DOI: 10.7589/2018-01-011

Journal of Wildlife Diseases, 55(2), 2019, pp. 000–000

EFFECTS OF BRUCELLOSIS SEROLOGIC STATUS ON PHYSIOLOGY AND BEHAVIOR OF ROCKY MOUNTAIN ELK (*CERVUS CANADENSIS NELSONI*) IN SOUTHWESTERN MONTANA

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ABSTRACT: Brucellosis, caused by bacteria in the genus *Brucella*, is an infectious zoonosis affecting animals and humans worldwide. Free-ranging Rocky Mountain elk (*Cervus canadensis nelsoni*) and bison (*Bison bison*) in the Greater Yellowstone Ecosystem (areas of southwestern Montana, eastern Idaho, and northwestern Wyoming, USA) are the self-sustaining reservoirs of bovine brucellosis (*Brucella abortus*) and elk are considered the primary source of livestock infections. It has been hypothesized that *Brucella*-exposed elk might have different physiologic status (pregnancy rates and body condition) and migration behaviors than would healthy elk. Here we tested the effects of brucellosis serologic status on pregnancy rates and winter ingesta free body fat of 100 female elk in southwestern Montana. We also evaluated the effects of serologic status on two characteristics of spring migration behavior, migration types (migrant, mixed migrant, resident, disperser, nomad, and undetermined type) and timing (start and end dates and duration). The migration behaviors were quantified using a model-driven approach based on the relative net squared displacement. We detected a significant difference (P=0.003) in pregnancy rates between seropositive and seronegative elk, with about a 30% drop in seropositive individuals. However, we did not detect differences in body fat between seropositive and seronegative elk or differences in either migration type or timing of spring migration. These results confirmed that the major effect of brucellosis in free-ranging elk is associated with reproduction.

Key words: Behavior, body condition, commingling, elk, migration, pregnancy, rNSD, serological status.

INTRODUCTION

Brucellosis is a highly infectious zoonosis affecting animals and humans worldwide caused by several species of Gram-negative, facultative, intracellular bacteria in the genus *Brucella* (Zheludkov and Tsirelson 2010). *Brucella abortus*, which typically infects cattle, is responsible for bovine brucellosis. Wildlife species, such as bison (*Bison bison*) and elk (*Cervus canadensis*), have been confirmed as important reservoirs of *B. abortus* (Davis 1990; O'Brien et al. 2017). Abortion and stillborn calves are the most-frequent clinical signs of brucellosis, potentially influencing elk reproduction rates and impacting population demography (Thorne et al. 1978; Peterson et al. 1991; Joly and Messier 2005). Brucellosis-induced arthritis and synovitis have also been reported in bison and cattle. Effects on joints could reduce an individual elk's foraging efficiency and potentially influence its long-term health, physiologic condition, and behavioral decisions (Tessaro et al. 1990; Joly and Messier 2005; Botzler and Brown 2014).

There has been a recent increase of reported brucellosis transmission from elk to livestock in the Greater Yellowstone Ecosystem (GYE; Smith and Anderson 1998; Bienen and Tabor 2006; Cross et al. 2010). Recent studies have employed genotyping (O'Brien et al. 2017) and next-generation sequencing (Kamath et al. 2016) to confirm multiple elk-cattle (*Bos taurus*) transmission events in the GYE. *Brucella* transmission between elk and livestock is hypothesized to be indirect and

due to spatial overlap (i.e., commingling) during the late-term elk pregnancy and calving period (March to May) when exposed elk may shed *Brucella* bacteria through abortion or calving events (Godfroid 2002; Proffitt et al. 2011; Cross et al. 2015). Commingling is difficult to prevent in the spring when elk are moving from winter to transitional and summer ranges; the populations are usually widely dispersed throughout the GYE during the spring migration period (Proffitt et al. 2011).

Current brucellosis management in the GYE is challenging considering the size and wide distribution of wildlife populations, their movement dynamics, and the unknown serologic status among elk populations (Schumaker et al. 2012; Brennan et al. 2017). Furthermore, because elk move between public and private lands, stakeholder values need to be considered in disease management practices (Proffitt et al. 2013). It has been hypothesized that brucellosis serologic status could indirectly impact the distribution and movement patterns of ungulates by affecting joint health (Joly and Messier 2005; Wadood et al. 2009). It is typical for elk to engage in spring migration close to the peak timing of brucellosis-induced abortion risk (March to May) in most average snow years (Cross et al. 2007, 2015). Thus, evaluating the predictability of migration timing and duration for exposed elk herds is important to develop practices that reduce elk-livestock commingling on livestock grazing areas such as fencing haystacks and hazing elk off the pasture (Schumaker et al. 2012). Differences in migration behaviors between brucellosis-exposed and naïve elk might help narrow down which elk groups to focus on for disease management.

