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HUMAN LAND USE INFLUENCES CHRONIC WASTING DISEASE PREVALENCE IN MULE DEER

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Abstract. Human alteration of landscapes can affect the distribution, abundance, and behavior of wildlife. We explored the effects of human land use on the prevalence of chronic wasting disease (CWD) in mule deer (*Odocoileus hemionus*) populations residing in north-central Colorado. We chose best approximating models estimating CWD prevalence in relation to differences in human land use, sex, and geographic location. Prevalence was higher in developed areas and among male deer, suggesting anthropogenic influences on the occurrence of disease. We also found a relatively high degree of variation in prevalence across the three study sites, suggesting that spatial patterns in disease may be influenced by other factors operating at a broader, landscape scale. Our results suggest that multiple factors, including changes in land use, differences in exposure risk between sexes, and landscape-scaled heterogeneity, are associated with CWD prevalence in north-central Colorado.

Key words: chronic wasting disease; CWD; epidemiology; landscape alteration; land use; model selection; mule deer; Odocoileus hemionus; *prion; urbanization.*

Introduction

In many areas of North America, alteration of landscapes by people has shaped the distribution and abundance of wildlife (Wiens et al. 1986, Turner 1989, McGarigal and McComb 1995, Crooks and Soule 1999, Dale et al. 2000). Less attention has been paid to the ways human action influences ecological processes, for example, the dynamics of pathogens and hosts (Van Buskirk and Ostfeld 1995, 1998, Augustine 1998, Daszak et al. 2001, Wasserberg et al. 2003). A variety of emerging, infectious diseases affect wildlife populations (Dobson and Meagher 1996, Dobson and Foufopoulos 2001, Williams et al. 2002), and the dynamics of these pathogen–wildlife systems are potentially shaped by human action.

Chronic wasting disease (CWD; Williams and Young 1980), a prion disease of mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), and Rocky Mountain elk (*Cervus elaphus nelsoni*), occurs naturally in free-ranging populations in several areas of North America, but the largest known outbreak occurs in a contiguous ~80 000-km^2 area of northeast Colorado and southeast Wyoming (Williams and Young 1992, Miller et al. 2000, Williams and Miller 2002). CWD apparently has been endemic in this area for over two decades, and field investigations and modeling suggest that the dynamics of this emerging disease may be best viewed as an epidemic with a protracted timescale (Miller et al. 2000, Gross and Miller 2001). More recent discoveries of other foci of CWD distant to this 80 000-km^2 "endemic area" have spawned interest in understanding spatial and temporal dynamics in order to develop management strategies for controlling CWD in affected populations and preventing or slowing its spread among unaffected populations.

The epidemic area also includes human communities that are growing more rapidly than almost any in the nation (Baron et al. 2000, Hansen et al. 2002). This population growth has caused dramatic change in mule deer habitat in some parts of the region. During 1970 to 2000, the area with housing density exceeding 1/20 ha more than doubled (40 636 to 81 836 ha) within game management units most affected by CWD (Theobald 2003). These trends are predicted to continue; by 2030, it is projected that 141 732 ha will be developed, almost another doubling relative to 2000. Much of this development is occurring on winter ranges where deer populations concentrate seasonally. The effects of land use change on disease processes in mule deer populations are poorly understood; however, two potential mechanisms affecting disease could exacerbate transmission in developed areas. First, if deer avoid areas of high human population density (Theobald et al. 1997, Theobald 2000) because of fences, dogs, and

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other sources of disturbance, then development could compress the area of the landscape used by deer, thereby increasing their density. It is plausible that increased density could accelerate rates of contact between infected and susceptible individuals. Second, development tends to reduce hunting pressure. As a result, adults, particularly adult males, tend to live longer in areas where hunting pressure is low. This might prolong the average clinical course by eliminating a prominent, competing source cause of mortality, and in so doing, prolong the total time that infected animals are able to transmit the disease.

Here, we explore how patterns of human land use influence variation in CWD prevalence across north-central Colorado. Based on the logic outlined above and observations of relatively high CWD prevalence among mule deer captured and tested in urban areas (Wolfe et al. 2002), we hypothesized that human development of mule deer habitat could result in higher CWD prevalence in developed areas. We also examined influences of gender and geographic location on prevalence because earlier analyses (Miller et al. 2000, Wolfe et al. 2004) suggested that these factors may affect patterns of CWD prevalence and thereby could confound underlying influences of land use patterns.

