Preventive Veterinary Medicine 113 (2014) 447–456

Contents lists available at ScienceDirect

Preventive Veterinary Medicine

journal homepage: www.elsevier.com/locate/prevetmed

Wildlife–livestock interactions in a western rangeland setting: Quantifying disease-relevant contacts

Heinrich zu Dohna[a,*], Dannele E. Peck[b], Bruce K. Johnson[c], Aaron Reeves[d], Brant A. Schumaker[e]

[a] School of Veterinary Medicine, University of California, Davis, CA, USA
[b] Department of Agricultural & Applied Economics, University of Wyoming, Laramie, WY, USA
[c] Oregon Department of Fish and Wildlife, LaGrande, OR, USA
[d] Department of Production Animal Health, University of Calgary Veterinary Medicine, Calgary, Alberta, Canada
[e] Department of Veterinary Sciences, University of Wyoming, Laramie, WY, USA

ARTICLE INFO

Article history:
Received 9 October 2013
Received in revised form
12 December 2013
Accepted 12 December 2013

Keywords:
Wildlife–livestock contacts
Spatial statistics
Spatio-temporal point processes
Rangeland systems

ABSTRACT

Disease transmission between wild ungulates and domestic livestock is an important and challenging animal health issue. The potential for disease transmission between wildlife and livestock is notoriously difficult to estimate. The first step for estimating the potential for between-species disease transmission is to quantify proximity between individuals of different species in space and time. This study estimates second-order statistics of spatio-temporal location data from radio-collared free-ranging deer, elk and cattle in northeast Oregon. Our results indicate, that when observed simultaneously, elk and cattle occur in closer proximity to each other than what would be expected based on general space use of these species. The same is true for deer and elk but not for deer and cattle. Our analysis also demonstrates that average distances between cattle and elk are largely driven by rare events of close co-mingling between the species, which extend over several hours. Behavioral causes for these co-mingling events are currently unknown. Understanding the causes for such events will be important for designing grazing practices that minimize wildlife–livestock contacts.

1. Introduction

Disease transmission between wild ungulates and domestic livestock is an important and challenging animal health issue. Diseases are generally easier to control in livestock than in wildlife populations, so an introduction or spillover of a disease into wildlife can severely impact the livestock industry's control efforts (Miller et al., 2013). Bovine brucellosis, for example, was introduced to North America via domestic cattle and later spilled over into wild bison (*Bison bison*) and elk (*Cervus elaphus*) populations. Although it has been eradicated from the U.S. cattle population, it still persists in wild bison and elk, and poses a continuous economic threat to rangeland cattle producers (Dobson and Meagher, 1996; Meagher and Meyer, 1994; Schumaker et al., 2012). Eradication of bovine tuberculosis and Johne's disease in the United States has also been complicated by spillover into wildlife (O'Brien et al., 2011; Sleeman et al., 2009).

Control of the last foot-and-mouth disease outbreak in the US was hampered by spillover of the disease into wildlife (Keane, 1927). If a highly contagious foreign animal disease, such as the foot-and-mouth disease virus, were introduced to the U.S. livestock system again, a spillover into wildlife (or a direct introduction to wildlife with the potential for spillover into livestock) would complicate control efforts and increase the risk of the disease becoming endemic. A prolonged outbreak or newly endemic

* Corresponding author. Current address: American University of Beirut, Lebanon. Tel.: +961 1 350000x3916; fax: +961 1 350 000x3888.
E-mail addresses: hb54@aub.edu.lb, heinrich.dohna@gmail.com (H.z. Dohna).

0167-5877/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.prevetmed.2013.12.004

situation could be catastrophic for the U.S. livestock industry (Boisvert et al., 2012; Highfield et al., 2010a,b; Ward et al., 2007). To minimize these economic consequences, it is crucial to understand how often livestock and wildlife interact closely enough to potentially transmit disease (Highfield et al., 2010a,b).

Rangeland systems are conducive to inter-species disease transmission because grazing livestock may easily encounter abundant wildlife over shared forage, cover, water, and mineral resources. Livestock graze three million km^2 of rangeland, pasture and forest in the U.S. (Mitchell, 2000). Roughly 2.12 million km^2 of rangeland and pasture occur west of the Mississippi River (Conner et al., 2001), eighty-percent of which is in the Rocky Mountain and Pacific Coast regions, or the 'western U.S.' (Mitchell, 2000). Rangelands in the western US, whether privately or publically owned, support diverse and abundant wildlife populations as well, including roughly 2.5 million mule deer (*Odocoileus hemionus*), 1 million elk, and 700,000 pronghorn antelope (*Antilocapra americana*) (Binfet and Lutz, 2003; Hoffmann et al., 2008; Rocky Mountain Elk Foundation, 2011).

Interactions between these wild ungulates and cattle are unique in rangeland systems compared to conventional systems. Cattle in conventional production systems are typically confined to fenced-in pastures or enclosed barns, and observed frequently by their owners. Cattle in rangeland systems, in contrast, range freely over hundreds or thousands of hectares, with limited supervision and ample opportunity to encounter wild ungulates in their shared habitats. Wildlife–livestock interactions in these settings are driven by many factors. Elk, mule deer and cattle select habitats with different attributes (Ager et al., 2005) and this habitat selection varies by season. In winter, for example, wild ungulates in mountainous regions might move to lower-elevations in search of native winter range (Coupal et al., 2004), where they could encounter cattle occupying private winter pastures and feed lines. In summer, rangeland cattle might be moved to higher-elevation public grazing allotments (Holechek and Herbel, 1982), where they could encounter wild ungulates occupying native summer range.

Wildlife biologists have developed a large body of literature on cattle–elk–deer interactions. Much of this research addresses questions about habitat use and resource competition, rather than disease transmission (Ager et al., 2005; Coe et al., 2005; Loft et al., 1993; Stewart et al., 2002; Torstenson et al., 2006). Forage competition between cattle, elk, and mule deer has been studied intensively at the U.S. Forest Service's Starkey Experimental Forest and Range in northeast Oregon, USA, particularly during spring, summer and fall. Previous work at this location has focused on wildlife responses to roads and traffic (Coe et al., 2005; Lyon, 1983; Rowland et al., 2000; Thomas et al., 1979; Witmer and DeCalesta, 1985), and patterns of resource selection by elk and mule deer in the presence or absence of cattle-grazing (Ager et al., 2005; Coe et al., 2005; Stewart et al., 2002). Results suggest that larger ungulate species generally displace smaller species (Coe et al., 2005; Stewart et al., 2002). It is unclear, though, how this displacement affects the risk of interspecific contact. Physical displacement might not preclude disease-relevant interactions. When cattle displace elk, the distance between them might remain small enough for transmission to occur. No previous studies have quantified the number of close contacts between domestic and wild ungulates at Starkey Experimental Forest and Range or analyzed the fine-scale spatiotemporal characteristics of such interactions.

