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ABSTRACT

Direct and indirect contacts among individuals drive transmission of infectious disease. When multiple interacting species are susceptible to the same pathogen, risk assessment must include all potential host species. Bovine tuberculosis (bTB) is an example of a disease that can be transmitted among several wildlife species and to cattle, although the potential role of several wildlife species in spillback to cattle remains unclear. To better understand the complex network of contacts and factors driving disease transmission, we fitted proximity logger collars to beef and dairy cattle ($n = 37$), white-tailed deer (*Odocoileus virginianus*; $n = 29$), raccoon (*Procyon lotor*; $n = 53$), and Virginia opossum (*Didelphis virginiana*; $n = 79$) for 16 months in Michigan's Lower Peninsula, USA. We determined inter- and intra-species direct and indirect contact rates. Data on indirect contact was calculated when collared animals visited stationary proximity loggers placed at cattle feed and water resources. Most contact between wildlife species and cattle was indirect, with the highest contact rates occurring between raccoons and cattle during summer and fall. Nearly all visits (>99%) to cattle feed and water sources were by cattle, whereas visitation to stored cattle feed was dominated by deer and raccoon (46% and 38%, respectively). Our results suggest that indirect contact resulting from wildlife species visiting cattle-related resources could pose a risk of disease transmission to cattle and deserves continued attention with active mitigation.

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1. Introduction

The cattle industry in the USA has been plagued by reoccurrences of bovine tuberculosis (bTB) caused by the *Mycobacterium bovis* (*M. bovis*) bacterium (Cosgrove et al., 2012; Miller and Sweeney, 2013; Palmer, 2013; Barasona et al., 2014). Historically, bTB occurred in 9 distinct locations in North America and persists in 3 of these areas (Miller and Sweeney, 2013). In northern Michigan's (MI) Lower Peninsula, USA, bTB is maintained in free-ranging white-tailed deer (*Odocoileus virginianus*) providing a source for reinfection in cattle and perpetuation of the problem (O'Brien et al., 2006; Fitzgerald and Kaneene, 2013; Palmer 2013). Free-ranging white-tailed deer represent a challenging reservoir in MI, which has motivated landscape-scale efforts to minimize potential for direct and indirect inter-species contact to reduce transmission of *M. bovis* from deer to cattle.

In the endemic zone of bTB in MI, raccoons (*Procyon lotor*) and opossums (*Didelphis virginiana*) are currently considered to be spillover hosts, testing positive for bTB at similar to higher rates than deer (Walter et al., 2013; Berentsen et al., 2010). Researchers from Michigan State University, USA reported it unlikely that bTB-infected opossums pose risk of pathogen transmission to large ruminants, although they can transmit pathogens via aerosol to other opossums in close contact (Fitzgerald et al., 2003). Such close contact within tightly knit family groups is a common characteristic of wildlife hosts of bTB (Fitzgerald et al., 2003). Both raccoons and opossums are found to share communal dens resulting in increased interaction when resources are abundant such as around feed stockpiled for livestock (Palmer et al., 2002; Atwood et al., 2009). Further, raccoons and opossums utilize the same stored feed, water sources, and feed being consumed by cattle and frequent

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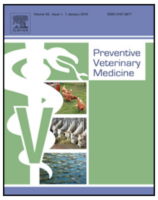

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farm buildings which house cattle and/or stored feed (Bruning-Fann et al., 2001; Atwood et al., 2009; Witmer et al., 2010; Walter et al., 2013). In other areas of the world where bTB is endemic, similar mesopredators including European badger (*Meles meles*) in Europe (Garnett et al., 2002; Bohm et al., 2009; Woodroffe et al., 2016) and brush-tailed opossum in New Zealand (Yockney et al., 2013) function as primary reservoirs of reinfection for cattle.

Transmission of *M. bovis* from animal to animal is possible through direct physical contact or exchange of air-borne pathogens, although transmission via contaminated feed or water is the most likely mode of transmission to cattle in the USA (Palmer et al., 2004a,b; Palmer and Whipple, 2006; Knust, 2008; Ribeiro-Lima et al., 2016). Human-manipulated environments, such as livestock production facilities, influence wildlife behavior and often provide unnatural foci for interaction such as at cattle-related resources including feed and water (Wobeser, 2006; Atwood et al., 2009; Gortazar et al., 2011; Barasona et al., 2014; Nunn et al., 2014).

Multi-host-species pathogens that are capable of being transmitted directly and indirectly, such as *M. bovis,* pose unique challenges to understanding risk and targeting mitigation to curb transmission (Cowie et al., 2015). Further, cryptic behavior of wildlife makes quantification of direct inter-species contact rates non-trivial and the ability to determine where, when, and how indirect interactions lead to transmission requires high-resolution contact data (Blyton et al., 2014). Fortunately, tools such as proximity loggers are now available and lend well to estimating previously unknown variables such as contact rates within and among species to provide a more accurate portrayal of the most relevant types and rates of interactions explaining disease dynamics (Cross et al., 2012; Lavelle et al., 2014). Our objectives were to, (1) quantify the extent of interaction occurring between wildlife and cattle in a landscape with bTB and, (2) evaluate the contributing role of cattle-related resources in exacerbating indirect contacts.

