



ARTICLE

Disease Ecology

Warm places, warm years, and warm seasons increase parasitizing of moose by winter ticks

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Abstract

Observed links between parasites, such as ticks, and climate change have aroused concern for human health, wildlife population dynamics, and broader ecosystem effects. The one-host life history of the winter tick (*Dermacentor albipictus*) links each annual cohort to environmental conditions during three specific time periods when they are predictably vulnerable: spring detachment from hosts, summer larval stage, and fall questing for hosts. We used mixed-effects generalized linear models to investigate the drivers of tick loads carried by moose (*Alces alces*) relative to these time periods and across 750 moose, 10 years, and 16 study areas in the western United States. We tested for the effects of biotic factors (moose density, shared winter range, vegetation, migratory behavior) and weather conditions (temperature, snow, humidity) during each seasonal period when ticks are vulnerable and off-host. We found that warm climatic regions, warm seasonal periods across multiple partitions of the annual tick life cycle, and warm years relative to long-term averages each contributed to increased tick loads. We also found important effects of snow and other biotic factors such as host density and vegetation. Tick loads in the western United States were, on average, lower than those where tick-related die-offs in moose populations have occurred recently, but loads carried by some individuals may be sufficient to cause mortality. Lastly, we found interannual variation in tick loads to be most correlated with spring snowpack, suggesting this environmental component may have the highest potential to induce change in tick load dynamics in the immediate future of this region.

KEYWORDS

Alces alces, climate change, *Dermacentor albipictus*, moose, parasite, snow, temperature, weather, winter tick

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INTRODUCTION

Tick (Acari: Ixodidae) populations and associated tick-borne disease are of increasing concern from both human health and ecosystem function perspectives. Shifts in geographic range and abundance may result from global climate change, although dynamics are complex and inferring cause and effect is difficult (Brunner et al., 2023; Gilbert, 2021). Northward expansion of several tick species in North America and Europe (Leighton et al., 2012) has been associated with warming temperatures and lengthened seasons of reproduction and questing, furthering concerns about their effects on both human and nonhuman hosts (Nuttall, 2022). Mechanisms behind widespread change include multiple pathways linking warmer temperatures to more successful tick populations in temperate regions (Ogden & Lindsay, 2016). Other weather parameters such as humidity and precipitation can also affect tick population parameters, as well as changes in host population dynamics and distributions (Elias et al., 2021).

Whereas multiple tick species carry pathogens of importance to human health (Dantas-Torres et al., 2012), the winter tick (*Dermacentor albipictus*) instead is notable for its effects on wildlife, in particular ungulates (hoofed-mammals). Winter ticks parasitize multiple ungulate species across North America (Chenery et al., 2023) but have most strongly affected moose (*Alces alces*) populations (Welch et al., 1991). Epizootics of winter ticks have been linked to decreased calf survival and population performance in New Hampshire, Maine, and Vermont (DeBow et al., 2021; Ellingwood et al., 2020; Jones et al., 2019), as well as to moose population crashes in Alberta (Samuel, 2007). Furthermore, the conservation status of moose in North America is increasingly precarious, with substantial population declines recently documented in portions of their southerly distribution (DeBow et al., 2021; Ellingwood et al., 2020; Harris et al., 2021; Lenarz et al., 2010; Murray et al., 2006; Nadeau et al., 2017). Common themes explaining such declines have invoked indirect effects of climate mediated by behavioral trade-offs, changes in forage nutrition, and parasitism (Ellingwood et al., 2020; Hoy et al., 2022; Monteith et al., 2015). In particular, the negative effects of warming temperatures on moose may be indirectly mediated by parasites, which themselves have complex responses to climate change (Pickles et al., 2013).

Winter ticks complete their life cycle on a single host, questing for hosts as larvae each autumn, living and feeding on hosts throughout winter where they molt twice into nymph and adult life stages, and finally detaching to lay eggs in the spring (Addison & McLoughlin, 1988; Leal et al., 2020). This one-host strategy links the survival of each winter tick cohort to environmental

conditions during three specific time periods when they are predictably vulnerable: spring detachment and egg-laying, summer larval stage, and fall questing. Research in moose–winter tick systems has suggested that relatively warm or snow-free conditions during spring detachment and fall questing periods can increase off-host tick survival and host attachment rates, thus leading to higher tick loads on moose (Drew & Samuel, 1986; Powers & Pekins, 2020; Samuel, 2007), and that such warm conditions have occurred more frequently in recent years (Ellingwood et al., 2020). Desiccation of eggs and larvae during summer and fall may also limit tick populations in some habitats (Addison et al., 2016; Yoder et al., 2016). Winter tick populations can also vary across vegetation types (Powers & Pekins, 2020) and with the densities of the host moose population (Samuel, 2007).

In relatively xeric environments of the western United States, winter ticks are known to parasitize moose, but evidence is mixed regarding the intensity of infections and demographic effects. Moose population growth rates in Utah were correlated with prior climatic patterns of summer rainfall and late-winter snow cover, which Ruprecht et al. (2020) attributed to climate-mediated links between populations of ticks and moose. High tick loads were also associated with the mortality of some individual adult moose in Washington (Harris et al., 2021). In contrast, Newby and DeCesare (2020) did not find evidence of tick-related effects on moose pregnancy rates in three Montana study areas. We currently lack research that clarifies conditions under which some moose in the mountainous west become heavily infested by winter ticks whereas others are unaffected. To that end, we investigated tick loads carried by moose across multiple years and study areas spread across the western United States with the objective of elucidating biotic and abiotic drivers of tick abundance. The counts of ticks on free-ranging moose are costly and time-intensive, but pooling data across multiple study areas and jurisdictions offered us a powerful and wide-ranging assessment of variation in tick loads in this less-studied ecoregion. Specifically, our objective was to quantify the spatiotemporal drivers of variation in tick loads carried by moose across the western United States, including the hypothesized effects of spatial variation in climate, annual variation in weather, host density, and migration behavior.

