

# An evaluation of historical mule deer fawn recruitment in North Dakota

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# Executive Summary

*Simone Ciuti, William F. Jensen, Scott E. Nielsen, Mark S. Boyce*

Since 1962 mule deer surveys have been conducted in North Dakota. Over the last 50 years the general pattern has been that mule deer numbers have increased while fall fawn recruitment rates have declined. However, in recent years both mule deer numbers and fall fawn recruitment rates have decreased to levels well below the long-term average, raising concern about recruitment and population trends. Indeed, fawn production during the period 2008-2012 is the lowest documented since demographic surveys began in 1962. These recent declines in abundance and recruitment of mule deer are coincident with substantial landscape changes attributable to energy development in mule deer habitats especially in the Little Missouri badlands.

The mule deer is one of the most sought after game species in North Dakota. In the past approximately 10,000 hunters applied during the first drawing for about 2,500 antlered mule deer licenses. In 2008, a total of 2,700 antlered mule deer hunting licenses were available for the badlands hunting units. Because surveys indicated reduced mule deer numbers, only 850 antlered mule deer licenses were allocated for these badlands hunting units in 2012. As a result of these declines, North Dakota Game and Fish Department is frequently questioned about the impacts of predation, winter weather, hunting pressure, range condition and, most recently, energy development. To find answers to these questions and to explain recent declines in mule deer abundance, a research project was initiated using one of the most complete time-series of wild Cervids in North America.

Seasonal climate can influence deer recruitment contributing to the population dynamics of large herbivores. Winter weather conditions were found to explain a consistent portion of the variability in fall fawn recruitment. Indeed, models that included both weather effects and the long-term trend explained about 71% of total variability. Average minimum temperature recorded during winter prior to the birth of fawns was the weather factor with the strongest influence on fawn recruitment. Fall fawn:doe ratios ranged from 0.85 when average minimum temperatures during the prior winter were about  $-16^{\circ}\text{C}$  in contrast with 1.2 fawns:female when minimum temperatures were about  $-8^{\circ}\text{C}$ . Mechanisms for this pattern are surely manifested through the nutrition and energy balance of the doe and if she is able to give birth, the resultant condition of the fawn.

We also showed that the North Pacific index (ocean oscillation) was a good predictor of mule deer fawn recruitment. This result is quite remarkable given the distance between North Dakota and the Pacific Ocean, yet these decadal oscillations influencing climate patterns are important because they

allow wildlife managers to anticipate patterns that could be incorporated in management plans. In practice, temperature recorded during a given winter is a good predictor of fawn recruitment expected during the following fall, allowing yearly harvest allocations to be adjusted.

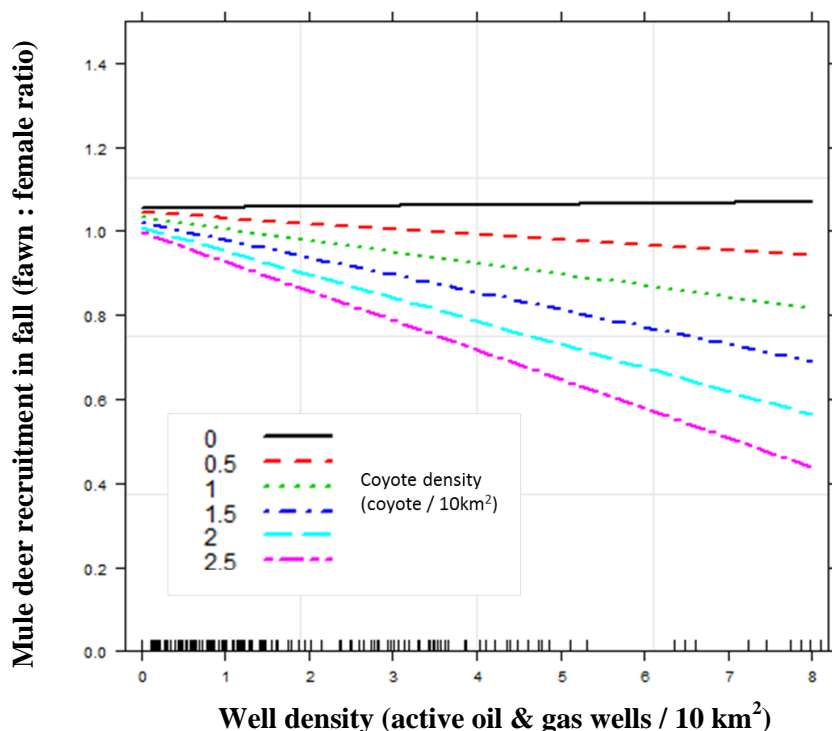
Even more important from a deer management perspective, we found that after accounting for winter temperatures the density of oil and gas wells and predator pressure by coyotes were important drivers of fall fawn recruitment, explaining about 85% of total variability. Our models predict little effect of increased coyote density on fawn recruitment where oil and gas wells are absent; and likewise, our models predict little effect of increased well density on fall fawn recruitment if coyotes are absent. However, industrial development and predation interact with each other affecting fall fawn recruitment in the North Dakota badlands. The lowest recruitment was recorded in areas where both coyote and well densities were high. Energy developments directly (well-pad surface) and indirectly (2-3 km from the well site) lead to habitat loss. We show, for the first time, how coyote densities and oil and gas development could have substantial consequences to fall mule deer fawn recruitment when occurring in an interacting or cumulative fashion.

|  |      | <i>Well density (active oil &amp; gas wells / 10 km<sup>2</sup>)</i> |      |      |      |      |      |      |      |      |
|--|------|--|------|------|------|------|------|------|------|------|
|  |      | 0  | 1    | 2    | 3    | 4    | 5    | 6    | 7    | 8    |
| <i>Spring coyote density (coyotes / 10 km<sup>2</sup>)</i> | 0    | 1.04   | 1.04 | 1.04 | 1.04 | 1.04 | 1.04 | 1.04 | 1.04 | 1.04 |
|  | 0.25 | 1.03   | 1.03 | 1.02 | 1.01 | 1.01 | 1.00 | 0.99 | 0.99 | 0.98 |
|  | 0.5  | 1.03   | 1.01 | 1.00 | 0.98 | 0.97 | 0.96 | 0.94 | 0.93 | 0.91 |
|  | 0.75 | 1.02   | 1.00 | 0.98 | 0.95 | 0.93 | 0.91 | 0.89 | 0.87 | 0.85 |
|  | 1    | 1.01   | 0.98 | 0.95 | 0.93 | 0.90 | 0.87 | 0.84 | 0.81 | 0.78 |
|  | 1.25 | 1.01   | 0.97 | 0.93 | 0.90 | 0.86 | 0.82 | 0.79 | 0.75 | 0.71 |
|  | 1.5  | 1.00   | 0.96 | 0.91 | 0.87 | 0.82 | 0.78 | 0.74 | 0.69 | 0.65 |
|  | 1.75 | 0.99   | 0.94 | 0.89 | 0.84 | 0.79 | 0.74 | 0.69 | 0.63 | 0.58 |
|  | 2    | 0.99   | 0.93 | 0.87 | 0.81 | 0.75 | 0.69 | 0.63 | 0.57 | 0.52 |
|  | 2.25 | 0.98   | 0.92 | 0.85 | 0.78 | 0.72 | 0.65 | 0.58 | 0.52 | 0.45 |
|  | 2.5  | 0.98   | 0.90 | 0.83 | 0.75 | 0.68 | 0.61 | 0.53 | 0.46 | 0.38 |
|  | 2.75 | 0.97   | 0.89 | 0.81 | 0.72 | 0.64 | 0.56 | 0.48 | 0.40 | 0.32 |
|  | 3    | 0.96   | 0.87 | 0.78 | 0.70 | 0.61 | 0.52 | 0.43 | 0.34 | 0.25 |

*When predator pressure and well density are absent in the North Dakota badlands, fawn : female ratio is above 1 with fluctuations due to winter harshness (milder winters, higher recruitment). However, a simultaneous increase of both oil & gas well density and coyote density resulted in a reduction of fawn recruitment to values lower than 0.40 fawns : female.*

***[numbers within the table are predicted fawn : female ratios]***

We emphasize that coyote density by itself does not affect fall fawn recruitment, and thereby predator control is not an effective long-term solution. Resilience of mule deer populations could therefore be weakened by the interaction of energy development with that of the interactions between predator and prey. The ultimate cause behind mule deer decline is still related to alteration in habitats. If habitat is adequate, predator-caused mortality should be compensatory. The ultimate cause for the decline in recruitment is therefore habitat loss and fragmentation caused by industrial development. This concentrates mule deer into smaller patches of habitat where the animals are more vulnerable to predation on fawns. Management to ensure persistence of mule deer in western ND should focus on securing adequate blocks of habitat with minimal disturbance.



*The largest decreases in mule deer recruitment have been recorded in the North Dakota badlands where oil & gas well density increased and where, at the same time, coyote density was high. Considering an average of more than 1 fawn : female during 1962-2012, mule deer subpopulations living in areas with more than 3 wells / 10 km<sup>2</sup> and 2 coyotes / 10 km<sup>2</sup> were characterized by a fawn:female ratio well below the long-term average (i.e., < 0.8 fawns : female)*

We are optimistic that future landscapes of North Dakota will continue to support thriving populations of mule deer and other wildlife. To ensure that this occurs, we must understand how to reduce cumulative effects, apply best management strategies, and pay particular attention to key habitats and how they might be affected by energy developments.

## Acknowledgments

Long-term data sets of big game population demographics are rare; particularly those that involve consistent methods over time. The North Dakota Game and Fish Department (NDGFD) began flying spring aerial mule deer surveys in 1956 and fall aerial mule deer surveys in 1962. Between 1956 and 1997, a span of 42 years, Jack Samuelson coordinated all surveys and flew as an observer for a large portion of the flights. Mr. Samuelson's dedication to detail and meticulous record keeping were key to the extensive dataset that is the basis of this report. Following Samuelson's retirement, Mike Oehler and Bruce Stillings took on the role of coordinating these surveys. Over the course of the 57 years represented in this work a tremendous amount of effort has been put forth by 24 observers and 18 pilots. The observers include: A. Anderson, P. Anderson, J. Feist, C. Grondahl, R. Gross, J. Gulke, A. Harmoning, L. Jacobson, J. Jasmer, W. Jensen, R. Johnson, J. Kolar, W. McDannold, J. McKenzie, R. Meissner, M. Oehler, R. Rostvet, J. Samuelson, B. Stillings, B. Stotts, J. Smith, B. Wiedmann, R. Witkowski, and J. Wynbrandt. Pilots include: F. Anderson, P. Anderson, D. Augustine, B. Berentson, J. Blair, J. Faught, E. Homelvig, T. Hendrickson, J. Jtachenko, R. Messer, R. Nelson, W. Plotskow, P. Redmond, J. Rubbert, R. Rubbert, B. Tester, D. Volesky, and C. Zimmer. Various aspects of this report were assisted by other NDGFD staff; these include S. Allen, A. Duxbury, J. Ermer, B. Hosek, S. Johnson, C. Penner, D. Repnow, and S. Tucker. Digitization of vegetation layers was conducted within the Geography Department at the University of North Dakota (UND); we thank Dr. B. Rundquist for his assistance. Coordination of the digitization at UND was carried out by M. Knudson and R. Thalacker. Technicians involved in the digitization process included A. Braget, R. Eckroad, M. Braget, B. Sergenian, and A. Schmaus. In total, the efforts of more than 50 individuals were involved in some aspect of this report. We apologize for any omissions and thank everyone for their contributions to the final product.

Simone Ciuti thanks Bill Jensen for his passionate dedication, commitment and enthusiasm that have made this work possible.

# Introduction

*Simone Ciuti, William F. Jensen, Scott E. Nielsen, Mark S. Boyce*

The evaluation of mule deer (*Odocoileus hemionus*) fawn-recruitment data is crucial to making sound management decisions regarding this important big game species. Young:female ratios have been declining and those recorded in western North Dakota during the past decade were well below the long-term average. Indeed, fawn production in 2008-2012 was the lowest documented since the first demographic surveys of mule deer began in 1962.

| 1967   | 1972   | 1977   | 1982   | 1987   | 1992   | 1997   | 2002   | 2007   | 2012   |
|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|
| 1.21:1 | 1.30:1 | 1.20:1 | 1.22:1 | 1.11:1 | 1.19:1 | 0.71:1 | 0.90:1 | 0.98:1 | 0.59:1 |

*Fawn:Female ratios recorded in the North Dakota badlands from 1967 to 2012*

Concern about the decline in fawn recruitment motivates a thorough analysis of these long-term data to identify factors affecting mule deer fawn recruitment. Many factors have been implicated in fluctuations in fawn recruitment including weather, harvest management, predation by coyotes (*Canis latrans*), and rapid landscape change associated with oil and gas development. How to efficiently manage and harvest wild ungulates in the presence of stochastic events, predation, and human disturbance has been a continuing challenge for ungulate managers.

Primary objectives of our investigation were to:

1. document associations between weather conditions and weather packages on variation in mule deer fall fawn recruitment (Chapter 1);
2. explore the possible role of coyote predation, using coyote population indices, on fall fawn recruitment (Chapter 2); and
3. evaluate the importance of increasing energy development on annual fall fawn recruitment rates and the probable consequences to the long-term sustainability of mule deer populations in the badlands (Chapter 2).

Data gathered for more than 50 years by the North Dakota Game and Fish Department (1326 survey units flown since 1962) gave us a unique opportunity to examine these ecological influences over time, and here we present main results on direct perturbations caused by weather (Chapter 1) and the indirect effects of predation and oil and gas developments on fall fawn recruitment (Chapter 2).

A secondary objective of this investigation was to produce a comprehensive dataset – available for a follow up analyses - including information collected from 1956 to 2013 in the North Dakota badlands. To create this library required us to re-screen and re-digitize a large part of data (e.g., from field forms), including original aerial survey records starting from 1950's. More importantly, compared with preliminary analyses carried out in the past (Nielsen, Jensen, Boyce unpublished) of large-scale patterns (e.g., study area subdivided into 4 macroregions), the new dataset includes yearly information at the resolution of each of the 28 mule deer study sites (*Fig.1.1, Fig. 1.2*). Although the total number of individual study areas surveyed was 28; however, we had sufficient information for 26 of these to include in the analyses presented in Chapter 1, and a total of 23 study sites could be included in the analyses for Chapter 2. Subsampling was necessary due to insufficient sampling in those areas eventually excluded by statistical analysis procedures. All of these data are now collected into a single database that will be the target of future analyses aimed to:

1. evaluate the effect of doe harvest on subsequent fawn recruitment;
2. identify density-dependent effects on fawn recruitment;
3. analyze how changing habitat conditions might influence fall fawn recruitment rates;
4. evaluate current and long-term harvest strategies for mule deer in the project area;
5. anticipate mule deer population resilience to stochastic events under an altered human-disturbance regimen (i.e., before and after the oil-development boom).

This library includes:

**1) mule deer aerial survey data:**

population size (spring surveys 1956-2012);

recruitment (fall surveys 1962-2012);

**2) predator indices and presence data (coyote, cougar *Puma concolor*)**

sources: mule deer aerial surveys (spring and fall, 1956-2012), Rural Mail Carrier data (1981-2011), trapper and hunter questionnaires (1995-2001), cougar harvest data .

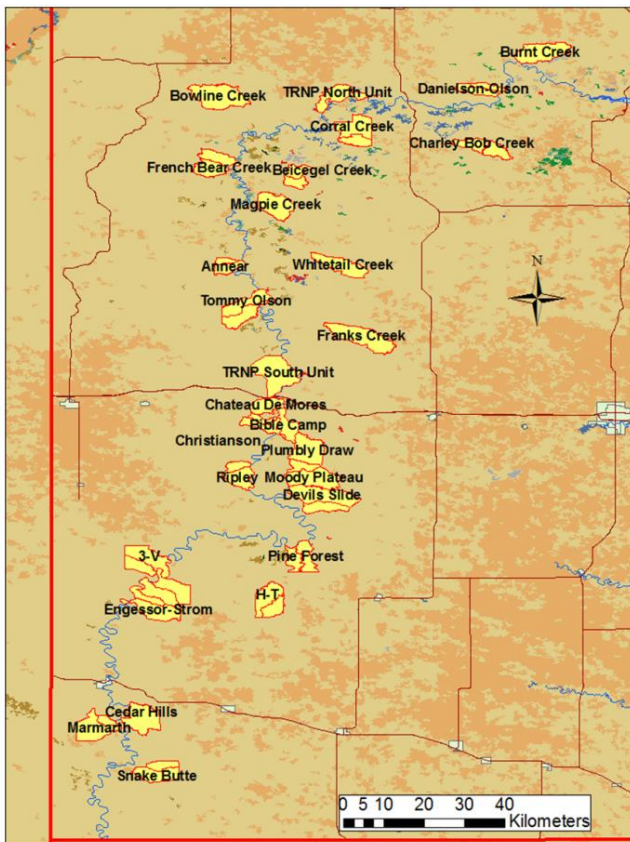
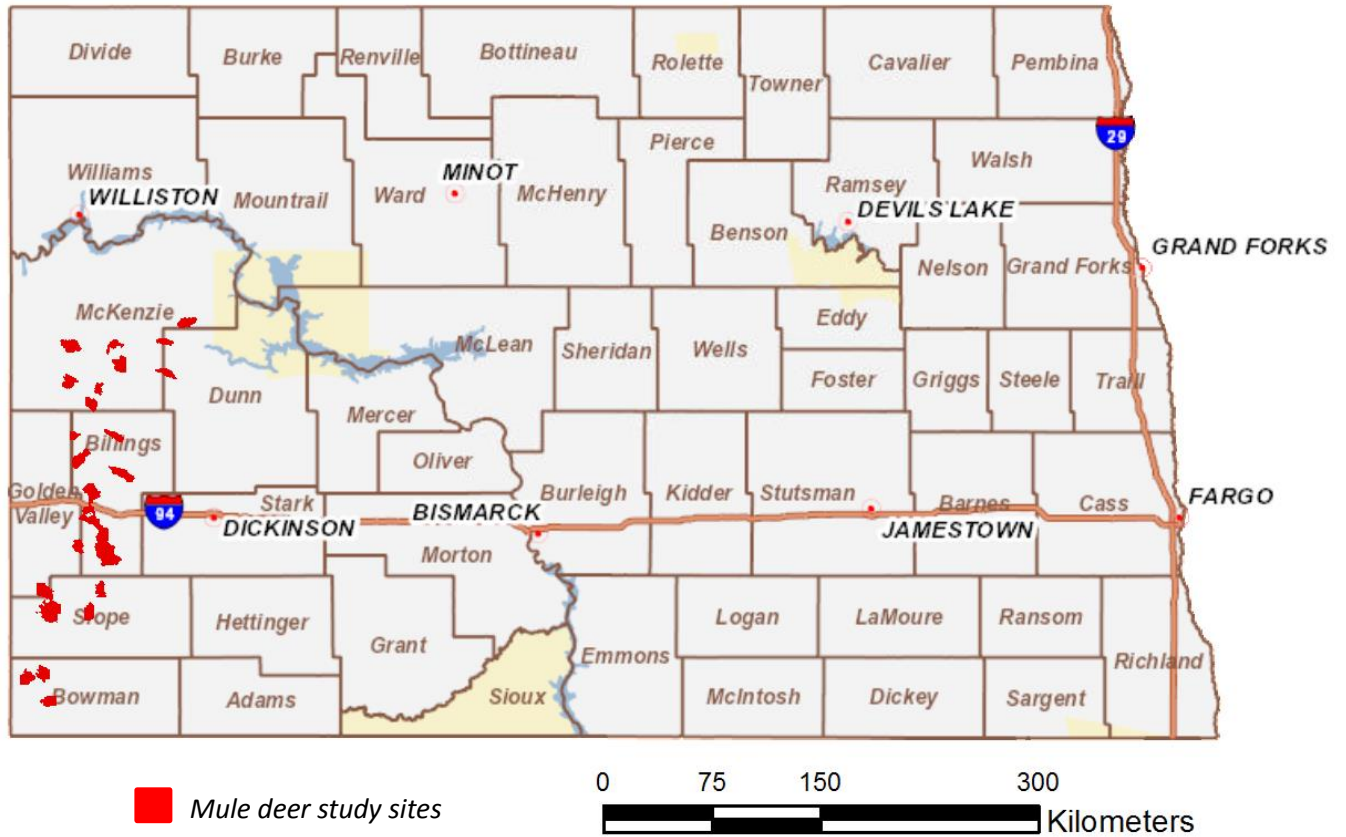
**3) harvest data** (rifle and archery license sales, harvest data)

**4) weather data** (winter-severity index, North-Pacific Oscillation, Pacific Decadal Oscillation, MEI El Niño La Niña; local weather stations, e.g. Medora, with data on precipitation, snow depth, temperature).



