonal range (Bethke et al. 1996, Taylor et al. 2001, Mauritzen et al. 2002), we subjectively chose 80% use to represent an area commonly used by each population unit; 80% was within the 70–90% used to describe seasonal range for these studies. Moreover, the 80% use contour eliminated outlying locations from deer making occasional forays outside of their seasonal range as well as locations of a few deer that moved to summer or winter range later than most ( $\geq 92\%$ ) of their population unit. Seasonal-range estimation and delineation were performed in ArcView GIS 3.2 (ESRI, Redlands, California, USA) with the animal movements extension (Hooge and Eichenlaub 2000).

#### *Dispersal and migration movements*

We used observed winter movement distances and historical data for mule deer in the study area (Siglin 1965, Carpenter et al. 1979, Medin and Anderson 1979, Kufeld et al. 1989, Kufeld and Bowden 1995; Colorado Division of Wildlife, *unpublished data*) to develop a criterion to define dispersal, and to distinguish migratory from sedentary movement patterns. From our data, 96% of movements made by radiocollared deer were  $\leq 6$  km during core winter months when there was no migration. Similarly, an earlier local deer movement study (Siglin 1965) found that migration distances varied between 5 km and 37 km for deer in the Poudre River section of the study area. Thus, we used a simple rule of 6 km as a lower limit for dispersal or migration movements; that is, a deer was considered to have dispersed if any winter location was  $\geq 6$  km from any winter location on a previous year and to have migrated if any summer location was  $\geq 6$  km from any winter location. Only deer with  $\geq 1$  yr or  $\geq 8$  mo of location data were used in analyses of dispersal and migration movements, respectively.

#### *Prevalence, exchange, and flow rates*

Local estimates of CWD prevalence were primarily based on data collected in conjunction with annual hunting seasons during October–November, and most

TABLE 1. Summary of cluster-analysis statistics for different numbers of clusters based on three clustering methods of median winter telemetry locations of 363 mule deer in north-central Colorado, USA, December 1996–January 2003.

No. clusters	UMGMA			Centroid			EML			
	CCC	PSF	ERS	CCC	PSF	ERS	CCC	PSF	ERS	AIC <sub>c</sub>
2	0.9	1317	0.65	0.9	1317	0.64	0.9	1314	0.64	55 666
3	-12.0	744	0.67	-12.0	744	0.76	-6.4	911	0.76	55 578
4	-19.0	531	0.69	-19.0	531	0.82	-9.6	772	0.82	55 450
5	-16.0	579	0.76	-16.0	579	0.86	3.3	1215	0.86	55 078
6	-3.3	950	0.87	-3.3	534	0.88	9.7	1511	0.88	54 652
7	-1.6	1004	0.89	-1.6	1004	0.90	9.4	1490	0.90	54 299
8	6.6	1347	0.93	6.6	1347	0.91	13.3	1704	0.91	54 063
9	3.7	1209	0.93	3.7	1209	0.92	16.7	1918	0.92	53 713
10	6.2	1318	0.94	6.2	1318	0.93	17.5	1974	0.93	53 425
11	14.0	1748	0.96	14.0	1748	0.94	16.7	1924	0.94	53 315
12	16.2	1891	0.97	16.2	1891	0.94	20.2	2181	0.94	53 164
13	18.1	2029	0.97	18.1	2029	0.95	22.8	2399	0.95	52 960
14	23.8	2488	0.98	23.8	2488	0.95	24.6	2559	0.95	52 792

Notes: Key to abbreviations for column headings: CCC, cubic clustering criterion; PSF, pseudo *F* statistic; ERS, expected *R*<sup>2</sup>; AIC<sub>c</sub>, Akaike's Information Criterion corrected for small sample sizes. For all three clustering methods, >14 clusters included groups with <4 members, which were not considered viable groups (Taylor et al. 2002).

likely represented a combined sampling of sedentary and migratory deer at any given location. We assumed that CWD exposure and transmission were more likely to occur on winter range when deer concentrate at relatively high densities compared to other seasons (Mackie 1994a). Because surveillance data came primarily from winter ranges, we regarded prevalence estimates in wintering deer population units as best representing the true rate of exposure and infection for each population unit, and thus used prevalence on winter range as an index of local infection rates. Prevalence on winter ranges was calculated as the number of CWD-positive deer divided by the total number of deer sampled within the 80% use contour.