MATERIALS AND METHODS

Study areas

We collected tick load data from free-ranging moose during research operations in 16 study areas distributed

among montane regions of Montana, Idaho, Wyoming, Utah, and Colorado during 2013–2022 (Table 1, Figure 1). In most cases, capture locations were aggregated within discrete study areas by design. In Idaho, where data collection was instead more widely dispersed, we aggregated samples into six study areas by geographically combining moose from adjacent management units to facilitate our statistical treatment of study areas as sources of spatial structure. Climate and vegetative conditions in the 16 study areas varied spatially and seasonally (see Nadeau et al., 2017). Elevations were generally highest in the Colorado study areas, followed by the Wyoming, Utah, Montana, and Idaho study areas, respectively. Mean temperatures across data collection locations ranged from -7.5 to 0.03°C during the spring drop-off period (15 March–30 April), from 4.85 to 10.38°C during the late summer (1 August–14 September), and from -3.59 to 0.65°C during the fall questing period (15 September–30 November; Appendix S1: Table S1).

Moose generally inhabited riparian valley bottoms and mountains coniferous forests (dominated by *Pinus* spp., *Abies* spp., *Picea* spp., *Psuedotsuga menziesii*, and in the most mesic study areas, *Thuja plicata* and *Tsuga heterophylla*). Aspen (*Populus tremuloides*) and black cottonwood (*P. trichocarpa*) were frequent overstory

deciduous dominants in wetter habitats. Foraging habitat for moose typically included willow (*Salix* spp.), often identified as the most frequently consumed plant in western North America (Nadeau et al., 2017). However, in warmer, more xeric study areas, moose forage habitat also featured shrubs such as serviceberry (*Amelanchier* spp.), dogwood (*Cornus* spp.), mountain mahogany (*Cercocarpus* spp.), and chokecherry (*Prunus virginiana*).

Tick load data and hypothesized covariates

We captured 750 adult moose (aged 1 or older) during winter (December, 13%; January, 52%; February, 20%; March, 16%), a period when winter ticks are reliably found on their hosts (Figure 2). Having no evidence of sex-based difference in tick infestation or its correlates (Appendix S1: Table S2), we included adult moose of both sexes (females = 732, males = 18) but excluded calves (DeBow et al., 2021; Sine et al., 2009). Across studies, moose were captured using a variety of methods including physical restraint via helicopter net-gunning and chemical immobilization via darting from both ground and helicopter following approved animal care

TABLE 1 Sample sizes of moose (aged 1+) captured during winters 2013–2022 on which ticks were counted, and which entered the analyses.

Study area	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022	Total
CONE	0	16	28	9	0	19	8	0	0	0	80
CONW	0	16	36	0	5	19	15	0	0	0	91
COSW	0	12	15	5	0	0	0	0	0	0	32
ID1	0	0	0	0	0	0	0	14	0	0	14
ID10	0	0	0	0	0	5	0	8	0	0	13
ID51	0	0	0	0	0	0	0	13	0	0	13
ID6	0	0	0	0	0	0	0	16	0	0	16
ID66	0	0	0	0	0	0	0	20	0	0	20
ID76	0	0	0	0	0	0	0	10	0	0	10
MTBH	12	18	6	4	7	8	6	6	7	0	74
MTCA	11	7	12	0	10	7	6	8	6	0	67
MTEF	11	8	6	5	7	11	9	4	11	0	72
UTNS	0	0	0	0	40	22	20	0	0	0	82
UTWS	0	0	0	0	41	22	21	5	0	0	89
WYJA	0	0	0	0	0	0	0	6	5	8	19
WYME	0	0	0	0	0	0	0	16	24	18	58
Total	34	77	103	23	110	113	85	126	53	26	750

Note: Study area abbreviations are: CONE, Colorado Northeast; CONW, Colorado Northwest; COSW, Colorado Southwest; ID1, Idaho northern panhandle; ID10, Idaho Clearwater River area; ID51, Idaho south-central; ID6, Idaho central panhandle; ID66, Idaho Targhee area; ID76, Idaho southeast; MTBH, Montana Big Hole Valley; MTCA, Montana Cabinet Mountains; MTEF, Montana East Front; UTNS, Utah North Slope; UTWS, Utah Wasatch Range; WYJA, Wyoming Jackson Hole; WYME, Wyoming Meeteetse.