2. Materials and methods

2.1. Study area

We conducted our study on 6 privately owned cattle farms including 3 cow-calf and 3 dairy farms in Michigan's Lower Peninsula within Montmorency, Presque Isle, and Alpena Counties. This area lies within the core endemic area of bTB in MI (Walter et al., 2012; Berentsen et al., 2014) and provides highly suitable habitat for white-tailed deer (Felix et al., 2007). High-use, cattle-related areas and feed storage sites were present on each farm. Land cover types adjacent to study farms were dominated by woody wetlands, alfalfa fields, deciduous forest, corn fields, and other non-alfalfa hay fields. Although cattle production occurs in this area, densities are low averaging one beef-cattle farm per 21.5 km^2 and one dairy-cattle farm per 130.0 km^2 (Berentsen et al., 2014). Elevations ranged from 150 to 390 m above sea level with average annual snowfall of 175 cm and 72.5 cm of rain (Eichenlaub et al., 1990). Winter snow depths typically peak at 25–50 cm which is typically melted off by mid-April (Beyer et al., 2010). Weather in this region is notably more variable than elsewhere in the state with average summer temperatures of 24.8C and average winter temperatures of – 10.8C (Beyer et al., 2010). Regional deer density is estimated at 10 deer/km^2 (O'Brien et al., 2011), though concentrations of deer around food sources during winter can result in densities exceeding 19 deer/km^2 (Beyer et al., 2010) to as high as 35 deer/km^2 (Sitar, 1996). Apparent bTB prevalence rates in deer, opossum, and raccoon in the region fluctuate around 2% (O'Brien et al., 2011), 6%, and 4% respectively (Walter et al., 2013).

2.2. Wildlife capture and monitoring

We captured free-ranging wildlife primarily in January; though also as needed throughout the study to maintain ≥ 3 monitored adult animals of each species per site, using numerous live trapping techniques. Trap sites were dispersed across each farm within suitable habitat thus all available animals were potential study animals. Pairs of animals making contact were the experimental unit. All procedures were approved by the Institutional Animal Care and Use Committee of the U.S. Department of Agriculture-Animal and Plant Health Inspection Service-Wildlife Services-National Wildlife Research Center (USDA-APHIS-WS-NWRC, QA-1940). All livestock producers providing access to their property provided informed consent and were present during the handling of their livestock.

We monitored wildlife interaction and movement on and around farms relative to cattle-related resources with proximity loggers. Proximity loggers ("loggers" from this point forward; E2C 181C, Sirtrack®, Havelock North, New Zealand) use ultra-high frequency (UHF) transceivers and receivers to transmit and receive unique identification codes and record time, date, and duration of events logged. We programmed loggers with a separation time of 60 s (duration loggers needed to separate before beginning to log a new "event") and range coefficient of 45, which translated to a mean distance of 0.88 m (SD = 0.95) ("contact").

To quantify indirect contacts resulting from visitation to cattle-related resources, we also installed stationary loggers (3 or 4 per farm) of the same model at stored feed sites, water sources, and cattle feeders to record visitation by logger-equipped individuals. The routine shift of stored feed from "stored feed" status to "fed feed" status was not tracked or quantified; thus indirect contacts resulting from contamination by wildlife being concentrated overnight and then delivered to cattle the very next day were underestimated. Stored feed sites including hay, potatoes, beets, high-moisture corn, silage, and haylage were typically accessed ≥ 1 time daily to provide feed to cattle. Where feed quantities changed frequently, loggers were relocated routinely to monitor access points (i.e., open end of agbag). Stationary loggers were maintained every 1–2 weeks by connecting to a laptop computer and downloading data. Over the duration of the study, we monitored 28 (mean = 5/farm; sd = 2.1) cattle-related resources including 8 feeders, 8 water sources, 7 enclosed feed storage facilities, and 5 elongated crop storage bags (agbags).

2.3. Contact data processing

2.3.1. Direct contacts

A direct contact was defined as when at least one of a pair of interacting animals' collars established a connection in any 15-s time window. To account for variability in transmission probability due to contact events of different duration, multiple contacts were counted if the duration of the contact was greater than 15 s. For example, if loggers indicated two animals were in contact for one minute, then we counted that as four contacts whereas if two animals were in contact for three seconds, it was counted as one contact. For each unique pair of individuals that made contact at least once during the study, we calculated daily contact rate per season. This involved taking the count of contacts between a unique pair of individuals (including pairs from 6 different farms) and dividing by the number of days the unique pair was co-monitored (denominator for pairwise contact rates) during the season. Each value of daily contact rate for a unique pair had the following factor data associated with it: species interaction, season, farm, unique ID. These data were analyzed in a statistical model described below. Also, we showed descriptive results in Table 1 by averaging over unique pairs of individuals within a season or within a species interaction level. Cow-cow contacts were excluded from analyses as they were not of interest.

2.3.2. Visitation to resources

We quantified visitation to cattle-related resources by all species and present descriptive statistics on particular species visiting and to which cattle-related resources they were visiting. Although visits to stored feed by wildlife and livestock were recorded, frequent delivery of this exposed feed to a particular group of livestock that may or may have not included a logger-equipped cow was not tracked, thus indirect contacts resulting from delivery of previously exposed stored feed to cattle were not included in analyses.