We estimated the probability that deer from one population unit overlapped (and thus potentially make direct or indirect contact) with deer from another population unit via their locations within the range of another population unit. We called this the potential exchange probability or rate, which we calculated separately for winter and summer for each population unit as

$$p_{ij} = \frac{\sum_{k=1}^{n_i} R_{ijk}}{n_i}$$

which represented the probability that a deer from population unit *i* was found within the range of population unit *j*. *R*<sub>ijk</sub> was an indicator variable that was 1 for each *k* location of a deer from population unit *i* found within the range of population unit *j* and a 0 otherwise, and *n*<sub>*i*</sub> was the total number of locations for all deer in population unit *i*. For winter ranges, where each location fell in a mutually exclusive space (either in 1 range or outside of any range), the exchange probability for each population unit *i*, which sums to 1, was the

probability that a location was within its population unit's winter range plus the probability that a location was outside its winter range. However, because locations on summer ranges sometimes fell in two to three overlapping ranges, potential exchange probabilities had to be calculated using basic set theory to count *n*<sub>*p*</sub> while accounting for intersections between summer ranges.

To evaluate likely paths of prion disease spread through the landscape, we estimated the flow of CWD from population unit *i* to population unit *j*. Potential disease flow was estimated by multiplying the matrix of estimated potential exchange probabilities on summer and winter range for each population unit by the difference in winter prevalence between the source and destination population units.

## RESULTS

### Population units

All 363 radiocollared deer were used in cluster analyses. For all three cluster analysis methods, when >14 clusters were identified in field data some of the clusters had <4 members and were not considered valid groups because inferences about movement for a population unit would be limited by so few members (Taylor et al. 2001); thus, only solutions with ≤14 clusters were considered. The UPGMA and centroid methods also had CCC ≤ -1.6 when there were <8 clusters. Using these criteria to eliminate poor solutions, we concluded that there were between 8 and 14 valid clusters discernable from our field data. For all methods, the CCC, ERS, and PSF statistic were highest for 14 clusters (Table 1). In addition, AIC<sub>c</sub> was the lowest (ΔAIC<sub>c</sub> ≥ 168) for the 14-cluster model using EML (Table 1). We therefore regarded 14 clusters as best representing population units in this study. Group memberships of

the 14 clusters did not vary substantially among methods. However, subsequent analyses revealed that in each of two identified population units, only two individual deer had sufficient data for migration and dispersal analyses. Consequently, all subsequent analyses were based on 352 individual deer (1653 locations), which represented the 12 remaining population units where sufficient sample sizes were available.

Fixed-kernel 80% use contours delineated summer and winter ranges for the 12 population units defined by cluster analysis. Analyses revealed <1% overlap between winter ranges of the respective population units (Fig. 2a), but >22% overlap of summer ranges (Fig. 2b). Lack of winter range overlap appeared attributable, at least in part, to the relatively small size of winter ranges compared to summer ranges. On average, winter ranges were 38% the size of summer ranges; the mean difference between summer and winter range size for the 12 population units was  $210 \pm 63$  km<sup>2</sup> (means  $\pm 1$  SE; range = 1–877 km<sup>2</sup>).

#### *Dispersal and migration movements*

Not all of the radiocollared deer were used in dispersal and migration analyses because data were not collected for a long enough time period on many of the deer due to mortalities and slipped or dropped collars; 151 of the 352 radiocollared deer had  $\geq 1$  year of location data and were used in dispersal analyses, and 223 had  $\geq 8$  months of location data and were used in migration analyses. Of 151 radiocollared deer with  $\geq 1$  year of location data, only three (2.0%) dispersed. By age, 2 of 101 adults, 0 of 24 yearlings, and 1 of 26 fawns dispersed. Dispersal distance for these three deer ranged between 7 km and 15 km, and their new home ranges were within established migration routes of their respective source population units. Because the proportion of deer dispersing was small relative to the proportion migrating (Table 2), and because distances moved and ultimate locations of dispersal were within established migration routes, we concluded that dispersal probably was not contributing measurably to the spread or spatial patterns of CWD in our study area. Consequently, we focused our remaining analyses on migration movements.