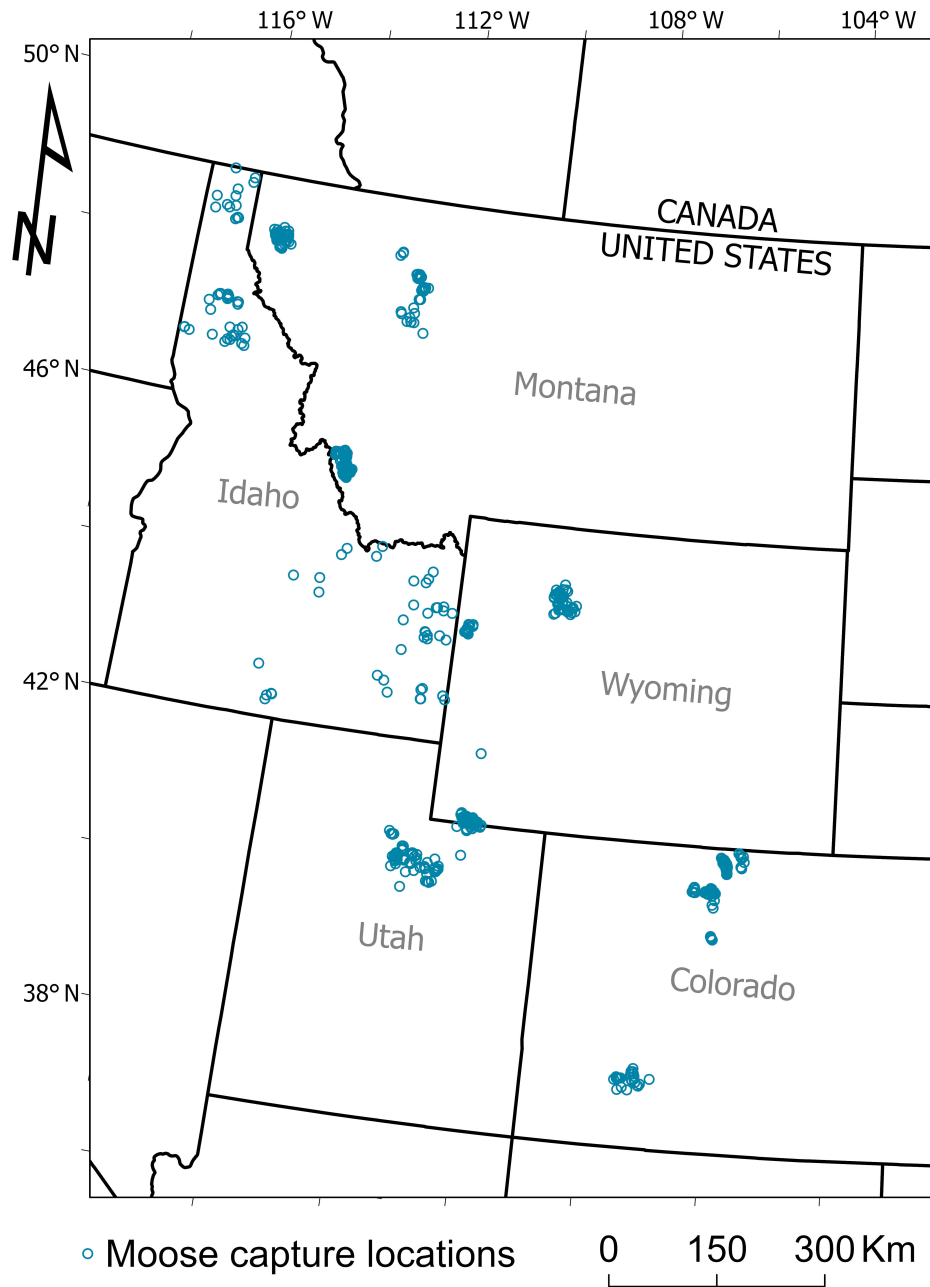


FIGURE 1 Moose capture locations where tick load data were collected in the western United States, 2013–2022.

and use protocols (e.g., Newby & DeCesare, 2020; FWP12-2012). Suitable tick load data were collected using quadrats or line transects through parted hair of moose along the rump, scapular, and/or loin regions following Sine et al. (2009). Protocols of individual studies varied in which sections of moose were sampled ($n_{\text{rump}} = 738$, $n_{\text{scapula}} = 472$, $n_{\text{loin}} = 472$). We restricted our analyses to counts of ticks on each moose's rump because the majority of records included it. For 12 moose from Idaho study areas that lacked tick counts from their rump areas but had corresponding counts from their scapular areas, we imputed rump tick counts from a model predicting rump

counts from scapular counts from all sampled moose (Appendix S1: Figure S1).

We investigated the putative drivers of winter tick loads on moose by evaluating four suites of candidate models, each corresponding to a hypothesized source of variation in tick loads throughout the annual life cycle of winter ticks (Figure 2, Table 2). First, we hypothesized that tick loads could vary due to the intrinsic characteristics of moose individuals and populations during the years of study. In this suite of models, we considered relative moose density (Bergeron & Pekins, 2014; Samuel, 2007), spatial overlap on winter range shared with other

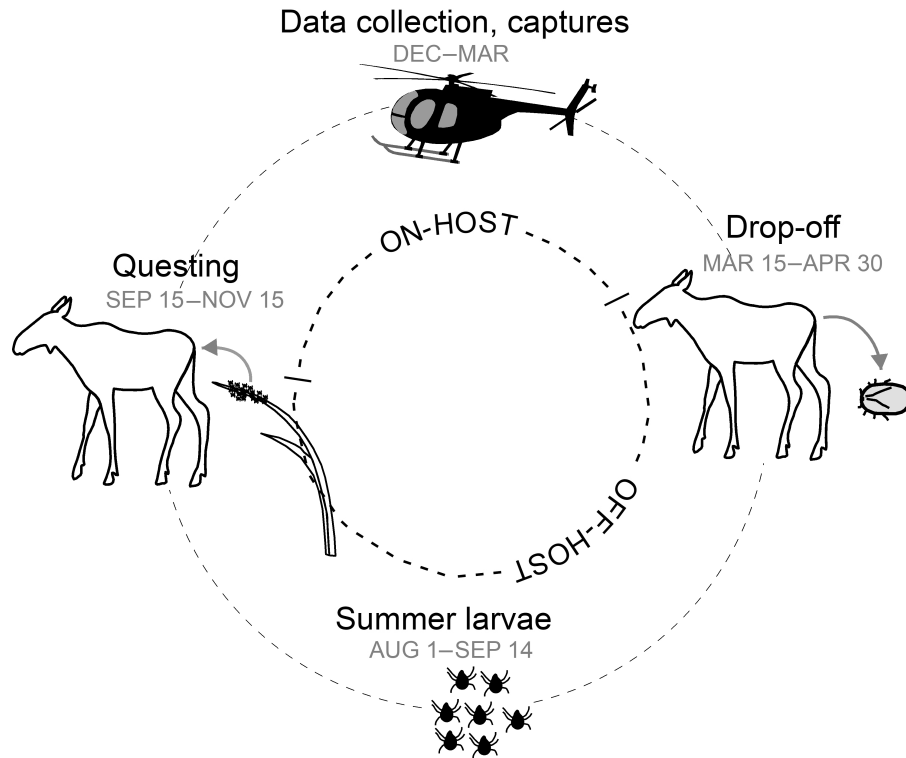


FIGURE 2 Schematic diagram of seasonal periods of study relating the life cycle of winter ticks during three off-host periods (spring drop-off, summer larvae, and fall questing) to on-host measurements of tick loads on moose collected during live-capture efforts, western United States, 2013–2022.

TABLE 2 Weather-related predictors considered in suites of candidate models during each of the three seasons, defined in terms of the life history of the winter tick–moose interaction.