A handful of studies have estimated parameters that describe livestock–wildlife interactions in the context of disease transmission (Brook and McLachlan, 2009; Richomme et al., 2006). These studies have shown that contacts between livestock and wildlife can be quite common, especially when livestock herds are unguarded (Richomme et al., 2006) or close to forested and/or protected areas (Brook and McLachlan, 2009). Moreover, there is evidence for some wildlife species that the propensity to associate with livestock varies between individuals and seasons (Berentsen et al., 2013). However, none of these studies have provided a detailed analysis of the spatio-temporal distribution of interspecific distances.

Detailed knowledge of the spatio-temporal distribution of livestock–wildlife distances is necessary to quantify the risk of interspecific disease transmission. Comparing the observed distribution of distances with expectations under various null hypotheses facilitates extrapolation of results to other settings. For example, if the distribution of distances between wildlife and livestock individuals does not differ from the expectation for random locations, one could easily extrapolate distributions of interspecific distances to any population densities. Second-order statistics of spatio-temporal point processes provide a framework to conduct such an analysis. Second-order statistics of point processes characterize the distribution of distances between points and can be used to detect spatial clustering or repulsion at different scales (Cressie and Wikle, 2011; Diggle et al., 1995; Lotwick and Silverman, 1982; Ripley, 1981).

In this study, we apply the theory of second-order statistics of spatio-temporal point processes to analyze two years of location data from free-ranging cattle, elk and mule deer in the Starkey Experimental Forest and Range in northeast Oregon (Rowland et al., 1997; Wisdom et al., 2005). Our study has three objectives: (i) characterize the distribution of distances between individuals of different species; (ii) characterize intra- and inter-annual variation in distances; and (iii) test to what degree distances between wildlife and livestock are driven by habitat selection or behavioral effects, such as attraction or avoidance. Our overarching goals in quantifying spatio-temporal interactions between cattle, elk and mule deer are to: (1) facilitate epidemiologists' efforts to incorporate interspecific contacts into mathematical models of disease spread, and (2) provide management-relevant insights about close encounters between cattle and wild ungulates that could lead to disease transmission.

2. Methods

2.1. Study area

Data were collected within the U.S. Forest Service's Starkey Experimental Forest and Range (Starkey), which

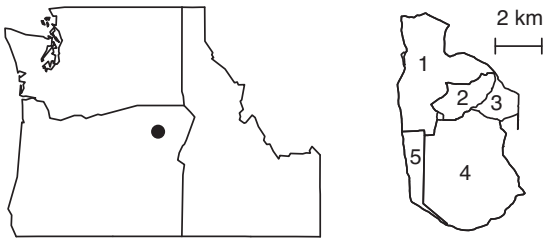

Fig. 1. Map of study area. Left panel shows location of Starkey experimental Forest within Oregon and right panel shows the Starkey Main study area with numbered cattle pastures: 1 = Smith–Bally, 2 = Meadow Creek (not available to radio-collared cattle), 3 = Lower Meadow Creek (not available to radio-collared cattle), 4 = Bear, 5 = Half Moon.

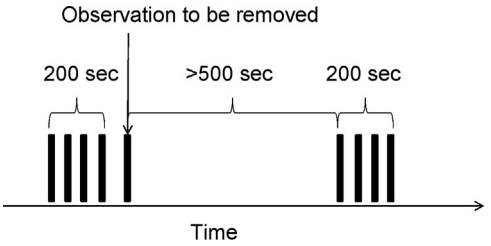

Fig. 2. Definition of observation periods. Vertical bars indicate observation times along the time axis. The plot shows two observation periods. A time interval of more than 500 s between two consecutive observations defines an interval between two separate observation periods. All observations that are more than 200 s after the first observation within the same period were removed to ensure observations within an observation period are somewhat simultaneous.

is located 45 km southwest of the town of La Grande in northeast Oregon, USA. Starkey comprises a 100-km^2 game-proof fenced enclosure (roughly 13 km north-to-south, and 8 km east-to-west) containing 500 cow/calf pairs, over 200 female elk, and roughly 200 mule deer. Starkey was established in 1989 to observe interactions between cattle, elk and deer in a rangeland and open-canopy forest setting. The area has climate and habitats similar to many National Forests in the Intermountain West (Rowland et al., 1997).

Starkey's fenced enclosure is sub-divided into two areas: Main study area, and Northeast study area. Data were gathered from animals within the Main study area that comprises 77.6 km^2 (Fig. 1). Elk and mule deer were free to roam throughout this area during the entire study period. Cattle locations, however, were influenced by a rotational grazing plan that systematically moved the herd between smaller pastures within the Main study area (Table 1; Fig. 1). These pastures are enclosed with cattle-proof fencing but not game-proof fencing, so elk and mule deer can freely enter and exit these pastures. Starkey's grazing plan resulted in cattle being rotated through the pastures in a clockwise direction in 2006, and in a counter-clockwise direction in 2007. As the cattle herd moves through pastures of different size, their density changes. Resource selection by all three species changed as plant phenology changed during summer (Ager et al., 2005) where selection of closed canopy forests and steeper slopes increased for both cattle and elk. Elk selected for steeper slopes and stands with more canopy cover when cattle were present in the sample pastures (Coe et al., 2005). Human activity also influenced elk distributions as elk selected resources that were further roads open to the public throughout summer (Ager et al., 2005; Rowland et al., 2000). Further details of the Starkey Project are described elsewhere (Rowland et al., 1997; Wisdom et al., 2006, 2005).