- 5) **GIS fine-scale data** (yearly variation of roads *Fig.1.4.*, oil and gas developments *Fig.1.6.*, and vegetation *Fig.1.5.*). More specifically: density of wells (air injectors, gas condensate, oil/gas, salt water disposals, water injectors, water supplies) active each year (1956-2013) within each MD study site and within a 1-km radius buffer around each study site *Fig.1.7.*. Basic GIS layers (digital elevation model, ruggedness, GAP data, etc.)
- 6) **potential mule deer competitors** (elk harvest and surveys, *Fig.1.3*, white-tail deer surveys, hunter observations)

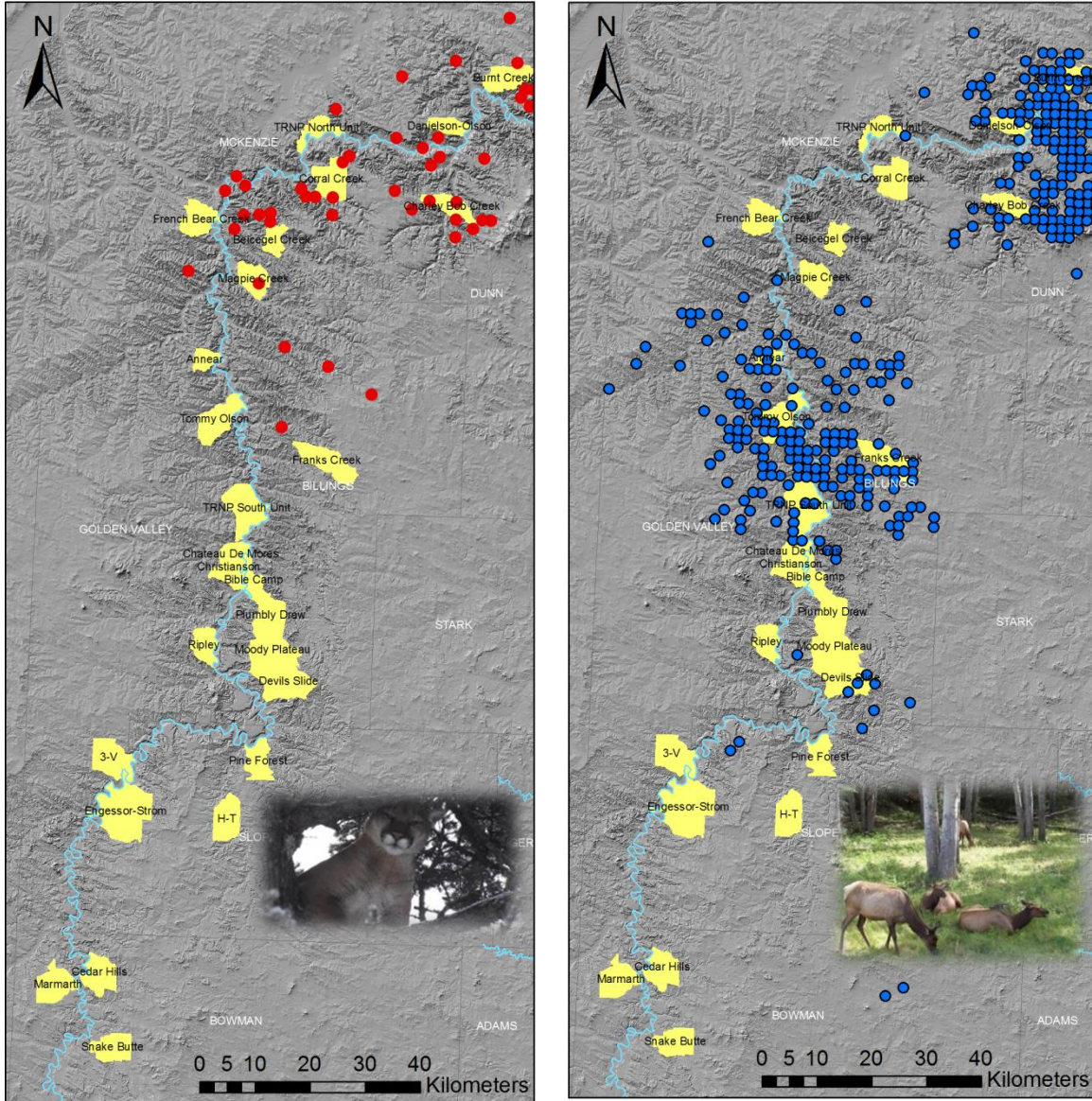
**Fig.1.1.** Location of the 28 mule deer study sites (in red) surveyed from 1956 to 2013 in south-western North Dakota USA



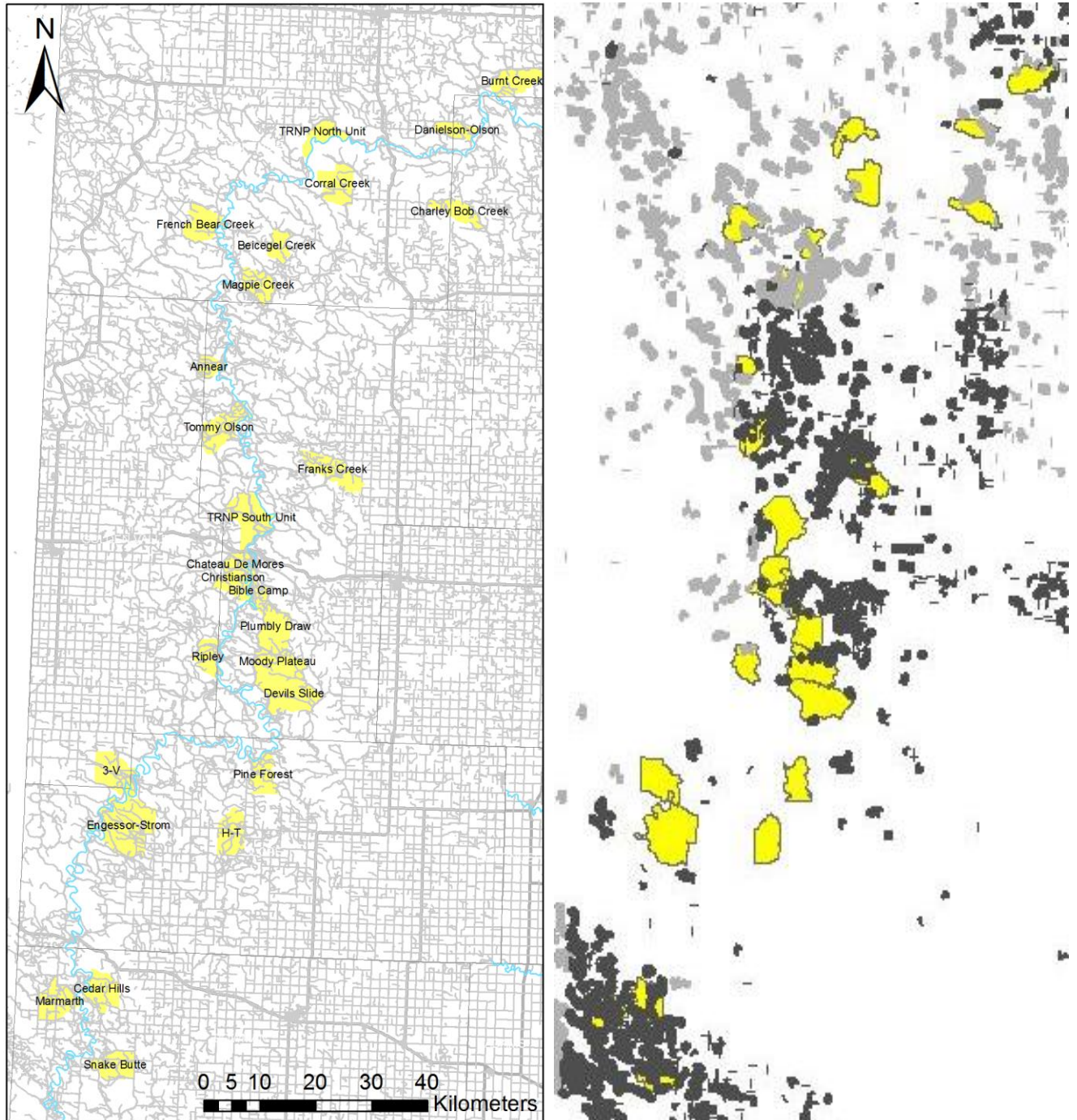
**Fig.1.2.** Names and locations of 28 mule deer study sites surveyed from 1956 to 2013 in southwestern North Dakota USA

■ Mule deer study sites

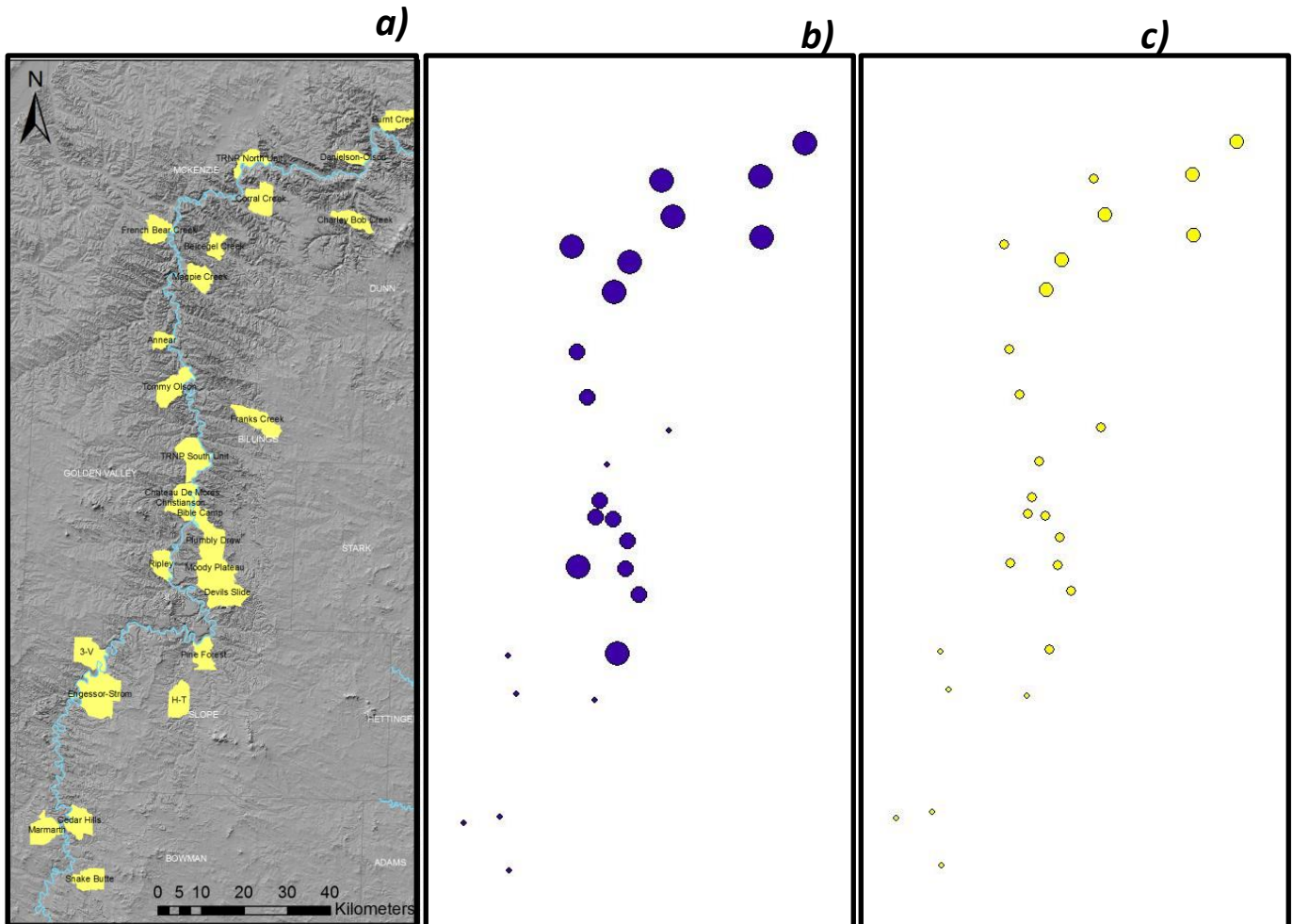
**Fig.1.3.** Spatial location of cougar (red dots) and elk harvest (blue dots) in the past decade.



**Fig.1.4.** Road network of the North Dakota badlands (left) and road segments added since 1990 during the oil boom (right) relative to the 28 mule deer study areas (in yellow).



**Fig.1.5.** North Dakota badlands' vegetation has changed appreciably during the past 50 years due to encroachment by woody vegetation (mainly Rocky Mountain Juniper, *Juniperus scopulorum*). a) location of mule deer study sites. b) study sites classified by the percentage of woody vegetation coverage in 2012 (larger the circle, higher the coverage). c) Study sites classified by encroachment rate over the period 1956-2012 (larger the circle, higher the encroachment rate over the period 1956-2012)



**Fig.1.6.** Well sites drilled since 1962 in the North Dakota badlands (black dots are wells located outside mule deer study areas, green dots are wells inside study sites and within the 1000-m buffer perimeter of each study area)

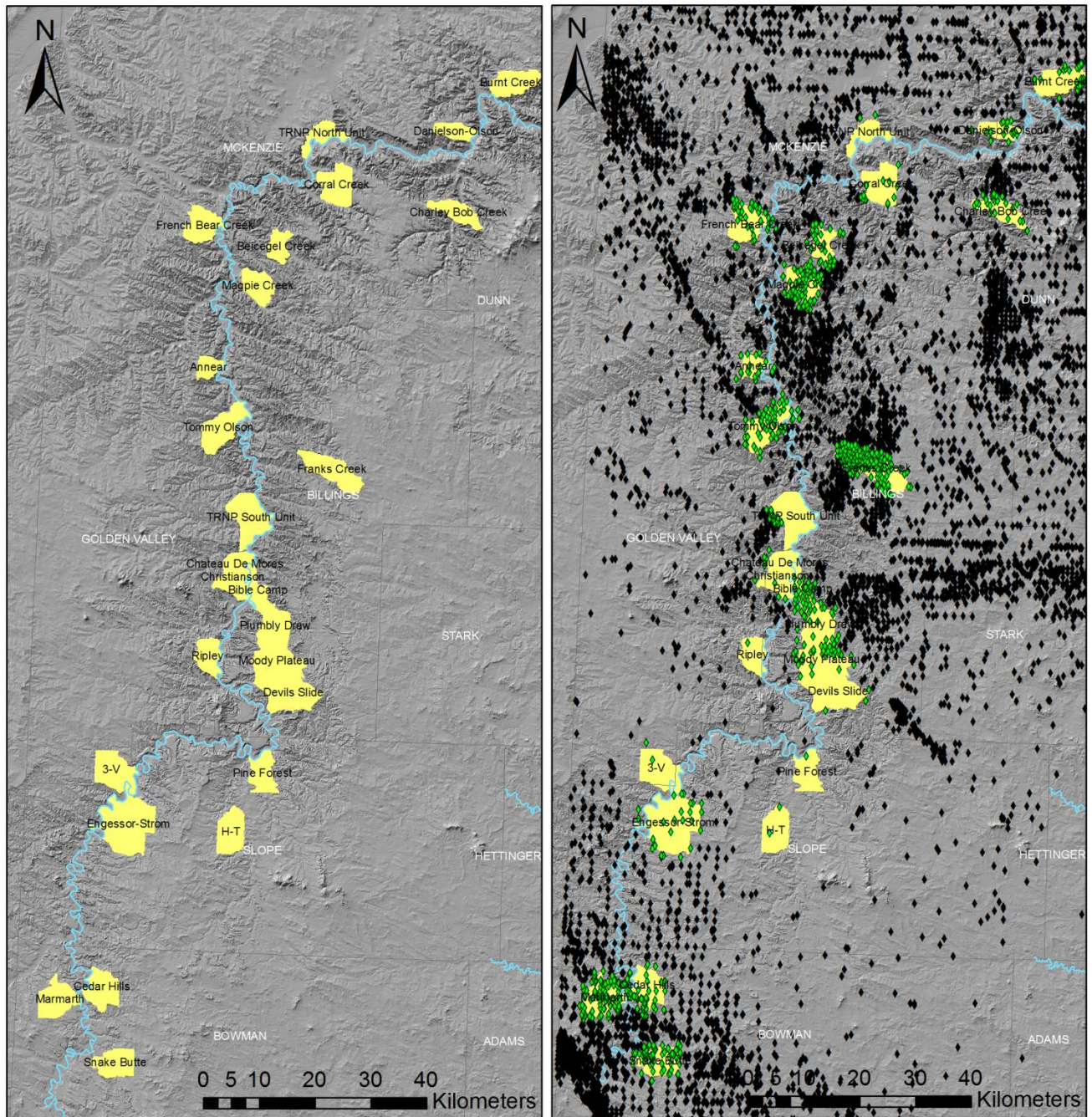
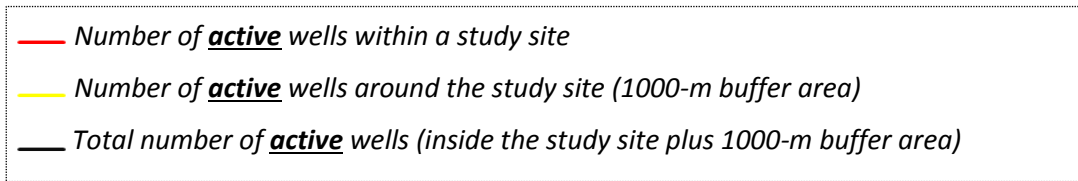
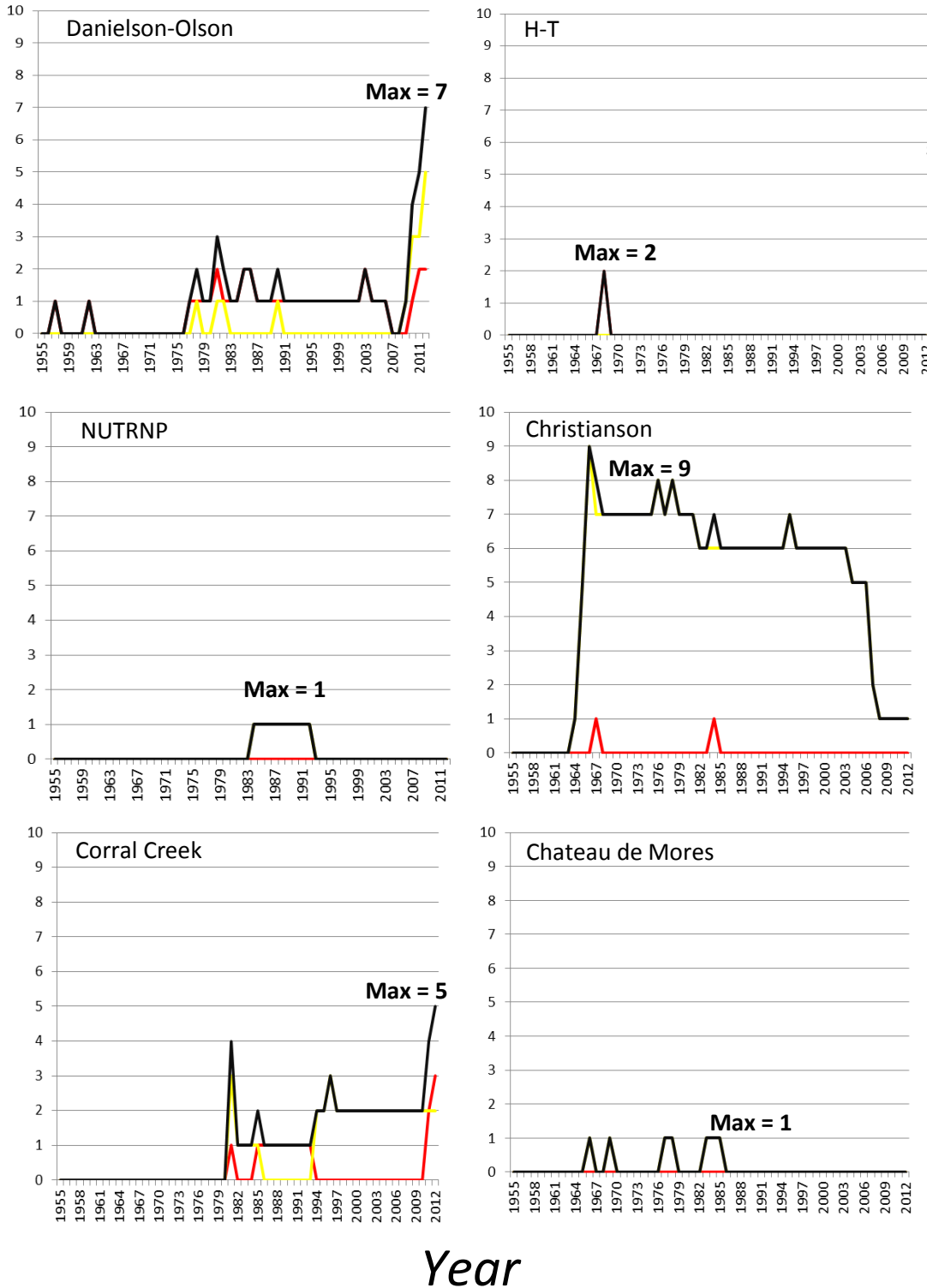


Fig.1.7. Number of active well sites (all types) present within mule deer study sites from 1956 to present.

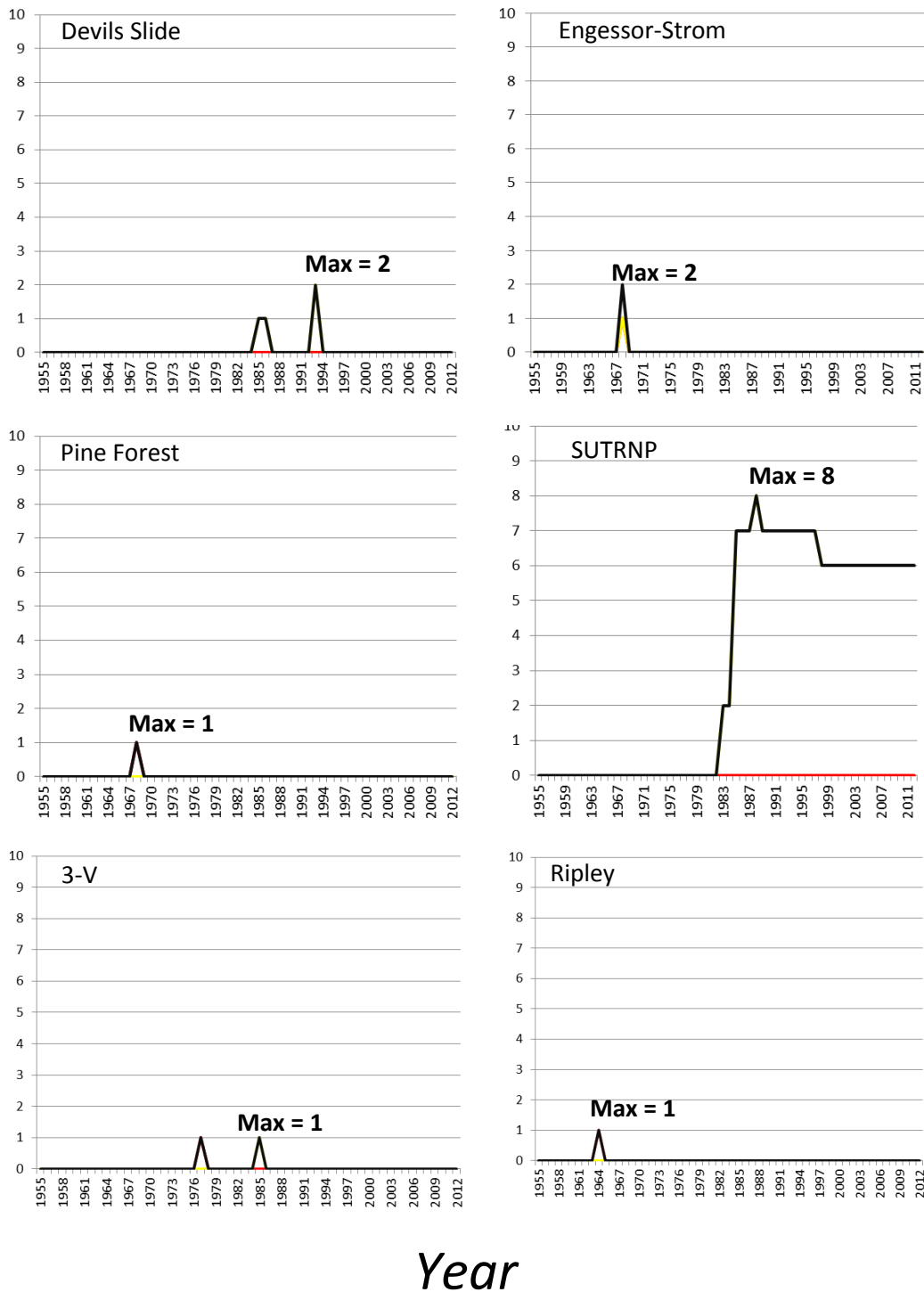
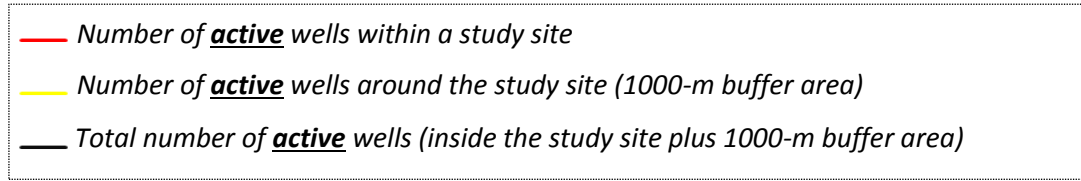