Hypothesized weather predictor	Spring drop-off	Summer larvae	Fall questing
Proportion of days with snow cover	✓		✓
Snow water equivalent mid-way in period	✓		✓
Snow water equivalent at end of period	✓		✓
Cumulative precipitation (including quadratic)		✓	
Mean temperature	✓	✓	✓
Days with temperature $<0^{\circ}\text{C}$	✓		✓
Days with temperature $<-20^{\circ}\text{C}$	✓		✓
Minimum relative humidity (including quadratic)		✓	✓
Maximum relative humidity (including quadratic)		✓	✓

ungulates (deer [*Odocoileus* spp.] or elk [*Cervus elaphus*]) that could serve as additional hosts (Welch et al., 1991), vegetation type (Addison et al., 2016; Drew & Samuel, 1986; Healy et al., 2018; Powers & Pekins, 2020), and individual moose migratory behavior (Blouin et al., 2021; Healy et al., 2018; Table 2). We characterized vegetation type at each capture site according to year-specific land cover data using the International Geosphere Biosphere Programme (IGBP) global vegetation classification of the

moderate resolution imaging spectroradiometer (MODIS) land cover product (MCD12Q1) at a 500×500 m resolution, following Liang et al. (2015). We simplified the six land cover types identified in the study areas (evergreen forest, woody savanna, savanna, grassland, cropland, and urban) into two land cover categories by aggregating together the first three (forest) and the latter three (open). We used expert opinion to characterize individual moose as being located within areas of low (<0.21),

medium (between 0.21 and 0.41), or high (>0.41) adult females per square kilometer, following quantitative delineation of moose densities with focus on adult females by Schmidt et al. (2007). When categorizing density, we relied on a rubric to standardize information and increase repeatability across study sites and to focus our treatment of density on relatively local (i.e., the size of individual home ranges) areas surrounding each capture location. Specifically, we imagined overlaying a 5×5 km neighborhood surrounding each winter capture location and the biologist with field experience in each area estimated how many adult female moose would be found in that neighborhood; our low-density category corresponded to ≤ 5 cows sharing that 25-km² neighborhood, medium density to 6–10 cows sharing that neighborhood, and high density to >10 . We similarly included a binary categorical variable concerning whether moose shared their winter range with deer or elk populations of equal or greater abundance based on field experience in each study area. We treated seasonal migration as a proxy for spatial overlap of individual moose during the tick drop-off and questing seasons, and assigned “resident,” “migratory,” or “unknown” categorical depictions of migration behavior according to project-specific spatial analyses or subjective assessments of seasonal movements. We assumed that migration behavior subsequent to capture was an adequate proxy for behavior during the year prior to capture, when measured tick loads would have accumulated on each moose.

Second, we hypothesized that winter tick loads could vary due to prevailing weather conditions during spring tick drop-off season (15 March–30 April), roughly 9–12 months prior to the winter when counts on moose were obtained (Figure 2, Table 2). Previous studies have shown that survival of adult female ticks after they drop from hosts in spring is depressed by cold temperatures (Drew & Samuel, 1986; Wilton & Garner, 1993) and snow cover (DelGiudice et al., 1997; Drew & Samuel, 1986; Ruprecht et al., 2020). We considered models containing all additive combinations of a suite of predictor variables related to temperature and snow cover during this time period (Table 2).

Third, we hypothesized that winter tick loads may vary according to survival of off-host tick larvae during late summer (1 August–14 September; Figure 2, Table 2). Larvae of many tick species are considered vulnerable to desiccation during hot and dry conditions (Addison et al., 2016; Leal et al., 2020), but warmer temperatures may also accelerate egg development and improve survival (Hoy et al., 2021). Here, we considered models containing all additive combinations of predictor variables related to precipitation, temperature, and relative humidity during

the late summer period (Addison et al., 2016; Leal et al., 2020; Yoder et al., 2016; Table 2).

Fourth, we hypothesized that winter tick loads may be driven by weather conditions during the prior autumn questing period (15 September–30 November; Figure 2, Table 2). In this suite of models, we considered the general hypotheses that tick abundance would be affected by temperature (Addison et al., 2016; Samuel, 2007), presence of snow (Holmes et al., 2018; Power & Pekins, 2020; Samuel, 2007), and relative humidity (Addison et al., 2016; Leal et al., 2020; Table 2).

Quantifying environmental conditions

We obtained weather data for each year, season, and moose capture location using publicly available gridded meteorological data from multiple sources. We quantified temperature as the mean of daily low temperatures across each of the late summer, questing, and drop-off periods using Daymet version 4 revision 1 data at a 1×1 km resolution (Thornton et al., 2022), accessed via the R package (Hufkens et al., 2018; R Core Team, 2018). To capture potential threshold effects of cold temperatures during the questing and drop-off seasons, we also used the same Daymet data to measure the number of days with low temperatures below thresholds of 0 (Powers & Pekins, 2020) and -20°C (Holmes et al., 2018). We also used multiple metrics to characterize the presence and amount of snow over time and space. We estimated the proportion of days with measurable snow across questing and drop-off periods according to daily gridded measures of normalized difference snow index (NDSI) detections of snow cover from MODIS version 6 MOD10A1 (Terra) and MYD10A1 (Aqua) data at a 500×500 m resolution (Hall et al., 2006). We merged Terra and Aqua NDSI data according to the maximum snow cover value measured between each platform per day (Tran et al., 2019) and used a threshold NDSI value of 0.1 to distinguish snow from non-snow, following Hussainzada et al. (2021). We also characterized the amount of snow using estimates of snow water equivalent (SWE) during the mid-point and end point of both the drop-off and questing periods using daily SWE data from Daymet V4R1 at 1×1 km resolution. We quantified daily minimum and maximum relative humidity during the late summer and questing seasons using daily minimum and maximum estimates of vapor pressure deficit and temperature produced by the parameter-elevation regressions on independent slopes model (PRISM) Climate Group at 4×4 km resolution (PRISM Climate Group, 2023) and following equations of Daly et al. (2015). Lastly, we used daily precipitation

data from PRISM, also at 4×4 km resolution, to quantify the total precipitation during the late summer period.

Statistical analyses

We fit candidate models using generalized linear mixed-effects models with negative binomial structures, considering ticks counted in the rump area as the response variable and hypothesized independent variables as fixed factor predictors. To account for heterogeneity in sampling conditions and dates, we included Julian date nested within study areas as random intercepts in all models. Julian date was included to account for additional variation or noise in tick load data resulting from variation across study areas and individual moose in the date of capture and measurement. Because response variables were integer counts but the area sampled on each moose varied, we included the logarithm of area sampled on each moose as offset terms in all models. We confirmed the absence of overdispersion in model residuals using the program DHARMA version 0.4.6 (Residual Diagnostics for Hierarchical Multi-level/Mixed; Hartig, 2021). To avoid multicollinearity within models, we added predictors to existing models only when uncorrelated ($r < 0.5$) with those already present, and we ensured variance inflation factors (VIF) for all covariates were < 3 . Because previous research had suggested that larval questing peaked at intermediate values of relative humidity (Leal et al., 2020), we included quadratic terms when examining both relative humidity and precipitation.