2.2. Data

During 2006 and 2007, Global position system (GPS) collars were placed on 29 and 30 of the 500 head of female cattle that graze Starkey (6% of the cattle population). Collared cattle mixed freely with collar-free cattle and were managed identically. Collars were placed on a similar proportion of adult female elk and female deer captured over the winter at a special feeding/trapping/handling facility within the Main study area (Table 1). Two trap sites for elk and >20 trap sites for deer were operated in winter to capture animals that did not enter the winter handling facility to minimize the potential for sampling bias. Summary statistics for cattle, elk, and mule deer populations at Starkey, including collared animals, are provided in Table 1. Fix rates were generally high (median fix rate >97% in 2006). Any temporal variation in fix rate was accounted for by our analysis methods (see below).

Sampling frequency of all locations was synchronized to occur on the hour in 2006 or every half-hour in 2007, which enabled animals to be observed almost simultaneously in time (i.e., within just a few minutes of each other). We ordered all location readings in time, calculated the time between all consecutive location readings and defined 'observation periods' by assigning any location readings separated by more than 500 s to different observation periods. A single observation period typically includes locations for several individuals. Duplicate readings of the same individual within an observation period were removed. In addition, any locations recorded more than 200 s (~3 min) after the first reading within that observation period were removed to ensure the remaining readings were sufficiently close in time to be treated as simultaneous (Fig. 2). This 200 s time window covers 65% of location readings in 2006 and more than 99% of location readings in 2007.

2.3. Data analysis

We used bivariate extensions of Ripley's K function (Lotwick and Silverman, 1982; Pfeiffer et al., 2008; Ripley, 1981) to summarize spatio-temporal distances between cattle, deer and elk and test for deviations from randomness. The core of our analysis was the bivariate K-function, $K_{xy}(r)$, which denotes the expected number of points of type y within distance r from a point of type x, standardized by the density of y. The standardization by density makes the $K_{xy}(r)$ function independent of the density of x and y. The expected values of the estimates are therefore not influenced by the number of animals collared or temporal variation in fix rates. We estimated this $K_{xy}(r)$ function to summarize distances between animals of different species.

Table 1
Data summaries.

Variable of interest	Year 2006			Year 2007		
	Cattle	Elk	Mule deer	Cattle	Elk	Mule deer
Population estimate	500	492	250	500	464	250
Number (percent) of collared animals	30 (6%)	59 (12%)	13 (5%)	29 (6%)	29 (6%)	17 (7%)
Dates on bear pasture (34.4 km^2)	July 10–August 21	–	–	August 8–September 22	–	–
Dates on half moon pasture (6.2 km^2)	August 22–29	–	–	August 1–August 7	–	–
Dates on Smith–Bally pasture (23.6 km^2)	August 30–October 15	–	–	June 15–July 30	–	–
Dates on entire main study area (77.6 km^2)	July 10–October 15	–	–	June 15–September 22	–	–

Given two sets of observed point locations $\mathbf{x} = \{x_1, x_2, \ldots, x_m\}$ and $\mathbf{y} = \{y_1, y_2, \ldots, y_n\}$ within an area of size A, an unbiased estimator of $K_{xy}(r)$ is:

$$\hat{\mathrm{k}}_{xy}(r) = \mathrm{A}\frac{\sum_{i=1}^{m}\sum_{j=1}^{n} a(x_i, y_j, r)}{mn} \quad (1)$$

where the function $a(x_i,y_j,r)$ equals $1/c$ if location x_i is more than r from location y_j, and zero otherwise; c is the proportion of the circumference of a circle around x_i that falls within the study area (Lotwick and Silverman, 1982).

If **x** and **y** are distributed randomly with respect to each other, the expectation of $\hat{\mathrm{k}}_{xy}(r)$ equals πr^2. $\hat{\mathrm{k}}_{xy}(r) > \pi r^2$ would, in contrast, indicate there are more points of type y within distance r of a point of type x than would be expected if points **x** and **y** are located randomly with respect to each other (Cressie and Wikle, 2011).

Deviation of $K_{xy}(r)$ from randomness (i.e., the difference between $K_{xy}(r)$ and πr^2) is often visualized using the L_{xy} function:

$$L_{xy}(r) = \sqrt{K_{xy}(r)} - \sqrt{\pi r^2} \quad (2)$$

$\hat{L}_{xy}(r)$ has an expectation of zero under the assumption that animals are located randomly with respect to each other (Cressie and Wikle, 2011; Lotwick and Silverman, 1982). The remainder of the paper deals exclusively with estimates of K and L. For notational simplicity, we will therefore drop the hat over $\hat{L}_{xy}(r)$ and $\hat{\mathrm{K}}_{xy}(r)$ from this point forward when describing our estimates.

To assess the potential for disease transmission between wildlife and livestock it is not only necessary to know the distances between animal locations but also how these distances are distributed in time. Two different species might, for example, use the same area but avoid each other. In that case, individuals of different species might visit the same location at different times, such that distances between simultaneous observations tend to be larger than distances between locations observed at different times.

We took advantage of temporal clustering of our location data to tease apart distance patterns between simultaneous observations versus observations at randomly chosen times, i.e. patterns due to general habitat use. We calculated different local K_{xy}-function and L_{xy}-functions per observation period and then averaged these values over the entire season to obtain global averages.

The first type of local K_{xy}-function is calculated using observed locations of individuals of species x and y within the same time period p, where p indexes the 200 s time windows described above. We denote this function by $K^0_{xp,yp}(r)$. This function describes the distribution of distances between simultaneous observations, i.e. the distances that are most relevant for disease transmission. The second type of local K_{xy}-function is calculated using observed locations of individuals of species x in observation

Table 2
Notation for various K-functions.

Notation	Meaning of function	Point set I	Point set II
$K^0_{xp,yp}(r)$	Expected number of points of one type (point set II) within radius r of a point of another type (point set I).	All location readings of species x in time period p	All location readings of species y in time period p
$K^l_{xp,yp+1}(r)$	"	All location readings of species x in time period p	All location readings of species y in time period $p+l$
$K^\rho_{xp1,yp2}(r)$	"	All location readings of species x in randomly chosen time period p_1	All location readings of species y in randomly chosen time period p_2 (chosen independently of p_1)
$K^\tau_{xp1,yp2}(r)$	"	All location readings of species x in randomly chosen time period p_1, with random toroidal shift	All location readings of species y in randomly chosen time period p_2 (chosen independently of p_1), with random toroidal shift
$\bar{K}^0_{x,y}(r)$	$K^0_{xp,yp}(r)$ averaged over all time periods p with p ranging from 1 to N.	–	–
$\bar{K}^l_{xp,yp+1}(r)$	$K^l_{xp,yp+1}(r)$ averaged over time periods p with p ranging from 1 to N–l.	–	–
$\bar{K}^\rho_{x,y}(r)$	$K^\rho_{xp1,yp2}(r)$ averaged over all pairs of randomly chosen time periods p_1 and p_2.	–	–
$\bar{K}^\tau_{x,y}(r)$	$K^\tau_{xp1,yp2}(r)$ averaged over all pairs of randomly chosen time periods p_1 and p_2.	–	–