Number of **active** wells



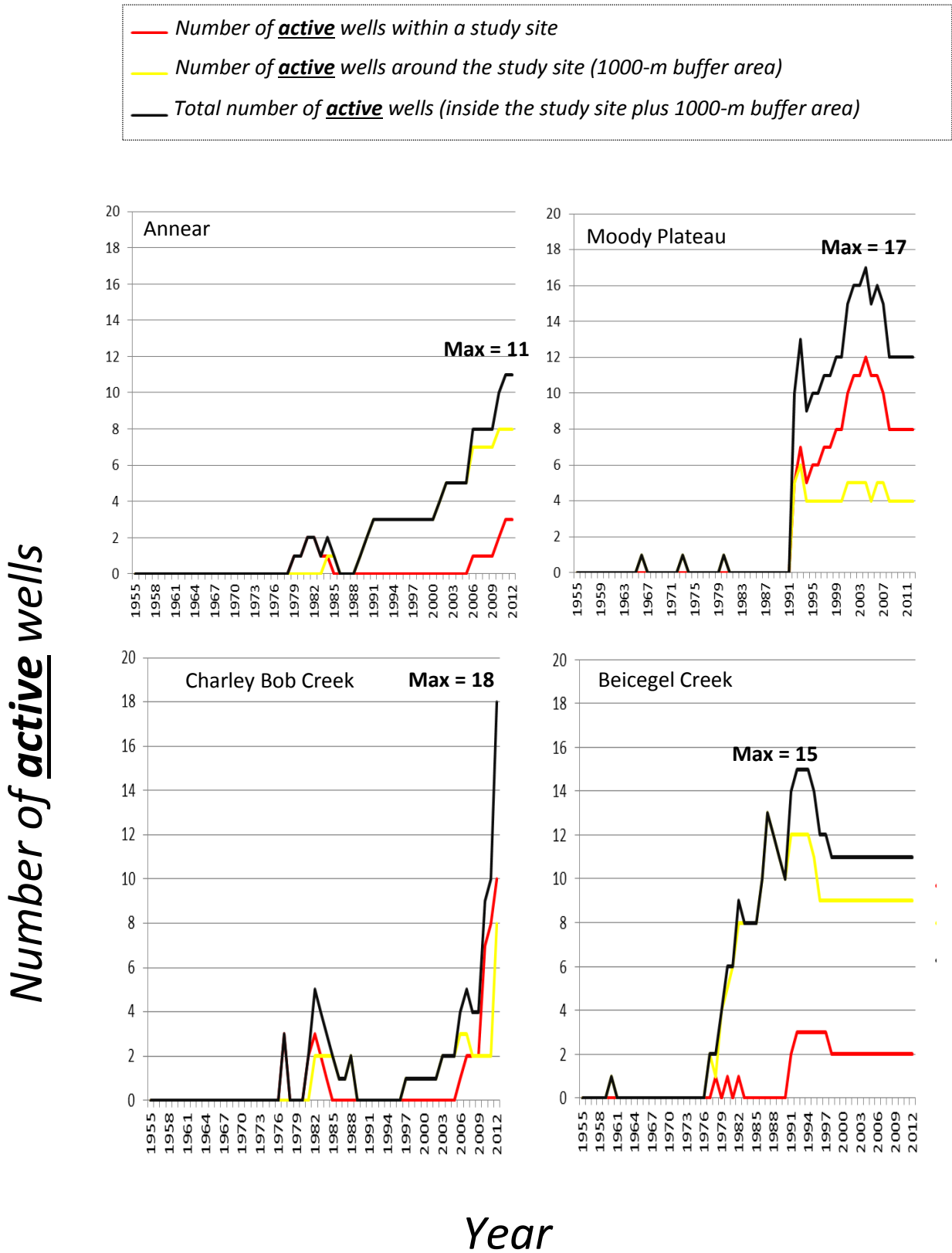
**Fig.1.7.** Number of active well sites (all types) present within mule deer study sites from 1956 to present. (continued)

**Number of active wells**

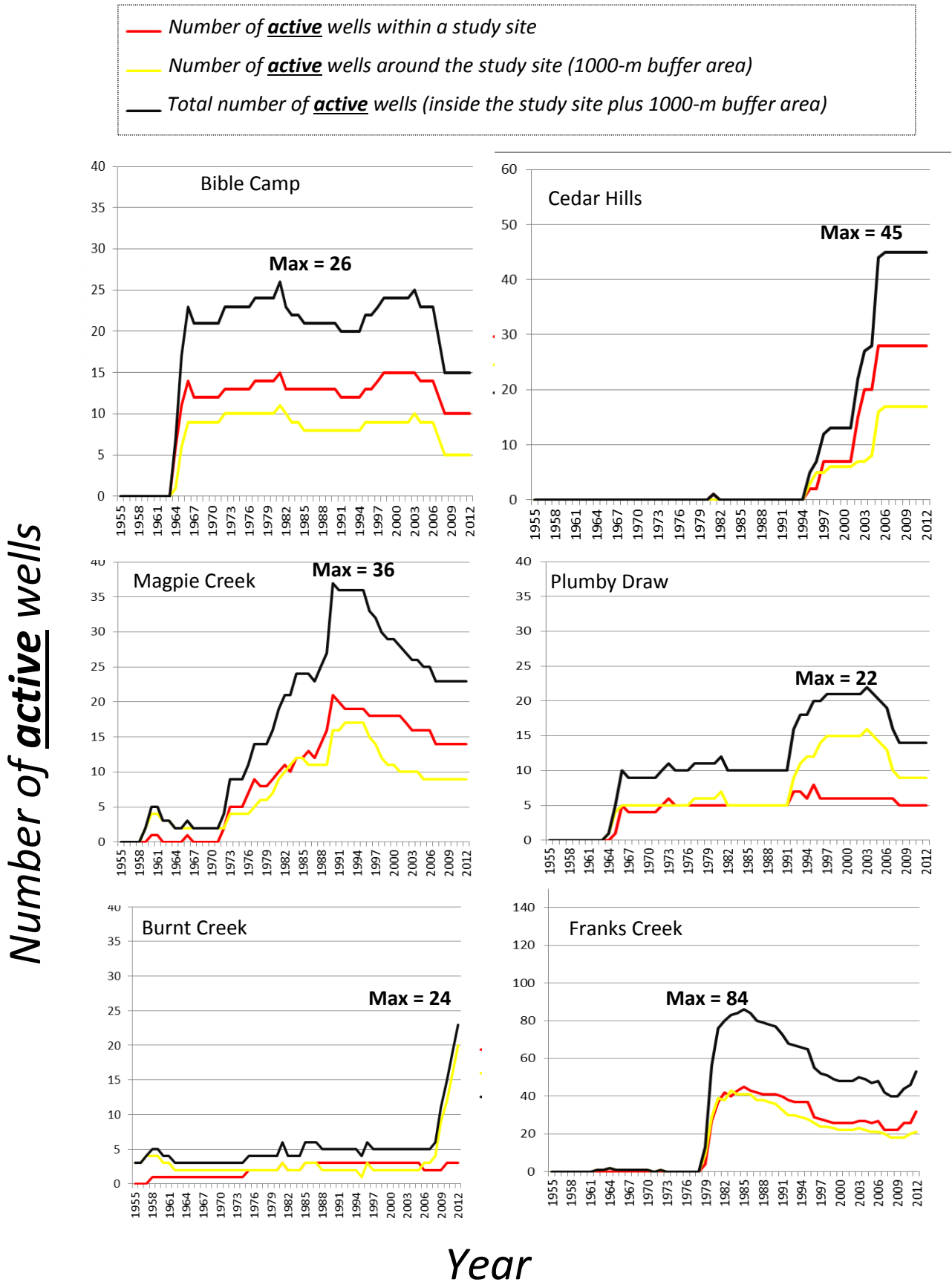




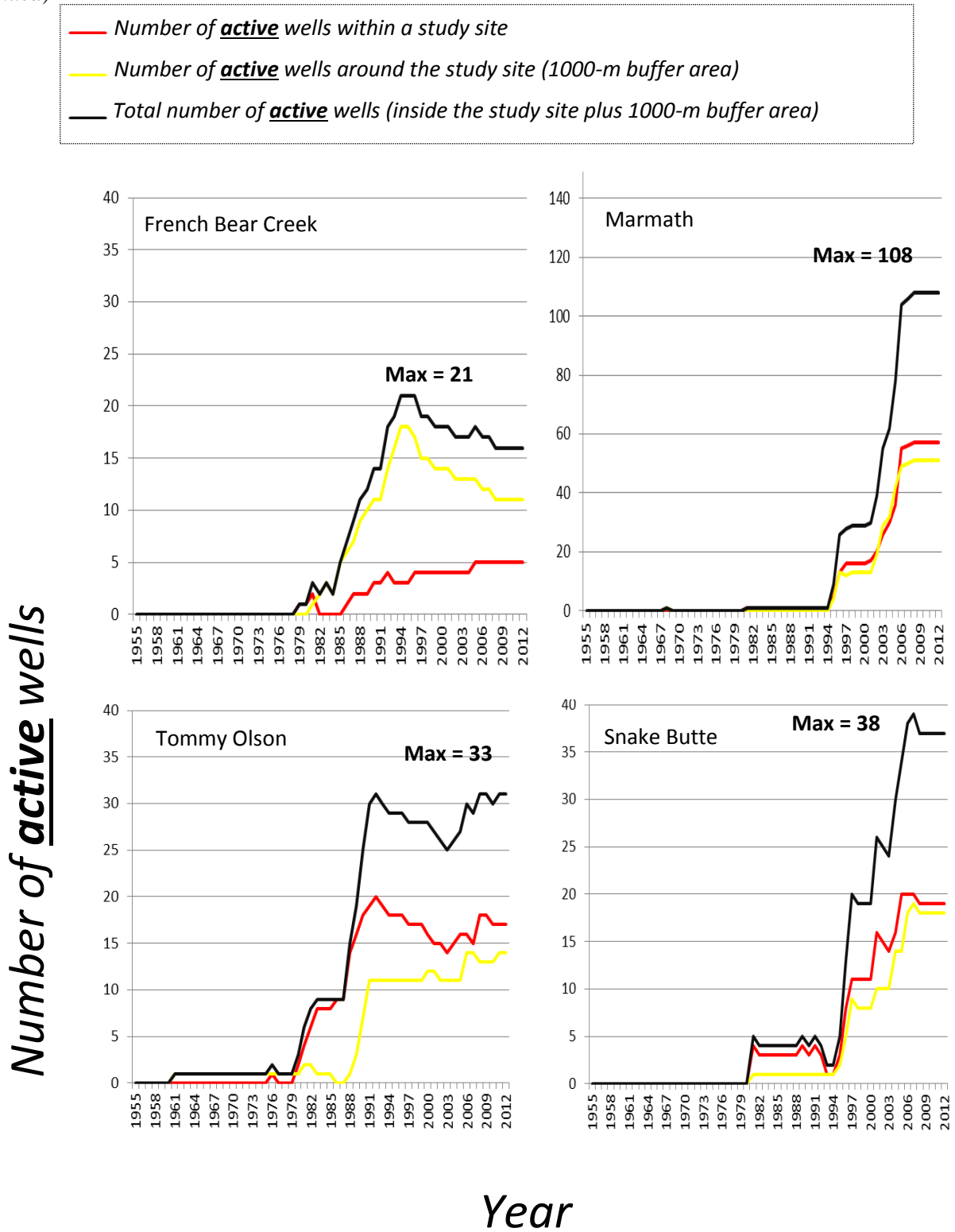
**Fig.1.7.** Number of active well sites (all types) present within mule deer study sites from 1956 to present. (continued)



**Fig.1.7.** Number of active well sites (all types) present within mule deer study sites from 1956 to present. (continued)

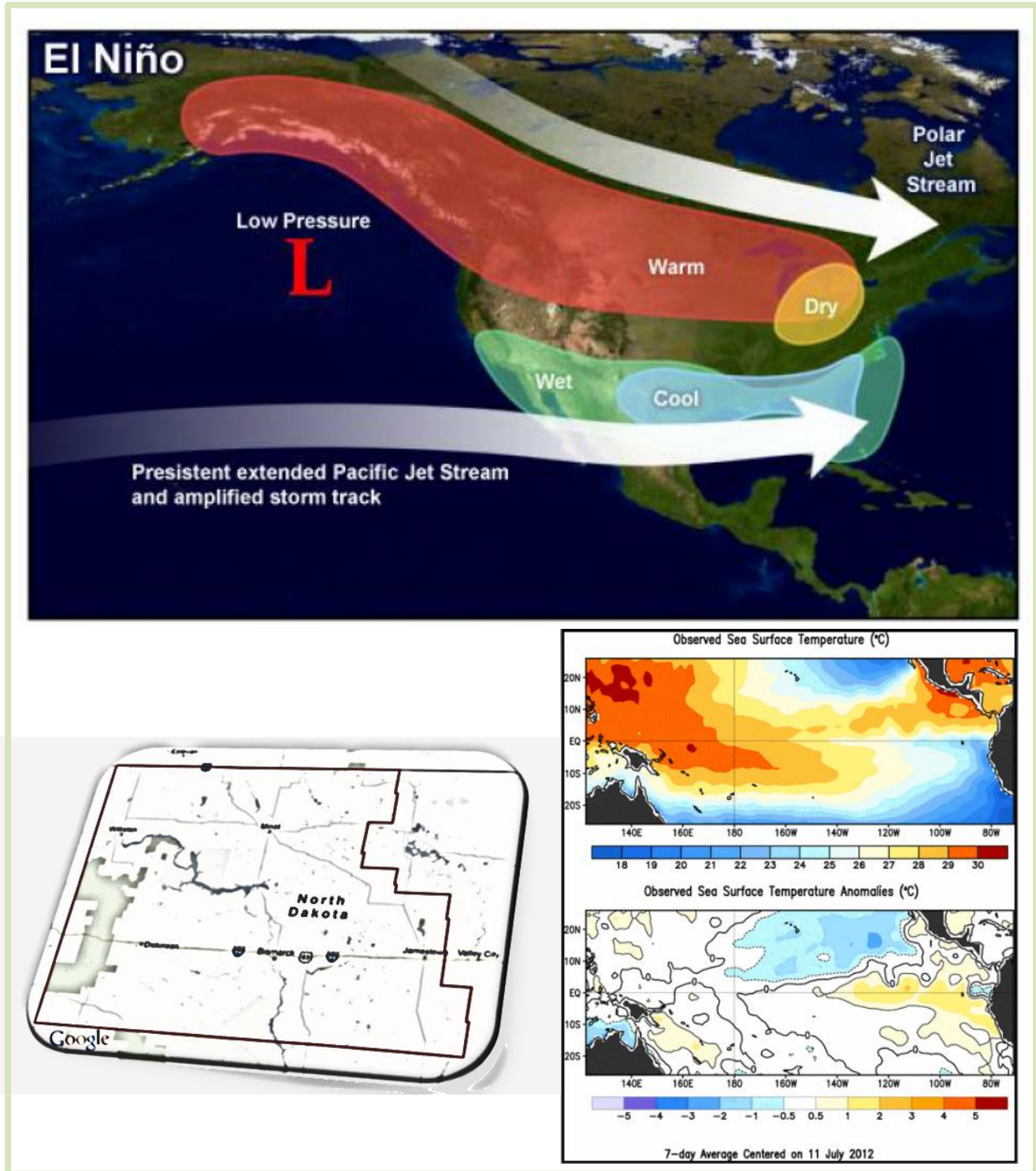


**Fig.1.7.** Number of active well sites (all types) present within mule deer study sites from 1956 to present. (continued)



# Chapter 1

## *Seasonal effects of local weather and Pacific-based climate on mule deer recruitment*



*Simone Ciuti, William F. Jensen, Scott E. Nielsen, Mark S. Boyce*

## Introduction

The effect of seasonal climate on fall fawn recruitment is critical for understanding factors ultimately responsible for the dynamics of large herbivore populations. Nutritional condition in mule deer has been reported to be the largest ultimate cause of mortality for fawns, with the exception of early summer fawn predation (Bishop et al. 2009, Forrester and Wittmer 2013). Mule deer are highly selective feeders that depend on forage quality more than quantity (Wallmo 1981), and annual weather effects on vegetation quality are expected to affect year-to-year mule deer dynamics (Parker et al. 2009, Forrester and Wittmer 2013).

Local weather stations can provide unique information on seasonal and yearly variation in climate at a fine scale that can be correlated with variation in fawn recruitment. However, recent research also has highlighted the predictive power of broad-scale climate indices. Indeed, the use of these large-scale indices as predictors of climate has the potential to shed light on our understanding of climate's influence on ecological patterns (Stenseth et al. 2003). Research on the influence of climate on large herbivores in western North America is still sparse (Griffith et al. 2002), and only a few studies have addressed the role of Pacific-based climate fluctuations (Hebblewhite 2005, Hegel et al. 2010a, Hegel et al. 2010b). However, in western regions of Europe and eastern North America, the North Atlantic Oscillation (NAO) index has been found to predict ecological processes even better than local weather because the index incorporates variation and interactions from multiple variables (e.g., temperature, precipitation) across multiple months and spatial scales (Stenseth et al. 2003, Hallett et al. 2004, Stenseth and Mysterud 2005). Large-scale indices are freely available online, are retrospectively available back to the early 1900's, and can be unique weather predictors for those areas where local weather stations are not available and /or are limited to short time series.

There is no information on the effect of large-scale indices on most continental areas of North America, where the distance from the closest ocean may exceed 2,000 km. In these continental areas characterized by cold and long winters, deer are constantly in negative energy balance during winter months because metabolic requirements cannot be met by foraging alone (Wallmo 1981, Torbit et al. 1985a, Torbit et al. 1985b, Parker et al. 1996). Deer survive by using fat and protein reserves accumulated during late summer and fall. Depletion rates of fat and muscle mass may vary depending on nutrient availability, winter severity, and energy expenditure. Combined, these factors have the potential to synergistically increase the rate at which nutrient body stores are depleted. If these impacts are of sufficient magnitude to cause increased overwinter deer mortality or reduced newborn fawn production and survival, dynamics of deer populations can be significantly affected by seasonal weather.

Weather can be related to recruitment through its influence on fecundity and/or fawn survival. Here we aim to test the effect of seasonal weather in a mule deer population of North Dakota, USA. We hypothesized that:

1) weather effects on mule deer recruitment are highly seasonal. Specifically, we expect that unfavourable weather conditions recorded prior (winter: November - March), during (spring: April - May) and after (summer: June - September) the birth of fawns negatively affect fawn survival and, consequently, fawn recruitment recorded during the fall (October). Harsh winter conditions are expected to weaken female condition with consequence on their reproductive success (Wallmo 1981, Torbit et al. 1985a, Torbit et al. 1985b, Parker et al. 1996). At the same time, snowy and cold spring weather can debilitate female body condition right at the end of the winter season when fat reserves in females are almost gone. Unfavourable spring weather makes the winter longer, with snow sometimes persisting on the ground for longer periods and delaying green-up. Finally, hot and dry summers are expected to reduce food quality and availability and reduce fawn survival;

2) a 1-year-lag effect of unfavourable seasonal weather conditions will persist on female deer body condition and thus on fawn recruitment;

3) the effect of Pacific-based climate indices (Pacific Decadal Oscillation PDO; North Pacific Index NPI, *a.k.a* North Pacific Patterns NP; Multivariate ENSO MEI, *a.k.a*. El Nino / La Nina fluctuations) on mule deer recruitment could occur even at >2,000 km from the Pacific Ocean coast. Specifically, we aim to verify i) the relationship between Pacific-based climate and local weather in the Great Plains, ii) the seasonal effect of Pacific-based climate on fawn recruitment, and iii) whether Pacific-based climate is a better predictor of deer recruitment than local weather covariates.

## Methods

### *1. Mule deer aerial surveys 1962 – 2012*

Data for our study were collected in the North Dakota badlands located in the south-western region of the state (Little Missouri River basin, **Fig. 2.1**). From 1962 to 2012, fall mule deer surveys were flown by staff of the North Dakota Fish and Game Department (Bismarck, North Dakota, USA) during the month of October. The mule deer study area (**Fig. 2.1**) has been surveyed each fall to determine deer population demographics and recruitment rates. A total of 54,744 mule deer was counted and classified over the monitored period (9,362 males, 22,699 females, 22,683 fawns). Yearly fall recruitment recorded in October (hereafter referred to as ‘recruitment’) is defined by the fawn : female ratio observed in the entire region. From 1962 to 2012, fawn : female ratio ranged from 0.59 to 1.52 (mean  $\pm$  SD, 1.07  $\pm$  0.22).

## 2. Local weather data

Local weather data including daily precipitation (mm), snowfall (mm), snow depth (mm), maximum temperature (degrees Celsius), and minimum temperature, were collected from 1962 to 2012 by the Medora weather station (station id: Medora ND US; elevation 686.1 m a.s.l.; Latitude 46.966°; Longitude -103.500°) centrally located in the mule study area (**Fig. 2.1**). Data are free online and are provided by the National Oceanic and Atmospheric Administration (NOAA, [www.noaa.gov](http://www.noaa.gov)). Daily observational raw data can be accessed through the GIS viewer at the following website: <http://gis.ncdc.noaa.gov/map/viewer/#app=cdo&cfg=cdo&theme=daily&layers=111&node=gis>.

Based on our knowledge of the ecology of mule deer and on available literature (Forrester and Wittmer 2013), we defined 3 main seasons when weather conditions were expected to affect female reproductive success and fawn survival, and, consequently, autumn recruitment (**Fig. 2.2**). We computed average local weather covariates on a seasonal scale; snow metrics were obviously not considered for summer (June – September). Also, we derived a Winter Severity Index (WSI) using data from the Medora station and according to a well-established protocol (Brinkman et al. 2005). To calculate this index of winter severity, we accumulated 1 point for each day in which mean ambient temperature was  $\leq -7^{\circ}\text{C}$ , and we accumulated an additional point for each day in which snow depth was  $\geq 35$  cm. WSI was computed for winters (November – March) and spring (April – May) of each year.

## 3. Pacific-based climate

We considered 3 Pacific-based climate indices

i) PDO (Pacific Decadal Oscillation). Data were freely available at the website

<http://www.esrl.noaa.gov/psd/data/climateindices/list/>

ii) NP (Trenberth and Hurrell monthly North Pacific Index, *a.k.a.*, NPI, also known as North Pacific pattern). NP data were freely available at the website

<https://climatedataguide.ucar.edu/climate-data/north-pacific-np-index-trenberth-and-hurrell-monthly-and-winter>

iii) MEI (multivariate ENSO, *i.e.*, El Niño / La Niña oscillations. El Niño occurs when MEI values are high, while La Niña occurs when MEI values are low)

MEI index (ranks) are freely available from the website

<http://www.esrl.noaa.gov/psd/enso/mei/#data>

All monthly Pacific-based indices were averaged on a seasonal scale (**Fig. 2.2**).

## 4. Data analyses

#### *4.1 Modelling fawn recruitment*

The primary objective of this work was to understand the effect of local weather data (1 weather station centrally located in the study area) and Pacific-based indices (same data for all North America) on fawn recruitment in the North Dakota badlands. We modelled the time series of fawn recruitment collected from 1962 to 2012 using the total number of fawns counted in the entire study area divided by total number of females counted in the same region each year. We did not attempt to test for the effect of local variation of weather conditions on fawn recruitment across different areas of the study region due to the lack of multiple weather stations with consistent reporting.