METHODS

Study area

We studied the relationship between CWD infection and human land use using four free-ranging mule deer subpopulations (Conner and Miller 2004) located across three study sites spanning roughly 1200 km^2 in Larimer County, Colorado, USA. One subpopulation resided in and around Estes Park (hereafter, EP), a second (Glacier View Meadows; GVM) was located west of Livermore, and the final two subpopulations were located west of Horsetooth Reservoir (HT). Deer habitat in the EP study area (elevation ~1850–2885 m) included coniferous forest and mountain shrub communities interspersed with deciduous forest and grasslands at lower elevations. The GVM (elevation ~1825–2450 m) and HT (elevation ~1580–2250 m) sites were composed of similar land cover and land use types as the EP site; however, the HT study area had a higher proportion of privately owned land and grass/shrubland than either the EP or GVM areas. Based on empirical studies of local mule deer movement patterns (Conner and Miller 2004), there was minimal range overlap between the HT and EV subpopulations and essentially no overlap between either of these and the GVM subpopulation. Winter range sizes (~10 km^2 for individuals; ~100 km^2 for population units) were similar for these three subpopulations, but migratory behavior differed somewhat among them: about half of the EP and GMV subpopulations migrated seasonally to high-elevation summer ranges, while only ~20% of the HT deer migrated seasonally (Conner and Miller 2004).

We chose these sites because they were typical of rapidly growing development patterns found in historical mule deer habitat in north-central Colorado where housing developments perforate the landscape (Theobald 2003). Each of the three study sites consisted of a developed zone nested within a larger undeveloped portion of the landscape (Fig. 1). We separated land use into developed and undeveloped categories based on a housing density map (Theobald 2001; D. M. Theobald and M. Kneeland, *unpublished report*). ''Developed'' zones were defined as having ≥1 dwelling per 8 ha, and ''undeveloped'' zones were remaining areas with <1 dwelling per 8 ha. These zones were defined so that developed areas contained dense-urban, urban, and suburban housing density classes and undeveloped areas contained rural housing density classes (Theobald 2001). We limited our analysis to two categories because we were concerned that including more categories would increase the likelihood that home ranges of individual deer included more than one development type. In the remainder of this paper, we use the terms developed and ''urban'' interchangeably when referring to that land use class and the deer that were sampled from it, and the terms undeveloped and ''nonurban'' when referring to the other land use class and the deer sampled from it.

Data collection

During 1997–2002, we collected geo-referenced data on presence/absence of CWD infection in individual deer sampled from urban and nonurban areas in conjunction with ongoing surveillance conducted by the Colorado Division of Wildlife (CDOW). Survey and diagnostic methods have been described in detail elsewhere (Miller et al. 2000, Miller and Williams 2002, Wolfe et al. 2002, Hibler et al. 2003); sampled deer were classified as CWD-infected or uninfected based on immunohistochemistry of retropharyngeal lymph node or tonsil tissue (Miller and Williams 2002). All samples were geo-referenced using either a global positioning system unit or by identifying sampled locations on standardized maps. We used a geographic information system to assign each deer sample location to a land use class (Fig. 1). Deer sampled in or within 1 km of core developed areas in each study site were categorized as urban deer; deer sampled >1 km from developed areas were categorized as nonurban deer. We chose to use the binary classification of deer as being from either urban or nonurban areas, rather than the use of a continuous variable such as ''distance to urbanization.'' Because land use practices within these two categories are distinctly different from one another (e.g., hunting is typically not permitted in urban areas), biologically it makes more sense to consider differences in disease prevalence between deer sampled from urban and nonurban areas, rather than as a function of distance from urban center. We labeled deer as being urban if they were nominally located 1 km beyond the