If exposed elk tend to migrate later or remain resident on the winter ranges that are shared with livestock, bacteria shed by elk may result in elk-to-livestock transmission events in the early spring and in areas where elk are not usually present during the risk season. Alternatively, if exposed elk engage in migration and start their spring migration early, they may move through spring livestock holding areas when the most bacteria are shed, increasing the risk of transmission to livestock in the holding areas. Additionally, if exposed elk seek out different resources than do naïve elk, migration might last longer, which increases the time and geographic extent of commingling, thus increasing the risk of transmission to a larger livestock population (Schumaker et al. 2012).

In this study, we focused on the effects of brucellosis serologic status on 1) pregnancy rates, 2) body condition, and 3) spring migration behaviors of elk in eight southwestern Montana herds. We expected to observe reduced pregnancy rates and poorer body conditions in brucellosis-exposed elk compared to naïve elk because brucellosis typically affects reproductive stages and potentially impacts long-term health. For spring migration behavior, we hypothesized that the serologic status of elk influences two characteristics of spring migration behaviors, migration type and migration timing (start dates, end dates, and durations). Specifically, we tested whether brucellosis-exposed elk have different migration types, or differences in their spring migration start dates, end dates, and durations, when compared to naïve elk. To test these hypotheses, we analyzed pregnancy status, body condition, and movement data from brucellosis-exposed and naïve global positioning system (GPS)-collared elk.

MATERIALS AND METHODS

Study areas and elk capture

Our study region in southwestern Montana included eight different elk herds: Black's Ford areas, Blacktail areas, Sage Creek areas, Tobacco Root areas, Red Mountain areas, Clark Canyon areas, South Pioneer Mountain areas, and West Pioneer Mountain areas (Fig. 1; Montana Fish, Wildlife, and Parks [MFWP] 2015). We captured elk via helicopter net gunning and deployed GPS collars following MFWP protocols (MFWP 2015). We programmed collars to record GPS fixes for 52–72 wk with 30-min, 1-h, or 2-h intervals. We assigned elk to herds based on the location of their captures. Capture, collaring, and sampling occurred mid-January to late February each year. We aged elk based on tooth eruption patterns. We collected a blood sample to determine serologic

