

Spatial structure of reproductive success infers mechanisms of ungulate invasion in Nearctic boreal landscapes.

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Abstract

1. Landscape change is a key driver of biodiversity declines due to habitat loss and fragmentation, but spatially shifting resources can also facilitate range expansion and invasion. Invasive populations are reproductively successful, and landscape change may buoy this success. 2. We show how modelling the spatial structure of reproductive success can elucidate the mechanisms of range shifts and sustained invasions for mammalian species with attendant young. We use an example of white-tailed deer (deer; *Odocoileus virginianus*) expansion in the Nearctic boreal forest, a North American phenomenon implicated in severe declines of threatened woodland caribou (*Rangifer tarandus*). 3. We hypothesized that deer reproductive success is linked to forage subsidies provided by extensive landscape change via resource extraction. We measured deer occurrence using data from 62 camera-traps in northern Alberta, Canada, over three years. We weighed support for multiple competing hypotheses about deer reproductive success using multi-state occupancy models and generalized linear models in an AIC-based model selection framework. 4. Spatial patterns of reproductive success were best explained by features associated with petroleum exploration and extraction, which offer early seral vegetation resource subsidies. Effect sizes of anthropogenic features eclipsed natural heterogeneity by two orders of magnitude. We conclude that deer populations are likely buffered from overwinter mortality by landscape change, wherein early seral forage subsidies support high springtime reproductive success to offset or exceed winter losses. 5. Synthesis and Applications. Modelling spatial structuring in reproductive success can become a key goal of remote camera-based global networks, yielding ecological insights into mechanisms of invasion and range shifts to inform effective decision-making for global biodiversity conservation.

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Summary

1. Landscape change is a key driver of biodiversity declines due to habitat loss and fragmentation, but spatially shifting resources can also facilitate range expansion and invasion. Invasive populations are reproductively successful, and landscape change may buoy this success.
2. We show how modelling the spatial structure of reproductive success can elucidate the mechanisms of range shifts and sustained invasions for mammalian species with attendant young. We use an example of white-tailed deer (deer; *Odocoileus virginianus*) expansion in the Nearctic boreal forest, a North American phenomenon implicated in severe declines of threatened woodland caribou (*Rangifer tarandus*).
3. We hypothesized that deer reproductive success is linked to forage subsidies provided by extensive landscape change *via* resource extraction. We measured deer occurrence using data from 62 camera-traps in northern Alberta, Canada, over three years. We weighed support for multiple competing hypotheses about deer reproductive success using multi-state occupancy models and generalized linear models in an AIC-based model selection framework.
4. Spatial patterns of reproductive success were best explained by features associated with petroleum exploration and extraction, which offer early seral vegetation resource subsidies. Effect sizes of anthropogenic features eclipsed natural heterogeneity by two orders of magnitude. We conclude that deer populations are likely buffered from overwinter mortality by landscape change, wherein early seral forage subsidies support high springtime reproductive success to offset or exceed winter losses.
5. *Synthesis and Applications*. Modelling spatial structuring in reproductive success can become a key goal of remote camera-based global networks, yielding ecological insights into mechanisms of invasion and range shifts to inform effective decision-making for global biodiversity conservation.

Key-words: fitness, invasive species, camera trapping, multistate occupancy models, reproduction, range shifts, landscape change

Introduction

Reproduction is vital to population persistence and distribution dynamics. Reproductive success is tightly linked to the quality and spatial distribution of available suitable habitat (Pulliam & Danielson 1991; Kurki *et al.* 2000) and so anthropogenic landscape change can markedly alter a species' spatial distribution. These effects are typically negative, through fragmentation and habitat loss (Fahrig 1997; Fahrig 2002; Fahrig 2003) but are positive for some species, facilitating range expansions or invasions (Ewers & Didham 2006; Didham *et al.* 2007). Linking spatial variability in reproductive success with landscape change (or disturbance) is key to understanding mechanisms of invasion and range shifts, an increasingly important endeavor under climate change (Lawler *et al.* 2008; Lawler *et al.* 2009).

Quantifying spatial variation in reproductive success has been mostly limited to taxa with stationary offspring such as plants (Muñoz & Arroyo 2006) and nesting birds (Rosenberg, Swindle & Anthony 2003; León-Ortega *et al.* 2017). Mammals are much harder to quantify due to their large size, widespread ranges, and vagile young. Camera trapping (Burton *et al.* 2015; Steenweg *et al.* 2016) can bridge this data gap, generating data on mammalian distribution and density. Many mammal species keep young at heel during early maternal care and this state can be likewise observed with camera traps. Applied to camera data for grizzly bears (Fisher, Wheatley & Mackenzie 2014) and European brown bears (Burton *et al.* 2018), we showed how spatial variation in reproductive success can be modelled to identify landscape mechanisms affecting success. Though further elaborated since (MacKenzie *et al.* 2017) the diverse opportunities of this approach have yet to be widely realized. Here, we illustrate how camera trap data can help infer mechanisms of species invasion and range expansion, using an example from the Nearctic boreal forest.