Models were fit using maximum likelihood procedures and ranked within each hypothesis-specific suite of candidate models using corrected Akaike information criterion (AIC_c). We constructed each of the four candidate suites by considering univariate models first, and then adding all other hypothesized predictors that met our collinearity criteria in manual forward stepping fashion. After developing hypothesis-specific final models related to each of our four hypotheses, we used similar procedures to identify an overall top model among candidate combinations of elements of the four hypothesis-specific sets.

Lastly, we also strove to understand the extent to which tick load variation was driven by broad spatial variation in climate among sites versus annual variation in weather within sites. To quantify the additive contribution of annual weather variation to the underlying climatic heterogeneity inherent in our study areas, we examined a variant of our top model in which we replaced weather covariate data with deviations from their respective study area means during 2013–2022. We

estimated the proportion of variance explained by top-ranked models using Nakagawa's approximate R^2 (Nakagawa et al., 2017). Generalized linear mixed-effects models were fit using glmmTMB version 1.1.5 (Brooks et al., 2017) and evaluated with Performance (Lüdtke et al., 2021), each implemented in R version 4.2.2 (R Core Team, 2018).

RESULTS

We found support for a number of metrics quantifying each of our four hypothesized drivers of winter tick loads on moose. The top model describing the effects of biotic factors on winter tick loads included positive effects of moose density, shared winter range with other wild ungulates, and “open” vegetation types (Table 3; Appendix S1: Table S3). The categorical variable migratory status had less support and did not appear in the top-ranking model. The top model relating only hypothesized weather factors during the previous spring drop-off period to winter tick loads included negative effects of both the number of days below freezing and the proportion of days with measurable snow cover (Table 3; Appendix S1: Table S4). The top model relating only hypothesized weather factors during the previous late summer period to subsequent winter tick loads included positive effects of mean temperature and negative effects of minimum relative humidity (Table 3; Appendix S1: Table S5). Lastly, the top model relating weather factors during the questing period to winter tick loads included the number of days $< 0^\circ\text{C}$, number of days $< -20^\circ\text{C}$, and proportion of days with measurable snow cover (Table 3). Winter tick loads decreased with days below the two threshold temperatures during questing and further decreased with higher proportions of days with ground covered by snow (Appendix S1: Table S6).

Considering all hypotheses comprehensively, our top model included predictive variables from all four hypotheses, including biotic conditions and all three seasonal periods (Tables 4 and 5; Figure 3). All covariates identified as important during our initial stages of modeling each hypothesis were retained in this top model except for the number of days $< 0^\circ\text{C}$ during the spring drop-off season, which was removed due to issues of multicollinearity with other covariates. Winter tick loads were positively associated with moose density on winter range, with moose at high density ($\beta = 0.542$, $\text{SE} = 0.217$, $p = 0.013$) predicted to have over twice the tick loads as those at low density ($\beta = -0.631$, $\text{SE} = 0.283$, $p = 0.026$). Similarly, moose sharing winter range with other ungulates were predicted to have more than twice the tick load of moose that did not ($\beta = 0.787$, $\text{SE} = 0.226$, $p < 0.001$).

TABLE 3 Four sets of a priori candidate models containing combinations of predictor variables hypothesized to affect loads of winter ticks on moose captured during winter in 16 study areas within the US Rocky Mountains, 2013–2022.

Candidate model	AIC _c	ΔAIC _c	df	Weight	R ² _c	R ² _m
Hypothesis 1: Biotic conditions						
1. Moose density + vegetation type + shared winter range	3188.5	0	7	0.758	0.324	0.112
2. Moose density + vegetation type + shared winter range + migratory	3191.1	2.6	9	0.204	0.327	0.115
3. Moose density + shared winter range	3195.6	7.1	6	0.022	0.311	0.098
4. Vegetation type + shared winter range	3198.0	9.5	9	0.007	0.323	0.082
5. Vegetation type shared winter range + migratory	3200.1	11.6	7	0.002	0.324	0.085
Hypothesis 2: Weather during spring drop-off						
1. Days <0°C + proportion days snow	3185.7	0	5	0.584	0.322	0.098
2. Days <0°C + proportion days snow + days <−20°C	3187.5	1.8	6	0.235	0.324	0.099
3. SWE at end of period	3190.4	4.7	4	0.055	0.328	0.094
4. Mean temperature + SWE middle of period	3191.2	5.5	5	0.037	0.308	0.074
Hypothesis 3: Weather during summer						
1. Mean temperature + minimum relative humidity	3182.0	0	5	0.701	0.297	0.131
2. Mean temperature + minimum relative humidity quadratic	3184.1	2.0	6	0.261	0.298	0.131
3. Mean temperature + maximum relative humidity	3189.3	7.2	5	0.019	0.293	0.112
4. Mean temperature	3190.8	8.7	4	0.009	0.293	0.104
5. Mean temperature + cumulative precipitation	3191.3	9.1	5	0.007	0.293	0.107
Hypothesis 4: Weather during fall questing						
1. Proportion days snow + days <0°C + days <−20°C	3182.1	0	6	0.858	0.316	0.121
2. Proportion days snow + days <0°C	3187.6	5.5	5	0.556	0.314	0.099
3. Mean temperature + days <−20°C	3188.6	6.5	5	0.033	0.317	0.110
4. Mean temperature + SWE middle of period	3188.9	6.8	5	0.028	0.329	0.116
5. Mean temperature	3189.5	7.4	4	0.021	0.318	0.103
Null (random effects only)	3223.6		3	<0.001	0.318	0.103

Note: See Appendix S1 for the top models of each candidate suite.

Abbreviations: AIC_c, corrected Akaike information criterion; SWE, snow water equivalent.

TABLE 4 Top models that integrate variables included in the four independent suites of candidate models (see Table 3) predicting tick loads of moose captured during winter in 16 study areas within the US Rocky Mountains, 2013–2022.

Candidate model	AIC _c	ΔAIC _c	df	Weight
Biotic + questing + summer + drop-off	3137.0	0.0	13	0.514
Biotic + questing + summer	3137.3	0.2	12	0.458
Biotic + drop-off + summer	3143.7	6.4	10	0.021
Null	3223.6	86.6	3	<0.001

Abbreviation: AIC_c, corrected Akaike information criterion.