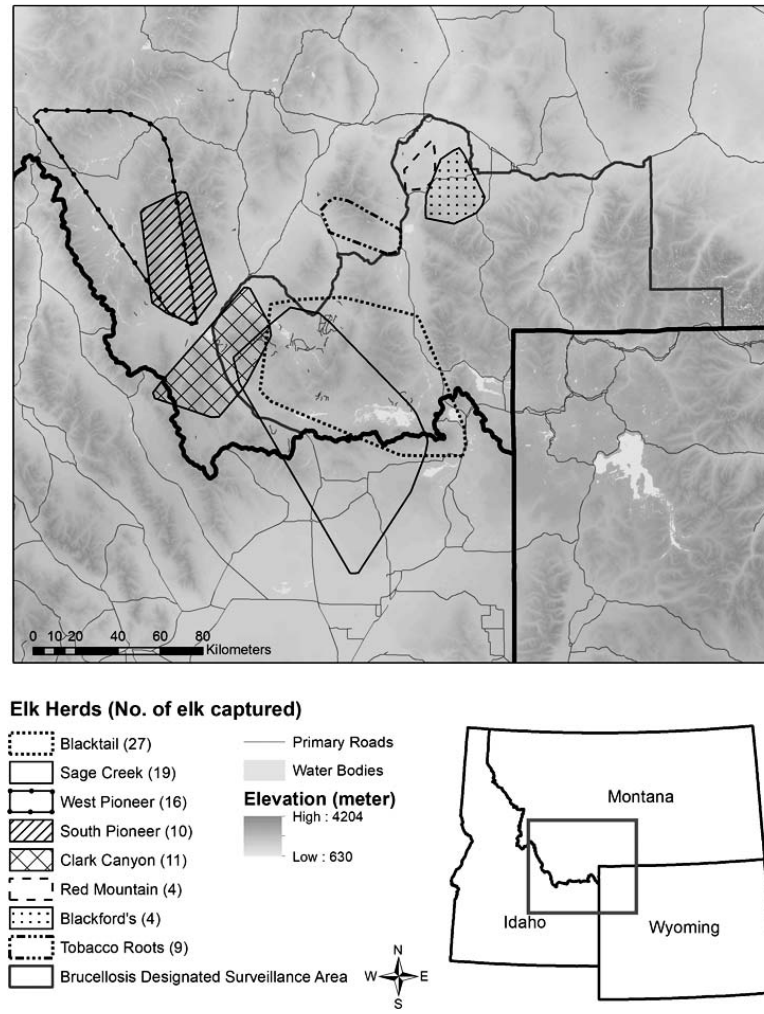

FIGURE 1. The southwest Montana study area of the Greater Yellowstone Ecosystem including the annual home ranges of eight Rocky Mountain elk (*Cervus Canadensis nelsoni*) herds, topography, primary roads, and waterbodies. Population level annual home ranges are represented by the minimum convex hull polygon of all the global positioning system fixes for all collared elk in each herd.

status from all individuals captured, and we collected pregnancy, body condition, and collar data from a sample of up to 30 individuals per herd.

Serological tests for *Brucella* spp. To determine the serologic status of each captured elk, serum samples were tested at the Montana Department of Livestock Diagnostic Laboratory (Bozeman, Montana). Serum samples were tested to determine exposure to *Brucella* using the buffered acidified plate antigen, the Rivanol test, fluorescence polarization assay (FPA) test (Ellie Labs, Milwaukee, Wisconsin, USA), and standard plate test. Final classification of serologic status (seropositive or seronegative) was confirmed using the FPA tube test (Nielsen and Gall 2001). According to the manufacturer's product instructions, the sensitivity and specificity of FPA test is 99.03% and 99.9%, respectively (Ellie 2013), such that errors due to misclassification can be disregarded. We assumed brucellosis-exposed and naïve elk were correctly identified to be seropositive and seronegative, respectively.

Pregnancy status and body condition

We determined pregnancy status based on pregnancy-specific protein-B levels in blood serum (Noyes et al. 1996). Ingesta free body fat

(IFBF) was measured as a proxy of body condition. To derive IFBF, we measured chest girth and assessed body fat using a portable ultrasound machine. We estimated IFBF following Cook et al. (2010). We did not estimate lactation status because the late-winter timing of sampling did not allow us to determine if elk had lactated the previous summer and fall. Both the pregnancy status and IFBF for seropositive and seronegative elk used in this study were tested from samples and measurements collected at capture events.

Testing for differences in physiologic status

We used generalized linear models (GLMs) and mixed models (GLMMs) to test the effects of brucellosis serologic status on pregnancy status and body condition. Because elk belonged to different herds and their physiologic conditions could vary across years, we included herd membership and year as random effects in the models. We tested the significance of serologic status and herd at α=0.05 by comparing the full model with models dropping the terms sequentially using a likelihood ratio test (Taper and Ponciano 2016). Pregnancy status models were constructed assuming that the dependent variable was binomially distributed while body condition was assumed to be log-normally distributed. The GLMs and GLMMs were developed using stats and lme4 packages in R v3.4.2, respectively (Bates et al. 2007; R Development Core Team 2017).

Testing for differences in migration behavior

To test the hypothesis that brucellosis serologic status influenced elk migration behaviors, we used a model-driven approach to classify each individual elk into one of five possible classic migration types: migrant, mixed migrant, resident, disperser, or nomad based on the relative net squared displacement (rNSD; Spitz et al. 2017). Relative NSD is defined as a straight-line distance from a relocated starting point of the trajectory to the location at a given time (see Supplementary Materials). Due to landscape heterogeneity across herds, however, migration movement patterns of some elk may not have been explained by these five migration behavior types. Reliable estimation of migration timing requires a clear classification of migration type. Therefore, we performed an additional goodness of fit test of each model by calculating the ratio between the residual sum of squares and the total sum of squares (SSr/SSt) of the best model for each individual. Individuals with 1-(SSr/SSt) lower than 0.50 were assumed to have an undetermined movement behavior and thus classified as a sixth type of migration: undetermined. After classifying each individual into one of the six migration types, we evaluated if serologic status influenced this classification of migration type by using a multinomial regression in which the type of migration was set as the dependent variable and serologic status as the independent variable. We evaluated the significance of the regression using a likelihood ratio test between the full regression and a null model in which serologic status did not influence the type of migration of elk. We, however, evaluated the effect of sampling size and unbalanced sampling using a series of simulations (see Supplementary Material).