Boreal landscapes have been markedly changed by widespread and economically important resource extraction (Schindler & Lee 2010; Venier *et al.* 2014). The epicenter of change are Canada's oil sands, the third largest global oil deposit and a driver of global economies (Bayoumi & Mhlesen 2006). Petroleum exploration and extraction create an altered landscape without analogs (Schneider, Dyer & Parks 2006; Pickell, Andison & Coops 2013; Pickell *et al.* 2015). Landscape change affects the entire boreal forest mammal community (Fisher & Burton 2018), but most notably manifest in woodland caribou declines (*Rangifer tarandus*)

(Hervieux *et al.* 2013; Hebblewhite 2017). Wolf predation is a primary cause (Boutin *et al.* 2012), with wolf populations bolstered by high-density invading white-tailed deer (deer; *Odocoileus virginianus*) (Latham *et al.* 2011; Latham *et al.* 2013).

White-tailed deer range expansion is a pan-continental phenomenon (Laliberte & Ripple 2004; Heffelfinger 2011) impacting entire ecosystems (Côté *et al.* 2004). Research on deer expansion south of the boreal has focused on population biology (DeYoung 2011), movement (Beier & McCullough 1990), and predation (Ballard *et al.* 2001). Boreal deer invasion has been linked to landscape and climate change (Dawe, Bayne & Boutin 2014; Fisher & Burton 2018; Fisher *et al.* 2020) but the mechanisms remain unidentified. We sought to examine whether anthropogenic landscape change is linked to spatial patterns of deer reproductive success, as a possible mechanism of boreal forest invasion.

Deer balance energy intake from early-seral deciduous forage (Ditchkoff 2011) with metabolic demands markedly increased by cold temperatures and deep snow, historically limiting white-tailed deer range (Parker, Barboza & Gillingham 2009; Hewitt 2011). In the boreal, climate change has produced warmer winters (Karl & Trenberth 2003); concurrently, landscape change has generated more abundant early-successional vegetation (Finnegan, MacNearney & Pigeon 2018; Finnegan, Pigeon & MacNearney 2019; MacDonald *et al.* 2020) that is strongly spatially linked to deer abundance and persistence (Fisher *et al.* 2020). Deer mortality risk is greatest in the first year of life (Lesage *et al.* 2001), decreasing markedly for 1-2 year-olds (Delgiudice *et al.* 2006). Fawn growth and survival is largely based on maternal body condition, governed by food availability (Therrien *et al.* 2008), so examining how spatial resource availability contributes to breeding success within the first year helps us understand how landscape change contributes to boreal deer expansion.

We hypothesized that anthropogenic landscape change in the northern boreal forest is providing resource subsidies that bolster reproductive success for invading white-tailed deer. If true, we predicted that anthropogenic features representing conversion of mature forest to early seral vegetation would explain variability in the spatial distribution of deer reproductive success. We define reproductive success as a deer occurrence with at least one attendant fawn in the summer months. This requires that a female achieve oestrus, breed, produce offspring, and maintain that offspring into the summer months, thus drawing close to recruitment—and is a measure that can be consistently applied to all mammal species with attendant young at heel.

Methods

Study Area

We surveyed white-tailed deer distribution in the boreal forest of northeast Alberta, Canada (Fig. 1). The 3500 km² landscape is a mosaic of aspen (*Populus tremuloides*), white spruce (*Picea glauca*), black spruce (*P. mariana*), and jack pine (*Pinus banksiana*) forests, interspersed with *Ledum groenlandicum*-dominated muskeg. Widespread petroleum exploration and extraction features, roads (car accessible), trails (off-road vehicle accessible), forest harvesting, and other anthropogenic features are dispersed throughout the study area (Fig. 1).

We deployed 62 camera-trap sites (Reconyx PC900 HyperfireTM infra-red remote digital; Holmen, WI, USA) in a constrained stratified random design (Supplementary Information), sampled continuously between November 2011– November 2014, as in Fisher and Burton (2018); Fisher *et al.* (2020). Following Burton *et al.* (2015), we define 'site' as the average area used by a deer (seasonally, in a 3-month window), centered on the camera detection zone. We define 'study area' as the *ca.* 3500 km² minimum convex polygon surrounding camera sites. Cameras were placed *ca.* 1m from the ground facing the wildlife trail and set to high sensitivity with 3-s delay.

