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Assessing Risk of Disease Transmission: Direct Implications for an Indirect Science

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By definition, contact *denotes the junction of at least two objects. In the context of disease transmission,* contact *implies interaction with potential to spread disease. Mischaracterization of contacts may result in inaccurate estimates of transmission rates. To collect more-accurate contact data among white-tailed deer (*Odocoileus virginianus*), we built a deer-borne contact detection system (DCDS) consisting of a camera and a proximity logger installed on a GPS (Global Positioning System) collar. We outfitted 26 adult male deer with DCDSs to record GPS locations, proximity of equipped deer to other equipped deer, and video of deer interactions in southern Texas during autumn 2010. From 17 continuously functional DCDSs, we documented 33 contacts with cameras, 61 with proximity loggers, and 16 with GPS, resulting in estimated mean daily contact rates of 0.29, 0.66, and 0.12, respectively. Cameras and GPS underrepresented contacts among deer, whereas proximity loggers provided credible estimates for epidemiological modeling.*

Keywords: camera, contact rate, disease transmission, Odocoileus virginianus, *white-tailed deer*

Research into the role of animal interactions in disease dynamics has benefited from a variety of animal-borne instruments, including GPS (Global Positioning System) and, more recently, proximity loggers, for collecting interaction data relevant to the transmission of diseases, such as bovine tuberculosis (Ramsey et al. 2002, Weihong et al. 2005, Prange et al. 2006), chronic wasting disease (Schauber et al. 2007, Grear et al. 2010, Habib et al. 2011), and brucellosis (Creech 2011, Cross et al. 2012). However, concerns over the intra- and interspecific transmission of pathogens have increased the demand for more-efficient and -accurate means for collecting behavioral data related to how animals interact, with particular emphasis on estimating contact rates (Schauber and Woolf 2003, Schauber et al. 2007, Silbernagel et al. 2011, Robert et al. 2012).

Technologies used to monitor the movement and behavior of animals, such as very-high-frequency (VHF) telemetry, GPS, and animal-activated cameras are well developed but provide information of only limited spatiotemporal resolution (Creech 2011, Robert et al. 2012). Infrequent interactions and, more specifically, meaningful physical contacts are often brief and probably missed with traditional monitoring. Other factors that limit the recording of contacts include the limited battery life and coarse spatiotemporal resolution of these devices, environmental constraints, and technological limitations (Creech 2011). Furthermore, most behavioral information collected with VHF telemetry or GPS is based on assumptions made by researchers and is laden with inherent error (Beringer et al. 2004, Prange et al. 2006, Hamede et al. 2009, Creech 2011).

VHF telemetry and GPS have been used to determine locations and movements; to estimate space use; and, more recently, to enable the quantification of contact rates of animals (Beringer et al. 2004, Schuler 2006, Creech 2011). Spatial imprecision up to 28 meters (m) with GPS and 600 m with VHF telemetry can be experienced (Frair et al. 2010). Collars that incorporate GPS minimize the field effort required to collect location data relative to those with VHF and enable improved accuracy, thus providing a better representation of animal-use areas and the potential for an increased collection frequency (D'Eon et al. 2002, Heard et al. 2008, Thompson et al. 2012). However, the level of activity, vegetative cover, and the orientation of the collar antenna can greatly affect the ability of GPS collars to successfully and accurately acquire locations (Prange et al. 2006, Heard et al. 2008, Frair et al. 2010). Without extensive monitoring of activity, locations, and the timing of interactions through direct observations, contacts among animals
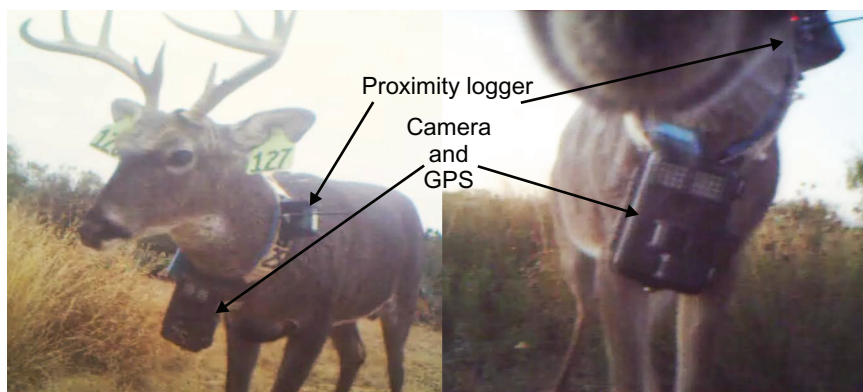
*Figure 1. Images of a deer-borne contact detection system, which included cameras, proximity loggers, and GPS (Global Positioning System) transmitters for documenting interactions among white-tailed deer (*Odocoileus virginianus*) near Zapata, Texas, in 2010. The red light-emitting diode of the proximity logger indicates whether a contact is being recorded. Photographs: Michael J. Lavelle. Deer 1 is on the right, and deer 25 is on left.*