Recruitment was modelled as a function of the variable year (representing a long-term trend) and one ( $x$ ) or more seasonal weather covariates using a linear model with the underlying assumption that residuals are independently normally distributed with mean 0 and variance  $\sigma^2$ .

$$\text{Recruitment} = \alpha + \beta_1 \times \text{Year} + \beta_2 \times x + \dots + \varepsilon_s$$

#### *4.2 identifying seasonal local weather and Pacific-based climate predictors of fawn recruitment*

We tested for collinearity between explanatory variables by calculating pairwise Pearson's correlation coefficients within seasons. We detected clear collinearity issues between seasonal local weather covariates, and also between seasonal Pacific-based climate indices (winter: **Table 2.1**; spring: **Table 2.2**; summer: **Table 2.3**). We thus fitted linear models (structured as defined above) with only one weather covariate at time and ranked them based on Akaike Information Criterion corrected for small sample size (AICc). Within each group of covariates, those included in the model with the lowest AICc values were selected as candidate predictors to be included in the modelling of fawn recruitment. In regard to local weather covariates, best predictors of fawn recruitment were the average minimum temperature recorded in winter, and the average max temperature recorded in spring and summer (**Fig. 2.3**). In regard to Pacific-based climate indices, we found small differences in AICc values among top ranked candidate predictors during winter and summer ( $\Delta\text{AICc} < 1$ ). Thus, we defined 2 sets of predictor variables

Set 1: MEI (winter), NP (spring), and PDO (summer)

Set 2: NP (winter), NP (spring), and MEI (summer)

#### *4.3 modelling the seasonal effect of local weather and Pacific-based climate on fawn recruitment*

We fitted 3 *a priori* sets of linear models using local weather covariates and Pacific-based climate indices (set 1 and set 2) as predictors of fawn recruitment. In contrast to local weather covariates, Pacific-



based climate indices also can be collinear among different seasons. We did not include collinear indices (including 1-year lags) in the same model (**Table 2.4**).

For all sets of models, we performed model selection using AICc (Burnham and Anderson 2002). Because there was not much support for a single best model, we chose a confidence set of models ( $w_i > 0.90$ ) (Burnham et al. 2011) and we used model averaging to get averaged coefficients and standard errors (Burnham and Anderson 2002). We also calculated the relative importance of each explanatory variable as a sum of Akaike weights across all the models in the confidence set that contained that variable (Burnham and Anderson 2002).

We verified if assumptions of linear models were met. Normality of residuals was checked by visually inspecting Quantile-Quantile (QQ) plots. Autocorrelation plots of residuals were drawn to exclude the possibility of temporal autocorrelations. Relationships between observed and predicted recruitment in top ranked-models were analysed with the Pearson correlation coefficient to quantify how well the models fit the data. All analyses were performed in R 3.0.2 (R Development Core Team 2011).

## Results

### *1. Correlation between Pacific-based climate and local weather covariates.*

During winter (November – March) (**Table 2.1, Fig. 2.4**), MEI values were directly correlated to warmer and drier winters in the North Dakota badlands. PDO values were directly correlated to warmer winters (significant correlation with average minimum temperature). NP index was strongly and positively correlated to local weather covariates: NP values were directly correlated with snowfall and inversely correlated with average temperatures. Pacific-based indices were not correlated with Winter Severity Index (WSI) values.

During spring (April – May) (**Table 2.2, Fig. 2.5**), higher values of MEI meant drier (significant direct correlation with precipitation) and warmer springs. Higher values of PDO were correlated with drier and warmer springs (significant direct correlation with temperatures and inverse with WSI). NP values were correlated with increased precipitation and colder springs.

During summer (June – September) (**Table 2.3, Fig. 2.5**), MEI values were significantly correlated with precipitation and inversely correlated with temperatures. Also PDO values were correlated with rainy and cool summers. NP values were weakly correlated with local weather covariates during summer.

### *2. Seasonal effect of local weather on fawn recruitment*

The confidence set of linear models ( $w_i > 0.90$ ) on the effect of seasonal local weather on fawn recruitment was reported in **Table 2.5**. Based on averaged parameters and relative importance in the *An evaluation of historical mule deer fawn recruitment in North Dakota – Ciuti et al. 2014* Page | 24

confidence set of models (**Table 2.5**), weather condition recorded during the winter prior to the birth of fawns and those of the spring one year earlier - i.e., average minimum temperature in winter, and average maximum temperature in spring<sub>t-1</sub> – had the strongest positive effect on mule deer fawn recruitment (**Fig. 2.6a,b**). Weather conditions recorded in the other seasons (**Table 2.5**) had little relative importance on the confidence set of models and weak effect on fawn recruitment.

### 3. Seasonal effect of Pacific-based climate on fawn recruitment

The confidence set of linear models ( $w_i > 0.90$ , set 1) on the effect of seasonal Pacific-based climate on fawn recruitment was reported in **Table 2.6**. AICc of top ranked model using local weather covariates (AICc = -65.68, **Table 2.5**) was less than 4 AICc points smaller than the most parsimonious model using Pacific-based climate predictors (AICc = -61.72, **Table 2.6**). Similarly to using local weather covariates as predictors, Pacific-based climate indices from the winter prior to the birth of fawns and those of the spring one year earlier - i.e. average MEI in winter, and average NP in spring<sub>t-1</sub>, – had the strongest effect on mule deer fawn recruitment (**Table 2.6**). Recruitment increased when NP recorded in spring<sub>t-1</sub> decreased and MEI recorded in winter increased (**Fig. 2.6c,d**). Pacific-climate indices recorded in the other seasons (**Table 2.6**) had little relative importance on the confidence set of models and weak effect on fawn recruitment.

The confidence set of linear models ( $w_i > 0.90$ ) using the set 2 of seasonal Pacific-based climate indices to predict fawn recruitment was reported in **Table 2.7**. AICc of top-ranked model of set 2 (AICc = -61.14, Table 6) was almost the same of that for set 1 (AICc = -61.72, Table 5), showing how predictive abilities of the 2 sets of Pacific-based climate indices were comparable. According to prediction of the second set of models (**Table 2.7**), fawn recruitment increased as NP index recorded in spring<sub>t-1</sub> and winter decreased (**Fig. 2.6e,f**).

### 4. Model validation

Autocorrelation plots for the residuals of top-ranked models ( $w_i > 0.90$ ) confirmed the absence of temporal autocorrelation issues and that the assumption of independence of residuals was met (**Fig. 2.7, 2.8, 2.9**). Relationships between observed and predicted mule deer recruitment in top-ranked models were inspected to verify goodness of fit in our models (**Fig. 2.10**). Models fit the data well with predicted and observed recruitment rates highly correlated ( $r_p > 0.84$ ,  $p < 0.001$ ).

## Discussion

Mule deer range from the northern Yukon Territories of Canada to central Mexico and from the 100th Meridian west to the Pacific coast. The species occupies habitats ranging from the tallgrass and

shortgrass prairie in the east, to mountain shrub, shrub steppe, woodlands and all forest types of the Rocky Mountains in the northwest, and the desert scrub of the southwest (Wallmo 1981). Mule deer habitats generally are characterized by early stages of plant succession, mixed plant communities and available browse (Baker et al. 1979, Carpenter et al. 1979, Wallmo 1981). Over such a wide distributional range, it is possible that the forage species may suffer from summer drought with consequences on fawn survival at least in the southern and western areas of mule deer range. However, recent research (Forrester and Wittmer 2013) has found that high winter snowfall can lower winter fawn survival across almost the entire mule deer range, with little evidence of summer precipitation affecting survival in the following year, indicating that increases in forage in summers following high snowfall years did not compensate for lower survival in high snowfall winters. This is in full agreement with what our models predicted for mule deer in southwestern North Dakota, with no detectable effect of summer conditions on fawn recruitment, even when we considered 1-year time lags. North Dakota badlands host a mule deer population more distant from the Pacific Ocean, where long and harsh winters appear to be the most limiting season in the mule deer biological cycle; at least concerning fawn recruitment. More specifically, we accurately predicted seasonal effects of local weather on fawn recruitment and found that weather conditions in the winter prior to the birth season, as well as in spring one year earlier, are the best predictors of mule deer fall recruitment in the North Dakota badlands. Harsh winter conditions likely weaken female body condition in the badlands prior to birth with negative consequences for their reproductive success, thus confirming what has been shown for other North American populations (Wallmo 1981, Torbit et al. 1985a, Torbit et al. 1985b, Parker et al. 1996). Additionally, we found a clear effect of weather recorded in the spring one year before the birth of fawns on the final output of population recruitment. Harsh springs (time lag year -1) are critical because they make the winter much longer and can further weaken females that face the next winter (the one just prior to birth) with reduced body condition.

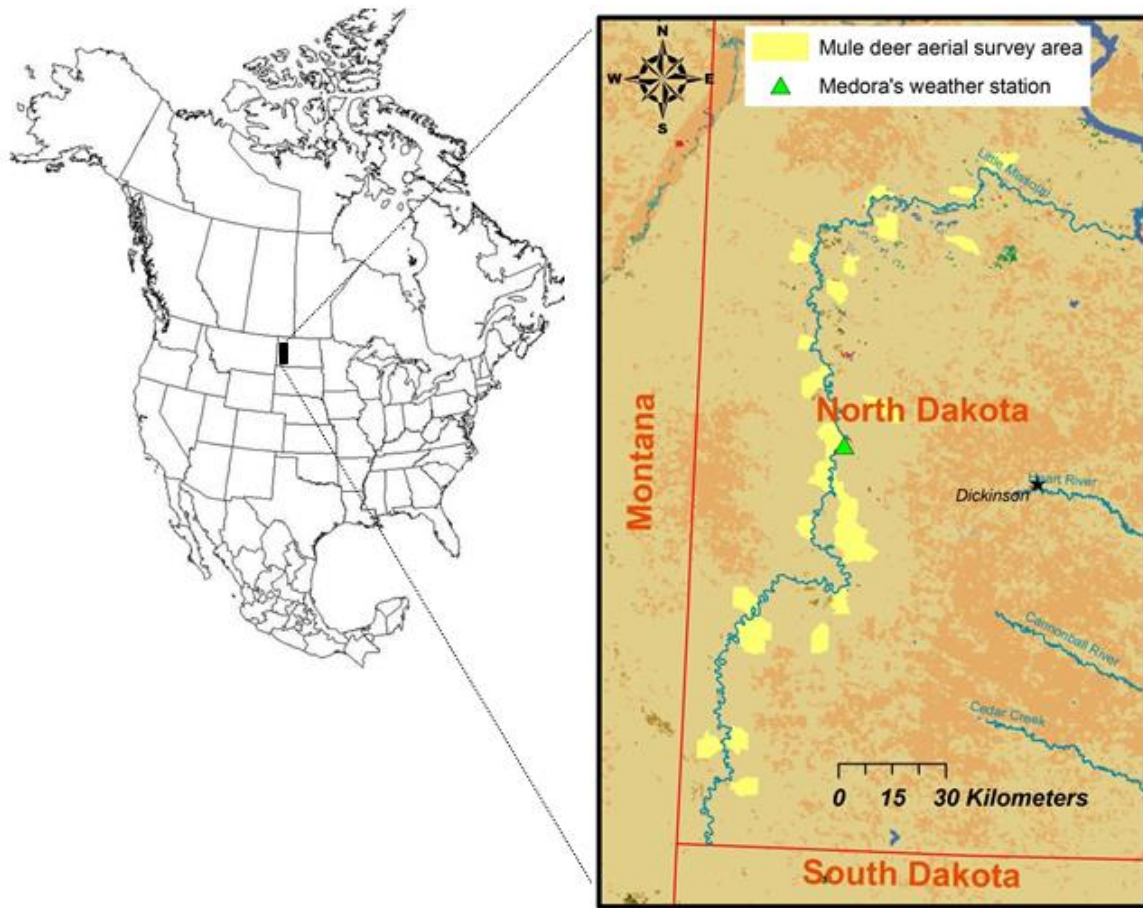
Interestingly, we did not find negative effects of 2 harsh winters in a row on fawn recruitment. Clearly, the first harsh winter negatively affect fawn recruitment, as confirmed by our analyses; however, females who did not give birth to a fawn or lost it due to weakened body condition due to adverse winter, reduced energy expenditure (no weaning) and were in a better condition to face the second harsh winter. This is likely the reason why our analyses did not detect any negative effect of 2 consecutive adverse winters.

Temperatures captured more variability in fawn recruitment than other metrics of local weather, such as snowfall or even more comprehensive covariates like the Winter Severity Index. For subpopulations spread over such a large area, as is the case in our study area, one single weather metric

(e.g., snow depth) derived from a single local weather station may not represent conditions experienced by all individuals. Temperature gradients are less spatially variable than snow depth or precipitation, which could be locally high at the weather station but not representative of the entire area and influenced by other parameters such as wind and freezing and thawing. In conclusion, temperature gradients are definitely better predictors of fawn recruitment, as also suggested by previous research (Melis et al. 2009, Hegel et al. 2010a, Hegel et al. 2010b).

Even at more than 2000 km from the Pacific coast, large-scale climatic indices remarkably had almost the same predictive power as local weather covariates. Pacific Oscillations still showed some predictive capacity with recruitment even with the thorough examination of other local factors. Pacific-based climate indices confirmed the same scenario depicted by local weather covariates, with winter prior to birth and 1-year time lag spring being the limiting seasons able to affect fawn recruitment. This opens new management opportunities for the Great Plains, where the predictability power of large-scale climate indices has been neglected due to the great distance from the Pacific Ocean. Large-scale climate indices are characterized by cycles that can be predicted in advance by statistical models and could be taken into account in management plans for a number of wildlife species. In North Dakota, NP and MEI have the best predictive power for explaining variability in mule deer fawn recruitment. The cyclic and predictive nature of NP and MEI also holds management implications for North Dakota in general; specifically for planning purposes by the farming and ranching communities.

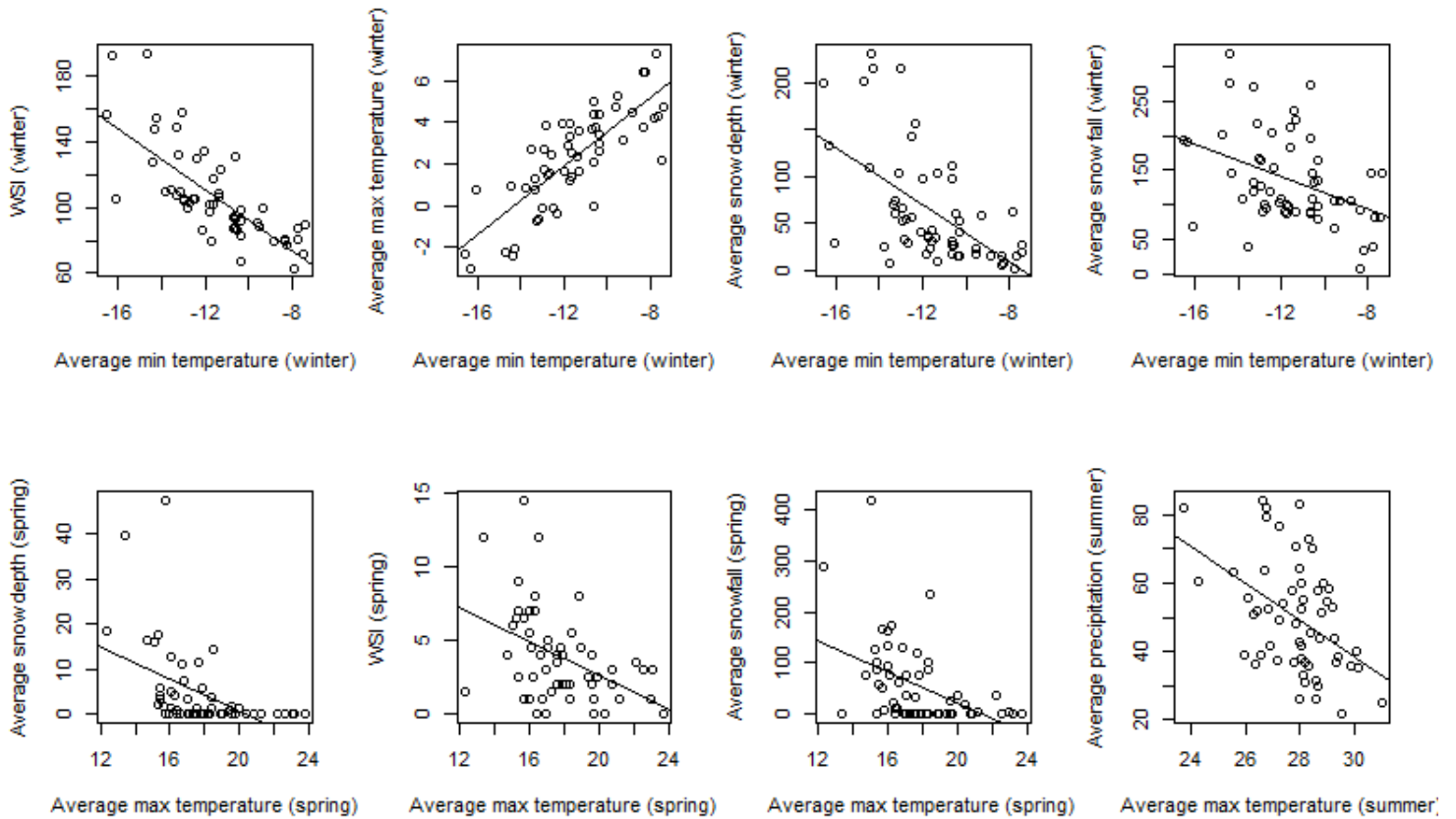
**Fig. 2.1.** Map of the mule deer study area located along the Little Missouri River, North Dakota badlands, where surveys were flown from 1962 to 2012. The location of the Medora weather station is indicated in the map (latitude: 46.96°; longitude: -103.50°; elevation: 686 m a.s.l.)



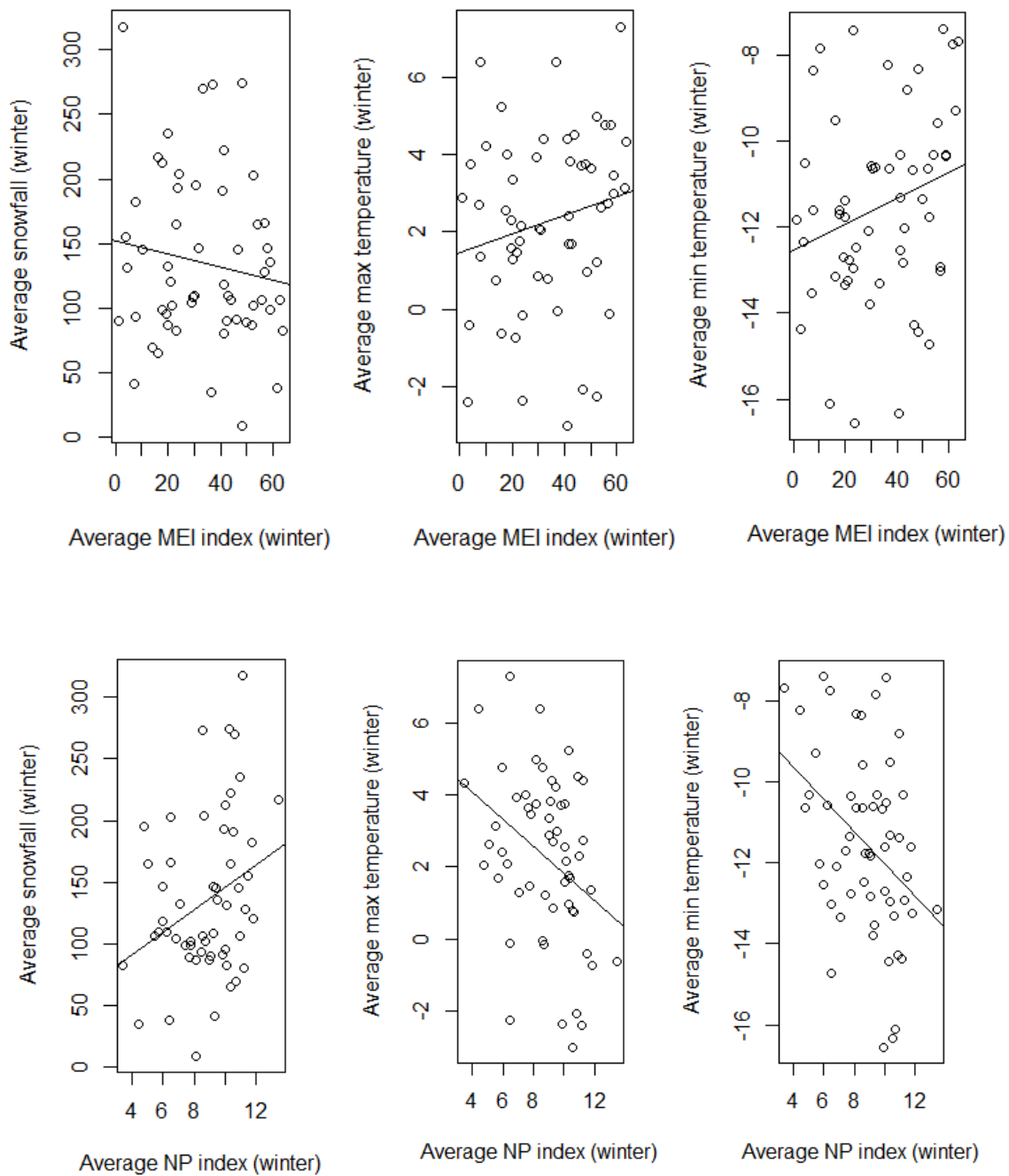
**Fig. 2.2.** Diagram depicting seasonal intervals at which local weather and Pacific-based climate covariates were computed as predictors of mule deer fawn recruitment. Seasons before, during and after the birth of fawns were considered, as well as those seasons when weather was expected to affect body condition of females on the long term (1-year lag).



**Fig. 2.3.** Relationship between best local weather predictors of fawn recruitment (upper panel: Average min temperature in winter; lower panel: average max temperature in spring and average max temperature in summer) with the other local weather covariates (1956-2012). Local weather data were collected by the Medora weather station, North Dakota, centrally located in mule deer study area. See **Table 2.1-2.3** for pairwise correlation coefficients; linear regression fits were added to improve readability of plots.