Most population units had a mix of sedentary and migratory deer. We observed large variation in the proportion of migratory individuals among population units, which averaged 52%, but ranged from 0% to 100% (Table 2). Mean maximum movement distance of migratory deer was  $27.6 \pm 1.4$  km ( $n = 117$ ); mean maximum movement distance of sedentary deer was  $2.6 \pm 0.1$  km ( $n = 106$ ). In general, most deer wintering north of the Poudre River migrated to the west or north-northwest to higher elevation summer ranges, while deer wintering south of the Poudre River in the low-elevation foothills tended to be sedentary (<25% migrated). The proportion of migratory deer in a popu-

lation unit did not correlate with CWD prevalence on winter ranges ( $R_{\text{adj}}^2 = -0.07$ ,  $P = 0.74$ ).

#### *Prevalence, exchange, and flow rates*

CWD prevalence varied 5–18% between population units on winter range (Table 3). We observed a general pattern in prevalence wherein highest prevalence ( $\geq 10\%$ ) occurred in the northern and southern portions of the study area, with relatively low prevalence ( $\sim 5\%$ ) in the central portion.

There was little exchange between population units during winter. Wintering deer from one population unit were located in the range of another population unit in only 6 of 960 (1%) possible population unit combinations, and the potential exchange rates between population units were small ( $\leq 2\%$ ). In contrast, we estimated higher potential exchange rates between population units on summer ranges (Table 4). Interaction was detected in 171 of 693 (25%) possible population unit combinations during summer, and potential exchange rates ranged from 1% to 54% among such cases (Table 4).

There was essentially no potential flow of CWD between population units during the winter. During the summer, however, the most distinct pattern and highest potential flows were into the Poudre River (PR) population unit (7.7%; Fig. 2c). Potential flows were also relatively high from the Red Mountain population unit to the nearby Big Hole and Campbell Valley population units (Fig. 2c).

#### DISCUSSION

Lloyd and May (1996) noted that one of the most exciting avenues for future work in epidemiology is the study of data sets containing both temporal and spatial data, which would provide information on the processes involved in epidemics and should aid in constructing more realistic spatial models. Empirically based spatial models of wildlife disease epidemics often combine georeferenced disease data with diffusion models to study spatial epidemiology in natural populations (e.g., Moore 1999, Hickling 2002). Relatively few models simulating epidemics in natural populations have incorporated more complex animal distribution and movement processes (e.g., Smith and Harris 1991, Rushton et al. 2000), perhaps because detailed data on locations and movement patterns are difficult to acquire for free-ranging animals. In addition, natural epidemics are often modeled using the constructs of anthropogenic boundaries (Jenkins and Winkler 1987, Moore 1999, Hickling 2002), such as counties or states, which may be too coarse a scale to discern movements that may greatly influence the patterns of disease spread in wildlife populations. Using georeferenced disease data in the absence of companion data on social structure and movements also may prove misleading when attempting to answer questions about the contribution of host or vector distribution and movements to the

origin, patterns, spread, and control of natural epidemics (Keeling 1999, Haydon et al. 2003). This appears to be particularly problematic in studies of large, gregarious ungulates with complex social structures and seasonal and geographic variation in movements and disease prevalence.

In this study, we wanted to use recently described advances in spatial methods and tools to explore relationships between mule deer movements and CWD epidemiology. To this end, following techniques described in cluster analyses of satellite telemetry location data (Bethke et al. 1996, Schaefer et al. 2001, Taylor et al. 2001, Mauritzen et al. 2002), we used mule deer radiotelemetry location data to define population units, as well as to estimate seasonal ranges and to describe distribution and potential exchange rates among these population units. This empirical approach, which embodied principles identified in more theoretical studies of contact networks and their influences on spatial epidemiology (e.g., Keeling 1999, Haydon et al. 2003), allowed us to combine independent movement and georeferenced disease data in assessing factors that could influence large-scale spatial patterns of CWD prevalence. Our goals were to develop an empirical basis for studying the origin and spread of CWD, as well as to generate parameter estimates for subsequent use in epidemic modeling and management experiments.