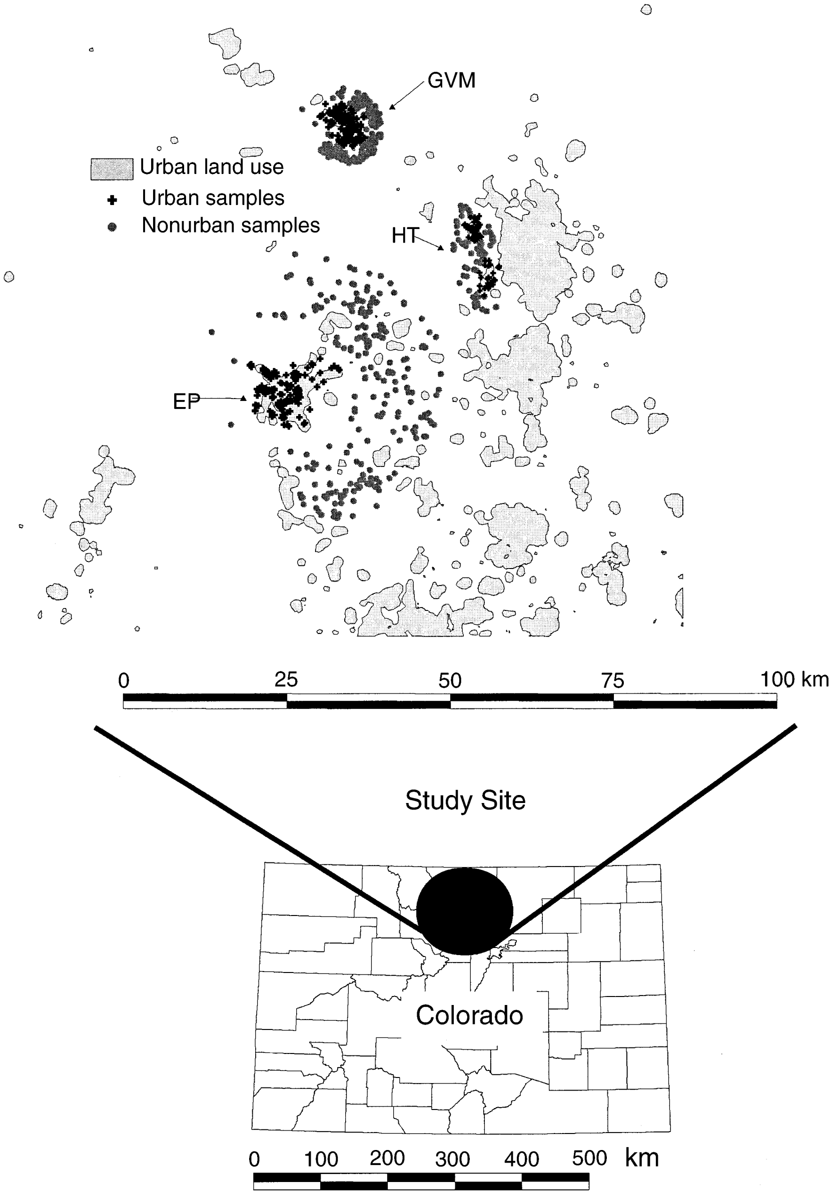

FIG. 1. Locations of the three study sites: Estes Park (EP), Glacier View Meadows (GVM), and Horsetooth Reservoir (HT), in north-central Colorado, USA.

developed boundary for two reasons. First, we wanted to reduce mapping errors associated with deer sampled near the boundary between developed and undeveloped zones. Second, although deer sampled in developed zones undoubtedly spent time in these areas, some deer residing in developed zones also may spend time in the periphery of these areas, where they could have been sampled. Nonurban deer were sampled from locations >1 km beyond the developed zone perimeter by using concentric rings extending out from the developed land use class in 0.5-km increments (Fig. 2) until we obtained a sample size of nonurban deer that was similar to the number of urban deer collected from the corresponding developed zone at each study site. Small pockets of developed land that occurred within the matrix of undeveloped land were excluded from the analysis to minimize confounding effects.

Formulation of competing models

We evaluated support for competing models portraying the relationship between CWD prevalence and the three variables of interest: land use type, sex, and study site.