2.3.3. Indirect contacts

We defined indirect contacts as environmental interactions that could result in the transmission of bTB via contaminated cattle-related resources (e.g., stored feed, water trough, etc.) where stationary loggers were installed. Bovine TB is known to survive in the environment and remain infectious depending on weather conditions (Fine et al., 2011; Cowie et al., 2015). We assumed a fixed 30-day infectious period for cooler periods (1 Oct–1 May) and 7 days for warmer periods (2 May–30 Sept; Fine et al., 2011) as an approximation to the average environmental persistence of bTB (i.e., appropriate intervals of indirect contact). We used the two different intervals to represent potential transmission pathways of bTB while accounting for seasonal variation in environmental persistence.

An indirect contact occurred when a source individual visited a cattle-related resource and other individuals subsequently visited the resource within the bTB persistence time window ("transmission risk period" – TRP). Indirect contact rates were non-directional: AB = BA. An indirect TRP was initiated from a source individual for each day that the source individual had at least one visit recorded at the resource (Fig. 1A). If any other individuals visited the resource within the TRP (30 or 7 days depending on season), the number of visits by the exposed individual to the resource were recorded as indirect contacts. Relative to direct contact rates, for indirect contact rates, calculating mean daily contact rate was more complicated because there were multiple TRPs within the time of co-monitoring of unique pairs, during which indirect contact could occur (Fig. 1A). Thus, first the number of indirect contacts for each unique pair were counted for each transmission risk period. These counts were each divided by the number of days in the transmission risk period. Then, for each unique pair of individuals, the average of indirect contact rates across all transmission risk periods within a season was calculated to generate mean daily indirect contact rates for the unique pair. These indirect contact rates for each unique pair had associated covariate data such as the species interaction type, stationary resource, farm, and season which were considered in the statistical models described below. For descriptive results, we calculated means across the levels of these main effects and presented them in Table 1.

2.4. Data analysis

2.4.1. Variation in contact rates

To quantify the effects of potential factors affecting contact rates, we used linear mixed model regression implemented in statistical software package R (R Core Team, 2015) and the package Bates et al. (2015). Response variables were direct (n = 269) and indirect daily contact rates (natural log-transformed, n = 169) for unique pairs of individuals for each level of covariate factors (Fig. 1B). Covariate factors included the species involved (i.e., raccoon-deer, cow-opossum, opossum-opossum, etc.) and the season when the contact occurred (Fig. 1B). Spring was defined to be during the months of March, April, and May; June, July, and Aug were considered summer; Sept, Oct, and Nov were the fall season; and winter was defined as the months of Dec, Jan, and Feb. Using Akaike Information Criterion (AIC) for models fit with restricted maximum likelihood (REML) given a saturated mean fixed effects structure (Zuur et al., 2009), we examined whether the following random effects should be included in the final models: unique animal pair (to account for repeated measures on the same pair within a season), one or both individuals in the pair, farm ID, type of farm (beef or dairy) and stationary logger (indirect contact models only). Unique animal pair (direct contact) and unique animal pair with unique stationary logger (indirect contact) explained most of the error correlation, such that other factors were redundant and thus excluded from the final models (Fig. 1B). We presented deviance and an approximate R^2 value for best models as goodness of fit measures where the R^2 statistic was the squared correlation between observed and predicted values. In order to show contact rates predicted by the model (i.e., which accounts for the sampling design), we predicted mean log daily contact rates and corresponding 95% confidence intervals for each factor level in each model using the *lsmeans* package in R (Lenth, 2016). These values were then back-transformed to reflect average daily contact rates on the original scale. We used Tukey pairwise comparisons to determine significant differences between factor levels.

Table 1

Means, with standard deviation, of daily direct and indirect contacts across species interaction type, season, and cattle-related resource type before the fence was installed from a 2012–13 multi-species interaction study in Michigan's Lower Peninsula, USA. Mean values include variation from unique pairs from 6 different farms.

		Direct Mean contacts/day (standard deviation)	Indirect Mean contacts/day (standard deviation)
Interaction	raccoon-cow	0.06 (0.01)	1.46 (1.27)
	opossum-cow	NA	1.02 (1.17)
	deer-deer	22 (78.61)	1.52 (2.54)
	raccoon-raccoon	3.78 (10.64)	1.32 (1.74)
	opossum-raccoon	1.82 (8.11)	0.91 (1.23)
	deer-raccoon	0.37 (0.98)	0.60 (0.52)
	opossum-deer	0.14 (0.11)	0.36 (0.43)
	opossum-opossum	4.63 (14.04)	0.18 (0.14)
Season	spring	7.30 (40.48)	0.93 (1.35)
	winter	14.90 (68.51)	1.21 (2.12)
	summer	2.21 (8.49)	1.53 (1.31)
	fall	3.47 (14.16)	0.22 (0.22)
Cattle-related resources	fed feed	NA	1.47 (1.32)
	stored feed	NA	1.06 (1.66)
	water source	NA	0.49 (0.49)