Our use of location and movement data revealed several results with respect to CWD epidemiology that would not have come to light using more traditional approaches. First, and perhaps most important, mule deer dispersal appeared unlikely to contribute to the geographic spread of CWD in our study area. Reported dispersal rates for mule deer vary widely across their western North American range (Mackie 1994a). In the Rocky Mountain region, estimated dispersal rates of yearlings ranged from 0% (Garrott et al. 1987) to 35% for females (Robinette 1966), and 60% for males (Robinette 1966); however, on the plains immediately east of our study area, fawn dispersal was estimated to be 89% (Kufeld and Bowden 1995). Because of high dispersal rates for fawns on the plains nearby, we initially hypothesized that dispersal might be an important mechanism for geographic spread of CWD. However, because observed dispersal rates were much lower than migration rates, and because relocation sites after dispersal remained within migration routes of source population units, we concluded that dispersal was not significantly contributing to the spread of CWD in our study area.

Second, data on estimated potential exchange and potential flow rates among population units revealed that CWD was relatively unlikely to spread between population units during the winter. Limited movement and remarkable fidelity to specific winter ranges combined to minimize potential for exchange of infected deer among wintering population units. However, these

same patterns may exacerbate disease transmission within mule deer population units during winter. The occurrence of different prevalences among different population units, coupled with the observations that within-unit potential exchange rates were greater during winter than summer and that winter range areas were, on average, 38% the size of summer range areas, suggests that CWD transmission may be greater within than between population units.

Although mechanisms have not been completely described, it appears that the CWD agent can be transmitted among mule deer both in the presence and in the absence of live, infected individuals (Williams and Young 1980, 1992, Williams and Miller 2002, Miller and Williams 2003; M. W. Miller, *unpublished data*). It follows that the potential for indirect transmission, combined with environmental persistence of CWD agent (Williams and Young 1992, Williams and Miller 2002, Miller and Williams 2003; M. W. Miller, *unpublished data*), could contribute to relatively high transmission probabilities on winter as compared to summer ranges. Because contact structures for contagious diseases in wildlife populations tend to be spatially localized, disease transmission is perhaps best viewed as a small-scale process wherein potential infectious contacts are limited to sympatric individuals and neighbors (Mollison and Levin 1995). Although mule deer population densities are generally not high across their year-round range, mule deer do tend to concentrate during winter (Mackie 1994a). This tendency is particularly common in mountain foothill habitats like those comprising part of our study area (Richens 1967, Mackie 1994a). Thus, although geographic spread of CWD between population units may be minimal during winter, amplification within population units may be highest during winter.

Third, analyses at a population unit level revealed that seasonal movement patterns appear to be a more plausible mechanism than dispersal for geographic spread of CWD among mule deer in our study area. The migratory patterns of population units that we studied are likely longstanding, thereby affording a solid temporal foundation for CWD spread. Based on data from previous studies conducted in the northern and central portions of our study area (Siglin 1965, Medin and Anderson 1979, Kufeld et al. 1989), both the migratory tendencies and destinations of contemporary mule deer population units that we studied remain largely unchanged from patterns observed 20–40 years ago. Mule deer elsewhere also show strong fidelity to summer and winter ranges (Russell 1932, Carpenter et al. 1979, Garrott et al. 1987, Kucera 1992). Such habits may be learned, and thus endure for generations (Russell 1932, Mackie 1994b). It follows that if migratory movements appear related to present patterns of CWD prevalence, then current epidemic patterns are likely at least a partial product of past migratory movements. Thus, it appears reasonable to consider such movement