The notation used for the L-functions (not shown here) is entirely analogous to the notation for the K-functions shown here.

period p and species y in observation period $p+l$, where l represents a lag time of either 1, 2 or 3 h. We denote this function by $K^{l}_{xp,yp+1}(r)$. This function describes the distribution of distances between lagged observations. These distances are relevant for diseases that can be transmitted through the environment. Furthermore, comparing of $K^{0}_{xp,yp}(r)$ with $K^{l}_{xp,yp+1}(r)$ provides evidence whether species avoid each other. The third type of local K_{xy}-function is calculated using observed locations of individuals of species x in a randomly chosen observation period p_1 and species y in another randomly chosen observation period p_2. For this calculation we used 1000 random samples of p_1 and p_2. We denote this function by $K^{\rho}_{xp1,yp2}(r)$. Testing whether $K^{0}_{xp,yp}(r)$ equals $K^{\rho}_{xp1,yp2}(r)$ indicates whether distances between simultaneous observations of different species simply result from general habitat use of those species. The fourth type of local K_{xy}-function, $K^{\rho}_{xp1,yp2}(r)$, is entirely analogous to $K^{\rho}_{xp1,yp2}(r)$, except that the locations were moved by a random toroidal shift. The random toroidal shift creates a pattern where species x and y occur randomly from each other while maintaining within-species clustering. Testing whether $K^{0}_{xp,yp}(r)$ equals $K^{\tau}_{xp1,yp2}(r)$ indicates whether distances between simultaneous observations of different species differ from distances expected if those species occur randomly with respect to each other.

Each of the local K_{xy}-functions were transformed into local L_{xy}-functions using Eq. (2) to obtain $L^{0}_{xp1,yp2}(r)$, $L^{l}_{xp1,yp2}(r)$, $L^{\rho}_{xp1,yp2}(r)$ and $L^{\tau}_{xp1,yp2}(r)$. The K_{xy} and L_{xy} functions were averaged over all observation periods within a season to obtain global averages $\bar{L}^{0}_{x,y}(r)$, $\bar{L}^{l}_{x,y}(r)$, $\bar{L}^{\rho}_{x,y}(r)$, $\bar{L}^{\tau}_{x,y}(r)$, $\bar{L}^{\rho}_{x,y}(r)$ and $\bar{L}^{\tau}_{x,y}(r)$. An overview of the notation is provided in Table 2.

K_{xy}-functions and L_{xy}-functions were estimated separately for each pair of species (cattle–elk, cattle–deer, elk–deer) in each year. K_{xy}-functions were estimated for distances from 20 m to 200 m, in 20 m intervals, using the *R* package *splancs* (Rowlingson and Diggle, 1993). Empirical distributions of $\bar{L}^{\rho}_{x,y}(r)$ and $\bar{L}^{\tau}_{x,y}(r)$ were generated by calculating 200 independent samples of $\bar{L}^{\rho}_{x,y}(r)$ and $\bar{L}^{\tau}_{x,y}(r)$. These distributions were then compared to $\bar{L}^{0}_{x,y}(r)$. *P*-values for the entire distance range were obtained by calculating for each sample $\Sigma^{200}_{r=20}\bar{L}^{\rho}_{x,y}(r)$ and $\Sigma^{200}_{r=20}\bar{L}^{\tau}_{x,y}(r)$ and comparing it to $\Sigma^{200}_{r=20}\bar{L}^{0}_{x,y}(r)$. Lagged L functions, $\bar{L}^{l}_{x,y}(r)$, are asymmetric, i.e. $\bar{L}^{l}_{x,y}(r) \neq \bar{L}^{l}_{y,x}(r)$, which is not true for un-lagged L functions. We therefore calculated a separate lagged L function for each order-permutation of each species pair.

3. Results

Throughout the distance range of 20–200 m, cattle co-occurred on average more frequently with elk and less frequently with deer than would be expected if they were located randomly with respect to each other (Fig. 3, $P<0.01$ in both years, Table 3). This pattern is also visible in the lagged L-functions' values, $\bar{L}^{l}_{x,y}(r)$, but less so in L-functions from randomly paired observation periods, $\bar{L}^{\rho}_{x,y}(r)$ (Fig. 4). Throughout the analyzed distance categories, elk are three to eight times more likely than deer to occur within a given

Table 3
Overview of statistical tests.

Test	Statistical interpretation of significant result	Biological interpretation	Graphical result	*P*-value*					
				Cow–deer		Cow–elk		Deer–elk	
				2006	2007	2006	2007	2006	2007
$L^{\tau}_{xp,yp}(r) \neq \bar{L}^{0}_{x,y}(r)$	The number of points of type y within distance r of a point of type x is different compared to points from randomly chosen observation periods with random toroidal shift	Individuals of species x and y do not occur randomly with respect to each other.	Fig. 3	0.665	0.01	<0.01	<0.01	<0.01	0.34
$L^{\rho}_{xp,yp}(r) \neq \bar{L}^{0}_{x,y}(r)$	The number of points of type y within distance r of a point of type x is different depending on whether points of type x and y were observed in the same or two randomly chosen observation periods	Distances between simultaneously observed individuals of species x and y differ from expectation based on general habitat use.	Fig. 4	0.95	0.025	0.03	<0.01	<0.01	0.125

* *P*-values were calculated by summing the squared deviation over all distance values.

distance from cattle, provided that deer and elk have the same population density (Fig. 3). To translate the $K^0_{x,y}(r)$ values (Fig. 3) into the expected number of individuals of species y found within a distance r from species x at any given instant, one has to multiply the $K^0_{x,y}(r)$ values by the density of species y. Examples of the expected number of individuals for two different density values are shown in Table 4.