Winter tick loads were negatively associated with the proportion of snow-covered days, with such effect being moderate during the questing period ($\beta = -1.702$,

SE = 0.946, $p = 0.072$) and weaker during the drop-off period ($\beta = -1.322$, SE = 0.885, $p = 0.135$). Tick loads were positively associated with warm temperatures

TABLE 5 Top model predicting tick loads on moose captured during winter in 16 study areas within the US Rocky Mountains, 2013–2022, as a function of biotic factors and weather conditions during the previous tick drop-off period, summer, and tick questing periods.

Model parameter	β	SE	z	p
Intercept	-3.827	0.702	-5.450	<0.001
Moose density high	0.542	0.217	2.490	0.013
Moose density low	-0.631	0.283	-2.228	0.026
Vegetation type: Open	0.470	0.177	2.656	0.008
Winter range shared with other species	0.787	0.226	3.484	<0.001
Drop-off: Proportion days with snow	-1.322	0.885	-1.494	0.135
Questing: Proportion days with snow	-1.702	0.946	-1.799	0.072
Questing: Days temperature <0°C	-0.020	0.009	-2.400	0.016
Questing: Days temperature <-20°C	-0.189	0.130	-1.454	0.146
Summer: Mean temperature	0.227	0.053	4.254	<0.001
Summer: Minimum relative humidity	-0.025	0.017	-1.468	0.142

Note: Model weight = 0.514, Nakagawa's marginal $R^2 = 0.238$.

during summer ($\beta = 0.227$, $SE = 0.053$, $p < 0.001$) and negatively associated with the number of days below 0°C ($\beta = -0.020$, $SE = 0.009$, $p = 0.016$) and below -20°C ($\beta = -0.189$, $SE = 0.130$, $p = 0.146$) during autumn questing. Lastly, tick loads were weakly negatively associated with minimum relative humidity during the previous summer ($\beta = -0.025$, $SE = 0.017$, $p = 0.142$). The top model was estimated to explain 33.1% of total variation, of which 23.8% came from the fixed effects of interest (Nakagawa's marginal $R^2 = 0.238$).

We also evaluated the relative contributions of spatial variation in climate among study areas versus annual variation in weather among years within study areas. Holding the heterogeneous climates of each study area at the means, the residual effects of days of snow-covered ground during the drop-off period ($\beta = -3.120$, $SE = 1.008$, $p = 0.002$) and days <0°C ($\beta = -0.021$, $SE = 0.012$, $p = 0.088$) and <-20°C ($\beta = -0.290$, $SE = 0.162$, $p = 0.073$) during the questing period each remained moderately significant (Appendix S1: Table S7). That is, annual variation in spring snow and autumn cold temperatures within each study area contributed a significant addition beyond spatial differences alone. In contrast, differences in summer temperatures ($p = 0.755$) or humidity ($p = 0.987$) from one year to the next were not significant predictors of tick burden. Comparing Nakagawa's marginal R^2 from the model that removed the effects of weather due solely to study area ($R^2 = 0.155$) with that from the full model ($R^2 = 0.238$, Table 5) suggested that approximately 35% of the variation explained by fixed effects in our best model was caused by broadscale spatial variation in climate, whereas the remainder was attributable to the combination of

annual variation in weather and biotic effects (e.g., host densities and vegetation type; Appendix S1: Table S7).

DISCUSSION

We found that warm climatic regions, warm seasonal periods within the annual tick life cycle, and warm years relative to long-term averages all contributed to increased tick loads incurred by moose in the western contiguous United States. In addition to the ubiquitous importance of temperature, we also found the important effects of snow and other biotic sources of variation in driving tick loads. Although we lacked fine-scale data necessary to examine how microsite-scale climate conditions affect tick demography (Yoder et al., 2017) or how fine-scale movement behavior of moose might affect tick encounter rates, these results indicate the existence of broadscale variation in tick loads across this region and that such variation can be partially explained by broadscale (500–5000 m resolution) metrics of climate and other biotic conditions.

Our finding of higher winter tick loads where moose shared winter range with other wild ungulates supports speculation by Welch et al. (1991) that offspring of ticks hosted by one species may use hosts of another. As a generalist parasite species, winter ticks are known to infect other ungulates sympatric with moose in this region, including elk, mule deer (*O. hemionus*), and white-tailed deer (*O. virginianus*; Haley et al., 2021; Samuel et al., 1980). Experimental studies indicate that moose carry the higher per capita tick loads relative to other ungulate species (Welch et al., 1991), but it remains uncertain whether other ungulates occurring at higher densities