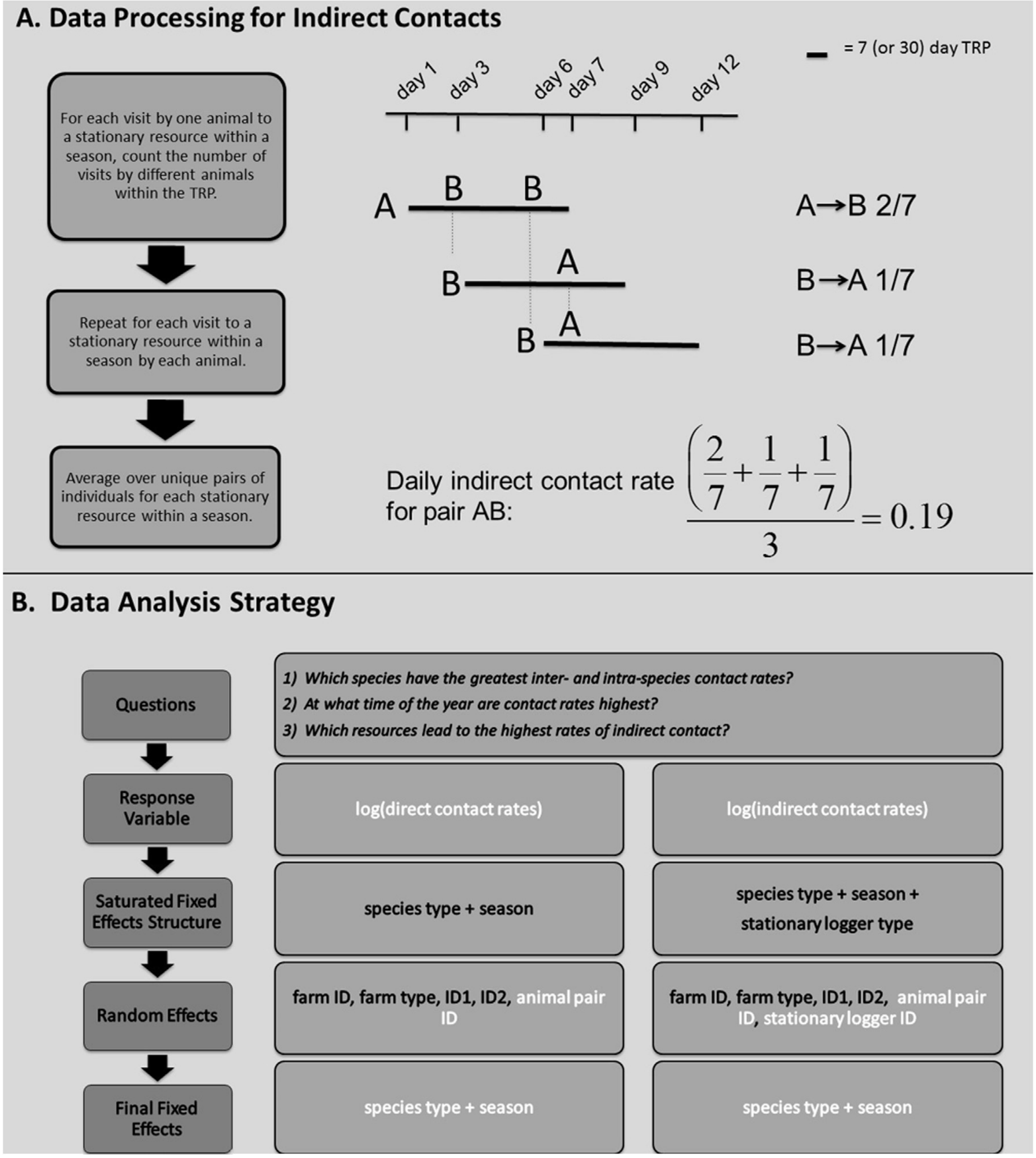

Fig. 1. Schematic of data processing and model analysis methods used in a 2012-13 multi-species interaction study in Michigan's Lower Peninsula, USA. A. Calculation of daily indirect contact rates for each unique pair within a season. We define "unique pair" as AB or BA where A and B are unique individuals which had at least one indirect contact event (i.e., A or B visited a stationary resource following the other within the TRP). Suppose that individual A visits the feeder on day 1 when the contact risk period is 7 days, and B visits the feeder on days 3 and 6. Then the indirect daily contact rate between animals A and B resulting from animal A's visit to the feeder on day 1 is 2/7 because of animal B's two visits to the feeder within the transmission risk period (TRP; which was 7 or 30 days based on environmental conditions and probable survival time of *Mycobacterium bovis*). Now suppose animal A visited the feeder again on day 7 after animal B who could have infected the feeder after animal A's initial visit. Since animal B visited the feeder twice, there are two more opportunities for exposure to animal A. Daily indirect contact rates arising from visits by either animal A or animal B were then averaged across the season. Thus, if these were the only visits made by animals A and B during the entire summer (92 days), then the daily indirect contact rate for the animal pair AB in the summer would be 2/7 + 1/7 + 1/7 divided by the three contact opportunities = 0.19. B. Outline of data analysis for both daily contact rate models. The leftmost column denotes the data analysis process, while the middle and rightmost columns describe the chosen model structures (highlighted in white) for direct and indirect contact rates before the fence. Model selection was done by first choosing the optimal random effects given a saturated fixed effects structure (including all variables of interest) using AIC with models fit using REML. Then, final fixed effects were chosen given the optimal random effect(s) using AIC with models fit using MLE. The final model was fit using REML.