Spatial reproductive success

We identified all camera trap images containing white-tailed deer and created a monthly detection-nondetection dataset with three states: breeding, non-breeding, or no deer detected. We discretized continuous camera sampling into monthly survey occasions. If a fawn(s) appeared in an image within the survey month, we classified that site as "breeding" for that survey (Fig. 2). If fawns were not detected, we classified

the site as "non-breeding" – which includes males and/or females that did not successfully rear a fawn into spring and summer

Multiple approaches are used for modelling serial occurrence data generated by camera traps (Rota *et al.* 2009; ; Burton *et al.* 2015). We therefore analysed camera data using two approaches. First, we sought to account for false absences which is a potential problem in wildlife surveys (MacKenzie 2005), including camera-trap surveys (Burton *et al.* 2015). Just as species may be detected imperfectly, age-sex classes may also be detected imperfectly, when neither age nor sex is known with accuracy. In our case, "breeding" sites could be misclassified as "non-breeding" if we missed photographing extant fawns at the cameras. To account for this error, we used occupancy models (MacKenzie *et al.* 2002) which estimate the probability of detecting that species if present (p) and based on p , the probability of site occupancy (ψ). With hierarchical multi-state occupancy models (Nichols *et al.* 2007; MacKenzie *et al.* 2009) we estimated the probability for each site that deer were either absent, present without breeding, or present with breeding. We also estimated the probability that deer were detected in each of the two occupied states. Occupancy models can be considered as simultaneous generalized linear models (GLMs) applied to the detection and occupancy submodels, with binomial errors (logistic link).

We separated continuous camera data into month-long (30.4 day) "secondary" survey periods *sensu* MacKenzie *et al.* (2003). Three such surveys comprised a three-month "primary" sampling season within which occupancy states were assumed to be closed. We considered only the fawning season (spring, April – June), and post-fawning (summer, July – September). We assumed non-Markovian variation in deer site-use among months within a 3-month season primary season (MacKenzie *et al.* 2006). In an occupancy framework this variation represents "detection error", attributed mainly to movement in and out of the camera detection zone (Burton *et al.* 2015). The full data frame for the study is thus 6 seasons, with 3 repeated monthly surveys within each season, for a total of 18 surveys at each site with each survey comprised of deer detection-nondetection within the month.

With this dataset, we ran several competing models, each with different assumptions about how detectability, breeding occupancy, and non-breeding occupancy varied through time and in relation to landscape features. We tested whether the probability of detection was either (1) constant over time, (2) varied among seasons, or (3) varied among surveys. We likewise tested whether site occupancy of breeders and non-breeders was either (1) constant across the study area, or (2) varied in relation to landscape features. We used hierarchical models in the program *Presence* (ver. 6.2) to estimate deer occupancy (ψ), detectability (p), and breeding state (R), where:

ψ_i = probability that site i is occupied, regardless of reproductive state

R_i = conditional probability that young occurred, given that site i is occupied

$\psi_{i(\text{breeding})}$ = unconditional probability that site i is occupied with breeding = $\psi_i * R_i$

$p(1)_{it}$ = probability that occupancy is detected for site i , period t , given that true state = 1 (non-breeding),

$p(2)_{it}$ = probability that occupancy is detected for site i , period t , given that true state = 2 (breeding),

δ_{it} = probability that evidence of successful reproduction is found, given detection of occupancy at site i , period t , with successful reproduction (Nichols *et al.* 2007).

Occupancy models provide a per-survey estimate of p , and from this we calculated the probability of false absence (PFA) across the three surveys in each sampling season as $[1-p]^3$ (Longet *et al.* 2008).

It has been argued that the variation among secondary surveys (months) due to deer movement is an important part of the ecological signal, and not error as assumed in occupancy models (Neilson *et al.* 2018; Stewart *et al.* 2018; Broadley *et al.* 2019). We therefore also treated zeros as signal, not error, and used an alternative modelling approach—generalised linear models (GLMs)—to determine whether fawn occurrence varied with landscape features. In this analysis each month can be considered an independent Bernoulli trial in which adult female deer with fawns were detected (1) or not (0). We summed the number of spring months

(April, May, June) with and without fawns across all three survey years creating a 0-9 response variable (3 spring months over 3 years). We modelled number of breeding-months as a binomial count model (GLM; binomial errors, log link) in R ver. 3.1.1 (R Foundation for Statistical Computing 2014) against explanatory variables from three spatial digital resource inventories (Supplementary Information Table S1).