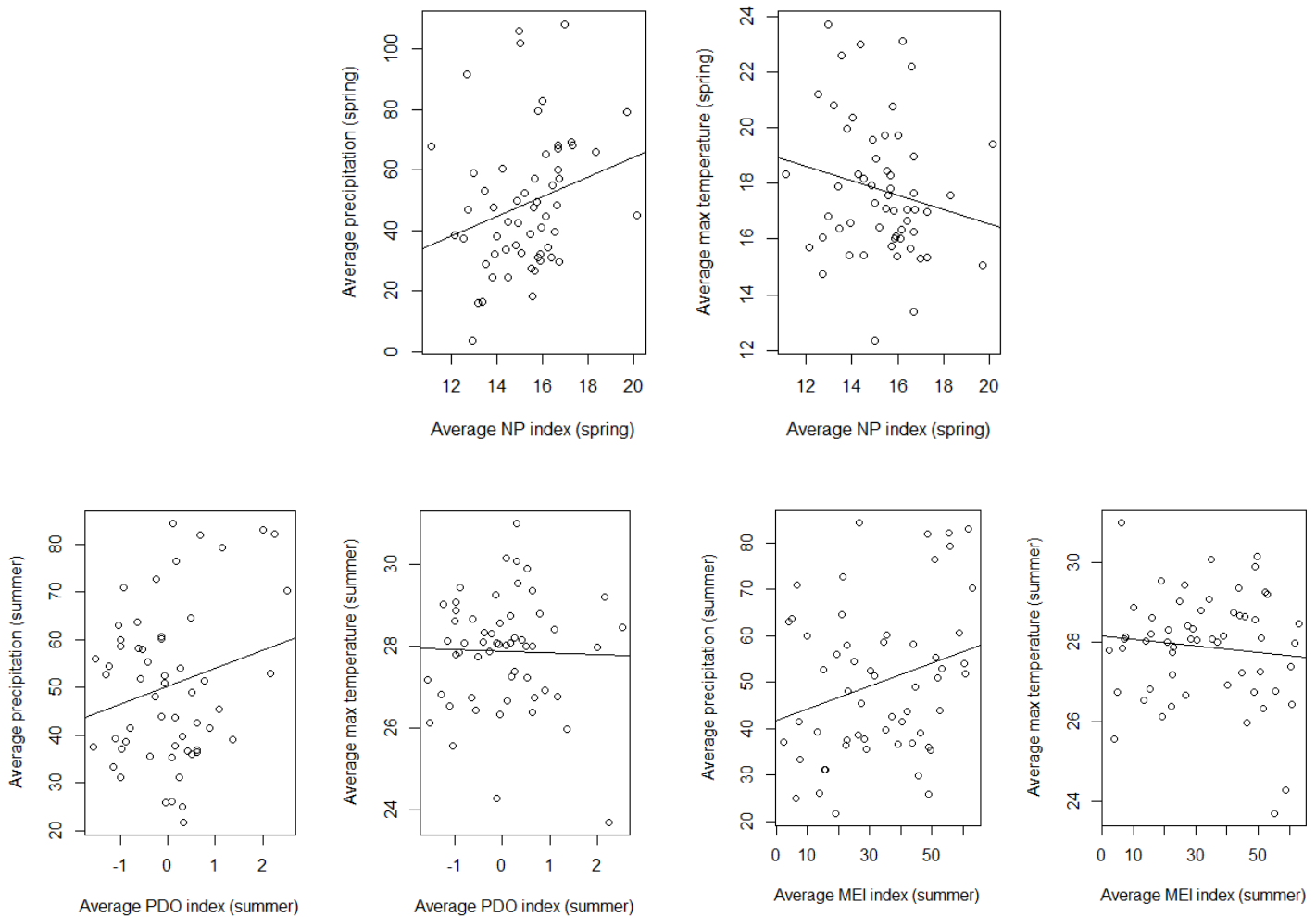


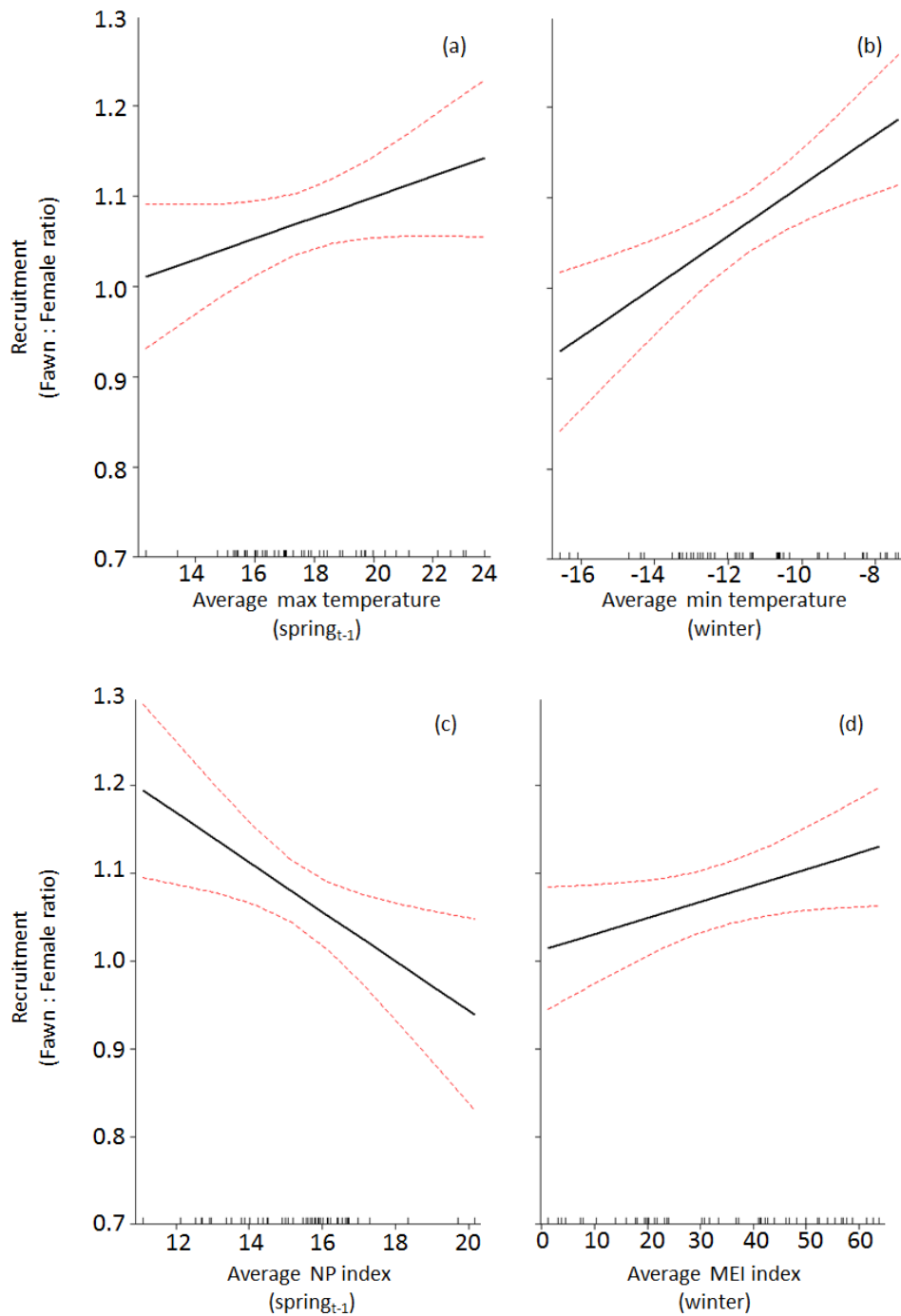
**Fig. 2.4.** Relationship between best Pacific-based climate winter predictors of fawn recruitment (upper panel: Average MEI index; lower panel: average NP index) with local weather covariates (1956-2012). Local weather data were collected by the Medora weather station, North Dakota, centrally located in mule deer study area. See **Table 2.1** for pairwise correlation coefficients; linear regression fits were added to improve readability of plots.



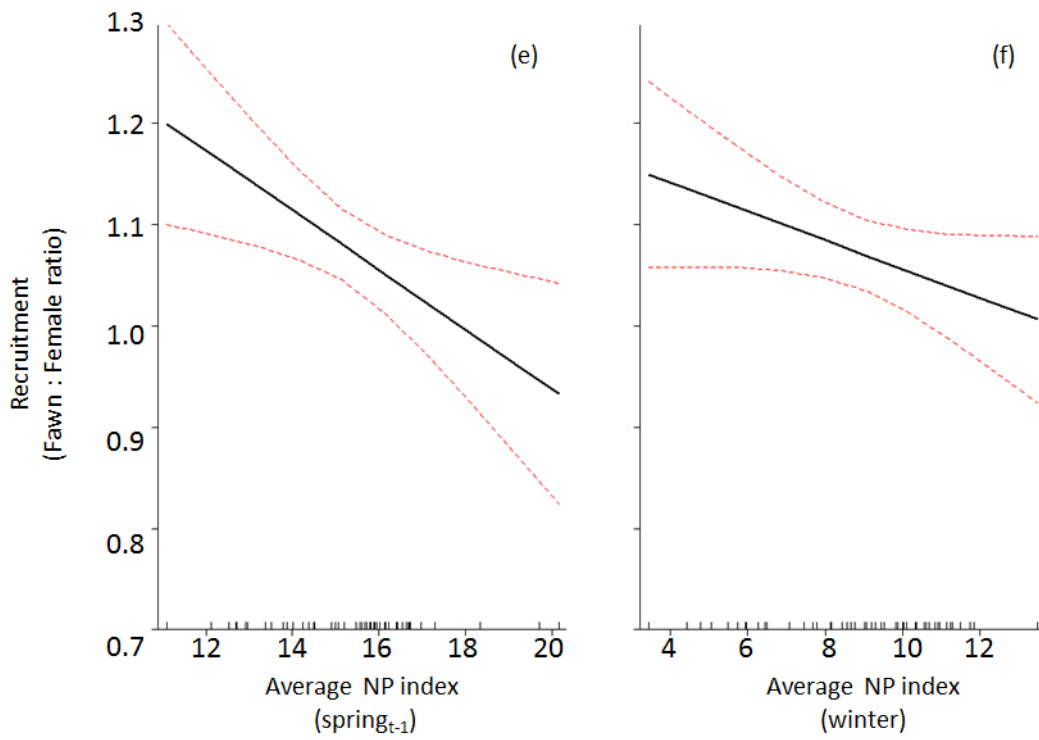


**Fig. 2.5.** Relationship between best Pacific-based climate predictors of fawn recruitment (upper panel: Average NP index in spring; lower panel: average PDO and MEI indices in summer) with local weather covariates (1956-2012). Local weather data were collected by the Medora weather station, North Dakota, centrally located in the mule deer study area. See **Table 2.2-2.3** for pairwise correlation coefficients; linear regression fits were added to improve readability of plots.



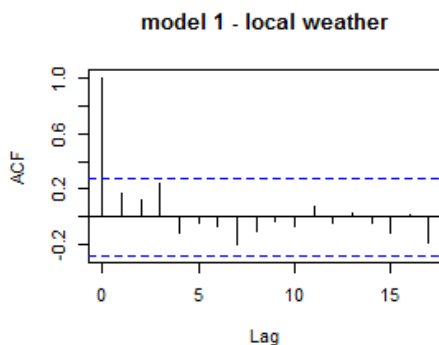


**Fig. 2.6.** Effects of local weather covariates (a,b) and Pacific-based indices (c-d, see next page for e-f) recorded during spring<sub>t-1</sub> (i.e., 1 year prior to the birth of fawns) and winter (i.e., during female pregnancy) on fall fawn recruitment (fawn:female ratio) in the North Dakota badlands (1962-2012). Predictions were estimated by Linear Models fitted using local weather predictors (a,b) and 2 different sets of Pacific-based climate predictors (set 1: c, d; set 2: e, f) [See bottom panels of **Tables 2.5, 2.6, and 2.7** for details on intercepts and slopes of linear models].

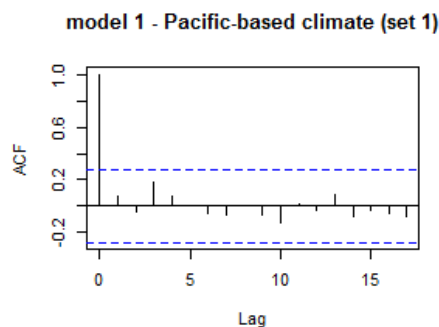


**Fig. 2.6.(continued)**

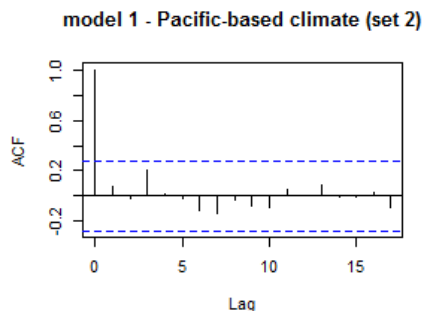
**Fig. 2.7** Autocorrelation plot for the residuals of the top ranked Linear Model of the effect of seasonal local weather on fawn recruitment in the North Dakota badlands (1962-2012). ACF values (auto-correlation function) are plotted against time lag (x-axis, year).



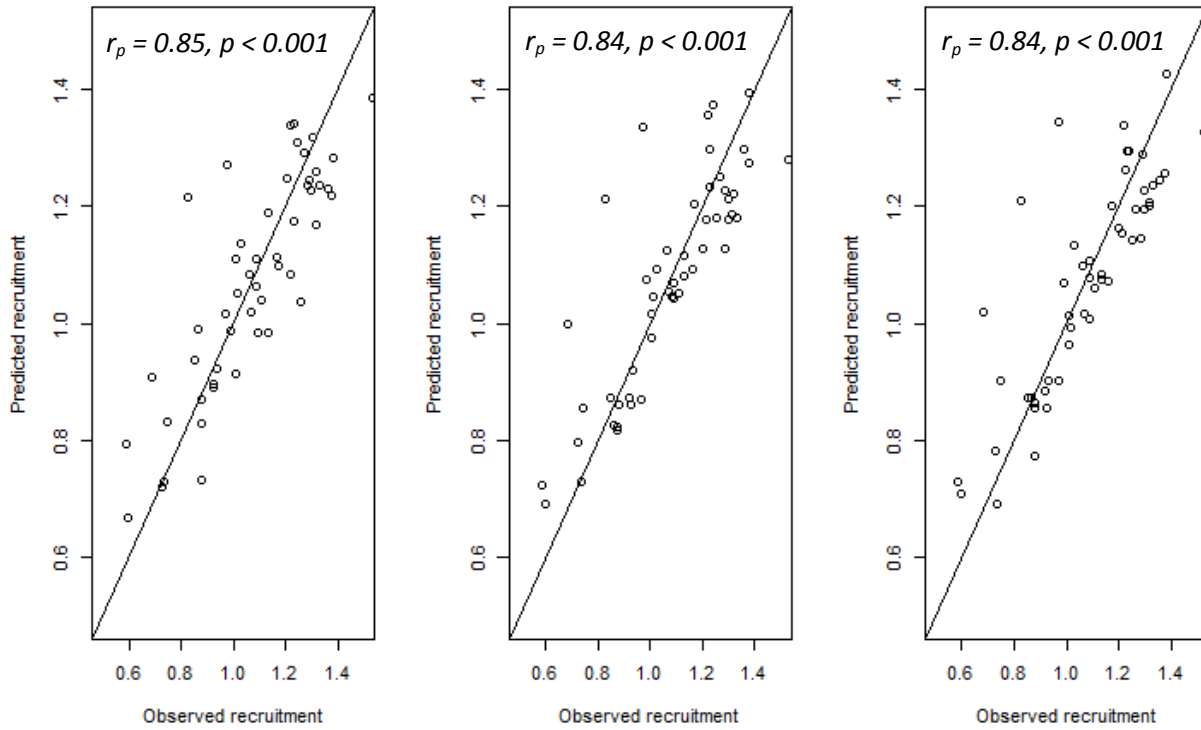
**Fig. 2.8** Autocorrelation plot for the residuals of the top ranked Linear Model of the effect of seasonal Pacific-based climate (set 1, i.e., using MEI, NP, and PDO indices recorded for winter, spring, and summer, respectively) on fawn recruitment in the North Dakota badlands (1962-2012). ACF values (auto-correlation function) are plotted against time lag (x-axis, year).



**Fig. 2.9** Autocorrelation plot for the residuals of the top ranked Linear Model of the effect of seasonal Pacific-based climate (set 2, i.e., using NP indices for both winter and spring, and MEI index for summer) on fawn recruitment in the North Dakota badlands (1962-2012). ACF values (auto-correlation function) are plotted against time lag (x-axis, year).



**Fig 2.10** – Relationship between observed and predicted mule deer recruitment rates in the North Dakota badlands (1962-2012). The diagonal line represents perfect correlation ( $r_p = 1.0$ ). Predicted recruitment rates were estimated by top-ranked Linear Models fitted with local weather covariates (left plot) and pacific-based indices (set 1: central plot; set 2: right plot). See **Tables 2.5-2.7** for details on Linear Models.



**Table 2.1.** Matrix of pairwise correlation coefficients between local weather covariates and Pacific-based climate predictors (1962 – 2012) during winter. Local weather data were collected by the Medora weather station, North Dakota, centrally located in the mule deer study area. Significant correlations ( $p < 0.05$ ) are bolded.

|                           | Average precipitation | Average snowfall | Average snow depth | Average max temp | Average min temp | Winter Severity Index WSI | Average MEI index | Average NP index | Average PDO index |
|---------------------------|-----------------------|------------------|--------------------|------------------|------------------|---------------------------|-------------------|------------------|-------------------|
| Average precipitation     |                       | <b>0.77</b>      | <b>0.52</b>        | <b>-0.51</b>     | <b>-0.28</b>     | <b>0.32</b>               | -0.14             | 0.24             | 0.00              |
| Average snowfall          | <b>0.77</b>           |                  | <b>0.64</b>        | <b>-0.62</b>     | <b>-0.41</b>     | <b>0.48</b>               | -0.14             | <b>0.30</b>      | 0.00              |
| Average snow depth        | <b>0.52</b>           | <b>0.64</b>      |                    | <b>-0.8</b>      | <b>-0.58</b>     | <b>0.79</b>               | -0.05             | 0.14             | -0.09             |
| Average max temp          | <b>-0.51</b>          | <b>-0.62</b>     | <b>-0.8</b>        |                  | <b>0.79</b>      | <b>-0.8</b>               | 0.19              | <b>-0.35</b>     | 0.14              |
| Average min temp          | <b>-0.28</b>          | <b>-0.41</b>     | <b>-0.58</b>       | <b>0.79</b>      |                  | <b>-0.75</b>              | 0.24              | <b>-0.38</b>     | <b>0.29</b>       |
| Winter Severity Index WSI | <b>0.32</b>           | <b>0.48</b>      | <b>0.79</b>        | <b>-0.8</b>      | <b>-0.75</b>     |                           | -0.01             | 0.10             | -0.07             |
| Average MEI index         | -0.14                 | -0.14            | -0.05              | 0.19             | 0.24             | -0.01                     |                   | <b>-0.46</b>     | <b>0.56</b>       |
| Average NP index          | 0.24                  | <b>0.30</b>      | 0.14               | <b>-0.35</b>     | <b>-0.38</b>     | 0.1                       | <b>-0.46</b>      |                  | <b>-0.72</b>      |
| Average PDO index         | 0.00                  | 0.00             | -0.09              | 0.14             | <b>0.29</b>      | -0.07                     | <b>0.56</b>       | <b>-0.72</b>     |                   |

**Table 2.2.** Matrix of pairwise correlation coefficients between local weather covariates and Pacific-based climate predictors (1962 – 2012) during **spring**. Local weather data were collected by the Medora weather station, North Dakota, centrally located in the mule deer study area. Significant correlations ( $p < 0.05$ ) are bolded.

|                           | Average precipitation | Average snowfall | Average snow depth | Average max temp | Average min temp | Winter Severity Index WSI | Average MEI index | Average NP index | Average PDO index |
|---------------------------|-----------------------|------------------|--------------------|------------------|------------------|---------------------------|-------------------|------------------|-------------------|
| Average precipitation     |                       | <b>0.36</b>      | 0.22               | <b>-0.45</b>     | 0.22             | -0.09                     | <b>-0.27</b>      | 0.25             | -0.25             |
| Average snowfall          | <b>0.36</b>           |                  | <b>0.5</b>         | <b>-0.46</b>     | <b>-0.27</b>     | 0.17                      | -0.03             | 0.13             | 0.06              |
| Average snow depth        | 0.22                  | <b>0.5</b>       |                    | <b>-0.48</b>     | -0.19            | <b>0.57</b>               | -0.06             | -0.05            | 0.05              |
| Average max temp          | <b>-0.45</b>          | <b>-0.46</b>     | <b>-0.48</b>       |                  | <b>0.52</b>      | <b>-0.44</b>              | 0.22              | -0.18            | <b>0.26</b>       |
| Average min temp          | 0.22                  | <b>-0.27</b>     | -0.19              | <b>0.52</b>      |                  | <b>-0.55</b>              | 0.15              | -0.12            | 0.22              |
| Winter Severity Index WSI | -0.09                 | 0.17             | <b>0.57</b>        | <b>-0.44</b>     | <b>-0.55</b>     |                           | -0.11             | 0.05             | <b>-0.27</b>      |
| Average MEI index         | <b>-0.27</b>          | -0.03            | -0.06              | 0.22             | 0.15             | -0.11                     |                   | <b>-0.48</b>     | <b>0.57</b>       |
| Average NP index          | 0.25                  | 0.13             | -0.05              | -0.18            | -0.12            | 0.05                      | <b>-0.48</b>      |                  | <b>-0.52</b>      |
| Average PDO index         | -0.25                 | 0.06             | 0.05               | <b>0.26</b>      | 0.22             | <b>-0.27</b>              | <b>0.57</b>       | <b>-0.52</b>     |                   |

**Table 2.3.** Matrix of pairwise correlation coefficients between local weather covariates and Pacific-based climate predictors (1962 – 2012) during summer. Local weather data were collected by the Medora weather station, North Dakota, centrally located in the mule deer study area. Significant correlations ( $p < 0.05$ ) are bolded.

|                         | Average precipitation | Average max temperature | Average min temperature | Average MEI index | Average NP index | Average PDO index |
|-------------------------|-----------------------|-------------------------|-------------------------|-------------------|------------------|-------------------|
| Average precipitation   |                       | <b>-0.45</b>            | -0.18                   | <b>0.29</b>       | 0.01             | 0.22              |
| Average max temperature | <b>-0.45</b>          |                         | <b>0.44</b>             | -0.11             | -0.02            | -0.02             |
| Average min temperature | -0.18                 | <b>0.44</b>             |                         | 0.18              | -0.16            | 0.19              |
| Average MEI index       | <b>0.29</b>           | -0.11                   | 0.18                    |                   | <b>-0.24</b>     | <b>0.60</b>       |
| Average NP index        | 0.01                  | -0.02                   | -0.16                   | <b>-0.24</b>      |                  | -0.16             |
| Average PDO index       | 0.22                  | -0.02                   | 0.19                    | <b>0.60</b>       | -0.16            |                   |



**Table 2.4.** Matrix of pairwise correlation coefficients between seasonal Pacific-based climate predictors (1962 – 2012), including 1-year time-lag seasons. Significant correlations ( $p < 0.05$ ) were bolded.