A comparison of estimated L_{xy} functions for years 2006 and 2007 reveals inter-annual differences (Fig. 4). The larger-than-random co-occurrence of elk and cattle around 100 m from each other, when observed simultaneously, was much more pronounced in 2007 than in 2006. Upon closer inspection of the raw data, we discovered that the strong spatial association between cattle and elk in 2007 was due to two phases of close-range co-mingling between a group of ten collared cattle and six collared elk (Fig. 5) on two consecutive days in mid-June for approximately six hours each day (Fig. 5). When these two phases of co-mingling were excluded from the calculation of $\bar{L}^0_{x,y}(r)$, the pattern of positive association disappears for 2007 (results not shown). A map of location readings from a single observation period during the first co-mingling phase shows the close proximity of several cattle and elk individuals (Fig. 6). An analysis of the distribution of $L^0_{xp,yp}(r)$ reveals that the proportion of observation periods p with $L^0_{xp,yp}(r) < \bar{L}^0_{x,y}(r)$ ranges from 0.99 ($r = 20$ m) to 0.86 ($r = 200$ m). This underscores the strong influence of a small set of observation periods on the average, $\bar{L}^0_{x,y}(r)$.

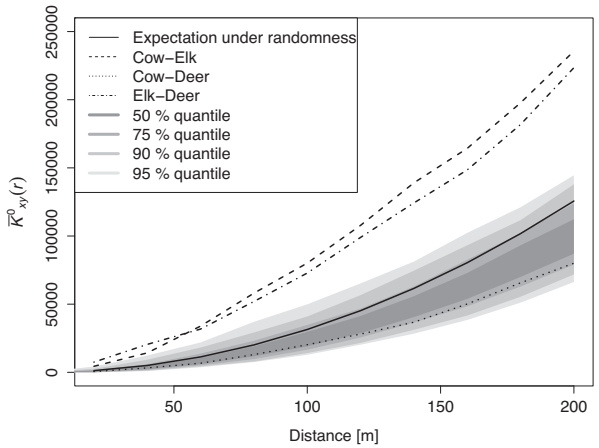

Fig. 3. $K^0_{xp,yp}(r)$ averaged over both years for distances between individuals of different species that were observed within the same observation period. Solid line shows $K^0_{xp,yp}(r) = \pi r^2$, which is the expectation if animals are randomly distributed with respect to each other. Grey areas show quantiles based on random toroidal shifts of 1000 randomly selected observation periods. $K^0_{xp,yp}(r)$ were estimated for each 20-m interval between 20 and 200 m.

In 2007, deer and cattle co-occurred less often (i.e., at larger distances from each other) when observed simultaneously than under random permutations of observation intervals (Fig. 4, $P = 0.025$, Table 3). However, this effect was not detectable in 2006 (Fig. 4, $P = 0.95$, Table 3). Elk and deer co-occurred more often when observed simultaneously

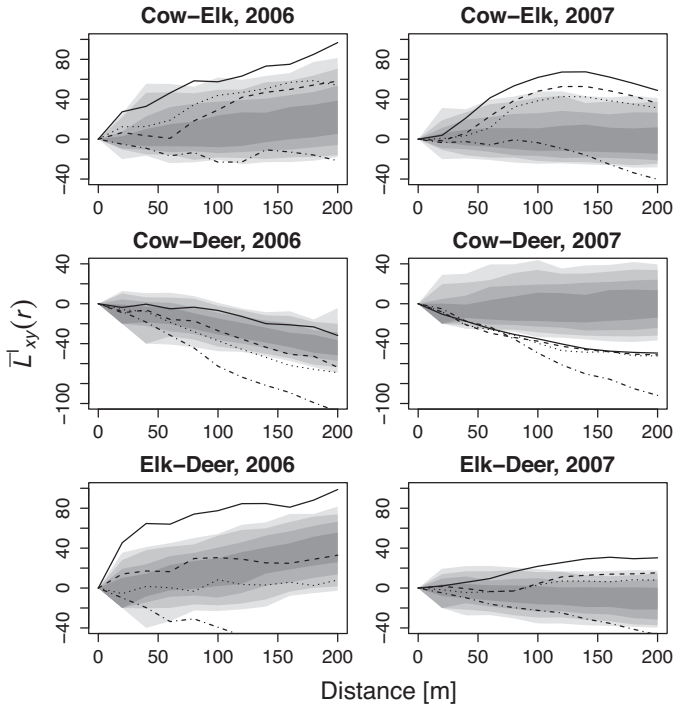

Fig. 4. Estimates of various types of L_{xy} functions for distances between individuals of species x and y. Functions are estimated for radius, r, ranging from 20 to 200 m in 20-m intervals. Shaded regions show the 50th, 75th, 90th and 95th percentiles for random observation periods calculated from $\bar{L}^\rho_{x,y}(r)$. Solid line shows $\bar{L}^0_{x,y}(r)$. Dashed, dotted and dashed-dotted lines show $\bar{L}^l_{x,y}(r)$ for time lags of one, two and three hours, respectively. See text for details.

Table 4
Number of wildlife–cattle contacts.

Deer or elk density (m^{-2})	20 m		200 m	
	Deer	Elk	Deer	Elk
Expected number of wildlife individuals within *r*-meters from a cow at a given instant in time.[a]				
6×10^{-6}	0.004	0.03	0.5	1.5
3×10^{-6}	0.002	0.015	0.25	0.75

[a] Values were obtained by multiplying $\bar{K}^0_{x,y}(r)$ values (shown in Fig. 3) with population densities shown in first column. The two densities used correspond roughly to the estimated elk and deer densities at Starkey. To convert the number of animals within a certain distance into disease transmission rates from livestock to wildlife would require an additional parameter, namely a distance-dependent transmission rate, i.e. the rate of transmission per unit time per animal-pair within that distance. If this distance-dependent transmission rate is low, the values in the table above have to be multiplied with this transmission rate to obtain a transmission rate per infected cow per unit time. If the rate is high one would need additional data about animal movement (turnover) to account for saturation effects.