Alberta Vegetation Inventory (AVI), a digital forest inventory dataset, provided percent cover of land cover types within a 1-km radius around each camera site (Fisher, Anholt & Volpe 2011; Fisher *et al.* 2020). Alberta Biodiversity Monitoring Institute (ABMI) 2010 Human Footprint Map Ver 1.1 provided percent of area of polygonal anthropogenic features. ABMI's Caribou Monitoring Unit (CMU) provided a GIS layer derived from 2012 SPOT satellite imagery to calculate area of linear features (buffered to create polygons from polylines) around each camera. In all models, we omitted correlated variables ($r > 0.7$) from multiple-variable models (Zuur, Ieno & Elphick 2010) to prevent multicollinearity. We combined variables only sparsely represented in the data (< 1 -2% of area) into a single, combination variable (Table 1), and rescaled each variable (mean=0, s.d.=1) to compare effect sizes.

In occupancy models, we placed covariates on ψ and R in hypothesis models or kept them constant in null models (Supplementary Information Table S2). In GLMs we created multiple *a priori* models, each corresponding to a hypothesis about the landscape features explaining variation in deer reproduction (Table 1). As *a priori* models may still contain uninformative parameters that should be discarded (Anderson 2007), we created a fully reduced model using AIC-based stepwise regression (R; *stepAIC* package) to determine the most parsimonious model explaining variation in deer reproduction.

For both the occupancy models and generalized linear models, we weighed the evidence in support of models corresponding to competing hypotheses using model selection in an information-theoretic framework (Burnham & Anderson 2002). Each model produces an Akaike Information Criterion (AIC) score that balances deviance explained by the model with model complexity – the number of parameters; low AIC scores suggest a best-supported model. We normalized AIC scores into 0-1 AIC weights, analogous to the probability that a given model is the best supported of the candidate set (Burnham & Anderson 2002). We further validated best-supported models using k-fold cross validation in R package *boot*, and calculated deviance explained (Zuur *et al.* 2009).

Results

Evidence of breeding

Of 112,648 deer images captured during the survey, 12,460 images (11.1%) had evidence of young-of-the-year. This included single fawns (92.9%), twins (7.6%) and triplets (0.6%), though these were not distinguished in models. There was a marked drop in the distribution of successful breeding across years. Of 62 sites, successful breeding was detected at 36 sites (58.1%) in 2012, 22 (35.5%) in 2013, and 12 (19.4%) in 2014. Among all years pooled together, 45 of 62 sites (72.6%) had evidence of breeding in at least one year.

Multi-state deer occupancy

Reproductively successful deer – does with fawns – were estimated to be widespread across the study area in spring 2012 ($\psi_b = 0.89$, SE = 0.14), 2013 ($\psi_b = 0.98$; SE = 0.02) and 2014 ($\psi_b = 0.95$; SE = 0.03) when modelled without landscape covariates. The estimated probability of false absences for deer with fawns was [?] 0.002 in all years, suggesting that we reliably detected fawns when they occurred.

Anthropogenic landscape features best explained conditional probability of fawns given occupancy by deer (R) in 2012 (well sites and seismic lines, cumulative $AIC_w = 0.83$), 2013 (seismic lines, $AIC_w = 0.84$) and 2014 (industrial features, forest cutblocks and total footprint, cumulative $AIC_w = 0.81$) (Supplementary Information Table S2). Models in which breeding varied only with natural vegetation, or was invariant, were not supported. Hence, occupancy of breeding deer differed from that of non-breeding deer, and varied with the area of anthropogenic features across the oil sands landscape. However, multistate occupancy models contained unresolvable “border estimates” for R (those close to 0 or 1; (MacKenzie *et al.* 2017)) and exhibited problems with model convergence, necessitating a companion approach.

Spatial patterns of reproductive success: GLMs

Months of occurrence of reproductively successful deer was positively related to anthropogenic landscape features, as well as natural landscape features. Models with petroleum features best explained deer with fawn occurrence, thus corroborating the multi-state occupancy models. Occurrence of deer with fawns increased with increasing seismic line density, 3D seismic line density, pipeline density, and deciduous forest cover; model 31 ($AIC_w = 0.88$) and 29 ($AIC_w = 0.11$) together carried 99% of the weight of evidence (Table 2; Table S3). The effect size (model β coefficients) of seismic lines on the occurrence of fawns was 100 times greater than the effect size of the best natural landcover feature: upland deciduous forests (Fig. 3). Projected across the northeast boreal forest surrounding the study area, areas of higher probability of deer reproduction correspond to intensive development (Fig. 4).