We included these variables because (1) increasing development will likely increase deer density at local scales and reduce hunting mortality, (2) previous ob-

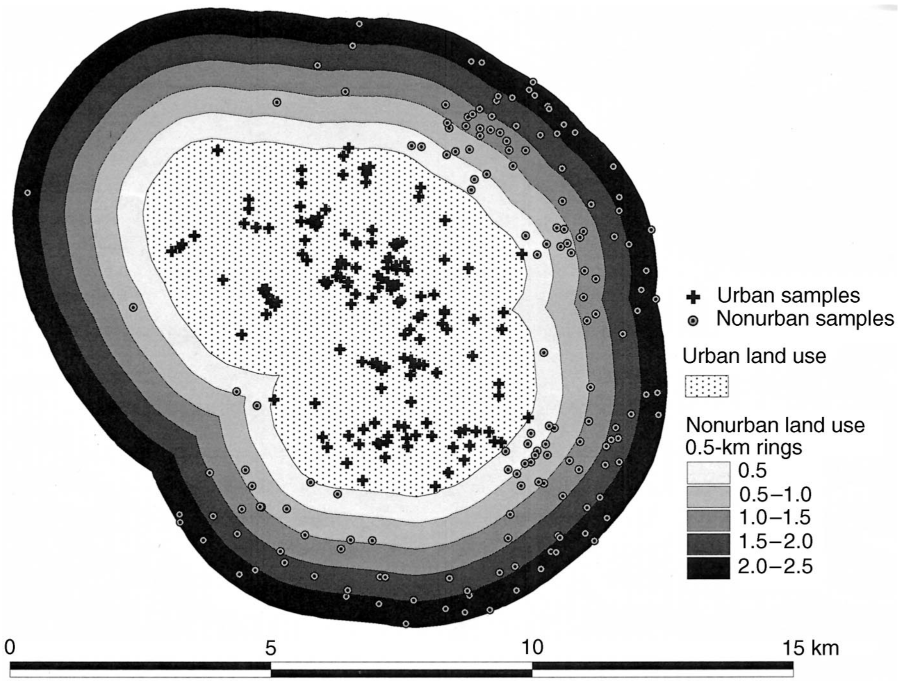

FIG. 2. Mule deer samples for the GVM site, showing the area defined as urban along with the 0.5-km annuli used for allocating deer to the nonurban land use class.

servations (Wolfe et al. 2002) suggested that higher CWD prevalence may occur in developed locations, (3) male mule deer have been observed to have higher prevalence than females (Wolfe et al. 2004, Miller and Conner 2005), and (4) previous observations have revealed substantial local variation in prevalence across large geographic areas (Miller et al. 2000, Conner and Miller 2004). To assess the contribution made by each of these variables to predicting observed CWD prevalence, we developed a suite of 16 candidate models that incorporated these variables in different combinations. Our primary hypothesis was that higher prevalence would be associated with developed areas as compared to nearby undeveloped areas. All models containing a land use effect were represented by the binary covariate ‘‘use’’ indicating whether a deer was sampled from the developed or undeveloped land use class. The influence of gender was coded as ‘‘sex’’ in candidate models; similarly, site level effects were coded as EP, GVM, and HT to represent site effects considered alone or in various combinations. Based on differences in infection rates between males and females apparent from our initial analyses, we subsequently separated the data by gender and developed candidate sets of models for each sex to investigate how the relative influence of land use and site effects on CWD prevalence differed between males and females. We determined relative support in the data for candidate models to assess the influence of each variable, both alone and in the presence of the other variables, on CWD prevalence.

Model selection

We used likelihood-based methods and information theoretics (Akaike's information criterion [AIC]; Burnham and Anderson 2002) to quantify the strength of evidence for alternative models and to estimate their parameters. Specifically, we used AIC adjusted for sample size ($\mathrm{AIC_c}$) to assess the relative information content of the models. Because model parameters were estimated based on data, there was some uncertainty that the ‘‘best’’ model would emerge as superior if different data were used to compare alternatives. We quantified this uncertainty with Akaike weights, w_r (Burnham and Anderson 2002); in the context of our analyses, we regarded normalized w_r as ‘‘probabilities’’ that the estimated model r was the best Kullback-Leibler model for the data at hand, given the set of models considered (Burnham and Anderson 2002). The w_r can be used to estimate the likelihood of the model, given the data, and in so doing offer a way to compare the relative weight of evidence for each model considered.

All models contained only additive effects, with maximum likelihood estimates, confidence intervals on model parameters, and $\mathrm{AIC_c}$ values obtained through logistic regression model fitting using SAS PROC GENMOD (SAS 2000).