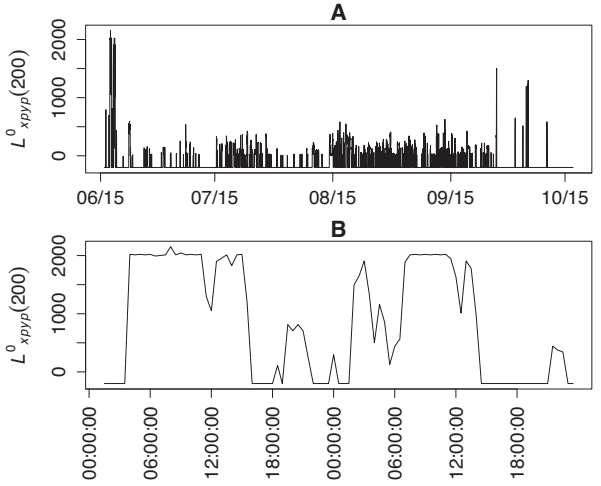

Fig. 5. $L^0_{xp,yp}(r)$ evaluated at $r = 200$ m for distances between cattle and elk, plotted against time of observation period *p*. Panel A shows the entire season of 2007 and panel B depicts a 48-h interval around June 18–19, 2007, which contains the two largest peaks that appear at the beginning of the season in panel A.

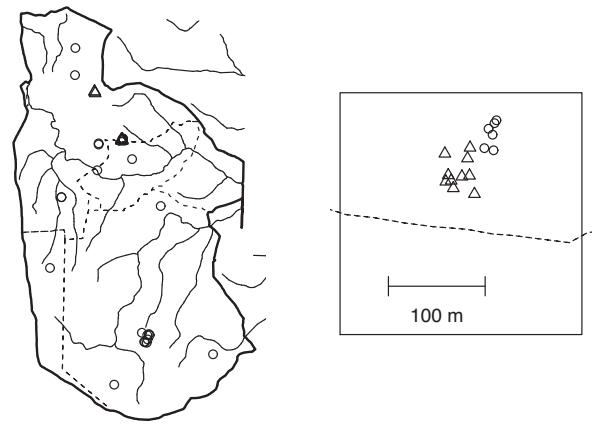

Fig. 6. Example of location readings from a single observation period during the first co-mingling phase depicted in Fig. 5B. Cattle readings are shown by triangles and elk readings by circles. Map on the left shows the entire study area (elk-proof fences shown by bold lines and cattle-proof fences by dashed lines; other lines represent drainages in the watershed); the square on the right is a close-up of the area where co-mingling occurred.

than under random permutations of observation intervals (Fig. 4). This effect was more pronounced in 2006 than in 2007 (Fig. 4). Reversing the order of species pairs for lagged *L*-functions produced very similar results as the ones shown here (results not shown).

4. Discussion

Our analysis shows that cattle and elk occur in closer vicinity of each other when observed in the same observation period than when observed in two different randomly chosen observation periods. The reverse is true for cattle and deer; they occur at larger distances from each other when observed simultaneously than when observed in two different randomly chosen observation periods. Based on these patterns of spatial co-occurrence, interspecies disease transmission is more likely between cattle and elk than between cattle and deer, all else being equal.

Calculating distances between observations from randomly chosen observation periods provides a measure for the distance distribution based on general habitat use within the observation season. This technique is therefore comparable to other approaches that predict transmission contacts based on general spatial overlap (e.g. Proffitt et al., 2011). Our results show that cattle and elk occur in closer vicinity of each other when observed simultaneously than what would be expected based on their general habitat use. This could be because both species use the same habitat at the same time or because one species actively seeks the other. Similarly, the larger distances between simultaneously observed cattle and deer could be due to the use of different habitats at the same time or because one species actively avoids the other. To simplify our language in the following discussion, we use the terms 'attraction' and 'avoidance' to refer to these patterns. It is important to keep in mind that the patterns could have been caused by mechanisms other than behavioral attraction and avoidance, as described above.

A time-series plot reveals temporal variation in the pattern of co-mingling between cattle and elk (Fig. 5). In one season there were two phases of close proximity between a group of cows and a group of elk. These two co-mingling phases strongly influenced the yearly average of spatio-temporal association and caused differences between years. These results show that average measures of co-occurrence can be strongly dependent on rare

events. The relative importance of rare interaction events is underscored by the fact that *K*-function values of the majority of observations (e.g. 99% for $r = 20$ m) are below the average value, indicating that the averages are driven by few observations.

It is currently unknown what triggers phases of close co-mingling between cattle and elk. One untested hypothesis is that a newly delivered salt block might have attracted cattle and mineral-deprived elk to the area, and held their attention until their micronutrient needs were satisfied. Understanding the behavioral mechanisms that lead to close co-mingling between cow and elk is an important direction for future research because it might help develop cattle management practices that reduce the probability of such events.

There is avoidance between mule deer and cattle according to our results. This avoidance was more pronounced in 2007 than in 2006. The difference between the two years does not seem to be attributable to rare events as it was for cattle and elk. It would be valuable, nonetheless, to understand drivers of variability in cattle–deer interactions in different years. The inter-annual variation in our results could be due to differences in weather conditions (e.g. snowpack levels in late spring) or differences in the direction of the cattle rotation plan between 2006 and 2007. More years of data should be analyzed to determine the most likely cause for the inter-annual variation in inter-specific association.

Our study suggests the existence of spatial attraction between cattle and elk, and spatial avoidance between cattle and deer. This might seem contradictory to results of a previous study by Stewart et al. (2002), which found avoidance of cattle by elk, and attraction of deer to cattle in an attempt to avoid elk. There are several possible reasons for this discrepancy.

Stewart et al. analyzed associations for 6-h (±3 h) and 7-day time windows. However, our study shows substantial variation in attraction or avoidance within a 3-h window. For example, at short distances, attraction between cattle and elk is not visible when location readings are separated by 3 h (Fig. 4). Similarly, simultaneous observations show an attraction between deer and elk, whereas observations that are lagged by three hours show avoidance, possibly due to grazing competition. Hence, the 6-h time window used by Stewart et al. seems to encompass very different behavioral patterns. It is also possible that the rare co-mingling events driving our measures of spatial association in 2007 were missed by Stewart et al.'s methods or did not occur in their dataset, which was collected years earlier than ours.

One final notable difference between Stewart et al.'s analysis and ours is that they disaggregated animal location data by time of year and ran separate regression models for spring (April–June), summer (July–September), and late summer (October). They detected seasonal differences in the species' habitat selections, and in the extent to which one species displaces another. We did not perform separate analyses for different seasons because we only had finely sampled location data from June to October. In the future, it might be interesting to repeat our analysis with more data for separate seasons.

Additional inspiration for future research comes from Berentsen et al. (2013), who showed that individual white-tailed deer differ in their propensity to interact with livestock. Our study could not analyze variation among individuals in the propensity to co-mingle with other species. This is because each individual was observed only once per observation period, whereas $K^0_{xp,yp}(r)$ can only be calculated with two or more location readings of species x and y per observation period (Lotwick and Silverman, 1982).