Discussion

As mammal distributions shift with climate change, decrease with habitat loss or capitalize upon change to invade, understanding the features facilitating reproduction in once barrens landscapes allow us to elucidate, and address, those mechanisms of change. Global camera-trap networks coupled with spatial distribution models can yield these insights.

In our example widespread landscape change from energy extraction is strongly linked to white-tailed deer reproduction where they have invaded the western Nearctic boreal forest. Deer invasion of the cold northern latitudes is consequent to expansion from southern agricultural areas, a continental phenomenon borne from widespread conversion of mature forest into early seral vegetation (Côté *et al.* 2004; Heffelfinger 2011). In the last few decades, new advances in forest harvesting and the dramatic growth of energy exploration and extraction have radically altered the Alberta boreal landscape (Pickell, Andison & Coops 2013; Pickell *et al.* 2015). The density of petroleum exploration “seismic” lines in the landscape had a 100 times greater effect on deer breeding success than did natural deciduous forest, an important predictor of adult white-tailed deer individual habitat selection and distribution (Darlington 2018; Fisher & Burton 2018; Fisher *et al.* 2020). Although we hypothesized that forest harvesting might play a substantial role (Fisher & Wilkinson 2005), we found no evidence to support this; and petroleum extraction features are much more widespread than forest harvest blocks in this region (Pickell, Andison & Coops 2013; Pickell *et al.* 2015). We conclude that the 1000s of kilometres of seismic lines, as well as pipelines and 3D seismic lines, spread across the western Nearctic boreal forest play a significant role in facilitating the northward expansion of white-tailed deer.

The mechanism for the relationship between linear features and deer reproductive success is centred on available forage. Nutrition affects ungulates’ probability of pregnancy, over-winter survival, parturition, and neonatal survival (Parker, Barboza & Gillingham 2009; Hewitt 2011). Greater nutrition from abundant available forage prevents metabolic stress, increasing deer survivorship and reproductive success (Hewitt 2011). However forage biomass is in itself not a good predictor of deer nutrition, as forage distribution relative to inedible vegetation plays a significant role (Spalinger & Hobbs 1992). In this landscape, abundant edible forage is available in linear features (Finnegan, MacNearney & Pigeon 2018; Finnegan, Pigeon & MacNearney 2019; MacDonald *et al.* 2020), and may be especially important in spring during green-up, when energetic demands of gestation are great (Pekins, Smith & Mautz 1998).

Research on deer pregnancy rates and recruitment suggests that female age and body condition affect breeding success (Ozoga, Verme & Bienz 1982; Ozoga & Verme 1986; Verme 1989; DelGiudice, Lenarz & Powell 2007); body condition, in turn, is primarily a function of nutrition afforded by available browse (Hewitt 2011). Winter induces substantial metabolic costs on white-tailed deer, but pregnancy and lactation induces markedly greater metabolic costs on females (Pekins, Smith & Mautz 1998; Therrien *et al.* 2008; Ditchkoff 2011). If female deer in this landscape were metabolically stressed after severe winters, female mortality, small fawns with low survival (Ditchkoff 2011), and starvation-induced abortions (Worden 1992, in Pekins *et al.* 1998) might be expected to reduce reproductive success. If the early seral vegetation abundant in anthropogenic landscape features provides forage subsidies, then metabolic costs would be offset and reproductive success enhanced. We contend our evidence here, as well as corroborating past research on adult

deer showing positive links to anthropogenic features (Darlington 2018; Fisher & Burton 2018), strongly infers that landscape change is enhancing breeding success and hence, facilitating and maintaining boreal deer invasions.

Caveats

Our research focussed on a heavily developed landscape in the western Nearctic boreal forest of Alberta, Canada. Extrapolating to other landscapes in this region should not be done without future research to understand the range of inference. In their province-wide analysis, (Dawe, Bayne & Boutin 2014; Dawe & Boutin 2016) concluded that deer expansion is likely facilitated in large part by climate change as the metabolic costs of cold temperatures and especially deep snow are ameliorated by contemporary mild winters. Evidence at landscape scales suggests climate is a contributory mechanism but abundant nutritional forage is pivotal for deer populations (Fisher *et al.* 2020), and historically the northern boreal forest has been dominated by largely inedible conifer (Fisher & Wilkinson 2005; Pickell *et al.* 2015). We contend forage subsidies induced by landscape change play a large role not yet disentangled from climate change; indeed it is likely the two act synergistically.