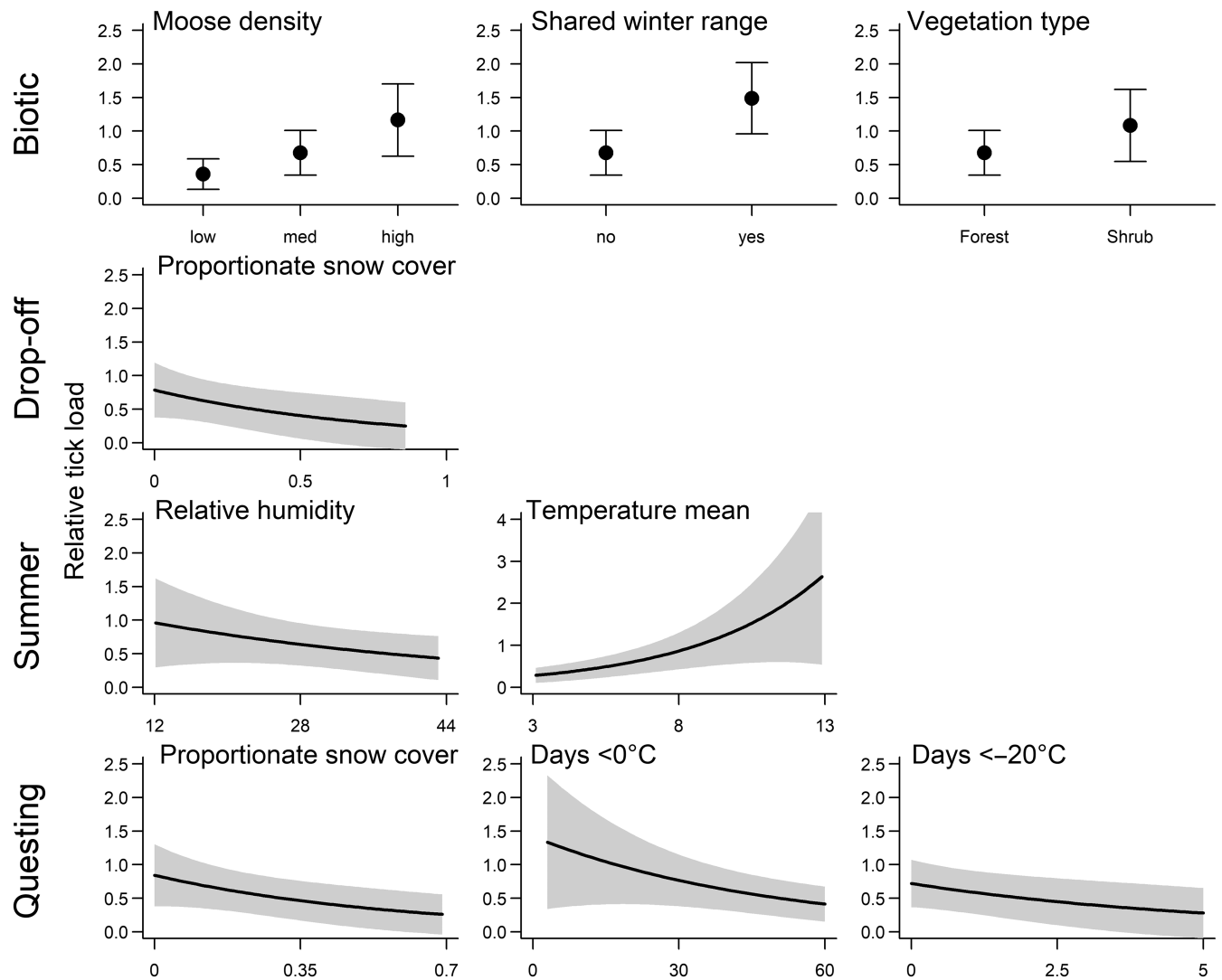


FIGURE 3 Predicted relative tick loads and 95% confidence limits (*y*-axes and shading) spanning the observed range of values for each covariate (*x*-axes) included in the final model and estimated using population-level predictions (i.e., random effects set to 0) and a 40-cm transect length. Predictions were made for each covariate while holding other continuous covariates at their means, categorical covariates at density = “medium,” shared winter range = “no,” and vegetation type = “forest,” and grouped by rows according to four hypothesized suites of covariates including biotic conditions, and weather conditions during the spring drop-off period, summer larvae period, and fall questing period, western United States, 2013–2022.

might yet make important contributions to tick populations in shared range. The common prevalence of winter ticks on ungulates such as white-tailed deer in ecosystems lacking moose indicates these species can themselves maintain tick populations (e.g., 22% prevalence on white-tailed deer in Georgia, USA; Wedincamp & Durden, 2016). In combination with previous findings, our results indicate that targeted reduction of moose density to reduce winter tick parasitism (e.g., as recommended by Ellingwood et al., 2020) may produce limited benefits in areas where sympatric host species also play important roles in tick abundance.

The patterns we observed relative to biotic predictors of tick loads on moose have been supported by previous

investigations elsewhere. Our finding that high winter tick loads were associated with high density of moose (even as categorically assessed here) corroborates suggestions of similar relationships (Bergeron & Pekins, 2014; Samuel, 2007). Our finding that winter tick loads were higher among moose captured in open, predominately shrub-type habitats compared with forested areas tends to corroborate work elsewhere, showing that off-host tick survival or abundance was greater in habitat types with open than closed canopies (Drew & Samuel, 1986). Alternatively, increased concentration of moose activity in relatively discrete shrub habitat patches may facilitate increased tick loads relative to more dispersed activity in forests (Sousa & Grosholz, 1991). That we found less

support for migratory status as a predictor of winter tick loads may result from our categorical assessments (i.e., migratory or not) being too geographically imprecise to capture the relevant information on spring and subsequent autumn locations.

Our models also corroborated previous work showing that winter-like conditions during the spring drop-off and fall questing periods reduced tick loads (Addison et al., 2016; Drew & Samuel, 1986; Power & Pekins, 2020; Ruprecht et al., 2020; Wilton & Garner, 1993). Our results were consistent with the findings of Holmes et al. (2018) that winter ticks are susceptible to mortality from inoculative freezing (i.e., direct contact with snow or ice) as well as from continuous or frequent exposure to cold temperatures.

We expected a positive relationship between relative humidity and tick loads, but relative humidity did not appear in any of the top five models relating autumn questing weather to tick loads. Its relationship with tick loads in models of summer weather was weakly negative. Yoder et al. (2016) discussed methods that larvae use to resist desiccation, and Yoder et al. (2017) noted that larvae may be more responsive to signals of host presence in drier than wetter conditions. Our study was limited to broadscale patterns, whereas ticks may have been responding to microclimates beyond our ability to characterize. Clarifying the effects of relative humidity on the subsequent attachment of ticks to moose would appear to require additional work; it appears from our analyses, however, that tick loads can be high among moose even in the most xeric habitats they inhabit of the western United States (e.g., Utah Wasatch Range [UTWS] study area, Appendix S1: Table S1).

Reflecting the study's design and data, our statistical models considered study areas as random intercepts. That is, we considered each study area a random offset of relationships characterizing moose in the United States Rocky Mountains generally. However, we note that our 16 study areas also varied in weather factors that, according to our analyses, were associated with tick loads in the fixed-effects portions of the models (Appendix S1: Table S1). For example, moose in southwest Colorado had, on average, the lowest tick loads (quantified by tick counts per square centimeter) of the 16 study areas, but also had the highest proportion of days with snow during the questing period and the lowest mean temperature during the drop-off period. In contrast, moose in Utah's Wasatch Range had the highest mean tick loads, but the lowest proportion of snow days and the highest mean temperature during questing. As a result, a portion of the predictive effects of weather were absorbed within the random component of our models, rendering our estimates of fixed weather effects slightly conservative. That

said, our analyses suggest that some weather effects on tick loads are more tightly associated with their geographic sources, whereas others are more temporally variable. The positive associations we documented with summer temperatures were associated with geography, with no difference arising from year-to-year variation. In contrast, temporal variation in snow cover in spring, and, to a lesser extent, the incidence of cold temperatures in autumn, affected tick loads on an annual basis for any given locality (Appendix S1: Table S7). These results suggest that the observed trends of reduced spring snow in western North America (Hamlet et al., 2005) have perhaps the highest potential to induce change in tick load dynamics in the immediate future of this region.