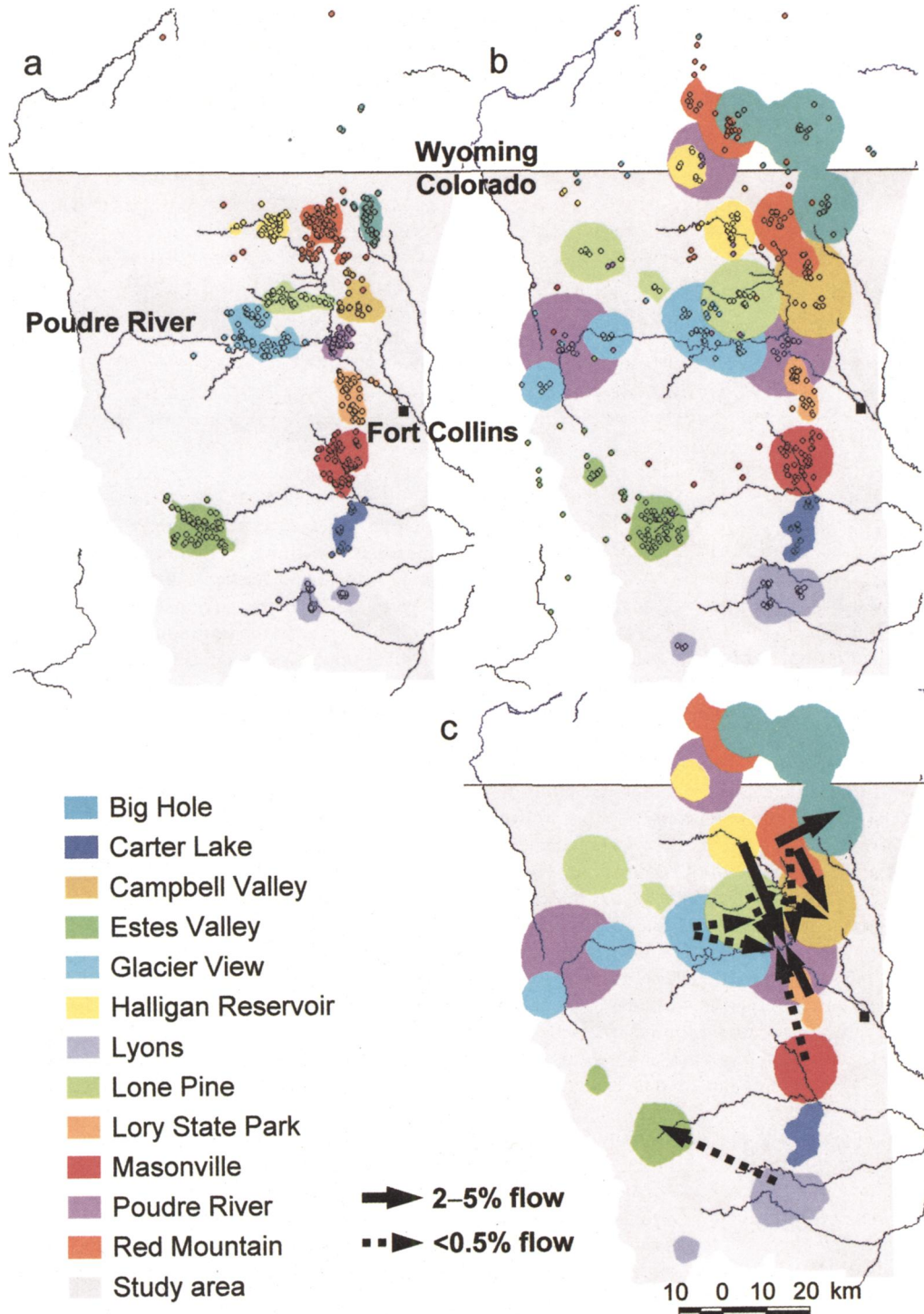


FIG. 2. Fixed-kernel 80% utilization contours for 12 population units identified by UPGMA cluster analysis of median winter locations of 352 radiocollared mule deer during (a) winter (1 December–28 February) and (b) summer (15 June–30 September) in north-central Colorado, December 1996–January 2003. (c) Likely paths of chronic wasting disease flow based on prevalence differentials on winter ranges and deer exchange rates between 12 population units based on locations of 352 radiocollared mule deer from December 1996 to January 2003.



TABLE 2. Migration statistics by population unit for 223 mule deer with  $\geq 8$  mo of location data, north-central Colorado, December 1996–January 2003.

Population unit†	<i>n</i>	Proportion migrating	Mean maximum migration distance (km)		
			1 SE	1 SE	
BH	18	0.89	0.07	23.4	2.4
CL	7	0.00			
CV	19	0.58	0.11	39.3	5.7
EV	37	0.49	0.08	20.2	2.0
GV	22	0.45	0.11	32.1	4.0
HR	9	0.67	0.16	22.3	6.2
L	9	0.11	0.10	21.2	<sup>b</sup>
LP	9	0.33	0.16	37.4	9.5
LSP	12	0.08	0.08	7.2	<sup>b</sup>
M	29	0.24	0.08	24.4	8.5
PR	11	1.00		37.6	5.4
RM	41	0.80	0.06	26.7	1.9

† The population unit abbreviations are: BH, Big Hole; CL, Carter Lake; CV, Campbell Valley; EV, Estes Valley; GV, Glacier View; HR, Halligan Reservoir; L, Lyons; LP, Lone Pine; LSP, Lory State Park; M, Masonville; PR, Poudre River; and RM, Red Mountain.