equipped with VHF or GPS collars cannot be meaningfully assessed (Heard et al. 2008, Frair et al. 2010).

A recent major development in technology that enables researchers to collect more-refined data on interactions is the proximity logger (Prange et al. 2006, Böhm et al. 2009, Hamede et al. 2009, Creech 2011, Walrath et al. 2011, Robert et al. 2012). Proximity loggers (or simply *loggers*) record events when equipped individuals are within a predetermined distance of one another (e.g., less than 1 m) with greater precision than was previously possible (Prange et al. 2006, Robert et al. 2012). Loggers enhance the ability to determine the frequency and extent of interactions and facilitate the creation of contact networks, which are helpful in effectively modeling the transmission of pathogens and the spread of disease (Böhm et al. 2009, Hamede et al. 2009, Creech 2011). The behavior of white-tailed deer (*Odocoileus virginianus*) has been studied previously through direct observation (e.g., Hirth 1977, Ozoga and Verme 1985). Direct observations, however, are labor intensive and provide limited inference when they are conducted on animals in confinement or unnatural settings where visibility is sufficient for consistent observation (Prange et al. 2006). Observations can be limited and biased by visibility, and it is difficult to directly and efficiently observe free-ranging deer without affecting their behavior (Beringer et al. 2004). Therefore, the collection of visually acquired and unbiased contact data on nocturnal or secretive animals is challenging (Creech 2011, Thompson et al. 2012). In attempts to collect candid behavioral data with broad population-based inference, researchers sought alternatives and employed automated cameras (e.g., Gysel and Davis 1956, Winkler and Adams 1968, Swann et al. 2004). The next evolutionary development in technology for monitoring behavior was mobile cameras that could be mounted on animals to capture imagery of what the equipped individuals were

seeing and doing (Marshall 1998, Moll et al. 2007, Lavelle et al. 2012, Thompson et al. 2012).

Although others have used GPS (e.g., Schauber et al. 2007) and loggers (Walrath et al. 2011) to infer physical contact among individual deer, the use of cameras enables documentation of true contacts for addressing the related potential for disease transmission through interactions (Lavelle et al. 2012, Thompson et al. 2012). Subsequently, researchers began investigating animal-borne video data collection systems for white-tailed deer (Beringer et al. 2004, Moll et al. 2007, Moll 2008). Imagery provides confirmatory evidence of events, whereas the methods mentioned above simply provide suggestions as to what may have occurred in proximity. In this observational study in which a large-scale deployment of animal-borne cameras was implemented, our primary objective was to document pre-breeding-season contacts among individual male deer equipped with cameras, loggers, and GPS to explore the reliability of the estimates of contact rates derived from the these devices for portraying the risk of disease transmission.

Measuring contact rates

We opportunistically captured 26 male white-tailed deer using helicopter net gunning inside a 405-hectare fenced property near Zapata, Texas (26 degrees [°] 54 minutes ['] north, 99°16' west), in the South Texas Plains region between 8:00 a.m. and 12:00 p.m. on 29 November 2010. We equipped each deer with a deer-borne contact detection system (DCDS), which included a camera and a logger (see below) installed on a store-on-board GPS collar (figure 1; TGW-4500, Telonics, Mesa, Arizona; see Lavelle et al. 2012 for details). We deployed DCDSs during the beginning of the breeding season for white-tailed deer in the region, which peaks on approximately 21 December (Illige 1951, Hellickson 2002). The weight of each DCDS was 1.5 kilograms, or approximately 2% of a deer's estimated body mass based on regional weights of adult male deer (Hellickson 2002). All of the collars had release mechanisms and were programmed to drop off the deer 14 days after deployment. All animal handling followed protocols approved by the Institutional Animal Care and Use Committee of the US Department of Agriculture's Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center (Quality Assurance protocol no. 1591).