To test the hypothesis that serologic status influenced migration timing, we compared the spring migration starting dates, ending dates, and durations between seropositive and seronegative migratory and mixed migratory elk. Starting and ending dates of migration were obtained from parameter estimates of the best model that classified each individual elk as a migrant or mixed migrant (see Supplementary Material). Date estimates were transformed into Julian dates starting on the first day of the year in which data were collected. Duration of migration was calculated by subtracting the starting Julian date from the ending Julian date.

We compared starting and ending migration dates and duration between seropositive and seronegative elk using a Cox-proportional hazard regression model. The Cox-proportional hazard regression model estimates a baseline of how the probability of an event happening changes through time and then estimates how covariates proportionally increase or decrease such probability (Cox 1972; Fox 2002). This type of analysis is increasingly used in animal behavioral studies (Lebreton et al. 1993; Moya-Laraño and Wise 2000). Coefficients of the Cox-proportional hazard larger than one indicated that the covariate increased the probability of occurrence of the event (hazard) while a coefficient smaller than one indicated that the covariate decreased the probability of occurrence of the event (Fox 2002). In our case, the baseline was set for seronegative elk. Thus, a Cox-proportional hazard coefficient greater than one indicated that seropositive elk started and ended migration earlier and spent less time migrating than did seronegative elk, as this predictor increased the probability of an individual elk to start or end migration.

It is possible that the synchrony and similarity of migration behaviors within a given herd or among years could influence migration timing irrespective of elk serologic status, misleading the results obtained (Bowyer 1981). To account for these potentially confounding factors, we included herd membership for each individual elk and year of data collection as random effects in the Cox-proportional hazard models. Finally, we assessed

TABLE 1. Sample size of radio-collared Rocky Mountain elk (*Cervus canadensis nelsoni*) included in migration type classification and estimation of migration timing. The table includes the number of seropositive and seronegative elk sampled for brucellosis exposure and the number of elk with complete movement data in eight herds in southwestern Montana.

	Elk captured			Elk with complete movements		
Herd	Positive	Negative	Subtotal	Positive	Negative	Subtotal
Black's Ford	2	2	4	2	2	4
Blacktail	7	20	27	7	16	23
Clark Canyon	0	11	11	0	7	7
Red Mountain	0	4	4	0	4	4
Sage Creek	5	14	19	4	12	16
South Pioneer	0	10	10	0	9	9
Tobacco Roots	0	9	9	0	5	5
West Pioneer	0	16	16	0	16	16
Total	14	86	100	13	71	84

the significance of the models by comparing model likelihood estimates to the likelihood of a null model with no explanatory variables. Cox-proportional hazard models were performed in the coxme R-package (Therneau 2012). For the above described analyses of migration behavior, elk were included if serologic lab results were assigned and movement data were complete for approximately 11 mo.

RESULTS

We captured and sampled 100 adult (>1 yr old) female elk in eight herds during 2011–2014 (Table 1). The brucellosis seroprevalence rate across the sampled population was 14% (95% CI: 8–23%). The historical brucellosis seroprevalence rate in elk sampled near winter feed grounds was 10–30%, but it was 2–3% away from feedgrounds around the GYE (Cross et al. 2010). Our study areas were all away from feedgrounds. We tested pregnancy status of all 100 elk and estimated the IFBF on 60 of these individuals. The mean (SD) pregnancy rates varied from about 85% (36%) to 93% (25%) in 2011–2014 and from 75% (50%) to 100% (0%) among the eight herds (see Supplementary Materials Table S1). The mean (SD) IFBF ranged from about 8% (±2%) to 9% (±4%) in 2011–2014 and from 8% (±2%) to 10% (±0%) in herds (see Supplementary Material Table S1). All 100 elk were GPS radio-collared. Given that we found that three of the eight herds sampled in our study included seropositive elk (Table 1), we repeated the aforementioned analyses to detect the effects of brucellosis on physiologic condition (GLM/GLMM) and migration (multinomial regression and Cox-proportional hazard regression model) including only elk members within these three herds. The results using the full and the reduced datasets were completely consistent. Given the consistency of the results, we herein present the results regarding the physiologic status and migration behavior only for the full dataset.