<sup>b</sup> Only one deer migrated.

patterns as stable for purposes of predicting future spread of CWD.

Fourth, despite apparently longstanding migration patterns that may have influenced CWD spread over the last several decades, the proportion of deer migrating did not appear related to prevalence within a wintering population unit. This observation conflicts with results from a stochastic simulation model of disease in metapopulations that predicted populations with low migration would remain relatively unexposed to infectious diseases (Hess 1996). This contradiction may be explained by temporal differences in local epidemic dynamics. In population units where deer migrate and spend part of the year off winter range, transmission rates may be lower and thus epidemic dynamics more protracted. Alternatively, epidemic dynamics may be more rapid in population units where deer are sedentary and have relatively small home ranges. An

TABLE 3. Estimate of chronic wasting disease prevalence of mule deer population units on winter range in north-central Colorado based on surveillance, culling, and biopsy data, September 1996–January 2003.

Population unit†	<i>n</i>	Prevalence	1 SE
CL	72	0.111	0.037
CV	116	0.052	0.021
EV	437	0.062	0.012
GV	435	0.076	0.013
HR	86	0.163	0.040
L	79	0.076	0.030
LP	239	0.063	0.016
LSP	156	0.096	0.024
M	174	0.201	0.030
PR	78	0.064	0.028
RM	144	0.167	0.031

† See Table 2 for abbreviations.

extreme example of this effect has been shown in CWD dynamics in captive mule deer, where incidence rose to over 50% within seven years of the start of an epidemic (Miller and Williams 2003). If CWD prevalence is a product of both transmission dynamics within a population unit and the time since CWD was introduced into that population unit (Miller et al. 2000), then point estimates of prevalence in two population units could be similar, even though the epidemic curves leading to those point estimates were quite different.

Finally, analyses of potential disease flow may provide insights into historical patterns of CWD's geographic spread. For example, our analyses revealed that movement of CWD into the PR population unit, which winters and summers along the Poudre River near Fort Collins, appears more likely than spread from the PR population unit to surrounding areas. This observation challenges the hypothesis (e.g., Spraker et al. 1997) that CWD originated in and spread from research facilities west of Fort Collins in the 1960s. The first documented CWD case in a free-ranging cervid was diagnosed in an elk from Rocky Mountain National

TABLE 4. Exchange rates from population unit *i* to population unit *j* on summer range for mule deer in north-central Colorado, December 1996–January 2003.

Population unit <i>i</i> †	Population unit <i>j</i> †												
	BH	CL	CV	EV	GV	HR	L	LP	LSP	M	PR	RM	OR‡
BH	0.79	0	0	0	0	0	0	0	0	0	0	0.15	0.21
CL	0	1.00	0	0	0	0	0	0	0	0	0	0	0
CV	0	0	0.84	0	0	0	0	0.05	0	0	0.11	0.21	0.11
EV	0	0	0	0.80	0	0	0	0	0	0	0.01	0	0.19
GV	0	0	0	0	0.87	0	0	0.13	0	0	0.44	0	0.07
HR	0	0	0	0	0	0.81	0	0	0	0	0.28	0	0.19
L	0	0	0	0.04	0	0	0.96	0	0	0	0	0	0.00
LP	0	0	0	0	0.12	0	0	0.96	0	0	0	0	0.04
LSP	0	0	0	0	0	0	0	0	0.96	0	0.54	0	0.04
M	0	0	0	0	0	0	0	0	0	0.85	0.02	0	0.13
PR	0	0	0	0	0.06	0.17	0	0.06	0	0	0.83	0	0.03
RM	0.38	0	0.12	0	0	0	0	0	0	0	0.03	0.78	0.16

† See Table 2 for abbreviations.

‡ OR represents the proportion of locations outside any population unit's range.