Applications to Ecology

In the western boreal forest, petroleum exploration features are increasing breeding success, and hence possibly (given lifetime success) fitness of individuals spatially associating with them. In the apparent competition “fulcrum” in which more deer boost wolf populations, which in turn drive declines in woodland caribou (DeCesare *et al.* 2010; Latham *et al.* 2011; Boutin *et al.* 2012), deer expansion is a substantial conservation threat. Conservation will require landscape management to mitigate the widespread resource subsidies afforded to deer, including active site restoration, which has been shown to be promising for mitigating white-tailed deer use of seismic lines (Tattersall *et al.* 2019). Dauntingly, this restoration is required for 10,000s of kilometres of seismic lines (Dabros, Pyper & Castilla 2018), as well as the other anthropogenic features associated with resource extraction (Fisher & Burton 2018; Fisher *et al.* 2020) lending urgency to the need for rapid application of ecological research to management decisions.

Biodiversity declines due to landscape change are a global problem (Maxwell *et al.* 2016) as are invasive species (Gurevitch & Padilla 2004; Clavero & García-Berthou 2005) and anthropogenic range shifts (Lawler *et al.* 2009; Chen *et al.* 2011). Understanding the ecological mechanisms facilitating and sustaining invasions is a key pursuit for and ecology. Global biodiversity networks can quantify variation in mammalian distribution and density at large scales (Steenweget *et al.* 2017) but abundance is not always a reliable metric for inference of mechanisms (Van Horne 1983; Schlaepfer, Runge & Sherman 2002; Battin 2004). Breeding success is more directly reflective of landscape change’s effect on mammalian fitness. These data can be garnered through camera-trap networks and modelled with data on landscape change to aid inference about the mechanisms of change: an intersection of fundamental ecology principles and applied ecology practice that can aid inferences and the decisions derived from them.

Authors’ Contributions

JTF conceived the research and the design and conducted statistical analyses; JTF and ACB conceived the questions and wrote the paper. Both authors reviewed and edited the draft and gave final approval for publication.

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Research Ethics

All research was permitted by the Government of Alberta, Ministry of Environment and Parks, Fish & Wildlife Division, Collection License 49143.

Animal Ethics

This research was reviewed and approved by InnoTech Alberta's Animal Care and Use Committee (ACUC), permit ACUC0524.frm /clj/IO.II.02.

Table 1. Hypotheses about the distribution of breeding white-tailed deer across the boreal forest study area.

Description	Model #	Hypothesis: White-tailed deer distribution is explained by % cover (within a buffer a
Global model	1	All variables
Natural landcover	2	Upland deciduous cover
	3	All mixedwood cover
	4	All conifer cover
	5	Upland spruce
	6	All deciduous + shrubs
	7	Wetland
	8	Upland forest
	9	Lowland forest
Non-forest	10	Early seral
Forestry	11	Cutblocks
Petroleum	12	Well sites
	13	3D seismic
	14	Seismic lines
	15	Pipelines
	16	Linear features
	17	Block features
Petroleum + Forestry	18	Block features incl. cutblocks
Access	19	Roads
	20	Trails
	21	Roads and trails
All anthropogenic	22	All anthropogenic features
Natural + forestry	23	Upland deciduous and cutblocks
	24	Shrubs and cutblocks
	25	Openings and cutblocks
	26	Upland deciduous and 3D seismic
Natural + petroleum	27	Upland deciduous and Seismic lines
	28	Upland deciduous and all anthropogenic
	29	Upland deciduous and all petroleum
	30	Upland deciduous and roads and trails
Natural + access	30	Upland deciduous and roads and trails
<i>Post-hoc</i> step-AIC model	31	Variables selected by stepwise regression

Table 2. Model selection of generalised linear models relating probability of occurrence of white-tailed deer with fawn(s) against natural and anthropogenic landscape features. Model numbers refer to candidate model sets in Table 2. K = number parameters.