To facilitate a comparison of tick loads in our western United States study areas to those of previous studies elsewhere in North America, we converted tick counts to tick densities (per square centimeter; assuming each cm of linear transect represented 1 cm² of area sampled) in both cases. We find these comparisons informative while recognizing that they do not adequately control for possible confounding factors such as differences in the timing of sampling, body locations of sampling, and sex and age classes sampled. Average tick densities in our study varied from 0.007 ticks/cm² (in Colorado Southwest [COSW]) to 0.315 ticks/cm² (in UTWS), with an overall mean of 0.089 ticks/cm² (SE = 0.007; Figure 4; Appendix S1: Table S1). In Vermont, where tick infestation was concluded to be the primary cause of moose mortality, median tick densities on adult and calf moose were 0.24 and 0.36 ticks/cm², respectively (i.e., 19 and 28.5 ticks counted across eight 10-cm² transects; DeBow et al., 2021). In New Hampshire, the mean tick density across study areas and sex and age classes during a relatively average year (2008) was 0.33 ticks/cm² (i.e., 53 ticks counted across 16 10-cm² transects; Bergeron & Pekins, 2014). In a subsequent study focused on calves in New Hampshire and Maine, the average tick densities at the time of capture for moose calves were 0.61 ticks/cm² (61 ticks counted along eight 10-cm² transects), with significant differences between calves that survived (0.51) versus those that died (0.65; Jones et al., 2019). These comparisons suggest that tick loads in our sampled moose were generally lower than where tick-related die-offs have occurred in New England states, but that the highest densities per individual moose in our sample approached densities associated with tick-caused mortality.

Our analyses suggest that similar biotic and abiotic drivers of tick abundance found in eastern and central North America are present in the western United States. We found that reservoirs among moose and conspecifics

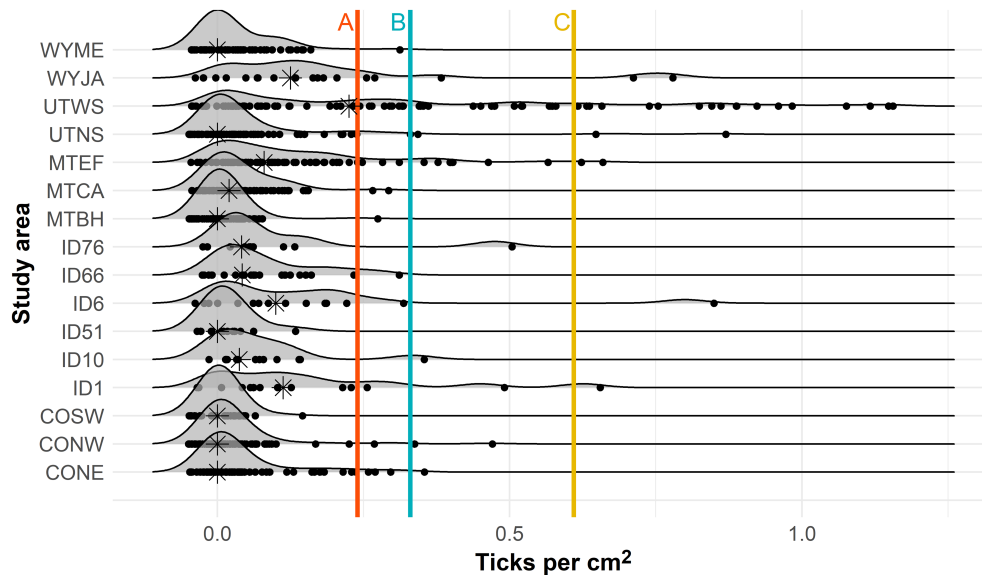


FIGURE 4 Density distributions (lines and shading), raw data values (dots), and median values (asterisks) for winter tick density measurements collected on the rump of moose across each of 16 study areas (CONE, Colorado Northeast; CONW, Colorado Northwest; COSW, Colorado Southwest; ID1, Idaho northern panhandle; ID10, Idaho Clearwater River area; ID51, Idaho south-central; ID6, Idaho central panhandle; ID66, Idaho Targhee area; ID76, Idaho southeast; MTBH, Montana Big Hole Valley; MTCA, Montana Cabinet Mountains; MTEF, Montana East Front; UTNS, Utah North Slope; UTWS, Utah Wasatch Range; WYJA, Wyoming Jackson Hole; WYME, Wyoming Meeteetse) in the western US, 2013–2022. Also shown are vertical line reference values corresponding to average tick densities in three studies from the northeastern United States: (A) average adult moose in Vermont (DeBow et al., 2021), (B) average across all sex and age classes, study areas, and during an average year in New Hampshire (Bergeron & Pekins, 2014), and (C) average among calves in New Hampshire and Maine (Jones et al., 2019).

can be important in perpetuating tick infestations (because tick loads were positively associated both with moose density and overlap with other ungulates). We found that snow cover during both spring drop-off and autumn questing periods strongly depressed subsequent tick loads, and that higher summer temperatures were associated with greater tick loads than lower temperatures. Because climate change is expected to produce both warmer summers (McGuire et al., 2012) and shorter winters (Evan & Eisenman, 2021; Musselman et al., 2021) in the Rocky Mountains, a trend toward higher tick loads among moose in these areas in the future is expected.

AUTHOR CONTRIBUTIONS

Nicholas J. DeCesare, Eric J. Bergman, and Kent R. Hersey conceived the study. All authors collected data and provided editorial advice. Richard B. Harris and Nicholas J. DeCesare analyzed the data. Nicholas J. DeCesare and Richard B. Harris wrote the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (DeCesare, 2024) are available from Dryad: <https://doi.org/10.5061/dryad.gqnk98svz>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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