|                                | Average MEI index (winter) | Average MEI index (spring) | Average MEI index (summer) | Average NP index (winter) | Average NP index (spring) | Average NP index (summer) | Average PDO index (winter) | Average PDO index (spring) | Average PDO index (summer) | Average MEI index (winter t-1) | Average MEI index (spring t-1) | Average MEI index (summer t-1) | Average NP index (winter t-1) | Average NP index (spring t-1) | Average NP index (summer t-1) | Average PDO index (winter t-1) | Average PDO index (spring t-1) | Average PDO index (summer t-1) |
|--------------------------------|----------------------------|----------------------------|----------------------------|---------------------------|---------------------------|---------------------------|----------------------------|----------------------------|----------------------------|--------------------------------|--------------------------------|--------------------------------|-------------------------------|-------------------------------|-------------------------------|--------------------------------|--------------------------------|--------------------------------|
| Average MEI index (winter)     |                            | <b>0.6</b>                 | 0.1                        | <b>-0.5</b>               | <b>-0.3</b>               | 0.1                       | <b>0.6</b>                 | <b>0.6</b>                 | <b>0.4</b>                 | 0.0                            | <b>0.4</b>                     | <b>0.9</b>                     | 0.1                           | -0.1                          | <b>-0.3</b>                   | 0.0                            | 0.1                            | <b>0.5</b>                     |
| Average MEI index (spring)     | <b>0.6</b>                 |                            | <b>0.7</b>                 | <b>-0.3</b>               | <b>-0.5</b>               | 0.0                       | <b>0.3</b>                 | <b>0.6</b>                 | <b>0.6</b>                 | -0.1                           | 0.2                            | <b>0.4</b>                     | 0.2                           | -0.3                          | -0.1                          | -0.1                           | 0.1                            | <b>0.4</b>                     |
| Average MEI index (summer)     | 0.1                        | <b>0.7</b>                 |                            | 0.0                       | <b>-0.3</b>               | -0.2                      | 0.1                        | 0.3                        | <b>0.6</b>                 | -0.2                           | -0.1                           | 0.0                            | 0.0                           | 0.0                           | 0.1                           | -0.1                           | 0.0                            | 0.1                            |
| Average NP index (winter)      | <b>-0.5</b>                | <b>-0.3</b>                | 0.0                        |                           | 0.1                       | <b>-0.3</b>               | <b>-0.7</b>                | <b>-0.6</b>                | <b>-0.3</b>                | 0.0                            | <b>-0.3</b>                    | <b>-0.5</b>                    | 0.0                           | 0.1                           | 0.0                           | -0.1                           | -0.1                           | <b>-0.3</b>                    |
| Average NP index (spring)      | <b>-0.3</b>                | <b>-0.5</b>                | <b>-0.3</b>                | 0.1                       |                           | 0.0                       | -0.2                       | <b>-0.6</b>                | <b>-0.5</b>                | -0.2                           | <b>-0.3</b>                    | -0.2                           | 0.1                           | <b>0.3</b>                    | -0.1                          | -0.1                           | <b>-0.3</b>                    | <b>-0.4</b>                    |
| Average NP index (summer)      | 0.1                        | 0.0                        | -0.2                       | <b>-0.3</b>               | 0.0                       |                           | <b>0.4</b>                 | 0.3                        | -0.2                       | 0.0                            | 0.2                            | 0.2                            | -0.1                          | -0.2                          | -0.2                          | 0.1                            | 0.2                            | <b>0.3</b>                     |
| Average PDO index (winter)     | <b>0.6</b>                 | 0.3                        | 0.1                        | <b>-0.7</b>               | -0.2                      | <b>0.4</b>                |                            | <b>0.7</b>                 | <b>0.4</b>                 | 0.2                            | <b>0.5</b>                     | <b>0.6</b>                     | -0.3                          | <b>-0.3</b>                   | -0.1                          | <b>0.3</b>                     | <b>0.5</b>                     | <b>0.7</b>                     |
| Average PDO index (spring)     | <b>0.6</b>                 | <b>0.6</b>                 | <b>0.3</b>                 | <b>-0.6</b>               | <b>-0.6</b>               | <b>0.3</b>                | <b>0.7</b>                 |                            | <b>0.7</b>                 | <b>0.3</b>                     | <b>0.5</b>                     | <b>0.5</b>                     | -0.2                          | <b>-0.3</b>                   | 0.0                           | <b>0.3</b>                     | <b>0.5</b>                     | <b>0.6</b>                     |
| Average PDO index (summer)     | <b>0.4</b>                 | <b>0.6</b>                 | <b>0.6</b>                 | <b>-0.3</b>               | <b>-0.5</b>               | -0.2                      | <b>0.4</b>                 | <b>0.7</b>                 |                            | 0.0                            | 0.1                            | <b>0.3</b>                     | -0.1                          | -0.1                          | 0.0                           | 0.2                            | 0.3                            | <b>0.3</b>                     |
| Average MEI index (winter t-1) | 0.0                        | -0.1                       | -0.2                       | 0.0                       | -0.2                      | 0.0                       | 0.2                        | <b>0.3</b>                 | 0.0                        |                                | <b>0.6</b>                     | 0.2                            | <b>-0.5</b>                   | <b>-0.3</b>                   | 0.1                           | <b>0.6</b>                     | <b>0.6</b>                     | <b>0.4</b>                     |
| Average MEI index (spring t-1) | <b>0.4</b>                 | 0.2                        | -0.1                       | <b>-0.3</b>               | <b>-0.3</b>               | 0.2                       | <b>0.5</b>                 | <b>0.5</b>                 | 0.1                        | <b>0.6</b>                     |                                | <b>0.7</b>                     | <b>-0.3</b>                   | <b>-0.5</b>                   | -0.1                          | <b>0.4</b>                     | <b>0.6</b>                     | <b>0.6</b>                     |
| Average MEI index (summer t-1) | <b>0.9</b>                 | <b>0.4</b>                 | 0.0                        | <b>-0.5</b>               | -0.2                      | 0.2                       | <b>0.6</b>                 | <b>0.5</b>                 | <b>0.3</b>                 | 0.2                            | <b>0.7</b>                     |                                | -0.1                          | -0.3                          | -0.3                          | 0.1                            | <b>0.3</b>                     | <b>0.6</b>                     |
| Average NP index (winter t-1)  | 0.1                        | 0.2                        | 0.0                        | 0.0                       | 0.1                       | -0.1                      | -0.3                       | -0.2                       | -0.1                       | <b>-0.5</b>                    | <b>-0.3</b>                    | -0.1                           |                               | 0.1                           | <b>-0.3</b>                   | <b>-0.7</b>                    | <b>-0.7</b>                    | <b>-0.3</b>                    |
| Average NP index (spring t-1)  | -0.1                       | -0.3                       | 0.0                        | 0.1                       | <b>0.3</b>                | -0.2                      | <b>-0.3</b>                | <b>-0.3</b>                | -0.1                       | <b>-0.3</b>                    | <b>-0.5</b>                    | -0.3                           | 0.1                           |                               | 0.0                           | -0.2                           | <b>-0.5</b>                    | <b>-0.5</b>                    |
| Average NP index (summer t-1)  | <b>-0.3</b>                | -0.1                       | 0.1                        | 0.0                       | -0.1                      | -0.2                      | -0.1                       | 0.0                        | 0.0                        | 0.1                            | -0.1                           | -0.3                           | -0.3                          | 0.0                           |                               | <b>0.3</b>                     | 0.2                            | -0.2                           |
| Average PDO index (winter t-1) | 0.0                        | -0.1                       | -0.1                       | -0.1                      | -0.1                      | 0.1                       | <b>0.3</b>                 | <b>0.3</b>                 | 0.2                        | <b>0.6</b>                     | <b>0.4</b>                     | 0.1                            | <b>-0.7</b>                   | -0.2                          | <b>0.3</b>                    |                                | <b>0.8</b>                     | <b>0.4</b>                     |
| Average PDO index (spring t-1) | 0.1                        | 0.1                        | 0.0                        | -0.1                      | <b>-0.3</b>               | 0.2                       | <b>0.5</b>                 | <b>0.5</b>                 | 0.3                        | <b>0.6</b>                     | <b>0.6</b>                     | <b>0.3</b>                     | <b>-0.7</b>                   | <b>-0.5</b>                   | 0.2                           | <b>0.8</b>                     |                                | <b>0.7</b>                     |
| Average PDO index (summer t-1) | <b>0.5</b>                 | <b>0.4</b>                 | 0.1                        | <b>-0.3</b>               | <b>-0.4</b>               | <b>0.3</b>                | <b>0.7</b>                 | <b>0.6</b>                 | <b>0.3</b>                 | <b>0.4</b>                     | <b>0.6</b>                     | <b>0.6</b>                     | <b>-0.3</b>                   | <b>-0.5</b>                   | -0.2                          | <b>0.4</b>                     | <b>0.7</b>                     |                                |

**Table 2.5.** Confidence set of linear models ( $w_i > 0.90$ ) predicting the effect of seasonal local weather on fawn recruitment in the North Dakota badlands (1962-2012) obtained from a starting set of 29 a priori models (including a null model:  $\log\text{Lik} = 5.31$ ,  $\Delta\text{AICc} = 59.3$ ). The models are ordered according to the corrected Akaike Information Criterion (AICc) with the most parsimonious model at the top of the list. Averaged parameters are reported in the lower panel along with their relative importance in the confidence set of models ( $\Sigma w_i$ ).

| #  | Model structure  | d.f. | AIC <sub>c</sub> | $\Delta$ AIC <sub>c</sub> | $w_i$ | ER   | logLik | adj R <sup>2</sup> |
|----|--|------|------------------|---------------------------|-------|------|--------|--------------------|
| 1  | spring <sub>t-1</sub> + winter   | 5    | -65.68           | 0                         | 0.28  | 1.0  | 38.51  | 0.71               |
| 2  | winter   | 4    | -65.04           | 0.64                      | 0.20  | 1.4  | 36.96  | 0.70               |
| 3  | winter <sub>t-1</sub> + spring <sub>t-1</sub> + winter                         | 6    | -64.02           | 1.67                      | 0.12  | 2.3  | 38.96  | 0.71               |
| 4  | winter + summer  | 5    | -63.29           | 2.40                      | 0.08  | 3.3  | 37.31  | 0.70               |
| 5  | winter <sub>t-1</sub> + winter   | 5    | -62.71           | 2.97                      | 0.06  | 4.4  | 37.02  | 0.69               |
| 6  | summer <sub>t-1</sub> + winter   | 5    | -62.66           | 3.03                      | 0.06  | 4.5  | 37     | 0.69               |
| 7  | winter + spring  | 5    | -62.62           | 3.06                      | 0.06  | 4.6  | 36.98  | 0.69               |
| 8  | winter <sub>t-1</sub> + spring <sub>t-1</sub> + winter + summer                | 7    | -61.77           | 3.91                      | 0.04  | 7.1  | 39.19  | 0.71               |
| 9  | winter <sub>t-1</sub> + spring <sub>t-1</sub> + summer <sub>t-1</sub> + winter | 7    | -61.41           | 4.27                      | 0.03  | 8.5  | 39.01  | 0.70               |
| 10 | winter <sub>t-1</sub> + spring <sub>t-1</sub> + winter + spring                | 7    | -61.36           | 4.33                      | 0.03  | 8.7  | 38.98  | 0.70               |
| 11 | winter <sup>t-1</sup> + winter + summer  | 6    | -60.79           | 4.89                      | 0.02  | 11.5 | 37.35  | 0.69               |

| Fixed effect                                     | $\beta$ | SE    | $\Sigma w_i$ |
|--|---------|-------|--------------|
| Intercept  | 27.29   | 2.60  | -            |
| Year   | -0.013  | 0.001 | 1.00         |
| Average min temperature (winter)                 | 0.028   | 0.008 | 1.00         |
| Average max temperature (spring <sub>t-1</sub> ) | 0.012   | 0.007 | 0.50         |
| Average min temperature (winter <sub>t-1</sub> ) | -0.006  | 0.009 | 0.30         |
| Average max temperature (summer)                 | 0.010   | 0.013 | 0.14         |
| Average max temperature (summer <sub>t-1</sub> ) | 0.003   | 0.012 | 0.09         |
| Average max temperature (spring)                 | 0.001   | 0.007 | 0.09         |

**Table 2.6.** Confidence set of linear models ( $w_i > 0.90$ ) predicting the effect of seasonal Pacific-based climate (set 1, i.e., using MEI, NP, and PDO indices recorded for winter, spring, and summer, respectively) on fawn recruitment in the North Dakota badlands (1962-2012) obtained from a starting set of 29 a priori models (including a null model:  $\log\text{Lik} = 5.31$ ,  $\Delta\text{AIC}_c = 55.3$ ). The models are ordered according to the corrected Akaike Information Criterion ( $\text{AIC}_c$ ) with the most parsimonious model at the top of the list. Averaged parameters are reported in the lower panel along with their relative importance in the confidence set of models ( $\Sigma w_i$ ).

| #  | Model structure  | d.f. | $\text{AIC}_c$ | $\Delta\text{AIC}_c$ | $w_i$ | ER   | $\log\text{Lik}$ | adj $R^2$ |
|----|--|------|----------------|----------------------|-------|------|------------------|-----------|
| 1  | spring <sub>t-1</sub> + winter   | 5    | -61.72         | 0                    | 0.36  | 1.0  | 36.53            | 0.69      |
| 2  | spring <sub>t-1</sub> + spring   | 5    | -60.37         | 1.35                 | 0.18  | 2.0  | 35.85            | 0.68      |
| 3  | winter <sub>t-1</sub> + spring <sub>t-1</sub> + winter                         | 6    | -59.25         | 2.47                 | 0.10  | 3.4  | 36.58            | 0.68      |
| 4  | winter <sub>t-1</sub> + spring <sub>t-1</sub> + spring                         | 6    | -57.81         | 3.91                 | 0.05  | 7.1  | 35.86            | 0.67      |
| 5  | winter <sub>t-1</sub> + spring <sub>t-1</sub> + winter + spring                | 7    | -57.70         | 4.02                 | 0.05  | 7.5  | 37.15            | 0.68      |
| 6  | winter   | 4    | -57.26         | 4.46                 | 0.04  | 9.3  | 33.06            | 0.65      |
| 7  | winter <sub>t-1</sub> + spring <sub>t-1</sub> + summer                         | 6    | -57.17         | 4.55                 | 0.04  | 9.7  | 35.54            | 0.67      |
| 8  | winter <sub>t-1</sub> + spring <sub>t-1</sub> + winter + summer                | 7    | -57.00         | 4.72                 | 0.03  | 10.6 | 36.8             | 0.68      |
| 9  | winter <sub>t-1</sub> + spring <sub>t-1</sub> + summer <sub>t-1</sub> + winter | 7    | -56.70         | 5.02                 | 0.03  | 12.3 | 36.65            | 0.67      |
| 10 | winter + spring  | 5    | -56.43         | 5.29                 | 0.03  | 14.1 | 33.88            | 0.65      |
| 11 | summer <sub>t-1</sub> + winter   | 5    | -56.13         | 5.59                 | 0.02  | 16.4 | 33.73            | 0.65      |
| 12 | spring   | 4    | -55.99         | 5.73                 | 0.02  | 17.5 | 32.43            | 0.64      |
| 13 | winter <sub>t-1</sub> + winter   | 5    | -55.93         | 5.79                 | 0.02  | 18.1 | 33.63            | 0.65      |
| 14 | summer <sub>t-1</sub> + spring   | 5    | -55.81         | 5.91                 | 0.02  | 19.2 | 33.57            | 0.65      |
| 15 | winter <sub>t-1</sub> + spring <sub>t-1</sub> + summer <sub>t-1</sub> + spring | 7    | -55.23         | 6.49                 | 0.01  | 25.6 | 35.92            | 0.66      |

| Fixed effect                         | $\beta$ | SE    | $\Sigma w_i$ |
|--------------------------------------|---------|-------|--------------|
| Intercept                            | 27.881  | 3.027 | -            |
| Year                                 | -0.013  | 0.001 | 1.00         |
| Average NP (spring <sub>t-1</sub> )  | -0.028  | 0.011 | 0.85         |
| Average MEI (winter)                 | 0.002   | 0.001 | 0.65         |
| Average NP (spring)                  | -0.016  | 0.011 | 0.36         |
| Average MEI (winter <sub>t-1</sub> ) | 0.000   | 0.001 | 0.33         |
| Average PDO (summer)                 | 0.020   | 0.021 | 0.07         |
| Average PDO (summer <sub>t-1</sub> ) | 0.011   | 0.030 | 0.08         |

**Table 2.7.** Confidence set of linear models ( $w_i > 0.90$ ) predicting the effect of seasonal Pacific-based climate (set 2, i.e., using NP indices for both winter and spring, and MEI index for summer) on fawn recruitment in the North Dakota badlands (1962-2012) obtained from a starting set of 29 a priori models (including a null model:  $\log\text{Lik} = 5.31$ ,  $\Delta\text{AICc} = 54.7$ ). The models are ordered according to the corrected Akaike Information Criterion (AICc) with the most parsimonious model at the top of the list. Averaged parameters are reported in the lower panel along with their relative importance in the confidence set of models ( $\Sigma w_i$ ).

| #  | Model structure  | d.f. | AIC <sub>c</sub> | $\Delta$ AIC <sub>c</sub> | $w_i$ | ER   | logLik | adj R <sup>2</sup> |
|----|--|------|------------------|---------------------------|-------|------|--------|--------------------|
| 1  | spring <sub>t-1</sub> + winter   | 5    | -61.14           | 0                         | 0.25  | 1.0  | 36.23  | 0.68               |
| 2  | spring <sub>t-1</sub> + spring   | 5    | -60.37           | 0.77                      | 0.17  | 1.5  | 35.85  | 0.68               |
| 3  | winter <sub>t-1</sub> + spring <sub>t-1</sub> + winter + spring                | 7    | -59.60           | 1.53                      | 0.12  | 2.2  | 38.1   | 0.69               |
| 4  | winter <sub>t-1</sub> + spring <sub>t-1</sub> + winter                         | 6    | -59.55           | 1.59                      | 0.11  | 2.2  | 36.73  | 0.68               |
| 5  | winter <sub>t-1</sub> + spring <sub>t-1</sub> + spring                         | 6    | -59.24           | 1.90                      | 0.1   | 2.6  | 36.57  | 0.68               |
| 6  | winter <sub>t-1</sub> spring <sub>t-1</sub> summer <sub>t-1</sub> spring       | 7    | -58.18           | 2.96                      | 0.06  | 4.4  | 37.39  | 0.68               |
| 7  | winter <sub>t-1</sub> + spring <sub>t-1</sub> + summer <sub>t-1</sub> + winter | 7    | -57.32           | 3.81                      | 0.04  | 6.7  | 36.96  | 0.68               |
| 8  | winter <sub>t-1</sub> + spring <sub>t-1</sub> + winter + summer                | 7    | -56.90           | 4.24                      | 0.03  | 8.3  | 36.75  | 0.67               |
| 9  | winter + spring  | 5    | -56.66           | 4.48                      | 0.03  | 9.4  | 34     | 0.65               |
| 10 | summer <sub>t-1</sub> + spring   | 5    | -56.45           | 4.68                      | 0.02  | 10.4 | 33.89  | 0.65               |
| 11 | winter <sub>t-1</sub> + spring <sub>t-1</sub> + summer                         | 6    | -56.20           | 4.93                      | 0.02  | 11.8 | 35.06  | 0.66               |
| 12 | winter   | 4    | -56.11           | 5.02                      | 0.02  | 12.3 | 32.49  | 0.64               |
| 13 | spring   | 4    | -55.99           | 5.14                      | 0.02  | 13.1 | 32.43  | 0.64               |
| 14 | winter <sub>t-1</sub> + spring <sub>t-1</sub> + summer <sub>t-1</sub> + summer | 7    | -55.80           | 5.34                      | 0.02  | 14.4 | 36.2   | 0.66               |

| Fixed effect                         | $\beta$ | SE    | $\Sigma w_i$ |
|--------------------------------------|---------|-------|--------------|
| Intercept                            | 28.581  | 2.921 | -            |
| Year                                 | -0.014  | 0.001 | 1.00         |
| Average NP (spring <sub>t-1</sub> )  | -0.029  | 0.011 | 0.92         |
| Average NP (winter)                  | -0.014  | 0.008 | 0.60         |
| Average NP (spring)                  | -0.018  | 0.011 | 0.52         |
| Average NP (winter <sub>t-1</sub> )  | 0.008   | 0.008 | 0.50         |
| Average MEI (summer <sub>t-1</sub> ) | 0.001   | 0.001 | 0.12         |
| Average MEI (summer)                 | 0.000   | 0.001 | 0.07         |

## Chapter 2

### *Effects of oil developments and predators on mule deer recruitment*



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## Introduction

Deer recruitment is a good proxy of population productivity because it represents the joint contribution of fecundity and fawn survival. Certainly recruitment is one of the most variable parameters in large herbivore populations and a key factor affecting population growth rates (Gaillard et al. 1998). However, observed temporal variation in many populations of large herbivores remains poorly understood. In a recent review (Forrester and Wittmer 2013), mule deer (including black-tailed mule deer and Sitka black-tailed deer) have been shown to be characterized by large population fluctuations across their range of distribution over the last century (Wallmo 1981, Unsworth et al. 1999). Efforts to understand observed population fluctuations have focused on habitat conditions and predators producing contrasting results (Ballard et al. 2001, Forrester and Wittmer 2013). Indeed, studies of the effects of habitat and predation across a range of environments has resulted into contrasting explanations of population fluctuations, including potential high predation rates, habitat change, and climate change (Ballard et al. 2001, Forrester and Wittmer 2013). In this complex scenario of uncertainty, human disturbance is another factor that is likely contributing to make this picture even more complex. Additionally, new ecological conditions created by human land use and development have the potential to alter delicate predator-prey equilibria, as shown by empirical studies on multi-predator prey systems (Muhly et al. 2011, Ciuti et al. 2012, Northrup et al. 2012, Muhly et al. 2013).

Among an array of human-caused sources of disturbance for wildlife, energy development effects can be tied to increased road density and traffic (Freddy et al. 1986, Stephenson et al. 1996), and, no less importantly, habitat loss (Sawyer et al. 2002, Sawyer et al. 2006, Naugle 2011). Energy expended by deer increases significantly as deer transition from lying to walking to running, particularly in snow (Freddy et al. 1986). As shown by classical examples available from the literature of the 1980's, Freddy et al. (1986) found that deer disturbed by humans increased energy expenditure from 9 kcal while lying to 54-127 kcal while running. Similarly, recent research on cow elk showed that relatively low traffic volumes decreased the time spent foraging by 20% (Ciuti et al. 2012).

Energy expenditures in response to disturbance are of greatest concern during winter months, when energy conservation is fundamental to survival and reproductive fitness in deer. Deer are constantly in negative energy balance during winter months because metabolic requirements cannot be met by foraging alone (Wallmo 1981, Torbit et al. 1985a, Torbit et al. 1985b, Parker et al. 1996, Parker et al. 2009). Deer survive winter by using fat and protein reserves accumulated during late summer and fall. Depletion rates of fat and muscle mass vary depending on nutrient availability, winter severity, and energy expenditure. Oil and natural gas development might negatively affect deer by increasing energy expenditure and decreasing forage availability. Combined, these factors synergistically could increase

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the rate at which nutrient body stores are depleted. If these impacts are of sufficient magnitude to cause increased overwinter deer mortality or reduced newborn fawn production and survival, deer populations could be expected to decline. Oil and gas development in critical deer habitat is expected to reduce availability of quality forage directly through habitat loss but also indirectly by influencing deer behavior and habitat-use patterns (Sawyer et al. 2002, Sawyer and Lindzey 2004, Sawyer et al. 2009). It follows that such an impact may be a cause for decreased survival and reproductive performance.

Populations of large herbivores typically are characterized by moderately variable fecundity rates and widely variable fawn survival (Gaillard et al. 1998, Gaillard et al. 2000b, Forrester and Wittmer 2013). For mule deer, average fecundity estimate is 1.70 (SE = 0.12) (Forrester and Wittmer 2013) fawns per female. However, a recent review (Forrester and Wittmer 2013) pointed out that despite high fecundity rates, mule deer may experience comparatively low (mule deer = 0.44 vs other ungulates = 0.64) and more variable (mule deer CV = 0.42 vs other ungulates CV = 0.27) summer fawn survival (Gaillard et al. 2000b). Higher fecundity rates (1.70 in mule deer vs. 0.82 for all ungulates) apparently enable mule deer to compensate for reduced summer fawn survival over longer time frames. As a consequence, mule deer populations might be characterized by strong resilience during the first years in which they are disturbed (e.g., colonization by a new predator, human developments, habitat change). However, this phenomenon could be detectable on the long term. This study is characterized by a mule deer population in an area with a long term and steady decline in fall fawn recruitment. This area also has been characterized by habitat change, variable predator pressure, and an exponential increase of energy development. Our objective with this study is to understand the main factors affecting fall fawn recruitment of mule deer in the North Dakota badlands.