Differences in physiologic status

We found that brucellosis serologic status affected pregnancy rates. Seropositive elk had an estimated probability of pregnancy at 64% (CI: 39–89%), which was, on average, 30% lower than seronegative elk with the pregnancy rates as 94% (CI: 89–99%; Table 2 and Fig. 2). We detected no significant relationship between serologic status and body condition (Table 2 and Fig. 2). Also, there were no significant herd or year effects on either pregnancy rates or body conditions for these elk herds, as the likelihood ratio tests suggested the model including only serologic status as a predictor was the top-selected for pregnancy

TABLE 2. Model comparisons for tests of the effects of brucellosis serologic status on pregnancy status and body condition of the Rocky Mountain elk (*Cervus Canadensis nelsoni*) in eight southwest Montana herds sampled in 2011–2014. Intercept and coefficient are presented with respective confidence intervals in parenthesis. For simplicity, we do not present the estimated variance, as no random effect was significant. Coefficients presented are in logit scale for pregnancy status and in logarithmic scale for body condition.[a]

	Intercept (95% CI)	Serologic status (95% CI)	Log-likelihood	χ^2	*P*
Pregnancy status					
Null	2.20 (1.86–2.53)	—	−32.50	—	—
Serologic status	2.79 (2.32–3.25)	−2.20 (−2.92 to −1.47)	−28.20	8.61	0.003
Serologic status+Herd+Year	2.79 (2.32–3.25)	−2.20 (−2.92 to −1.47)	−28.20	0.00	1.000
Body condition					
Null	2.12 (2.09–2.16)	—	−129.28	—	—
Serologic status	2.12 (2.09–2.16)	−0.01 (−0.11 to 0.14)	−129.28	0.01	0.915
Serologic status+Herd+Year	2.12 (2.09–2.16)	−0.01 (−0.11 to 0.14)	−130.28	0.00	1.000

[a] A dash (—) indicates_____.

analysis, and the best model for body condition test was the null model.

Differences in migration behaviors

Sixteen elk died during the year before completing their migration, leaving us with 84 elk (13 seropositive and 71 seronegative) that had both complete movement data and serologic results across all eight herds (Table 1). We found that serologic status did not influence migration type (Fig. 3; likelihood ratio test with P=0.484). The majority of elk (62) were classified as migratory animals (migrants or mixed migrants) regardless of serologic status. Fifteen seronegative elk were classified as having the undetermined migration type while only one seropositive elk was classified in this group.

Similar to analysis of migration types, we found that brucellosis serologic status did not influence the start date, end date, or duration of spring migration (Table 3 and Fig. 4). Even though the likelihood ratio tests between the serologic status model and the null model of start date, end date, and migration duration all showed that the model which included serologic status, herd, and year significantly explained more variability than did the null model, the significance was driven by the large variability in migration timing among herds and in migration ending dates among years (Table 3; see Supplementary Material Table S2;). The coefficients of the fixed effects in the Cox-proportional hazard model were not significant at α=0.05 (Table 3).

Given no significant difference in migration timing between seropositive and seronegative elk, we found that elk left winter ranges on a mean (SD) of Julian day 100 (±32) of the year (10 April) and reached the summer ranges on a mean of Julian day 151 (±41) of the year (31 May). The mean (SD) time that elk spent migrating was 51 (±46) d. Migration behavior was variable with some elk starting migration as early as late January or early February (2.5% quantile of spring migration starting Julian day 36; 5 February) and ending as late as mid-August (97.5% quantile of spring migration ending Julian day 226; 14 August). Consequently, migration duration varied widely with 95% of the individuals spending between 6 and 124 d migrating (Fig. 4).

DISCUSSION

Overall, our results showed a relatively high *Brucella* seroprevalence rate (14%) for female elk in southwestern Montana, which had a strong impact on pregnancy rates. *Brucella* infection decreased pregnancy rates in this sample population by about 30%, supporting the hypothesis that brucellosis significantly impacts the reproductive stages of seropositive animals. In contrast, we found no support