RESULTS

Statistical modeling

Of the 16 candidate models fit to the entire data set, the top two models (Table 1) suggested that sex, land

TABLE 1. Candidate sets of models used to understand the relative influence of covariates on the probability that an individual mule deer tested positive for CWD (chronic wasting disease).

Model (all deer)	K†	Log-lik‡	ΔAIC_c§	w_r
Sex Use EP GVM	5	−224.359	0.000	0.601
Sex Use EP	4	−226.063	1.385	0.301
Sex EP GVM	4	−227.742	4.743	0.056
Sex EP	3	−229.516	6.273	0.026
Use EP GVM	4	−229.581	8.420	0.009

Notes: Only the top five models are shown for clarity. Abbreviations are: EP, Estes Park; GVM, Glacier View Meadows.

† Number of estimable parameters.

‡ Maximized value of the logarithm of the likelihood function.

§ Difference in AIC_c between a given model, r, and the model with the minimum AIC_c.

use, and site effects all were important predictors of CWD prevalence. The combined w_r for the top two models indicated a 90% probability that the best approximating model for our field data contained all three covariates as additive effects, with the other 14 models sharing the remaining 10% of the support. Estimates of slope terms from the top model suggested that deer in developed areas were almost twice as likely to test positive for CWD than deer in undeveloped areas (odds ratio = 1.98, $P = 0.011$, 95% CI = 1.17, 3.34), and that males were nearly 2.5 times more likely to be infected than females (odds ratio = 2.35, $P = 0.001$, 95% CI = 1.39, 3.97). Deer sampled from the EP site were approximately one-fourth as likely to be infected with CWD as those sampled from the HT site (odds ratio = 0.27, $P < 0.001$, 95% CI = 0.14, 0.51) and deer from the GVM site were about one-half as likely to be infected as deer in the HT site (odds ratio = 0.55, $P = 0.062$, 95% CI = 0.30, 1.03), although this comparison was not highly significant given a confidence interval coverage that included 1.00.

Modeling sexes separately (Tables 2 and 3) offered additional insight into the relative influences of land use and site-specific effects on CWD prevalence. Summing w_r values for the top male-only models (first two models in Table 2), each of which included both the EP site and land use effects, showed that these models captured 75% of the total weight of evidence. Because we wished to account for model selection uncertainty (Burnham and Anderson 2002) in our estimates of the effect of urban land use on CWD prevalence for each sex, we averaged the estimates of this effect across all models that included it. Based on the model averaged estimates, males in developed areas were more than twice as likely to be infected as males sampled from undeveloped areas (odds ratio = 2.27, 95% CI = 1.17, 4.42). Males in the EP site had approximately one-third the probability of testing positive for CWD relative to those at the HT site (odds ratio = 0.35, $P = 0.011$, 95% CI = 0.16, 0.78). When the EP and land use effect were uncoupled (last six models in Table 2) in male-only models, the support in the data diminished; for the next best model, $w_r = 0.08$ (Table 2).

TABLE 2. Candidate sets of models used to understand the relative influence of covariates on the probability that an individual male deer tested positive for CWD.

Model (males only)	K	Log-lik	ΔAIC_c	w_r
Use EP	3	−125.615	0.000	0.458
Use EP GVM	4	−125.026	0.863	0.297
Use	2	−128.343	3.425	0.083
EP	2	−128.530	3.800	0.068
EP GVM	3	−127.876	4.522	0.048
Use GVM	3	−128.155	5.080	0.036
Intercept	1	−131.891	8.501	0.007
GVM	2	−131.607	9.955	0.003

Note: See Table 1 for explanation of column headings.

The top four female-only models (Table 3) encompassed 95% of the support in the data with the EP covariate present in each of these models. Unlike the top male-only models, the EP and land use effects did not always appear together in the top female-only models (first four models in Table 3), with the land use effect appearing in two of the top four models. Based on model averaged estimates of the effect of land use on prevalence for the female-only models, female deer in developed areas showed a relatively insignificant difference in the probability of testing positive for CWD compared to females in undeveloped settings (odds ratio = 1.73, 95% CI = 0.75, 3.99). In the top female-only model containing an EP effect, we observed a more pronounced effect of site, with females sampled from the EP site being approximately one-sixth as likely to be infected as females sampled at the HT site (odds ratio = 0.17, $P = 0.002$, 95% CI = 0.05, 0.53). Overall, the site effect appeared to be the most informative predictor of CWD prevalence in females, while both land use and site effects contributed almost equally as predictors of prevalence in males.