Our study's overarching goal was to translate a rich set of animal location data into a concise quantitative measure of interaction, which epidemiologists could incorporate into a disease simulation model. The Starkey Project is a multi-million dollar effort that cannot be easily replicated in other regions with wildlife–livestock disease concerns. It is therefore important to tease out generalizable insights from the Starkey Project dataset, without sacrificing too much realism. Our results demonstrate that wildlife–livestock interactions are not simply a result of random interactions conditioned on the two species' densities. Nor is average habitat use of each species sufficient to predict average distances between animals. Instead, the distances between individuals are governed by complex behavior that is highly variable in time.

One way to generalize our results is to apply the average *K*-function estimates we obtained for simultaneous observations to other densities of the interacting species. If one assumes that different densities simply means varying the number of spatial locations while keeping the observed spatio-temporal correlation structure, one can extrapolate our results to different densities by multiplying the *K*-function estimates with population density as demonstrated in Table 4. This assumption would predict a linear increase of disease-relevant contacts with density. Epidemiological analysis has shown that brucellosis transmission among elk increases with elk density, but data were not sufficient to determine whether this increase was linear (Cross et al., 2010a,b). Our results show that *K*-function values are driven by complex behavioral processes. It is therefore unclear to what degree spatio-temporal correlations remain constant across different densities–an assumption implicit in multiplying *K*-function values with animal densities.

Future research on the behavioral mechanisms that drive co-mingling events might lead to models that predict interaction patterns based on behavioral processes. A tradeoff exists, though, between incorporating more biological information to enhance the realism of epidemiological models, and the difficulty of obtaining and incorporating such detailed biological information. Even without modeling, a better understanding of the behavioral mechanisms that drive the co-mingling can produce insights of practical relevance.

5. Conclusion

Overall, this study shows that elk and deer do occur within distances of free-ranging cattle that might allow disease transmission. The average spatial proximity between cattle and elk is much closer than between cattle and deer,

but is driven largely by rare events of close co-mingling. Hence, our analysis does not disprove the well-accepted notion that larger ungulates displace smaller ungulates. Instead, it shows that, under rare conditions, elk appear willing to associate closely with cattle. Reasons for these close co-mingling events are unknown. Although close co-mingling events are rare, they could dramatically change the dynamics of a disease outbreak.

Our results show that aggregate measures of interaction vary across years due to rare co-mingling events and possibly due to variation in climate or grazing practices. These results highlight two challenges for understanding wildlife–livestock interactions. Location data have to be sampled at short intervals to capture rare events and data collection has to be performed for multiple years to capture inter-annual variation. The high variability of interaction patterns means that any quantitative prediction of disease transmission is associated with a high degree of uncertainty. However, the fact that the average distances between livestock and wildlife are strongly influenced by rare co-mingling events also implies some good news. It means that understanding and avoiding the behavioral mechanisms that lead to these co-mingling events bears the potential to strongly reduce the risk of disease transmission.

Acknowledgements

This study was funded by the National Center for Foreign Animal and Zoonotic Disease Defense, a Department of Homeland Security Science and Technology Center of Excellence. The authors are grateful to Mike Wisdom, Priscilla Coe, Marty Vavra, and other colleagues associated with the Starkey Experimental Forest and Range Lab. Any opinions expressed here are the authors, however, and should not be attributed to the funding agency or any agencies for whom the authors work. The authors take full responsibility for any errors or omissions.

References

Ager, A.A., Johnson, B.K., Coe, P.K., Wisdom, M.J., 2005. Landscape simulation of foraging by elk, mule deer, and cattle on summer range. In: Wisdom, M.J. (Ed.), The Starkey Project: A Synthesis of Long-Term Studies of Elk and Mule Deer. Alliance Communications Group, Lawrence, KS, pp. 170–184.

Berentsen, A.R., Miller, R.S., Misiewicz, R., Malmberg, J.L., Dunbar, M.R., 2013. Characteristics of white-tailed deer visits to cattle farms: implications for disease transmission at the wildlife–livestock interface. Eur. J. Wildl. Res., 1–10.

Binfet, J., Lutz, D.W., 2003. Deer and elk population status and harvest structure in western North America: a summary of state and provincial status surveys. In: Proceedings of the Fifth Western States and Provinces Deer and Elk Workshop, pp. 48–68.

Boisvert, R.N., Kay, D., Turvey, C.G., 2012. Macroeconomic costs to large scale disruptions of food production: the case of foot-and-mouth disease in the United States. Econ. Model. 29, 1921–2193.

Brook, R.K., McLachlan, S.M., 2009. Transdisciplinary habitat models for elk and cattle as a proxy for bovine tuberculosis transmission risk. Prev. Vet. Med. 91, 197–208.

Coe, P.K., Johnson, B.K., Stewart, K.M., Kie, J.G., 2005. Spatial and temporal interaction of elk, mule deer and cattle. In: Wisdom, M.J. (Ed.), The Starkey Project: A Synthesis of Long-Term Studies of Elk and Mule Deer. Alliance Communications Group, Lawrence, KS, pp. 150–158.

Conner, R., Seidl, A., Van Tassel, L., Wilkins, N., 2001. United States Grasslands and Related Resources: An Economic and Biological Trends Assessment. Texas A&M University, Wildlife and Fisheries Sciences.

Coupal, R., Beauvais, G., Feeney, D., Lieske, S., 2004. The Role and Economic Importance of Private Lands in Providing Habitat for Wyoming's Big Game (B-1150). University of Wyoming Extension.

Cressie, N., Wikle, C.K., 2011. Statistics for Spatio-Temporal Data. John Wiley & Sons, Hoboken, NJ.

Cross, P.C., Cole, E.K., Dobson, A.P., Edwards, W.H., Hamlin, K.L., Luikart, G., Middleton, A.D., Scurlock, B.M., White, P.J., 2010a. Probable causes of increasing brucellosis in free-ranging elk of the Greater Yellowstone Ecosystem. Ecol. Appl. 20, 278–288.

Cross, P.C., Heisey, D.M., Scurlock, B.M., Edwards, W.H., Ebinger, M.R., Brennan, A., 2010b. Mapping brucellosis increases relative to elk density using hierarchical Bayesian models. PLoS ONE 5, e10322.