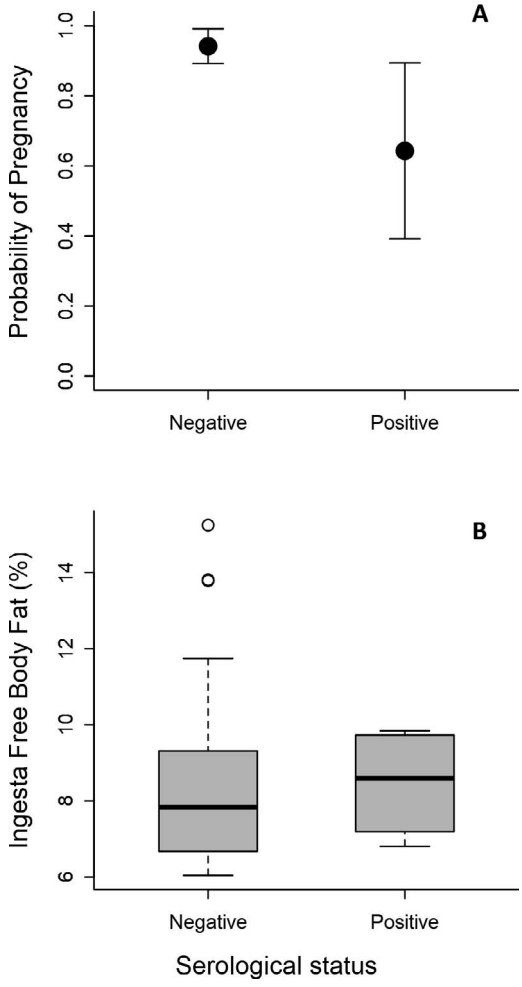

FIGURE 2. Pregnancy probability (panel A) and percent ingesta free body fat (panel B) for *Brucella* seropositive and seronegative individuals of Rocky Mountain elk (*Cervus Canadensis nelsoni*) in southwestern Montana. The plotted pregnancy probabilities (or ingesta free body fat [IFBF]) presented for seronegative and seropositive individuals are parameter estimates and 95% confidence intervals from a generalized linear model with pregnancy status (or IFBF) as the dependent variable and serologic status as the independent variable.

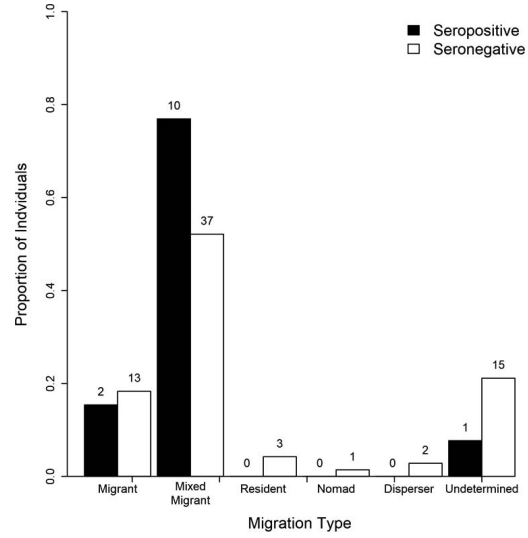

FIGURE 3. Proportion (bars) and number (shown above bar) of seropositive and seronegative elk migratory behaviors classified as migrant, mixed migrant, resident, disperser, nomad, and undetermined type.

for the hypotheses that brucellosis affected body condition or migration behaviors. Seropositive elk did not have poorer body condition (as measured by IFBF) or adopt different movement behaviors compared to brucellosis-naive elk.

The effects of brucellosis on ungulate population dynamics are controversial. For example, Daszak et al. (2003) argued that a significant number of disease-induced mortality events is a general criterion to demonstrate the impacts of a disease on population declines. Other studies suggested that brucellosis affects population dynamics by causing reduced reproduction rates and the production of dead or weak calves (Peterson et al. 1991; Joly and Messier 2005). Recent studies on long-term elk population demographic dynamics suggest that pregnancy rate has a minor effect on elk population growth rates while juvenile survival has a major impact (Gaillard et al. 2000; Raithel et al. 2007; Eacker et al. 2017). Eacker et al. (2017) showed that fecundity, a variable related to pregnancy rate, had little influence on population growth rate. They showed that population growth rates can still be positive even in cases where fecundity is much lower than the pregnancy rates we found in seropositive elk in this study (Eacker et al. 2017). Alternatively, brucellosis is not expected to have a significant impact over population growth rate if brucellosis-exposed elk only abort their first calf following the initial exposure but continue to be fertile through the rest of their

TABLE 3. Results of mixed effects Cox-proportional hazard regression models testing for differences in starting, ending dates, or duration of spring migration between brucellosis seropositive and seronegative elk in eight Rocky Mountain elk (*Cervus canadensis nelsoni*) herds in southwestern Montana during 2011–2014.

			Fixed effects		Random effects	
			Seropositive			
	Log-likelihood	Integrated *P*	Exp(Coef)[a]	*P*	Herd SD[b]	Year SD[b]
Starting Date	−187.95	<0.001	1.74	0.140	0.80	0.02
Ending Date	−191.69	0.016	0.53	0.086	1.07	0.80
Duration	−193.44	0.077	0.85	0.640	1.03	0.32

[a] Exp(Coef) refers to the proportional hazard coefficient that maximizes the likelihood of the data and the *P*-value reports the significance of such coefficient.

[b] SD refers to the conditional standard deviation of the random effects Herd and Year.

reproductive life (Thorne et al. 1978). Consequently, although we estimated a 30% lower pregnancy rate in seropositive elk, this decrease may not affect the elk population growth rate, despite the relatively high seroprevalence.