3. Results

3.1. Descriptive results

Throughout the entire study, we outfitted 79 opossum, 53 raccoon, 29 deer, and 37 cattle with proximity loggers and collected usable data from 40, 43, 29, and 37 respectively. From Jan 2012–June 2013, we recorded 265,929 direct contacts among 180 pairs of individuals of which raccoon and deer intraspecies contacts were highest (65% and 33% of overall total respectively, excluding cattle-cattle). No direct contacts were documented between cattle and opossums or cattle and deer, but three cattle-raccoon

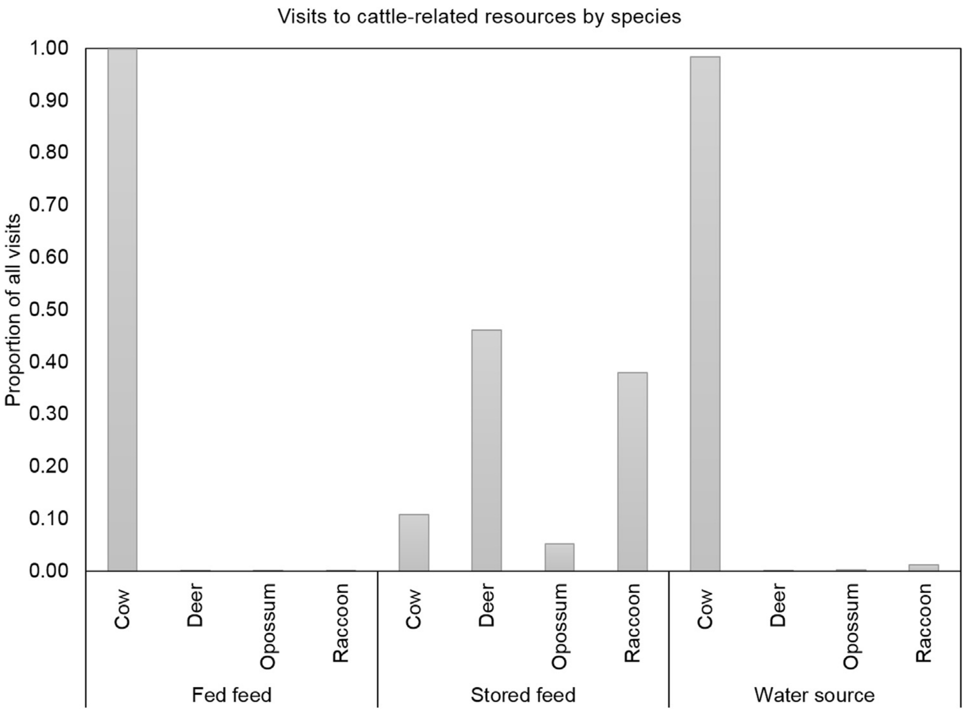

Fig. 2. Overall proportion of visits, as recorded by proximity loggers on cattle, deer, opossums, and raccoons, to each cattle-related resource including fed feed available within cattle confinement areas, stored feed areas, and water sources including automatic waterers and ponds. Results are from a multi-species interaction study in Michigan's Lower Peninsula, USA.

pairs were recorded having direct contact in the summer and fall (total = 9 contacts). Considering descriptive statistics of the raw data, daily contact rates were highest for deer-deer pairs followed by opossum-opossum and raccoon-raccoon pairs (Table 1). Mean direct contact rates peaked in winter when deer typically congregate in wintering areas in this region (Sitar, 1996; Beyer et al., 2010). Winter was also when visitation by deer to stored feed peaked during this study as well (Fig. 2; 91% of all deer visits to stored feed) resulting in observed congregations at stored feed sites.

We recorded a total of 101,670 visits by wildlife and cattle to cattle-related resources over the duration of the study (Fig. 2). The majority of visitation to fed feed and water sources was by cattle (>98%) as expected, while wildlife visitation to these same resources remained relatively low (Fig. 2). The majority of visitation to stored feed however, was by deer and raccoon (46% and 38%, respectively), yet there was also unanticipated visitation by cattle (>10%) to stored feed resulting in spatial overlap between wildlife in cattle.

Throughout the study, we recorded 72,919 indirect contacts involving 72 pairs of wildlife and cattle (excluding cattle-cattle). Indirect contact rates resulting from visitation to cattle-related resources were highest for deer-deer contacts followed by those of raccoon-cow (Table 1). Deer-deer indirect contacts at stored feed dominated indirect contacts of all species and resource type (55% of total). Indirect contact rates were slightly higher (38.7%) at fed feed relative to stored feed and were higher (113.3%) at feed sites relative to water sources (Table 1).