Model #	K	AIC	Δ AIC	AIC _w	Cumulative AIC _w	-2LL
Model 31	5	406.41	0	0.88	0.88	-197.66
Model 29	7	410.64	4.23	0.11	0.99	-197.26
Model 28	11	415.69	9.28	0.01	1	-194.15
Model 27	4	428.09	21.68	0	1	-209.69
Model 16	7	430.79	24.38	0	1	-207.34
Model 22	10	431.07	24.67	0	1	-203.34
Model 14	3	433.95	27.54	0	1	-213.77
Model 1	11	438.14	31.73	0	1	-205.38
Model 4	6	438.53	32.12	0	1	-212.49
Model 7	4	441.22	34.81	0	1	-216.25
Model 6	6	441.28	34.87	0	1	-213.86
Model 26	4	443.1	36.7	0	1	-217.19
Model 23	4	443.16	36.76	0	1	-217.23
Model 30	5	443.69	37.28	0	1	-216.3
Model 2	3	444.64	38.23	0	1	-219.11
Model 8	5	446.73	40.32	0	1	-217.82
Model 15	3	447.25	40.84	0	1	-220.41
Model 17	4	451.05	44.65	0	1	-221.17
Model 10	7	452.6	46.19	0	1	-218.24
Model 18	5	452.79	46.38	0	1	-220.85
Model 20	3	452.86	46.45	0	1	-223.22
Model 12	3	453.11	46.7	0	1	-223.34
Model 5	3	453.16	46.75	0	1	-223.37
Model 21	4	454.68	48.27	0	1	-222.98
Model 19	3	454.7	48.3	0	1	-224.14
Model 9	5	454.79	48.39	0	1	-221.85
Model 13	3	454.8	48.39	0	1	-224.19
Model 11	3	455.07	48.67	0	1	-224.33
Model 3	4	455.97	49.56	0	1	-223.63
Model 25	5	456.41	50	0	1	-222.66
Model 24	4	457.37	50.96	0	1	-224.33

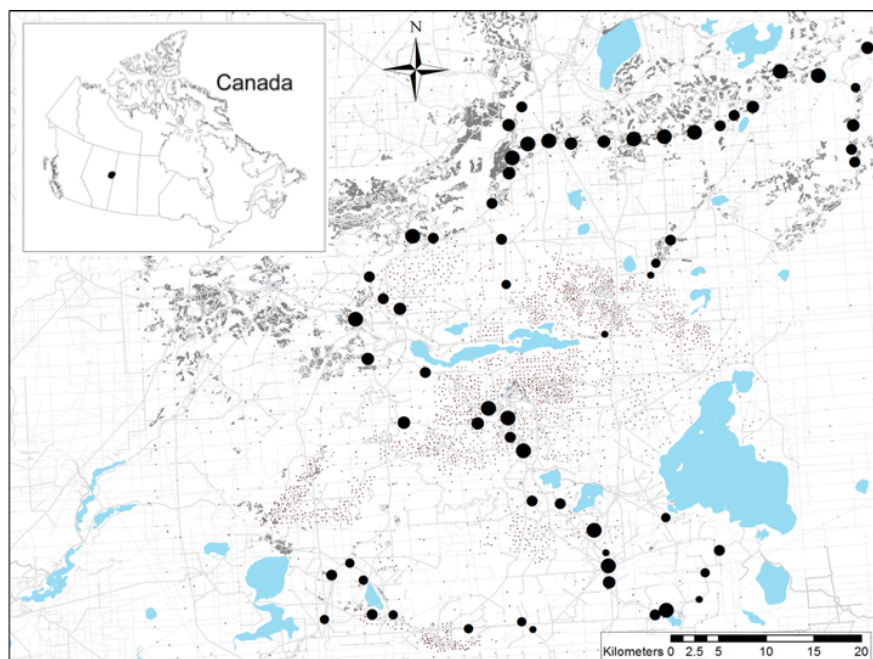


Fig. 1. Occurrence of white-tailed deer does with fawns at heel (inset, lower left) was surveyed at 62 camera sites (large block dots, scaled to the 0-9 month response variable) in the boreal forest of northeast Alberta, Canada. Anthropogenic landscape features are widespread across this landscape, including forest harvesting cutblocks (grey polygons), well sites (square dots), seismic lines (grey), and roads and trails (dark grey and colored lines). Lakes are in blue.



Fig. 2 . In the boreal forest of Alberta, Canada, camera-traps quantified sites with white-tailed deer fawns –

characterized by their small size, and for younger animals, the presence of spots. Sites with fawns appearing in a survey month were recorded as “breeding” for that month.