## **Methods**

### *Mule deer aerial surveys*

Mule deer in North Dakota are predominantly found in that portion of the state south and west of the Missouri River. The Little Missouri Badlands is considered the primary mule deer range. The annual spring mule deer census is based on fixed-wing aerial coverage of 28 permanent study areas located in the Badlands of western North Dakota. Each study area is usually flown after the snow has melted, but prior to the time the trees "leaf out" (mid April). Early morning flights on each area are used as a basis for establishing population indices and trends of mule deer in the Badlands. The survey is conducted from approximately one-half hour before to about one hour after sunrise of the survey day. The entire study area is intensively searched from as low an altitude and air speed as is possible in small fixed-wing aircraft (e.g., PA-18), and deer are tallied (but not classified) by study area. The sex and production

surveys are conducted on the same permanent study areas in the autumn after leaves have dropped and prior to the deer-gun season (mid October). Aerial surveys are conducted in the same manner as the spring surveys, but deer are classified as an antlered male, adult female (>1 year old), and young-of-the-year (i.e., <6 months old). Two study sites (Bowline Creek, Whitetail Creek) were dropped from the starting dataset because they had only been monitored since 2009. Additionally, 3 other study sites were excluded because of monitoring inconsistency between the spring and the fall survey, with these areas scarcely surveyed during spring (e.g., Bible Camp, Southern and Northern Units of the Theodore Roosevelt National Park). The total number of study sites included in this set of analysis is 23.

#### *Predictors of fawn recruitment: local weather data*

Local weather data were collected from 1962 to 2012 by the Medora weather station (station id: Medora ND US; elevation 686.1 m a.s.l.; Latitude 46.966°; Longitude -103.500°) centrally located in the mule study area. Data are free online and are provided by the National Oceanic and Atmospheric Administration (NOAA [www.noaa.gov](http://www.noaa.gov)). Daily observational raw data can be accessed through the GIS viewer at the following website:

<http://gis.ncdc.noaa.gov/map/viewer/#app=cdo&cfg=cdo&theme=daily&layers=111&node=gis>. Based on our knowledge of the ecology of mule deer, on available literature (Forrester and Wittmer 2013), and on results of our concurrent research dealing with the effect of seasonal weather on mule deer recruitment (Chapter 1), we computed winter minimum temperature (November-March) to be used as weather predictor of female reproductive success and fawn survival, and, consequently, autumn fall recruitment (Fig. S9).

#### *Other predictors of fawn recruitment*

Coyote (*Canis latrans*) density indices (coyote/ 10km<sup>2</sup>) were estimated from spring mule deer aerial surveys for each study site per year. Coyote densities ranged from 0 coyote / 10 km<sup>2</sup> to slightly more than 3 coyotes / 10 km<sup>2</sup> (Figure S3). These indices positively correlated with the overall estimate of coyote density for the region (Fig. S7); and more importantly, with independent estimates of coyote density (Fig. S8, e.g., relative coyote index recorded by Mail Carriers in April). Mule deer density (deer / km<sup>2</sup>) was estimated in spring during aerial surveys. Both mule deer and coyote densities were thus recorded during the April just prior to the birth season and the fall in which we recorded recruitment data. The density of active oil and gas wells (wells / 10 km<sup>2</sup>) was estimated each year inside mule deer survey units and within a buffer of 1 km around the boundary (Fig S1-S2). Inactive wells (e.g., abandoned) were not considered in our well-density estimation. Wells considered to have lower disturbance rates (e.g., air



injection, salt water disposal, water injection) were excluded from the analysis (source: Official Portal for North Dakota State Government <https://www.dmr.nd.gov/oilgas/>). Woody vegetation was digitized from 54 random plots for which we had replicated aerial photos from 1939 to present: for each plot, we digitized woody vegetation coverage for the first sampling period (1939-1970), and a second sampling period (2012). We thus modelled encroachment rate using linear regression and a set of candidate predictors (latitude, longitude, aspect, habitat class, geological features, and ruggedness). Starting from a full model, we selected the best linear model using backward step-wise model selection. The best model explained 40% of the variability in woody vegetation covering mule deer study sites. This model was used to rebuild the degree of yearly encroachment per study site. Terrain ruggedness was computed using a 30-m resolution Digital Elevation Model of the study site (Riley et al. 1999).

### *Modelling fawn recruitment in mule deer*

We used linear mixed-effects models with a Gaussian distribution of errors to model deer recruitment (fawn : female ratio) as a function of a set of covariates which included predator pressure, energy development, habitat characteristics and mule deer population density (see Table 2.1 for the full set of covariates used to build a set of 60 *a priori* models). Variability of fawn recruitment within and across study sites was reported in Fig. S3 and Fig. S6. We did not find collinearity issues between explanatory variables by calculating pairwise Pearson's correlation coefficients within seasons. Collinearity also was checked using Variance Inflation Factors (VIF) metrics. Year (covariate) was included within fixed factors (i.e., trend) to account for possible long-term trend in recruitment. The random structure took the form (1|YEAR)+(year|StudyArea), thus YEAR (factor) and Study area (factor) were fitted as random intercepts (crossed, i.e. non-hierarchical random effects), while year (covariate) was fitted as a random slope because we could not assume a constant effect across different study areas. Variability explained by top ranked models was computed using both a null model and a model including the random factor only.

Models were estimated using Maximum Likelihood (ML). For all sets of models, we performed model selection using Akaike Information Criterion (AIC) (Burnham and Anderson 2002). Because there was not much support for a single best model, we chose a confidence set of models ( $w_i > 0.90$ ) (Burnham et al. 2011) and we used model averaging to get averaged coefficients and standard errors (Burnham and Anderson 2002). We also calculated the relative importance of each explanatory variable as a sum of Akaike weights across all the models in the confidence set that contained that variable (Burnham and Anderson 2002).

We verified if assumptions of linear models we ran were met. Normality and homogeneity of residuals was checked by visually inspecting Quantile-Quantile (QQ) plots and residual plots. Autocorrelation plots for the residuals were drawn to exclude the presence of temporal autocorrelations. Finally, semivariance plots were inspected to exclude spatial autocorrelation of residuals between mule deer study sites. All analyses were performed in R 3.0.2 (R Development Core Team 2011).

## Results

We reported the set of *a priori* models predicting fawn recruitment in 23 study sites monitored from 1962 to 2012 in the North Dakota badlands in Table 2.1. Eleven top linear models ( $\Delta AIC < 4$ ) were reported in Table 2.2, and averaged parameters were shown in Table 2.3. Top-ranked models explained 85% of total variability ( $\text{adj. } R^2 = 0.85$ , null model as a reference), and 46% of variability when compared to a model including the random factor only ( $\text{adj. } R^2 = 0.46$ ). The major drivers of fawn recruitment (Table 2.3) were the average min temperature recorded during the winter prior to birth (at low temperatures recruitment was lower, see Fig. 2.1), and the interaction between coyote density and well density (Table 2.4, Fig. 2.2, Fig. 2.3, Fig. 2.4).

As shown in Fig. 2.2-2.4, coyote density has little effect on mule deer recruitment when oil and gas wells are absent. However, the two factors interact when simultaneously occurring at high densities, with the lowest deer recruitment rates recorded when well densities exceeded 3 wells / 10 km<sup>2</sup> and coyote density exceeded 1.5 coyotes / 10 km<sup>2</sup>.

We report 3 scenarios predicting fawn recruitment in Table 2.4. After an average winter (average min temperature of -11.2 degrees Celsius), fawn:female ratio is expected to be 1.04 if both coyotes and wells are absent (Table 2.4, upper panel). However, top-ranked models predict a significant decrease of recruitment if densities of wells and coyotes increase. Two more scenarios were built depending on the harshness of winter temperatures prior to birth (Table 2.4, middle and bottom panels).

Woody coverage, terrain ruggedness, mule deer density were included in top-ranked models but played little role in affecting mule deer recruitment in the North Dakota badlands (Table 2.3).

We did not find sign of temporal (Fig S4) or spatial (Fig S5) autocorrelation in the residuals of top-ranked models.

## Discussion

One of the strongest factors affecting fawn recruitment in the North Dakota badlands is the average minimum temperature recorded in the winter prior to the birth season. This is fully in agreement with what was shown in Chapter 1. More importantly, our analyses clearly show how oil and gas well density and coyote density interact and negatively affect fawn recruitment in the North Dakota badlands. In our analyses we only included oil and gas wells that were active in a given year. This makes our model stronger if compared to approaches using road densities instead. The inclusion of active wells in our analyses takes into account human use and traffic volumes in the road network, while road density lacks of this predictive power, because inactive wells reached by the road network received little if any vehicle traffic. We thus believe that our analyses takes into consideration the actual degree of human disturbance related to activity linked to active well sites. Fox (1989) showed that mule deer in the North Dakota badlands are displaced by energy development. Intuitively, mule deer populations might be negatively affected by energy development, and the level of thresholds of population-level impacts are likely related to oil/gas well densities and amount of human activity associated with development and production activities, but these threshold levels have not been assessed scientifically until now. For the first time, our study predicts the density of oil and gas wells that are responsible for reduced mule deer recruitment in conjunction with relatively medium-high coyote densities (1.5 – 3 coyotes / 10 km<sup>2</sup>; **Fig.2.2-2.4, Fig. S3**). Densities of 2 to 4 coyotes / 10 km<sup>2</sup> are common over much of the range. However, densities are usually lower in North Dakota, with estimates of 0.3 to 0.7 adults / 10 km<sup>2</sup> (Seabloom 2011); consequently, local coyote density higher than 1.5 coyotes / 10 km<sup>2</sup> are considered a common figure in several areas of North America, but are medium-high relatively to the North Dakota scenario.

Our models predict little effect of increased coyote density on fawn recruitment if well sites are absent; at the same time, the model predicts little effect of increased well density on fawn recruitment if the main predator (i.e., coyote) is absent. However, the two factors interact to reduce fawn recruitment in the North Dakota badlands, with the lowest recruitment rates recorded in areas with simultaneous high coyote density and high well density. Energy developments are clearly responsible of direct (well-pad surface) and indirect (2-3 km from the well site) habitat loss, as documented by recent research in Wyoming (Sawyer et al. 2002, Sawyer and Lindzey 2004, Sawyer et al. 2005, Sawyer et al. 2006, Sawyer et al. 2009). Our study adds a new piece to the puzzle of these complex interactions and cumulative effects, because we documented how coyote density and oil and gas development had little effect when occurring as isolated factors, but may be dramatic if occurring in an interacting and/or cumulative fashion. Habitat loss due to energy development could be responsible for fragmentation and a decrease in the spatial randomness of mule deer fawn bedding sites. Thus fawn bedding sites could be more

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predictable and localized in areas away from well pads. Under such condition, coyotes might be more effective at finding and preying upon fawns. This could be one of the explanations as to why the two factors negatively interact and decrease fall mule deer fawn recruitment. The decreased recruitment we recorded in areas with high well densities and high coyote densities also could be the end result of cumulative factors. Indeed, coyote pressure always has been considered a compensatory factor (Hurley et al. 2011, Forrester and Wittmer 2013), meaning that is expected to have little effect on recruitment rates. However, recruitment can significantly decrease when coyote pressure and disturbance by energy developments (e.g., mortality due to car collisions, habitat loss and decreased body condition of animals using suboptimal habitats) are occurring simultaneously. We caution against predator removal programs to limit the impacts of predation on declining mule deer fall fawn recruitment rates. There is as long history of bounties and predator programs being ineffective, wasteful, and resulting in unintended consequences (Boersma et al, in press). This has been shown on both a national level (Bolen and Robinson 1999, Boal and Ballard 2013), as well as here in North Dakota (North Dakota Outdoors 2011). The challenges currently facing mule deer are analogous to the challenges agencies faced in management of waterfowl in the 1970s and 1980s (Cowardin et al. 1983). The same comprehensive approach used by waterfowl managers is needed to managing mule deer and other affected wildlife species in the badlands. For further discussion on the interaction between oil and gas developments and coyote pressure in affecting mule deer recruitment, see the final section of this report ‘*Final remarks*’.

Sawyer and colleagues (Sawyer et al. 2002, Sawyer and Lindzey 2004, Sawyer et al. 2005, Sawyer et al. 2006, Sawyer et al. 2009) showed that mule deer might respond negatively to energy development because of: 1) direct reduction in forage availability from development activities, 2) indirect reduction of forage quality and quantity by shifting their distribution away from development activity to less-preferred habitats, 3) negative physiological responses where deer maintain fidelity in areas exposed to development activities, and 4) fragmentation of their habitats exposing them to increased vehicle collisions or shifting their migration patterns away from traditional seasonal ranges. However, our study for the first time highlights how indirect and/or cumulative effects could affect mule deer recruitment.

The effect of predation on ungulate recruitment is particularly debated (Gaillard et al. 1998, Gaillard et al. 2000a, Pierce et al. 2012). Both bottom–up and top–down mechanisms may simultaneously affect large herbivorous dynamics and often interact (Sinclair and Arcese 1995, Boyce and Anderson 1999, Sinclair and Krebs 2002). The interactions between forage and predation also are likely to be mediated by environmental conditions such as weather (Hopcraft et al. 2010, Pierce et al. 2012). Overall, in regard of mule deer, research has shown that coyote (Hurley et al. 2011) and at times mountain lion predation (Forrester and Wittmer 2013) was compensatory rather than additive. This fits well with our

data, which show that coyotes have little effect on recruitment rates when human disturbance is absent (e.g., very low densities or even absence of energy developments).

Hebblewhite (2011) reviewed studies on impact of energy developments on ungulates, and pointed out that impacts started to manifest on ungulate species including mule deer, pronghorn, and elk from 0.1-0.4 wells km<sup>-2</sup> and 0.18-1.05 linear km of roads km<sup>-2</sup>. Our study showed that, considering only oil and gas well sites – thus excluding the other wells affected by lower human disturbance (e.g., air injectors, saltwater disposals, water injectors, etc.) – some of the mule deer study sites exceeded 0.8 wells km<sup>-2</sup>, markedly higher than the threshold indicated by Hebblewhite (2011). North Dakota badlands' energy development on survey units ranged from 0.012 wells km<sup>-2</sup> (e.g., study site: 3V) to more than 0.8 wells km<sup>-2</sup> (e.g., study site: Franks Creek). Only Sawyer and colleagues (Sawyer et al. 2002, Sawyer and Lindzey 2004, Sawyer et al. 2005, Sawyer et al. 2006, Sawyer et al. 2009) performed studies on the effects of energy developments on ungulate populations that were comparable or exceeded (1.01 wells km<sup>-2</sup>) well densities recorded in North Dakota; all other studies on the impact of energy developments on ungulate populations refer to sites with well densities lower than that recorded in the North Dakota badlands (e.g., 0.001 – 0.27 wells km<sup>-2</sup>, reviewed in Hebblewhite 2011).

Mule deer studies in southwestern Wyoming (Sawyer et al. 2002, Sawyer and Lindzey 2004, Sawyer et al. 2005, Sawyer et al. 2006, Sawyer et al. 2009) reported expanding development over a 5-year period with about 0.3 wells km<sup>-2</sup>. They showed that mule deer avoided areas close to developments, responses to development occurred rapidly (within 1 year from development), and avoidance of development increased over the course of the 3-year study. One of those studies (Sawyer et al. 2006) reported lower predicted probabilities of use by mule deer within 2.7-3.7 km of well sites, confirming that indirect habitat losses far exceeded direct losses (i.e., space actual occupied by the development). They also showed that mule deer shifted habitat use away from high-quality habitats to marginal habitats in response to development.

Anthropogenic changes to habitat can lead to lower nutritional capacity and/or large changes in predator and/or alternative prey species. These changes are potentially able to modify mule deer carrying capacity and predation risk, and are likely to destabilize mule deer population dynamics. This pattern is likely to occur where human activities alter the landscape in a way that lowers nutritional carrying capacity (i.e., by development) or changes species interactions within food webs. Mule deer are particularly susceptible to any alteration resulting in lower survival of adults (Robinson et al. 2002). Both food web and community composition and the spatial distribution of species are likely to be important in this scenario. Other direct impacts of energy development, such as deer-vehicle collisions (not evaluated

in this report), will add further downward pressures on mule deer numbers in the badlands. In today's rapidly changing world, these cumulative effects will become more important in the future. We recommend monitoring those areas affected by medium to high oil/gas well densities to identify and reduce long-term negative effects on mule deer recruitment and population dynamics.

**Table 2.1.** A priori set of linear mixed models predicting fawn recruitment in the North Dakota badlands (1962-2012). A confidence set of linear models ( $\Delta AIC < 4$ ) has been averaged (11 top-ranked models) and highlighted in bold. Models were run using ML Maximum Likelihood. Year (covariate) was included as a fixed factor in all models to account for possible long-term trend in recruitment. The random structure took the form  $(1/YEAR)+(year|StudyArea)$ , thus YEAR (factor) and Study area (factor) were fitted as random intercepts (crossed, i.e. non-hierarchical random effects), while year (covariate) was fitted as a random slope because we could not assume a constant effect across different study areas. The top ranked model explained 85% of total variability ( $adj. R^2 = 0.85$ , null model as reference), and 46% of variability when compared to a model including the random factor only ( $adj. R^2 = 0.46$ ).

| #         | model structure   | df        | logLik        | AIC           | $\Delta AIC$ | wi          |
|-----------|---|-----------|---------------|---------------|--------------|-------------|
| <b>1</b>  | <b>winter min temp + coyote density + year + well density + (well density * coyote density)</b>   | <b>11</b> | <b>-38.57</b> | <b>99.14</b>  | <b>0.00</b>  | <b>0.16</b> |
| <b>2</b>  | <b>winter min temp + coyote density + year + well density + woody coverage + (well density * coyote density)</b>  | <b>12</b> | <b>-37.61</b> | <b>99.22</b>  | <b>0.08</b>  | <b>0.15</b> |
| <b>3</b>  | <b>winter min temp + coyote density + year + well density + terrain ruggedness + (well density * coyote density)</b>                                      | <b>12</b> | <b>-37.75</b> | <b>99.50</b>  | <b>0.37</b>  | <b>0.13</b> |
| <b>4</b>  | <b>winter min temp + coyote density + year + mule deer density + well density + (well density * coyote density)</b>                                       | <b>12</b> | <b>-38.37</b> | <b>100.73</b> | <b>1.59</b>  | <b>0.07</b> |
| <b>5</b>  | <b>winter min temp + coyote density + year + well density + terrain ruggedness + woody coverage + (well density * coyote density)</b>                     | <b>13</b> | <b>-37.58</b> | <b>101.17</b> | <b>2.03</b>  | <b>0.06</b> |
| <b>6</b>  | <b>winter min temp + coyote density + year + mule deer density + well density + woody coverage + (well density * coyote density)</b>                      | <b>13</b> | <b>-37.67</b> | <b>101.34</b> | <b>2.20</b>  | <b>0.05</b> |
| <b>7</b>  | <b>winter min temp + coyote density + year + mule deer density + well density + terrain ruggedness + (well density * coyote density)</b>                  | <b>13</b> | <b>-37.72</b> | <b>101.44</b> | <b>2.31</b>  | <b>0.05</b> |
| <b>8</b>  | <b>winter min temp + coyote density + year + well density</b>   | <b>10</b> | <b>-40.95</b> | <b>101.90</b> | <b>2.76</b>  | <b>0.04</b> |
| <b>9</b>  | <b>winter min temp + coyote density + year + well density + woody coverage</b>  | <b>11</b> | <b>-40.14</b> | <b>102.28</b> | <b>3.14</b>  | <b>0.03</b> |
| <b>10</b> | <b>winter min temp + coyote density + year + mule deer density + well density + terrain ruggedness + woody coverage + (well density * coyote density)</b> | <b>14</b> | <b>-37.25</b> | <b>102.50</b> | <b>3.36</b>  | <b>0.03</b> |
| <b>11</b> | <b>winter min temp + coyote density + year + well density + terrain ruggedness</b>  | <b>11</b> | <b>-40.34</b> | <b>102.69</b> | <b>3.55</b>  | <b>0.03</b> |
| 12        | winter min temp + coyote density + year + mule deer density + well density  | 11        | -40.79        | 103.57        | 4.43         | 0.02        |
| 13        | winter min temp + coyote density + year + (winter min temp * coyote density)  | 10        | -41.81        | 103.62        | 4.48         | 0.02        |
| 14        | winter min temp + coyote density + year + well density + (winter min temp * coyote density)   | 11        | -40.86        | 103.73        | 4.59         | 0.02        |
| 15        | winter min temp + coyote density + year + mule deer density + well density + woody coverage   | 12        | -39.88        | 103.75        | 4.62         | 0.02        |
| 16        | winter min temp + coyote density + year + well density + terrain ruggedness + woody coverage  | 12        | -40.14        | 104.28        | 5.14         | 0.01        |
| 17        | winter min temp + coyote density + year + well density + terrain ruggedness + (terrain ruggedness * coyote density)                                       | 12        | -40.21        | 104.42        | 5.28         | 0.01        |
| 18        | winter min temp + coyote density + year + well density + terrain ruggedness + (winter min temp * coyote density)  | 12        | -40.23        | 104.46        | 5.32         | 0.01        |
| 19        | winter min temp + coyote density + year + well density + woody coverage + (woody coverage * coyote density)   | 12        | -40.26        | 104.52        | 5.38         | 0.01        |
| 20        | winter min temp + coyote density + year + mule deer density + well density + terrain ruggedness   | 12        | -40.44        | 104.89        | 5.75         | 0.01        |
| 21        | winter min temp + coyote density + year + well density + woody coverage + (winter min temp * coyote density)  | 12        | -40.49        | 104.98        | 5.84         | 0.01        |
| 22        | winter min temp + coyote density + year + mule deer density + well density + (mule deer density * coyote density)   | 12        | -40.78        | 105.57        | 6.43         | 0.01        |

| #  | <i>model structure</i>   | <i>df</i> | <i>logLik</i> | <i>AIC</i> | <i>Δ AIC</i> | <i>wi</i> |
|----|--|-----------|---------------|------------|--------------|-----------|
| 23 | winter min temp + coyote density + year + mule deer density + well density + woody coverage + (woody coverage * coyote density)                          | 13        | -39.82        | 105.64     | 6.51         | 0.01      |
| 24 | winter min temp + year   | 8         | -44.86        | 105.72     | 6.58         | 0.01      |
| 25 | winter min temp + coyote density + year + mule deer density + well density + terrain ruggedness + woody coverage   | 13        | -39.87        | 105.75     | 6.61         | 0.01      |
| 26 | winter min temp + coyote density + year + mule deer density + well density + terrain ruggedness + (terrain ruggedness * coyote density)                  | 13        | -39.95        | 105.91     | 6.77         | 0.01      |
| 27 | winter min temp + coyote density + year + mule deer density + well density + terrain ruggedness + (winter min temp * coyote density)                     | 13        | -39.99        | 105.99     | 6.85         | 0.01      |
| 28 | winter min temp + coyote density + year + well density + terrain ruggedness + woody coverage + (terrain ruggedness * coyote density)                     | 13        | -40.00        | 106.00     | 6.86         | 0.01      |
| 29 | winter min temp + coyote density + year + mule deer density + terrain ruggedness + woody coverage  | 12        | -41.12        | 106.25     | 7.11         | 0.00      |
| 30 | winter min temp + coyote density + year + mule deer density + well density + woody coverage + (winter min temp * coyote density)                         | 13        | -40.17        | 106.34     | 7.20         | 0.00      |
| 31 | winter min temp + coyote density + year + well density + terrain ruggedness + woody coverage + (woody coverage * coyote density)                         | 13        | -40.21        | 106.41     | 7.28         | 0.00      |
| 32 | winter min temp + coyote density + year + mule deer density + well density + (winter min temp * coyote density)  | 12        | -41.23        | 106.46     | 7.32         | 0.00      |
| 33 | winter min temp + coyote density + year + mule deer density + well density + woody coverage + (mule deer density * coyote density)                       | 13        | -40.28        | 106.57     | 7.43         | 0.00      |
| 34 | winter min temp + coyote density + year + mule deer density + well density + terrain ruggedness + woody coverage + (woody coverage * coyote density)     | 14        | -39.34        | 106.69     | 7.55         | 0.00      |
| 35 | winter min temp + coyote density + year + mule deer density + well density + terrain ruggedness + (mule deer density * coyote density)                   | 13        | -40.44        | 106.89     | 7.75         | 0.00      |
| 36 | winter min temp + coyote density + year + well density + terrain ruggedness + woody coverage + (winter min temp * coyote density)                        | 13        | -40.46        | 106.92     | 7.78         | 0.00      |
| 37 | winter min temp + coyote density + year + mule deer density + terrain ruggedness + woody coverage + (woody coverage * coyote density)                    | 13        | -40.58        | 107.15     | 8.02         | 0.00      |
| 38 | winter min temp + coyote density + year + mule deer density + well density + terrain ruggedness + woody coverage + (terrain ruggedness * coyote density) | 14        | -39.72        | 107.43     | 8.29         | 0.00      |
| 39 | winter min temp + coyote density + year + mule deer density + well density + terrain ruggedness + woody coverage + (winter min temp * coyote density)    | 14        | -39.77        | 107.53     | 8.40         | 0.00      |
| 40 | winter min temp + coyote density + year + mule deer density + well density + terrain ruggedness + woody coverage + (mule deer density * coyote density)  | 14        | -39.87        | 107.74     | 8.60         | 0.00      |
| 41 | winter min temp + coyote density + year + mule deer density + terrain ruggedness + woody coverage + (terrain ruggedness * coyote density)                | 13        | -40.93        | 107.87     | 8.73         | 0.00      |
| 42 | winter min temp + coyote density + year + mule deer density + terrain ruggedness + woody coverage + (winter min temp * coyote density)                   | 13        | -40.99        | 107.98     | 8.84         | 0.00      |
| 43 | winter min temp + coyote density + year + mule deer density + terrain ruggedness + woody coverage + (mule deer density * coyote density)                 | 13        | -41.12        | 108.24     | 9.10         | 0.00      |
| 44 | coyote density + year + well density + (well density * coyote density)   | 10        | -44.83        | 109.65     | 10.51        | 0.00      |
| 45 | winter min temp + year + mule deer density + well density + terrain ruggedness + woody coverage  | 12        | -42.91        | 109.81     | 10.67        | 0.00      |
| 46 | coyote density + year  | 8         | -48.04        | 112.09     | 12.95        | 0.00      |
| 47 | coyote density + year + mule deer density + well density + terrain ruggedness + woody coverage + (well density * coyote density)                         | 13        | -43.61        | 113.21     | 14.08        | 0.00      |
| 48 | coyote density + year + woody coverage + (woody coverage * coyote density)   | 10        | -46.82        | 113.63     | 14.50        | 0.00      |
| 49 | coyote density + year + mule deer density + (mule deer density * coyote density)   | 10        | -47.79        | 115.58     | 16.44        | 0.00      |