Motion-activated cameras. We affixed cameras (model 119435C, Trophy Cam, Bushnell Outdoor Products, Overland Park, Kansas) to the GPS unit housings. The cameras were activated by a passive-infrared motion sensor set

at the medium sensitivity setting. The manufacturer-stated specifications for the sensor were a range of 0–13.7 m and a trigger speed of less than 1 second. Video was captured at 30 frames per second, in color during daylight and in black and white at night, with the aid of 32 infrared-emitting diodes. We programmed the cameras to record a 30-second video segment followed by a time lag of 5 minutes before triggering again when the motion sensor was triggered. We reviewed the video and identified most deer captured on video by the distinguishing characteristics of the individuals (e.g., antler points, ear tags, collars). A *contact* was defined as an event in which at least two equipped deer were at most 1 m apart.

Proximity loggers. We attached loggers (E2C 181C, Sirtrack, Havelock North, New Zealand; as described in Prange et al. 2006, Böhm et al. 2009, and Hamede et al. 2009) on the dorsal aspect of the collars. The loggers scanned continuously at 1.5-second intervals, and we programmed them to record contacts at the most sensitive setting when at least two equipped deer were at most 1 m apart (figure 1). We conducted controlled testing to determine the detection distances of 20 randomly selected loggers. The mean distance at which the loggers recorded contacts was 0.95 m (standard deviation [SD] = 1.11). Because of prior experience with loggers and reported variation in their ability to detect contacts (Walrath et al. 2011), we considered all data recorded by the loggers as contacts, whether or not both loggers recorded an event. We assumed that no false contacts were recorded and that at least one logger would record an event when an equipped deer approached to within 1 m of another. Loggers similar to those that we used were previously determined to be 87% effective in detecting contacts when they were at most 1 m apart (Walrath et al. 2011). Likewise, we estimated the probability of detection (Z) of our loggers using $Z = A/B$, where A is the number of contacts recorded by the cameras that were also recorded by the loggers and B is the total number of contacts recorded by the cameras. We adjusted the number of contacts and contact rates for the loggers to reflect the probability of detection using $X = Y/Z$, where Y is the number of contacts recorded by the loggers and X is the adjusted number of contacts.

GPS collars. We programmed the GPS collars to obtain a fix every 15 minutes with a fix timeout of 3 minutes (the maximum allowable time to collect a fix before shutting down before another attempt). Accuracy testing at a fixed reference location ($n = 1586$ fixes truthed with a Trimble GEOXH 2008; Trimble Navigation, Sunnyvale, California) revealed a median position error of 4.7 m and a 95% circular error of probability of 20.4 m. In previous studies in which GPS collars were used on deer to infer contacts, paired locations were used within 10–25 m and during the fix timeout of the GPS (2–3 minutes) to represent contacts though the reportedly underestimated true numbers of

contacts (Schauber et al. 2007, Kjær et al. 2008, Habib et al. 2011). For comparison, we categorized the locations that that fell within 20.4 m and our 3-minute timeout period to be GPS contacts. We calculated the distance from one GPS location to another using ArcGIS (ESRI, Redlands, California).

Data analysis. To extract concurrent data relative to contacts, we pooled the data from all three sources into one spreadsheet and sorted by date and time. We considered the contacts from the cameras to be true contacts, which provided specific data points for comparison with the contacts derived from the logger and GPS data, so we reduced the combined data set to include only dyads of collared deer that were involved in contacts recorded by the cameras. We determined the time during which at least one camera within a dyad was functional and available to record a contact (i.e., the time from when the first of the two collars was deployed until the last of the two collars failed or the collar's memory became full) and labeled them *dyad focal periods*. We omitted contacts that were recorded outside of these focal periods. We reviewed the contacts logged by the cameras and examined the events from the loggers and GPS that occurred within 10 minutes of the camera events, classified them as *confirmed* contacts for each particular device, and calculated the percentage of camera contacts also detected by the loggers and GPS.

We used Pajek network analysis software (Pajek, Ljubljana, Slovenia) to create a simple network diagram depicting the contact networks derived from the camera data (figure 2). The nodes (dots) in figure 2 represent the individual equipped deer, and the edges (lines) represent interactions between individuals. The edges were weighted on the basis of the number of camera-documented contacts, with the lines' widths reflecting the number of occurrences.