Diggle, P., Chetwynd, a., Haggkvist, R., Morris, S., 1995. Second-order analysis of space-time clustering. Stat. Methods Med. Res. 4, 124–136.

Dobson, A., Meagher, M., 1996. The population dynamics of brucellosis in the Yellowstone National Park. Ecology 77, 1026–1036.

Highfield, L.D., Ward, M.P., Laffan, S.W., Norby, B., Wagner, G.G., 2010a. The impact of potential mitigation strategies on the predicted spread of foot and mouth disease in white-tailed deer in south Texas. Prev. Vet. Med. 94, 282–288.

Highfield, L.D., Ward, M.P., Laffan, S.W., Norby, B., Wagner, G.G., 2010b. Critical parameters for modelling the spread of foot-and-mouth disease in wildlife. Epidemiol. Infect. 138, 125–138.

Hoffmann, M., Byers, J., Beckmann, J., 2008. *Antilocapra americana*. In: IUCN Red List of Threatened Species 2013.

Holechek, J.L., Herbel, C.H., 1982. Seasonal suitability grazing in the western United States. Rangelands 4, 252–255.

Keane, C., 1927. The outbreak of foot and mouth disease among deer in the Stanislaus National Forest. Mon. Bull. Dep. Agric. State Calif. 16, 213–225.

Loft, E.R., Kie, J.G., Menke, J.W., 1993. Grazing in the Sierra-Nevada – home-range and space use patterns of mule deer as influenced by cattle. Calif. Fish Game 79, 145–166.

Lotwick, H., Silverman, B., 1982. Methods for analysing spatial processes of several types of points. J. R. Stat. Soc. Ser. B 44, 406–413.

Lyon, L.J., 1983. Road density models describing habitat effectiveness for elk. J. For. 81, 592–613.

Meagher, M., Meyer, M.E., 1994. On the origin of brucellosis in bison of Yellowstone National Park: a review. Conserv. Biol. 8, 645–653.

Miller, R.S., Farnsworth, M.L., Malmberg, J.L., 2013. Diseases at the livestock–wildlife interface: status, challenges, and opportunities in the United States. Prev. Vet. Med. 110, 119–132.

Mitchell, J.E., 2000. Rangeland Resource Trends in the United States: A Technical Document Supporting the 2000 USDA Forest Service RPA Assessment. Health San Francisco.

O'Brien, D.J., Schmitt, S.M., Rudolph, B.A., Nugent, G., 2011. Recent advances in the management of bovine tuberculosis in free-ranging wildlife. Vet. Microbiol. 151, 23–33.

Pfeiffer, D.U., Robinson, T.P., Stevenson, M., Stevens, K.B., Rogers, D.J., Clemens, A.C.A., 2008. Spatial Analysis in Epidemiology. Oxford University Press, New York, NY.

Proffitt, K.M., Gude, J.A., Hamlin, K.L., Garrott, R.A., Cunningham, J.A., Grigg, J.L., 2011. Elk distribution and spatial overlap with livestock during the brucellosis transmission risk period. J. Appl. Ecol. 48, 471–478.

Richomme, C., Gauthier, D., Fromont, E., 2006. Contact rates and exposure to inter-species disease transmission in mountain ungulates. Epidemiol. Infect. 134, 21–30.

Ripley, B.D., 1981. Spatial Statistics. John Wiley & Sons, New York, NY.

Rocky Mountain Elk Foundation, 2011. Elk Hunt Forecast 2011.

Rowland, M.M., Bryant, L.D., Johnson, B.K., Noyes, J.H., Wisdom, M.J., Thomas, J.W., 1997. The Starkey Project: History, Facilities, and Data Collection Methods for Ungulate Research, PNW-GTR-396. La Grande, OR.

Rowland, M.M., Wisdom, M.J., Johnson, B.K., Kie, J.G., 2000. Elk distribution and modeling in relation to roads. J. Wildl. Manage. 64, 672–684.

Rowlingson, B.S., Diggle, P.J., 1993. SPLANCS: spatial point pattern analysis code in S-plus. Comput. Geosci. 19, 627–655.

Schumaker, B.A., Peck, D.E., Kauffman, M.E., 2012. Brucellosis in the greater yellowstone area: disease management at the wildlife–livestock interface. Human–Wildlife Interact. 6, 48–63.

Sleeman, J.M., Manning, E.J.B., Rohm, J.H., Sims, J.P., Sanchez, S., Gerhold, R.W., Keel, M.K., 2009. Johne's disease in a free-ranging white-tailed deer from Virginia and subsequent surveillance for *Mycobacterium avium* subspecies paratuberculosis. J. Wildl. Dis. 45, 201–206.

Stewart, K.M., Bowyer, R.T., Kie, J.G., Cimon, N.J., Johnson, B.K., 2002. Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. J. Mammal. 83, 229–244.

Thomas, J.W., Black, H., Scherzinger, R.J., Pedersen, R.J., 1979. Deer and elk. In: Wildlife Habitats in Managed Forests – the Blue Mountains of Oregon and Washington: Agricultural Handbook Number 553. United States Department of Agriculture, Forest Service, Washington, DC, pp. 104–127.

Torstenson, W.L.F., Mosley, J.C., Brewer, T.K., Tess, M.W., Knight, J.E., 2006. Elk, mule deer, and cattle foraging relationships on foothill and mountain rangeland. Rangeland Ecol. Manag. 59, 80–87.

Ward, M.P., Laffan, S.W., Highfield, L.D., 2007. The potential role of wild and feral animals as reservoirs of foot-and-mouth disease. Prev. Vet. Med. 80, 9–23.

Wisdom, M.J., Cimon, N.J., Johnson, B.K., Garton, E.O., Thomas, J.W., 2005. Spatial partitioning by mule deer and elk in relation to traffic. In: Wisdom, M.J. (Ed.), The Starkey Project: A Synthesis of Long-Term Studies of Elk and Mule Deer. Alliance Communications Group, Lawrence, KS, pp. 53–66.

Wisdom, M.J., Meczarski, L., Lekovic, D., Cimon, N.J., 2006. A GPS-Based Automated Telemetry System for Ungulate Research at the Starkey Experimental Forest and Range, Northeast Oregon, USA. La Grande, OR.

Witmer, G.W., DeCalesta, D.S., 1985. Effect of forest roads on habitat use by Roosevelt elk. Northwest Sci. 59, 122–125.