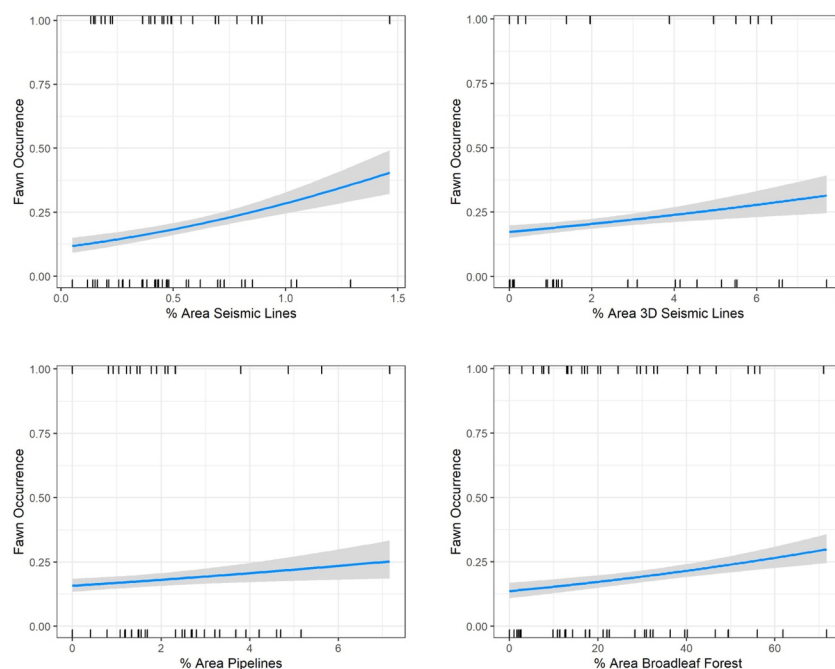


Fig. 3. Spatial variation in white-tailed deer reproductive success in the oil sands of the western Nearctic boreal forest of Alberta, Canada was best explained by petroleum extraction features – conventional seismic lines, 3D seismic lines, and pipelines – as well as upland deciduous forest.

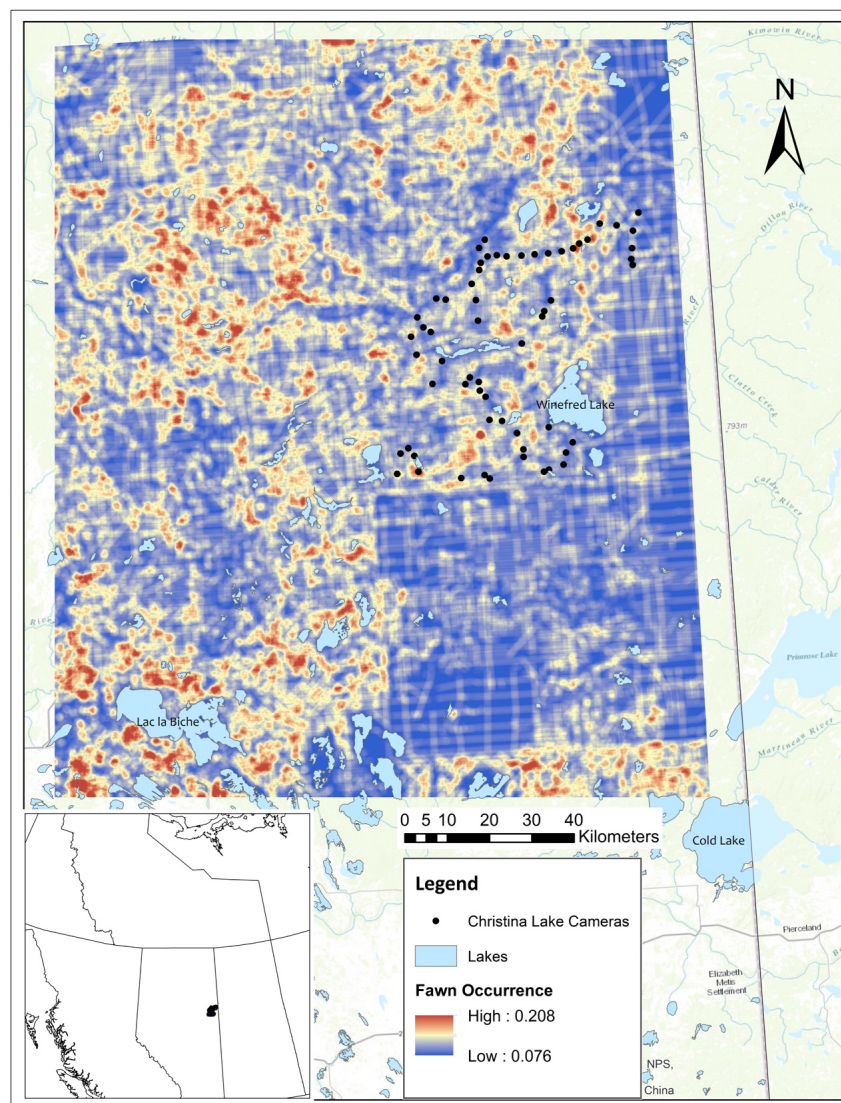


Fig. 4. The probability of white-tailed deer reproduction across Alberta's northeast boreal forest oil sands' region. Beta coefficients from the best-supported generalized model explaining spatial variation in fawn occurrence were extrapolated across the region using the same spatial data from the models were derived.

Data Accessibility Statement

Data used in these analyses are made available in Supplementary Information.

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