The lack of a significant relationship between *Brucella* serologic status and body fat in the elk herds implied that the impact of *B. abortus* on elk fitness is primarily on reproduction and abortion but not necessarily on physical condition or body fat. Similar results have been reported in other ruminants, in which brucellosis does not appear to affect body condition or parity, and seroprevalence is not influenced by sex (Wadood et al. 2009). Winter IFBF reflects nutritional resources acquired during the previous summer's growing season minus the fat lost during the winter and is strongly dependent on summer-fall lactation status. The IFBF is often used as a proxy to reflect the nutritional status over previous weeks and months (Milner et al. 2003). Any parturition events, including both normal and brucellosis-induced early parturition, could impact the short-term nutritional conditions within only days or weeks (Parker et al. 2009). However, due to quick recovery, when elk aborted shortly before being tested these effects would more likely be reflected in blood chemistry rather than in body fat (Milner et al. 2003).

Although we expected that seropositive elk might become more resident than seronegative ones, the three elk classified as resident in this study were seronegative. Also, most seropositive elk were not classified as the undetermined migration type, though 21% of seronegative elk were classified into this group. The majority of elk included in this study were classified as migratory animals (migrants and mixed migrants) across herds, which might be explained by the strong genetic basis for migration behaviors in large ungulates which overrides the impacts of the disease (McDevitt et al. 2009; Hebblewhite and Merrill 2011). However, some individual elk may switch migration status between migrants or mixed migrants and residents across their lives (Hebblewhite and Merrill 2011), suggesting that factors other than brucellosis (e.g., land use practices, predators, climatic variability, or social cues) are required to understand the decision of elk to switch between migration types (Eggeman et al. 2016).

Because the timing of spring migration and movement vectors of elk herds determine their spatiotemporal use of landscape, our estimates may be used to improve spring grazing practices of livestock in a manner that avoids commingling and reduces elk-livestock transmission risks. Our results suggested significant elk movements through summer ranges starting as early as the beginning of February until as late as the end of July, with the highest concentration starting migration in early April and ending in late May. Suitable

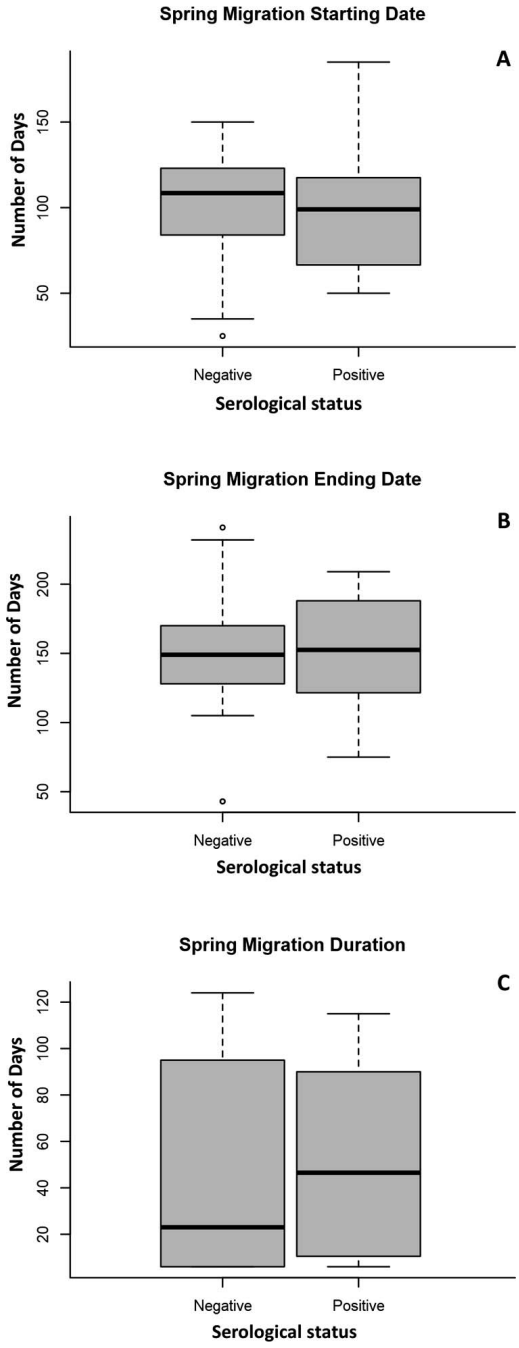

FIGURE 4. Boxplots comparing spring migration starting (panel A) and ending (panel B) dates and total duration (panel C) between *Brucella* seropositive and seronegative individuals of Rocky Mountain elk (*Cervus canadensis nelsoni*) in eight southwest Montana populations during 2011–2014. For starting and ending migration dates, the Y-axis shows the number of days from 1 January of the year in which data were collected until migration either started or ended.