3.2. Variation in direct contact rates

Direct contact rates were significantly higher in winter than in the summer (p-value = 0.005) or fall (p-value = 0.003) (R^2 for full model fit = 0.85; Fig. 3, left; Fig. S1 in the online version at DOI: http://dx.doi.org/10.1016/j.prevetmed.2016.10.009). There were no significant differences between the levels of the 'species type' factor but visual trends did exist (Fig. 3). For example, intra-species direct contact rates were higher than inter-species direct contact rates, and raccoons generally had higher inter-species contact rates relative to deer and opossum (Fig. 3, right; Fig. S1 in the online version at Doi: http://dx.doi.org/10.1016/j.prevetmed.2016.10.009). Most direct contacts in the fall were intra-species contacts between raccoon-raccoon and deer–deer pairs. In contrast, many intra-species direct contacts between opossums occurred in the summer and winter.

3.3. Variation in indirect contact rates

Indirect contact rates were significantly lower in the fall than in the summer (p-value < 0.001) or winter (p-value = 0.003), and higher in the summer than in the spring (p-value < 0.001). As in the direct contact rate model, there were no significant differences between the levels of the 'species type' factor but trends did exist. Raccoon-cow daily indirect contact rates were highest, followed by deer-deer, opossum-opossum, cow-opossum, and raccoon-deer which were similarly high (R^2 for full model fit = 0.64, Fig. 4, Fig. S2 in the online version at DOI: http://dx.doi.org/10.1016/j.prevetmed.2016.10.009). The type of resource was not a significant factor in the model, therefore we did not include this factor in the final model (Fig. 1B).

4. Discussion

Our predominant objective was to explore the dynamic web of inter- and intra-species interactions occurring among cattle and wildlife commonly found on and around farms in Michigan's Lower Peninsula to pinpoint how (i.e., indirectly or directly and inter- or intra-species), where (i.e., particular cattle related resource), and when (i.e., season) transmission of bTB could be occurring. In agreement with previous research, we also did not document direct contacts between cattle and deer, emphasizing the importance of other areas where resources are shared discretely (Hill, 2005; Berentsen et al., 2014). Few direct contacts occurred between

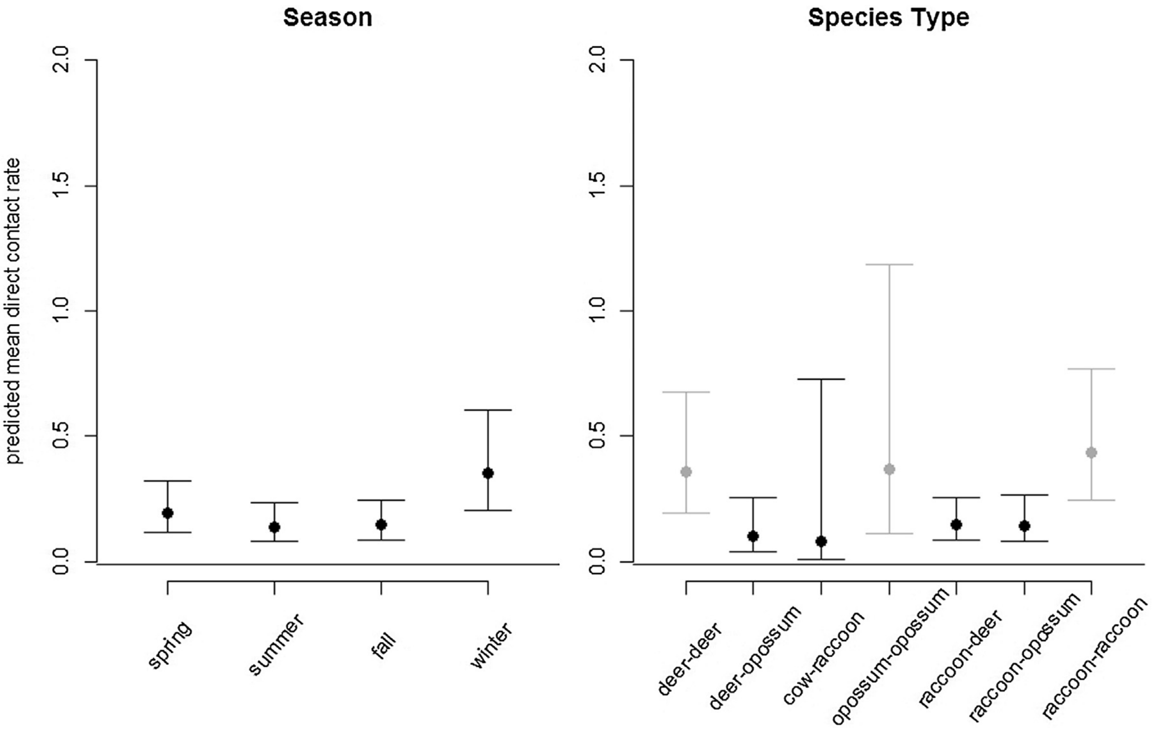

Fig. 3. Predicted mean daily direct contacts and 95% confidence intervals for direct contacts model. Fixed effects included species interaction type and season with log-transformed daily direct contacts as the response. Animal pairs were included as a random effect. Winter had significantly higher direct contact rates than summer (p-value = 0.005) or fall (p-value = 0.003). There was a trend of intraspecies contact rates being higher than interspecies contact rates but there were no significant differences in this 2012–2013 multi-species interaction study in Michigan's Lower Peninsula, USA.