DISCUSSION

CWD in north-central Colorado occurs in an environment undergoing marked human-induced changes

TABLE 3. Candidate set of models used to understand the relative influence of covariates on the probability that an individual female deer tested positive for CWD.

Model (females only)	K	Log-lik	ΔAIC_c	w_r
EP GVM	3	−99.580	0.000	0.288
Use EP GVM	4	−98.679	0.240	0.255
EP	2	−100.865	0.540	0.220
Use EP	3	−100.014	0.869	0.186
Intercept	1	−104.104	4.997	0.024
Use	2	−103.711	6.231	0.013
GVM	2	−103.999	6.808	0.010
Use GVM	3	−103.554	7.949	0.005

Note: See Table 1 for explanations of column headings.

(Hansen et al. 2002). The human population in this region grew by 68% during the last two decades, making it one of the fastest growing in the United States (Baron et al. 2000). Expanding human habitation has altered land cover as landscapes have been developed. These alterations in land use and land cover, in turn, have changed the amount and configuration of wildlife habitat in this region (Theobald et al. 1997), including specific habitats used by mule deer. Our work suggests that these changes in land use and land cover may play a role in shaping the dynamics of CWD in mule deer.

Land use effects

Prevalence of CWD in deer sampled from developed areas was almost twice as high as in undeveloped areas (~10% vs. 6%), and models that included land use tended to be strongly supported by our field data (Tables 1–3). Land use modifications that accelerate contact rates with the infectious agent might account for observed differences in prevalence between developed and undeveloped areas. Wolfe et al. (2002) suggested that higher prevalence observed in deer sampled from developed locations could be due to local factors such as artificial feeding around residences that concentrate deer at a few points on the landscape. CWD transmission can occur via exposure to infected animals or to environments contaminated by excreta or carcasses from infected animals (Miller et al. 2004). Therefore changes in deer distribution or movements effected by human alteration of deer habitats could plausibly lead to higher local prevalence in developed areas. Consumable resources, including both vegetation and artificial feed, are more likely to be replenished in urban areas than in nonurban areas, thereby allowing deer to meet foraging needs within smaller home ranges. It follows that land use effects may be more pronounced in populations where a higher proportion of deer are sedentary. Such a pattern is suggested in our data for female deer: land use effects appear to be most pronounced in the study area (HT) with the lowest seasonal migration rate (~16%; Conner and Miller 2004). Differences in the timing of data collection could have been partially responsible for observed differences in prevalence between land use types, but also may reflect underlying influences on CWD transmission: deer sampled in developed areas during the summer and early fall were more likely to be year-round residents than harvested deer sampled during the fall in undeveloped areas. Also, these year-round residents may have been subjected to greater exposure because their overall home ranges were smaller than those of migratory deer (Wolfe et al. 2002).

In addition to altering movements or habitat use, urbanized areas also may offer refuge from natural predators and human hunting, thereby allowing CWD-infected deer to survive and shed the infectious agent longer than in areas where predators are more abundant. The relative paucity of predators in urban areas also could allow infected carcasses to persist longer.

Finally, elimination of suitable habitat by development might concentrate mule deer populations on smaller areas of undeveloped winter range, and in so doing, increase population density and accelerate transmission. All of these mechanisms could contribute to higher CWD prevalence in developed areas. Future work should focus on identifying which, if any, of these mechanisms are responsible for the effects of land use we observed.

Sex effects

Differences in CWD prevalence between sexes in our three study areas are consistent with patterns observed on a broader geographic scale throughout north-central Colorado (Miller and Conner 2005). Prevalence among male mule deer in our study was nearly twice as high as among females (~10% vs. 6%). Sex-specific analyses revealed that males sampled from developed locations were more than twice as likely to test positive for CWD as males in undeveloped settings, while females showed less difference between land use types. Model selection results also reflected this trend: support for land use effects on CWD prevalence was stronger in field data from males ($w_r = 0.84$) than from females ($w_r = 0.44$).