environmental conditions in the spring can promote *B. abortus* persistence for up to 81 d in fetal tissue and 43 d in soil (Aune et al. 2012), although other studies suggest much-shorter survival under normal conditions (Cook et al. 2004; Maichak et al. 2009; Rushton 2009). To completely avoid exposure to *B. abortus*, livestock would need to be grazed on pastures several weeks or month after elk have occupied the ranges (Schumaker et al. 2012).

Changing spring grazing practices of livestock could be challenging, however, due to limited forage and the high cost of grazing livestock on private, brucellosis-free pastures (Roberts 2011). Winter supplemental elk feedgrounds were established to avoid elk-livestock commingling in southern GYE in Wyoming (Smith 2001; Cotterill et al. 2018), but this strategy likely increased brucellosis seroprevalence in elk populations (Cross et al. 2007). Additional management practices have been employed including vaccination (Herriges et al. 1991), habitat enhancement (Clause et al. 2002), test-and-remove (Ragan 2002; Cotterill et al. 2018), and temporary sterilization (Killian et al. 2009; Cotterill et al. 2018). Livestock producers outside feedground areas also take various activities to prevent commingling such as fencing haystacks, hazing elk off the pasture, and asking local wildlife agencies for assistance (Schumaker et al. 2012). Some producers also join calfhood and adult-booster vaccination programs and spray heifers (Schumaker et al. 2012). All of these options can be alternatives to the change in spring grazing practices and might be easier to align with the timing of elk migration reported here.

In addition to the lack of support for the hypothesis that elk migration behavior is influenced by brucellosis serologic status, we observed high variability among herds and years in the timing of elk migration (Table 3; see Supplementary Material Table S2), suggesting that it is other ecologic and biogeographic factors that determine migration timing (Alerstam et al. 2003; White et al. 2010). Similar results suggest high variability in elk movements among years and herds

(Boyce 1991; Irwin 2002; White et al. 2010). Predicting migration type, timing, and duration of elk migration based on environmental variables could help livestock producers and wildlife managers make decisions that reduce commingling between elk and livestock. Climatic variability among years might influence the level of photosynthetic greenness and snowpack in the spring, which affect the decisions of individual elk to start or end migration. The same factors can potentially have an influence in the variability among herd migration timing, as environmental conditions are variable in space and time. The variability among elk herds could also be explained by their gregariousness. Social cues, such as the density of conspecifics in the herd, could result in the similarity of migration patterns and dates of individuals within the same herd (White et al. 2010). Additionally, migration behavior is contingent wherein individual elk could adopt different migration strategies due to their different physiologic status, such as body condition and pregnancy, and to interactions with environmental suitability and social cues (White et al. 2010). Consequently, the significant influence of annual variation and herd membership on migration timing was an interesting result that warrants further study at a finer spatiotemporal resolution than this current study.

It is possible that the seropositive category included both infected and recovered individuals, biasing our results. *Brucella* infection can be detected several years after initial infection, depending on age (Thorne et al. 1978; Benavides et al. 2017). Therefore, seropositive elk in our sample could have included healthy animals that were no longer infected. Currently, serologic testing is still the primary means to infer prevalence for most wildlife disease monitoring programs, including bovine brucellosis (Gilbert et al. 2013; Benavides et al. 2017). Based on the available evidence, we confirmed that the major pathology of brucellosis was related to elk reproduction. Although no significant impacts of brucellosis on body condition and spring migration behavior were detected, our identification of migration types and the estimates of migration timing for elk herds might improve management of brucellosis and wildlife to avoid elk-livestock commingling, which could have important public health and economic implications.

ACKNOWLEDGMENTS

We are grateful for the assistance of Montana Fish, Wildlife, and Parks for data collection and data sharing. Partial funding for this study was provided by the National Institutes of Health Grant 1R01GM117617-01 to J.K.B. Funding for data collection was supplied by the US Department of Agriculture-Animal and Plant Health Inspection Service through an agreement with Montana Department of Livestock and Montana Fish, Wildlife, and Parks. We thank L.R. Morris for preliminary contributions to this study.

SUPPLEMENTARY MATERIAL

Supplementary material for this article is online at http://dx.doi.org/10.7589/2018-01-011.

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Submitted for publication 14 January 2018.
Accepted 18 May 2018.