We calculated daily contact rates, standardized for variable-length focal periods, for each device dyad by dividing the total number of contacts recorded by the length (in days) of the focal period for that dyad. We estimated mean contact rates (contacts per day) across dyads for each device using the PROC GLIMMIX function in SAS (version 9.1; SAS Institute, Cary, North Carolina) using restricted maximum likelihood, with an identity link, Gaussian error distribution, and Kenward–Roger degrees of freedom. Residual-side (i.e., no random effects; Littell et al. 2006) heterogeneous variance estimation (variance components by device) was used to account for nonhomogeneous variance among the residuals observed for the "contact_rate = device" model. We compared contact rates among the devices using linear contrasts (δ) and reported standard errors (SE), degrees of freedom (df, expressed in parentheses adjacent to δ), and 95% confidence intervals (95% CI) for the device means and contrast estimates. Various additional descriptive statistics (the mean and SD) were estimated using the SAS PROC MEANS function.
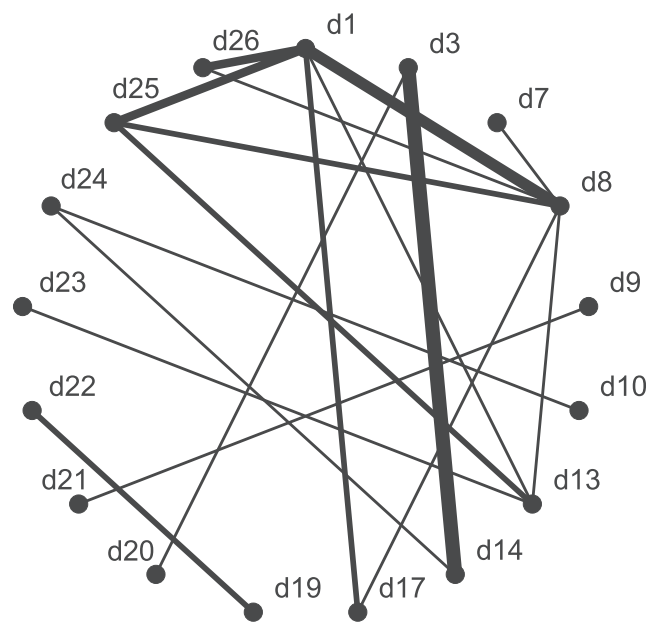
*Figure 2. Network diagram depicting camera-documented contacts among individual white-tailed deer (*Odocoileus virginianus*) near Zapata, Texas, in 2010. Each node represents an individual deer (e.g., d1 is deer 1), and the connecting lines represent contacts between individuals (the weighted line widths indicate the number of distinct contacts) collected from camera imagery.*

Calculating contact rates

We recovered 24 of 26 DCDSs on the 14th day after deployment and downloaded the data from all of the devices. Our data set was reduced to the information collected by 17 functional cameras, which recorded 20,976 videos; the other 7 cameras did not yield data because of damage that occurred during the study period (e.g., water damage, lens puncture, tampering). From this reduced data set, we documented 33 contacts between equipped deer derived from the cameras. These contacts involved 18 dyads among 17 individuals during an average focal period of 6.71 days (SD = 3.03). During these dyad focal periods, we also recorded 61 and 16 contacts derived from the loggers and the GPS, respectively. Twenty-seven of the camera contacts (82%) were also recorded by the loggers and 16 by the GPS. Adjusting for our logger probability of detection ($Z = .82$) increased the number of logger contacts from 61 to 74. Furthermore, 16 camera contacts (48%) were documented by all three types of devices, 5 were captured solely by the cameras, and 3 were recorded concurrently by the cameras on both equipped deer.

The contact data from the cameras enabled us to construct a network diagram that provides a depiction of the interactions among the individuals within our study area (figure 2). The equipped deer contacted an average of two other individuals (SD = 1.54), and one individual contacted six others. An average of 1.83 (SD = 1.20) contacts occurred

between individuals with a maximum of five occurring between two individuals.

We estimated mean daily contact rates of 0.29 for the cameras (SE = 0.03), 0.66 for the loggers (SE = 0.15), and 0.12 for the GPS (SE = 0.03), with df = 17 for each estimate (figure 3). The contact rates varied between the cameras and loggers ($\delta(18.62) = 0.37$, SE = 0.15, 95% CI = 0.04–0.69), between the cameras and GPS ($\delta(33.91) = -0.18$, SE = 0.05, 95% CI = -0.27 to -0.08), and between the loggers and GPS ($\delta(18.46) = -0.54$, SE = 0.15, 95% CI = -0.87 to -0.22). We experienced 100% success in logger and GPS collar function and a 99% successful GPS fix rate; therefore, missed GPS contacts due to a fix rate bias were not a concern.