Park in 1981 (Spraker et al. 1997). Although we doubt that this was the first case to occur in the wild, it shows that CWD became established in the southwestern portion of our study area over 20 years ago. For CWD to have spread this far in the first 10–15 years of a free-ranging epidemic, relatively strong disease flow still should be evident. The location of this index case falls within the Estes Valley winter range in our study, but a direct connection between this site and mule deer wintering in the PR area west of Fort Collins appears improbable based on the movement patterns we observed. The pattern of potential disease flow that we observed seems more consistent with an alternative hypothesis (Miller et al. 2000) that CWD originated well north of Fort Collins and spread southward. However, spatial patterns of prevalence and potential disease flow probabilities also suggest the possibility that CWD may have arisen in more than one location independent of natural movements of infected mule deer. In light of recent, unexplained changes in the geographic distribution of CWD (Williams and Miller 2002, 2003), potential sources of epidemics in natural populations clearly warrant further investigation.

Although our data represent a substantial improvement in understanding spatial epidemiology of CWD in north-central Colorado mule deer, we know of two key limitations of our data set. First, we have no information on the movements or localized CWD prevalence for mule deer population units in southeastern Wyoming, immediately north of our study area. A proportion of mule deer from several of our northern population units migrated into Wyoming (Fig. 2b). Because CWD prevalence is quite high in southeastern Wyoming (Miller et al. 2000; T. J. Kreeger, *personal communication*), the role of mule deer population units north of our study area in spatial dynamics may be important in understanding the patterns observed in north-central Colorado. Second, we may not have captured deer on all winter ranges in our study area, and thus the population units we identified are probably best viewed as a representative rather than a complete sample. If all population units were not identified, then we may have underestimated rates of potential exchange and hence spread of CWD. Although we believed sampling to be relatively uniform over the study area, there may be more connectivity among some population units than generally represented by our potential exchange rates. Related to this second limitation is a bias in potential exchange rates, which probably underestimated true exchange between population units because we did not collect data continuously and hence may have missed occasions when deer were located in ranges of other population units. Thus, the potential exchange rates reported here serve only as a proxy for the probability of exchange and disease flow. In general, it is likely that the connectivity between population units is greater than we could measure, and con-

sequently disease flow may be greater than we predicted.

Advances in computing technology coupled with geographically indexed disease data have resulted in advances in methodology and applications of spatial epidemiology (Elliot et al. 2000). However, much of the recent spatial work in wildlife diseases still omits animal movements and uses anthropogenic or possibly artificial units such as counties (Moore 1999, Miller et al. 2000, Hickling 2002) or grids (Mollison and Levin 1995, Rushton et al. 2000) as the sampling unit. In this study, we were concerned with linkage between deer population units via movements, and how linkage influenced the spatial epidemiology of CWD. Thus, we were interested in population units that had some probability of exchange with each other. If we had used anthropogenic boundaries such as game management units (GMU), which are based on road and county boundaries and used to distribute hunters, as the sampling unit, then we would have come to some erroneous conclusions. First, because GMUs are large relative to deer movements so that much of the migration and dispersal occurs within a GMU, we would have underestimated the proportion of deer that dispersed or migrated. Second, because GMUs are large relative to winter and ranges of population units, we would have missed almost all of the exchange between sample units. Finally, because migration and exchange would have been grossly underestimated or fully missed, we would not have been able to evaluate potential pathways of disease flow. In the end, we would have lacked the resolution necessary to conclude that the disease was being spread by movement and contact among population units. Thus, for species with seasonal and geographic variation in movements or where animal movements occur at a finer scale than an anthropogenic unit, we recommend moving away from using simple diffusion models within anthropogenic boundaries as a basis for spatial epidemiological modeling of wildlife diseases.

From a management standpoint, we concur with Barlow (1996) that improvements in model-based evaluation of the relative merits of disease control strategies will require spatially explicit models in which animal movement and spatial interactions can be adequately incorporated. Given the advent of improved telemetry data acquisition methods, such as GPS collars, explicit incorporation of population distribution and movements into spatial epidemiological models is now more feasible. Moreover, basing models on population units and not on artificial anthropogenic boundaries greatly enhances a manager's ability to detect population units with high probabilities of transmitting the disease to other population units or contracting the disease, as well as likely paths of disease flow. Using a spatial approach and populations as the sample unit, disease control and monitoring efforts can be strategically targeted at populations of concern.

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