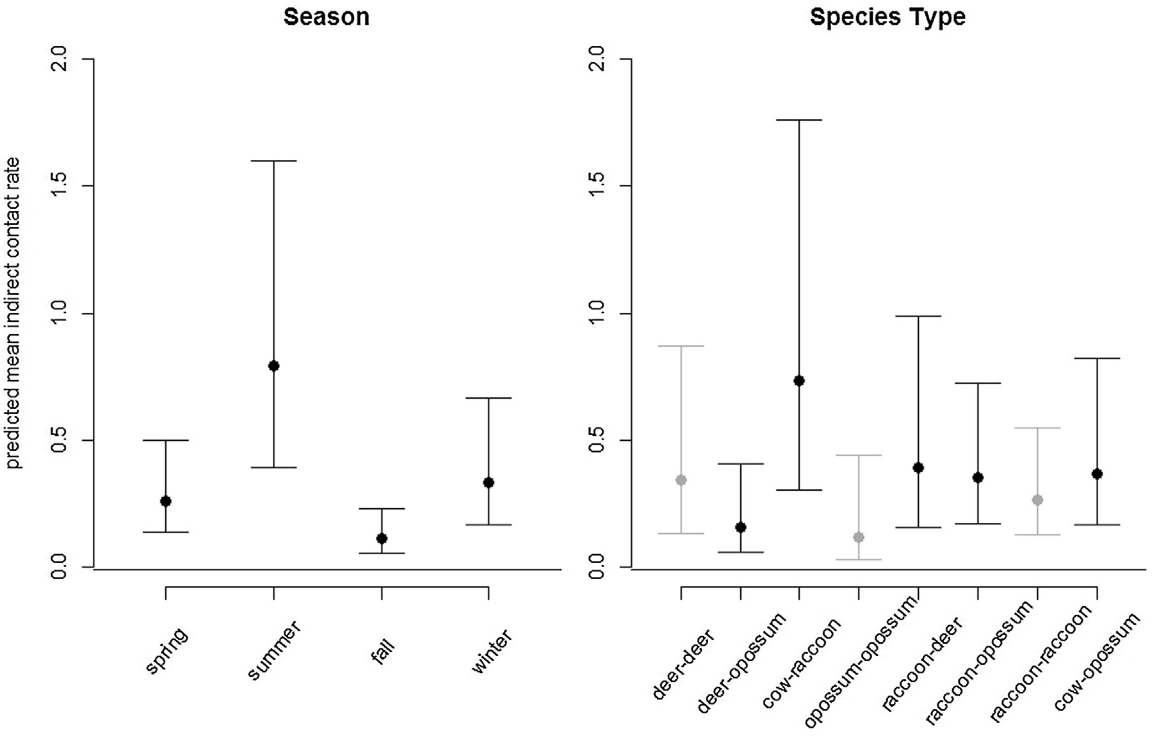

Fig. 4. Predicted mean daily indirect contact rates and 95% confidence intervals in the indirect contacts model. Fixed effects included season and species interaction type with log-transformed daily indirect contacts as the response. Animal pairs and stationary loggers were included as random effects. Indirect contact rates in the fall were significantly lower than in the summer (p-value < 0.001) or winter (p-value = 0.003), and indirect contacts in the summer were significantly higher than in the spring (p-value < 0.001). There was a trend of cow-raccoon indirect contact rates being higher than all other pairs but were no significant differences among species pair types in this 2012–2013 multi-species contact study in Michigan's Lower Peninsula, USA.

cattle and raccoons and none between cattle and opossums. However, indirect contacts between cattle and all wildlife species we monitored occurred routinely, peaking in winter and summer seasons suggesting increased vigilance in mitigating contacts is needed during those seasons. Further, higher level of contacts associated with fed feed and stored feed indicates the need for continued focus on only feeding as much feed as cattle will eat in a single day, leaving minimal feed residue overnight, and excluding wildlife from stored cattle feed.

Consistent with previous work (Gortazar et al., 2011, 2015), we focused on characterizing indirect contacts through cattle-related resources such as feed and water which are likely hot spots for pathogen contamination by wildlife species (Atwood et al., 2009; Joseph et al., 2013; Palmer and Whipple, 2006; Ward et al., 2006; Walter et al., 2012). Our findings demonstrate indirect contacts resulting from wildlife visitation to unprotected resources are of primary concern, especially when that same feed is delivered shortly afterwards to cattle. Concern mainly revolves around the highly-desired foodstuffs stored in agbags or bunkers such as silage, haylage, and high-moisture corn that have a localized access point where contamination by wildlife is concentrated overnight and then delivered to cattle the very next day. Although quantification of where, when, to whom, and how frequently stored feed transitioned to fed feed was not tracked, the level of visitation to stored feed provides a rough portrayal of this situation. As such, the documented relatively high levels of visitation to stored cattle feed by deer and raccoons followed by daily delivery of this potentially contaminated feed results in an undeniably risky source for transfer of bodily fluids from wildlife to cattle (Fig. 2). On the contrary, if stored feed that was exposed overnight was disposed of prior to extracting feed to be fed to cattle, resultant waste contributes to economic loss. Although debatable, risks associated with potential delivery of pathogens from a source directly to susceptible individuals outweigh the costs associated with routine disposal of exposed feed. Fortunately, both situations could be mitigated through installation of fences to exclude wildlife from valuable stored cattle feed and eliminate the potential flow of wildlife contaminants to susceptible cattle.