From the camera images, we documented 146 occasions when unmarked deer were within 1 m of an equipped deer, of which 84 resulted in physical contact. From these 84 contacts, 61 involved sparring, 15 were nose-to-nose contacts, 2 were nose-to-rump, 5 were mutual grooming, and 1 was a breeding event. From those 61 sparring events, 40 deer were identifiable by unique characteristics, including collars and ear tags.

Conclusions

Within this maiden deployment of DCDSs, we sought to maximize our chances of capturing images of interactions, and therefore chose to collar males just prior to the breeding season, when they are highly mobile and interactive (Hirth 1977, Miller and Conner 2005, Grear et al. 2010). One difficulty in capturing behavioral data using animal-borne devices is the possibility of altering the behavior of the animal being monitored. To assess this possibility, researchers conducted a preliminary evaluation of the potential stress on deer resulting from collars representative of our DCDS and found no evidence of increased stress levels due to the collars (Moll et al. 2009). We also conducted visual observations 5 hours after the deployment of the last DCDS, during which three observers documented three separate equipped deer acting naturally and demonstrating behaviors representative of adult males at that time of year. For example, one collared deer was tending a female, and two were feeding in association with other deer.

Our findings demonstrate the value of cameras not only for estimating contact rates but also for collecting descriptive information on the nature of contacts that may have implications for the transmission of pathogens. For example, observations of specific behaviors, such as muzzle contact with an aborted fetus in the case of brucellosis epidemiology, are needed to confirm meaningful disease transmission events (Creech 2011). Furthermore, documentation of an exchange of bodily fluids and infectious pathogens that may result from social interactions (e.g., mutual grooming, breeding) is reliant on visual evidence; collection of this evidence is now possible through the use of animal-borne cameras.

Unfortunately, we were able to retrieve video data from only 17 of the 26 cameras; therefore, we are unsure that our data represent all contacts that took place during the study among all of the equipped individuals. However, from the
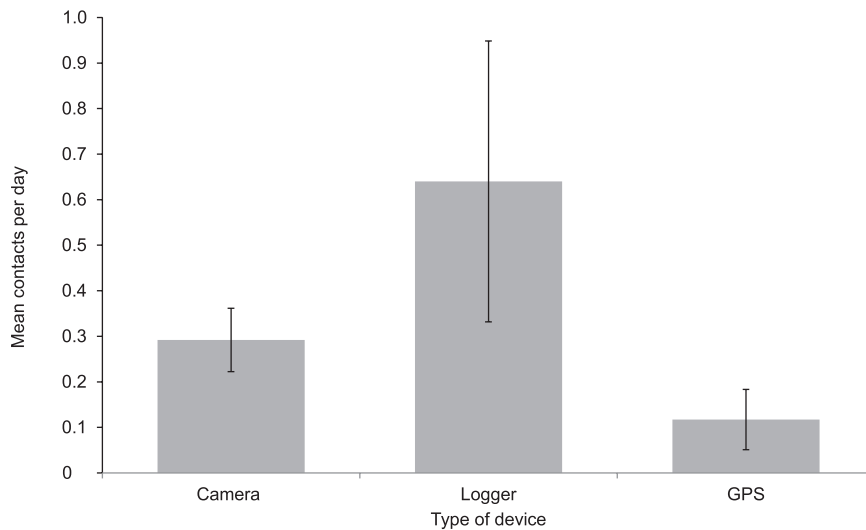
Figure 3. Mean daily contact rates among male white-tailed deer (Odocoileus virginianus) before the breeding season, derived from data collected by cameras, proximity loggers (adjusted to reflect an 82% probability of detection), and GPS (Global Positioning System) transmitters near Zapata, Texas, in 2010. The contact rates are based on user-selected sampling inputs for the devices used and will, therefore, vary accordingly. The error bars represent the 95% confidence interval.

26 equipped individuals, we do know that 96% (25 of 26) and 100% were documented by the loggers and the GPS, respectively, as being involved in contacts, although we have no video confirming these additional potential contacts. The rates derived from the cameras were likely biased low because the cameras were programmed to record for 30 seconds with a 5-minute delay between triggers. With improved technology, continuous collection of video could overcome this challenge.