The relationship observed here between land use and sex effects may have arisen from differences in sex and age structure of mule deer populations in the two land use categories. Because CWD is always fatal (i.e., the infected class is an absorbing state), older age classes will have more opportunity to be exposed to the infectious agent, and thus should exhibit higher prevalence. Comparisons of CWD prevalence among male and female deer (Miller et al. 2000) showed a pattern of increasing prevalence with age in both sexes, although this rise was much more dramatic in 4–6-year-old males than in females (Miller et al. 2000, Miller and Conner 2005). The mechanism driving this difference is unclear, but similarities to patterns observed in white-tailed deer (*O. virginianus*) infected with bovine tuberculosis (O'Brien et al. 2002) suggest that sex-specific social behavior may play an important role (Miller and Conner 2005). Hunting is virtually absent from developed areas, and in undeveloped areas hunting pressure on males is much greater than on females. Consequently, land use may have had an additional effect on the composition of male herd segments in our study areas. Higher prevalence in male deer from urban areas could be a product of relatively light hunting pressure that preserves a larger proportion of middle-aged males than in more heavily hunted populations in undeveloped areas. Because land use-associated differences in hunting pressure are smaller for females, this effect would be less evident among female subpopulations. It seems plausible that circumstances leading to differences in male mule deer subpopulations between developed and undeveloped areas could partially explain the patterns we observed. To test these biological hypotheses, data on age structures of mule deer residing in developed and undeveloped areas are needed, along with a better understanding of relationships between mule deer behavior and CWD exposure risk.

Site effects

Heterogeneous landscapes can give rise to spatial heterogeneity in disease prevalence (Barlow 1996). Observations of CWD prevalence across north-central Colorado show strong spatial heterogeneity (Miller et al. 2000), and our finer scale results are consistent with these observations. All of the supported models in our study included a site effect, with differences in prevalence among three study sites. Geographic heterogeneity in CWD prevalence may be structured in part by differences in the time since disease introduction (Miller et al. 2000), deer migration patterns (Conner and Miller 2004), demography (Miller and Conner 2005), harvest rates (Miller and Conner 2005), and habitat (see *Results*) among infected mule deer subpopulations. Which factor or combination of factors gave rise to the differences observed among our three study areas cannot be determined with certainty. The size, duration, and intensity of human development do differ somewhat among the GVM, HT, and EP areas, and these may have produced differential effects on deer habitats and deer use of altered habitats. Among females, differences in migration rates among these subpopulations (HT < EP or GVM; Conner and Miller 2004) may have contributed to observed site effects; among males, differences in harvest pressure (EP < HT < GVM) and resulting male age structure (Miller et al. 2000, Miller and Conner 2005) may have contributed. In addition, the ''site'' effect we observed may have been influenced in part by sampling artifact associated with the EP study area: the undeveloped EP area covered a much larger geographic area then either the HT or GVM sites (Fig. 1), and EP had relatively imbalanced sampling between land use classes within each sex. Additional work will be needed to understand the interactions and relative importance of these various factors in affecting CWD prevalence across north-central Colorado.

Management implications

Based on our findings, it appears that mule deer wintering in developed locations need to be included in control efforts intended to reduce overall CWD prevalence in north-central Colorado. Modification of land use practices and other human activities that foster congregation or sedentary behavior in urban mule deer populations could have beneficial effects on reducing opportunities for CWD transmission. Because urban areas may serve as refugia from hunting, alternative management strategies like the ''test-and-cull'' program under evaluation by the Colorado Division of Wildlife (Wolfe et al. 2004) may be necessary adjuncts to more traditional population management approaches (Williams et al. 2002) in such areas. A better understanding of the specific features of urban landscapes that have the greatest potential influence on CWD transmission among mule deer should aid in further refining landscape-level control strategies.

CONCLUSIONS

We offer strong evidence that land use influences prevalence of CWD in north-central Colorado mule deer populations. Future work is needed to resolve mechanisms responsible for the phenomena we observed, in particular the relative importance of land use on: (1) frequency of local contact with infectious material; (2) differences in exposure due to differences in population, sex, and age structures; and (3) mixing of subpopulations with different levels of prevalence.

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