Complex multi-host systems, such as that in MI, complicate disease eradication efforts particularly when free-ranging wildlife species are involved (Bohm et al., 2009; Palmer, 2013; Barasona et al., 2014). Dairy and beef cattle production in MI is reliant on cultivation, storage, and daily delivery of high-quality food resources to cattle resulting in the presence of abundant highly desired foodstuffs frequently leading to the congregation of free-ranging species when left accessible which was evident at all of our study sites.

Recurring bTB-positive cattle and deer within MI emphasize persistent challenges despite expansive management actions focused on deer and cattle. Such actions include, but are not limited to increased opportunity for harvesting antlerless deer on cattle farms, assistance in fencing stored cattle feed, and excluding cattle from within and adjacent to areas of high deer concentrations such as low-lying coniferous swamp. Heterogeneity of direct contact rates within and among involved species and indirect contact rates at cattle-related resources all play into the overall complexity of disease dynamics and further complicate control, especially when physical abilities and means for excluding species differ (Grear et al., 2013; Craft, 2015; Pepin et al., 2016). White-tailed deer are relatively easy to exclude from an area with fences given routine maintenance (VerCauteren et al., 2006; Lavelle et al., 2015); however, the efficacy of such fences in deterring other species is questionable. Solid barriers and electrified fences proved effective in reducing badger visitation to farm resources in England (Judge et al., 2011).

One major challenge to bTB eradication efforts relates to the persistence of the pathogen (Fine et al., 2011; Palmer et al., 2012). A second is due to the generalist nature of the pathogen in host range combined with insufficient knowledge of contact and disease transmission ecology within the assemblage of transmitting host species (Palmer et al., 2012; Palmer 2013). A third challenge is that multiple, and occasionally conflicting interest groups and governmental agencies all play into potential success of eradication efforts (Gortazar et al., 2015). For example, rules regarding supplemental feeding and baiting practices for wildlife continue to be issues of contention, while cattle producers are actively implementing measures to eliminate potential congregation of wildlife around similar foodstuffs associated with cattle production (Rudolph et al., 2006; Palmer et al., 2012). Lastly, reluctance of hunters to increase harvest of antlerless deer has hampered localized population reductions directed at minimizing potential for disease transmission (Cosgrove et al., 2012).

Although white-tailed deer in proximity of bTB-positive farms are the primary wildlife target for disease control, efforts to reduce visitation by other suspected spillover species are also recommended (O'Brien et al., 2006). These other suspect species may not replicate the pathogen to high enough levels to serve as reservoirs, but it is possible that they act as mechanical vectors or are competent enough hosts to amplify pathogen persistence for short times (Foil and Gorham, 2000; Wobeser, 2006), making it important to determine their contact rates and potential routes of transmission to cattle (Palmer et al., 2004b).

Existing and developing technologies such as interacting proximity loggers enable quantification of a key process driving disease transmission: contact (Cross et al., 2012; Lavelle et al., 2014). Proximity loggers enable researchers to collect data relative to contact rates, yet there are still several shortcomings of using them to estimate contact rates among individuals. First, a large enough sample of the population must be outfitted with loggers to capture the level of variability between individuals. Second, the variability in function of loggers themselves results in some uncertainty (Prange et al., 2006). Third, to capture any information pertaining to indirect contacts, a minimum of 3 loggers have to be functioning simultaneously and present (i.e., one stationary logger at the resource and two logger-equipped animals) at the same location to acquire meaningful information. Fourth, with contact studies it is unknown a priori whether collared individuals will occupy home ranges within proximity to enable contact. Also, without concurrent locations data it is difficult to know whether pairs that don't make contact are zeros due to a social reason or simply because their home ranges do not overlap. Future studies which concurrently collect locational data could shed light on the contribution of no-contact pairs (i.e., how many there are which are within reasonable spatial range) in explaining variation in contact rates. Lastly, as other researchers have demonstrated, occasional detection failures due to the nature of the technology used in proximity loggers are to be expected further reducing estimates of contact rates below reality (Walrath et al., 2011; Tosa et al., 2015). Regardless of these shortcomings, we documented both direct and indirect contacts among multiple loggers on multiple farms.

5. Conclusions

Proximity loggers are a novel tool useful for examining interactions among individuals including difficult-to-observe wildlife species. We collected proximity logger data from cattle, wildlife, and cattle-related resources to evaluate the extent to which direct and indirect contacts occur. Our data reflect a conservative estimation of reality and the absolute minimum of what truly occurred. Most contact between wildlife species and cattle was indirect, with the highest contact rates occurring between raccoons and cattle during summer and fall. We identified unprotected stored feed destined for consumption by cattle as sites where disease transmission is most likely to occur due to focused activity by deer, opossums, and raccoons. Ultimately, mitigation measures to eliminate this focused activity, along with other ongoing actions will further progress towards controlling bTB in wildlife and livestock.

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