The cameras used in this study enabled the creation of a network diagram (figure 2), which can improve the understanding of the connectedness of individuals and the potential effects of social structure within the dynamics of disease transmission. For example, deer 8 contacted six other equipped deer directly and an additional two indirectly. Conversely, deer 7 directly contacted only one other equipped deer (deer 8) and, as a result of contacting such a gregarious individual, may have indirectly interacted with another seven equipped deer. Furthermore, network diagrams elucidate the variability in the sociality of individuals and the significance of interacting with particularly risky individuals (i.e., super spreaders) and thereby amplifying the risk for spreading infectious agents of disease.

The recent introduction of innovative loggers enabled the collection of finescale (i.e., 1-m resolution) interaction data. Our 82% probability of detection was consistent with the 87% experienced by Walrath and colleagues (2011) for detecting contacts with the loggers. Consequently, we suggest that users of loggers consider adjusting their data accordingly in order to account for the probability of

detection. Furthermore, the loggers conclusively provided the contact rate estimates that were the most representative of the actual rate in our study, because they operated continuously and limited logged contacts to much closer distances than was detectable with GPS. Therefore, we found the loggers to be the best single option that we evaluated for estimating contact rates.

The accuracy of GPS receivers has improved, although inherent error still imposes an uncertainty of true locations that renders these data weak for inferring physical contact. For example, two deer equipped with GPS collars may exchange saliva at the same physical location, or, conversely, they may be 40 m apart and still recorded as being in the same location. The rates derived from GPS were biased low, given the magnitude of difference between GPS and both the logger and the camera rates, as well as the reduced frequency of data acquisition and the associated contact detection.

Previous researchers have concluded, "Proximity does not provide enough information to determine whether contact has occurred between individuals or whether sufficient interaction has occurred to allow for disease transmission, but high frequency of close proximity events suggests active association between individuals and thus a higher probability of physical contact" (Silbernagel et al. 2011, p. 1454). A combination of devices such as our DCDS provides a more complete story, with photo documentation characterizing interactions and GPS providing the approximate locations of those interactions. However, without electronically linked components, it is virtually impossible to consistently collect concurrent data, because of the nature of the technologies. For example, successfully obtaining a fix with GPS is not always temporally predictable, and attempts are not continuous. The integration of GPS and loggers could enable loggers to trigger a GPS fix attempt when they detect another collar in order to record the location where the interaction occurred.

To date, loggers or VHF or GPS collars verified by direct observation have been the only option for researchers to acquire verified contact data, although that process is very labor intensive, costly, and challenging. With time, devices such as our DCDS will undoubtedly alter the approaches to obtaining such data. Comparisons of multiple technologies for collecting contact data are rare (Creech 2011), and, hopefully, these results provide insight into the value of various sampling schemes and technologies. Although our evaluation provides a better understanding of contact data collected with various technologies, the data shared herein may not be representative of that exhibited elsewhere; we

therefore caution against using our contact rates for modeling efforts without careful consideration and interpretation. Furthermore, we compared contact rates on the basis of our sampling regimes and programming parameters for each device (e.g., camera motion detection sensitivity and programmed down time, logger sensitivity, GPS fix attempt frequency). One must realize that unlimited combinations of user-selected inputs are available, and contact rates reflect these inputs. We provide information that can facilitate prescribing the most appropriate tool for estimating contact rates and elucidating the potential for disease transmission. We also provide means for improving the reliability and relevance of the contact rates estimated from data collected with various monitoring devices.

Short of conducting direct observations, only camera technology, such as that used in our DCDS collars, documents true physical contact but, currently, can be deployed only for a short time because of battery limitations. The nature of GPS data, with spatial imprecision and a lack of temporal synchronization, creates challenges when attempting to make meaningful inferences relative to contact rates for epidemiological modeling. Our results suggest that the contact rates derived from GPS data can be an underrepresentation of reality, and such data should be reserved for purposes in which (spatiotemporally) less precise information does not affect greater outcomes, such as the predicted rate of the spread of a disease and the emergency disease management responses. Great care should be taken in selecting the techniques used to estimate contact rates because considerably varied estimates can result. Study objectives and the nature of a particular disease being studied should influence the selection and programming of the specific tool or combination of tools in order to optimize the results.

Acknowledgments

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