**Table 2.1.(continued)**



| #  | <i>model structure</i>   | <i>df</i> | <i>logLik</i> | <i>AIC</i> | <i>Δ AIC</i> | <i>wi</i> |
|----|--|-----------|---------------|------------|--------------|-----------|
| 50 | coyote density + year + terrain ruggedness + (terrain ruggedness * coyote density)   | 10        | -47.84        | 115.69     | 16.55        | 0.00      |
| 51 | coyote density + year + mule deer density + well density + terrain ruggedness + woody coverage   | 12        | -46.18        | 116.36     | 17.22        | 0.00      |
| 52 | year + well density  | 8         | -50.27        | 116.54     | 17.40        | 0.00      |
| 53 | year + woody coverage  | 8         | -50.40        | 116.80     | 17.66        | 0.00      |
| 54 | year + terrain ruggedness  | 8         | -50.47        | 116.94     | 17.80        | 0.00      |
| 55 | coyote density + year + mule deer density + well density + terrain ruggedness + woody coverage + (woody coverage * coyote density)     | 13        | -45.71        | 117.41     | 18.27        | 0.00      |
| 56 | year + mule deer density   | 8         | -51.00        | 117.99     | 18.85        | 0.00      |
| 57 | coyote density + year + mule deer density + well density + terrain ruggedness + woody coverage + (terrain ruggedness * coyote density) | 13        | -46.06        | 118.12     | 18.98        | 0.00      |
| 58 | coyote density + year + mule deer density + well density + terrain ruggedness + woody coverage + (mule deer density * coyote density)  | 13        | -46.59        | 119.18     | 20.04        | 0.00      |
| 59 | model with random factor only  | 6         | -68.49        | 148.98     | 49.84        | 0.00      |
| 60 | null model   | 2         | -204.30       | 412.60     | 313.47       | 0.00      |

**Table 2.1.(continued)**

**Table 2.2** Top linear mixed models ( $\Delta AIC < 4$ ) predicting fawn recruitment in the North Dakota badlands (1962-2012). Models were run using ML Maximum Likelihood. Year (covariate) was included as a fixed factor in all models to account for possible long-term trend in recruitment. The random structure took the form  $(1/YEAR)+(year|StudyArea)$ , thus YEAR (factor) and Study area (factor) were fitted as random intercepts (crossed, i.e. non-hierarchical random effects), while year (covariate) was fitted as a random slope because we could not assume a constant effect across different study areas. The top ranked model explained 85% of total variability ( $adj. R^2 = 0.85$ , null model as reference), and 46% of variability when compared to a model including the random factor only ( $adj. R^2 = 0.46$ ).

| #  | model structure  | d.f. | logLik | AIC    | $\Delta AIC$ | wi   |
|----|--|------|--------|--------|--------------|------|
| 1  | winter min temp + coyote density + year + well density + (well density * coyote density)   | 11   | -38.57 | 99.14  | 0.00         | 0.20 |
| 2  | winter min temp + coyote density + year + well density + woody coverage + (well density * coyote density)  | 12   | -37.61 | 99.22  | 0.08         | 0.19 |
| 3  | winter min temp + coyote density + year + well density + terrain ruggedness + (well density * coyote density)                                      | 12   | -37.75 | 99.50  | 0.37         | 0.16 |
| 4  | winter min temp + coyote density + year + mule deer density + well density + (well density * coyote density)                                       | 12   | -38.37 | 100.73 | 1.59         | 0.09 |
| 5  | winter min temp + coyote density + year + well density + terrain ruggedness + woody coverage + (well density * coyote density)                     | 13   | -37.58 | 101.17 | 2.03         | 0.07 |
| 6  | winter min temp + coyote density + year + mule deer density + well density + woody coverage + (well density * coyote density)                      | 13   | -37.67 | 101.34 | 2.20         | 0.07 |
| 7  | winter min temp + coyote density + year + mule deer density + well density + terrain ruggedness + (well density * coyote density)                  | 13   | -37.72 | 101.44 | 2.31         | 0.06 |
| 8  | winter min temp + coyote density + year + well density   | 10   | -40.95 | 101.90 | 2.76         | 0.05 |
| 9  | winter min temp + coyote density + year + well density + woody coverage  | 11   | -40.14 | 102.28 | 3.14         | 0.04 |
| 10 | winter min temp + coyote density + year + mule deer density + well density + terrain ruggedness + woody coverage + (well density * coyote density) | 14   | -37.25 | 102.50 | 3.36         | 0.04 |
| 11 | winter min temp + coyote density + year + well density + terrain ruggedness  | 11   | -40.34 | 102.69 | 3.55         | 0.03 |

**Table 2.3** Averaged parameters and their relative importance ( $\Sigma w_i$ ) in the confidence set of 11 linear mixed models ( $\Delta AIC < 4$ ) predicting fawn recruitment in the North Dakota badlands (1962-2012). Models were run using ML Maximum Likelihood. Year (covariate) was included as a fixed factor in all models to account for possible long-term trend in recruitment. The random structure took the form  $(1|YEAR)+(year|StudyArea)$ , thus YEAR (factor) and Study area (factor) were fitted as random intercepts (crossed, i.e. non-hierarchical random effects), while year (covariate) was fitted as a random slope because we could not assume a constant effect across different study areas. The top ranked model explained 85% of total variability ( $adj. R^2 = 0.85$ , null model as reference), and 46% of variability when compared to a model including the random factor only ( $adj. R^2 = 0.46$ ).

| <i>Fixed effect</i>                  | $\beta$       | SE           | 95% CI<br>(lower) | 95% CI<br>(upper) | $\Sigma w_i$ |
|--------------------------------------|---------------|--------------|-------------------|-------------------|--------------|
| <b>intercept</b>                     | <b>1.735</b>  | <b>0.111</b> | <b>1.519</b>      | <b>1.952</b>      | -            |
| coyote density                       | -0.025        | 0.022        | -0.067            | 0.017             | 1            |
| well density                         | 0.001         | 0.010        | -0.019            | 0.021             | 1            |
| <b>winter min temperature</b>        | <b>0.030</b>  | <b>0.008</b> | <b>0.014</b>      | <b>0.046</b>      | 1            |
| <b>year</b>                          | <b>-0.011</b> | <b>0.001</b> | <b>-0.014</b>     | <b>-0.009</b>     | 1            |
| <b>coyote density * well density</b> | <b>-0.030</b> | <b>0.013</b> | <b>-0.055</b>     | <b>-0.004</b>     | 0.88         |
| woody coverage                       | -0.001        | 0.001        | -0.004            | 0.001             | 0.40         |
| terrain ruggedness                   | -0.001        | 0.001        | -0.003            | 0.001             | 0.37         |
| mule deer density                    | 0.007         | 0.008        | -0.009            | 0.023             | 0.25         |

**Table 2.4** Recruitment rates predicted by top ranked mixed linear models depending on varying oil and gas well density, coyote density, and average min winter temperature (3 scenarios) while keeping the other predictors **constant to mean values** (year, woody coverage, terrain ruggedness and mule deer density)

|                                |      | well density (wells / 10 km2) |      |      |      |      |      |      |      |      |      |
|--------------------------------|------|-------------------------------|------|------|------|------|------|------|------|------|------|
|                                |      | 0                             | 1    | 2    | 3    | 4    | 5    | 6    | 7    | 8    |      |
| coyote density (head / 10 km2) | 0    | 1.04                          | 1.04 | 1.04 | 1.04 | 1.04 | 1.04 | 1.04 | 1.04 | 1.04 | 1.04 |
|                                | 0.25 | 1.03                          | 1.03 | 1.02 | 1.01 | 1.01 | 1.00 | 0.99 | 0.99 | 0.99 | 0.98 |
|                                | 0.5  | 1.03                          | 1.01 | 1.00 | 0.98 | 0.97 | 0.96 | 0.94 | 0.93 | 0.93 | 0.91 |
|                                | 0.75 | 1.02                          | 1.00 | 0.98 | 0.95 | 0.93 | 0.91 | 0.89 | 0.87 | 0.87 | 0.85 |
|                                | 1    | 1.01                          | 0.98 | 0.95 | 0.93 | 0.90 | 0.87 | 0.84 | 0.81 | 0.81 | 0.78 |
|                                | 1.25 | 1.01                          | 0.97 | 0.93 | 0.90 | 0.86 | 0.82 | 0.79 | 0.75 | 0.75 | 0.71 |
|                                | 1.5  | 1.00                          | 0.96 | 0.91 | 0.87 | 0.82 | 0.78 | 0.74 | 0.69 | 0.69 | 0.65 |
|                                | 1.75 | 0.99                          | 0.94 | 0.89 | 0.84 | 0.79 | 0.74 | 0.69 | 0.63 | 0.63 | 0.58 |
|                                | 2    | 0.99                          | 0.93 | 0.87 | 0.81 | 0.75 | 0.69 | 0.63 | 0.57 | 0.57 | 0.52 |
|                                | 2.25 | 0.98                          | 0.92 | 0.85 | 0.78 | 0.72 | 0.65 | 0.58 | 0.52 | 0.52 | 0.45 |
|                                | 2.5  | 0.98                          | 0.90 | 0.83 | 0.75 | 0.68 | 0.61 | 0.53 | 0.46 | 0.46 | 0.38 |
|                                | 2.75 | 0.97                          | 0.89 | 0.81 | 0.72 | 0.64 | 0.56 | 0.48 | 0.40 | 0.40 | 0.32 |
| 3                              | 0.96 | 0.87                          | 0.78 | 0.70 | 0.61 | 0.52 | 0.43 | 0.34 | 0.34 | 0.25 |      |

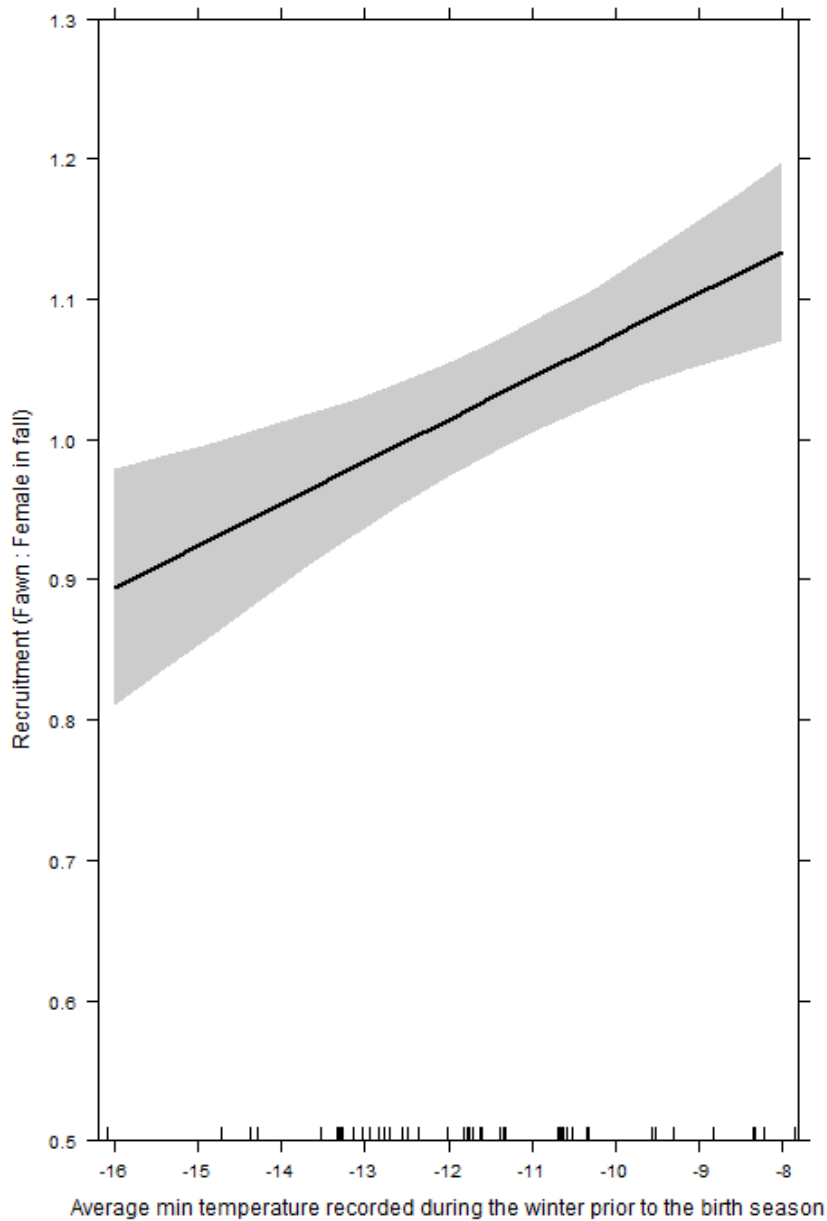
Average winter temperature kept to mean values recorded over the period 1962-2012 (-11.2 Celsius degrees)

|                                |      | well density (wells / 10 km2) |      |      |      |      |      |      |      |      |      |
|--------------------------------|------|-------------------------------|------|------|------|------|------|------|------|------|------|
|                                |      | 0                             | 1    | 2    | 3    | 4    | 5    | 6    | 7    | 8    |      |
| coyote density (head / 10 km2) | 0    | 0.98                          | 0.98 | 0.98 | 0.98 | 0.98 | 0.98 | 0.99 | 0.99 | 0.99 | 0.99 |
|                                | 0.25 | 0.97                          | 0.97 | 0.96 | 0.95 | 0.95 | 0.94 | 0.93 | 0.93 | 0.93 | 0.92 |
|                                | 0.5  | 0.97                          | 0.95 | 0.94 | 0.92 | 0.91 | 0.90 | 0.88 | 0.87 | 0.87 | 0.85 |
|                                | 0.75 | 0.96                          | 0.94 | 0.92 | 0.90 | 0.87 | 0.85 | 0.83 | 0.81 | 0.81 | 0.79 |
|                                | 1    | 0.95                          | 0.93 | 0.90 | 0.87 | 0.84 | 0.81 | 0.78 | 0.75 | 0.75 | 0.72 |
|                                | 1.25 | 0.95                          | 0.91 | 0.88 | 0.84 | 0.80 | 0.77 | 0.73 | 0.69 | 0.69 | 0.66 |
|                                | 1.5  | 0.94                          | 0.90 | 0.85 | 0.81 | 0.77 | 0.72 | 0.68 | 0.63 | 0.63 | 0.59 |
|                                | 1.75 | 0.94                          | 0.88 | 0.83 | 0.78 | 0.73 | 0.68 | 0.63 | 0.58 | 0.58 | 0.52 |
|                                | 2    | 0.93                          | 0.87 | 0.81 | 0.75 | 0.69 | 0.63 | 0.58 | 0.52 | 0.52 | 0.46 |
|                                | 2.25 | 0.92                          | 0.86 | 0.79 | 0.72 | 0.66 | 0.59 | 0.52 | 0.46 | 0.46 | 0.39 |
|                                | 2.5  | 0.92                          | 0.84 | 0.77 | 0.69 | 0.62 | 0.55 | 0.47 | 0.40 | 0.40 | 0.32 |
|                                | 2.75 | 0.91                          | 0.83 | 0.75 | 0.67 | 0.58 | 0.50 | 0.42 | 0.34 | 0.34 | 0.26 |
| 3                              | 0.90 | 0.82                          | 0.73 | 0.64 | 0.55 | 0.46 | 0.37 | 0.28 | 0.28 | 0.19 |      |

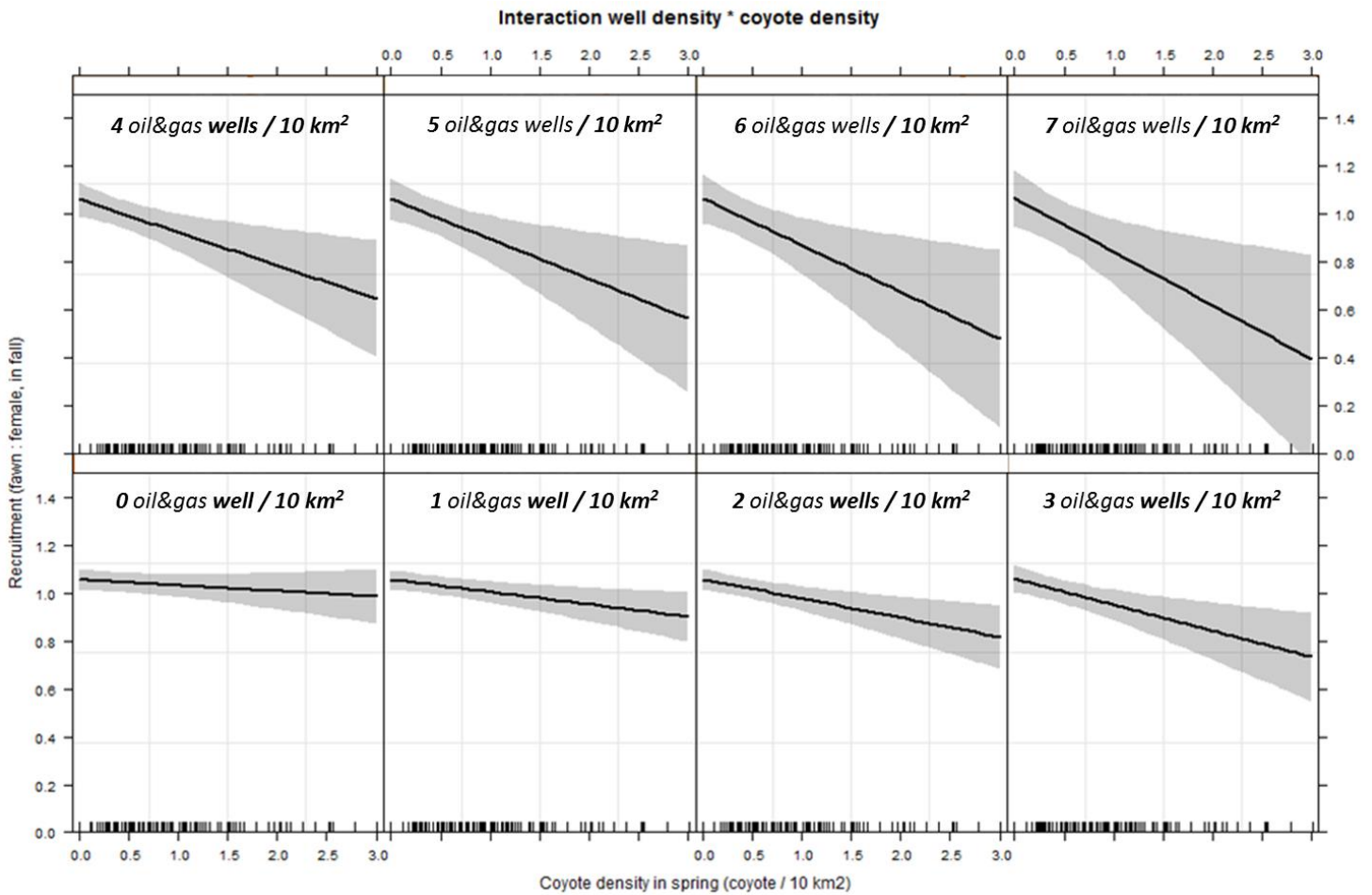
Particularly cold winters (average min winter temperature -13.2 Celsius degrees)

|                                |      | well density (wells / 10 km2) |      |      |      |      |      |      |      |      |      |
|--------------------------------|------|-------------------------------|------|------|------|------|------|------|------|------|------|
|                                |      | 0                             | 1    | 2    | 3    | 4    | 5    | 6    | 7    | 8    |      |
| coyote density (head / 10 km2) | 0    | 1.10                          | 1.10 | 1.10 | 1.10 | 1.10 | 1.10 | 1.11 | 1.11 | 1.11 | 1.11 |
|                                | 0.25 | 1.09                          | 1.09 | 1.08 | 1.07 | 1.07 | 1.06 | 1.05 | 1.05 | 1.05 | 1.04 |
|                                | 0.5  | 1.09                          | 1.07 | 1.06 | 1.04 | 1.03 | 1.02 | 1.00 | 0.99 | 0.99 | 0.97 |
|                                | 0.75 | 1.08                          | 1.06 | 1.04 | 1.02 | 0.99 | 0.97 | 0.95 | 0.93 | 0.93 | 0.91 |
|                                | 1    | 1.07                          | 1.05 | 1.02 | 0.99 | 0.96 | 0.93 | 0.90 | 0.87 | 0.87 | 0.84 |
|                                | 1.25 | 1.07                          | 1.03 | 1.00 | 0.96 | 0.92 | 0.89 | 0.85 | 0.81 | 0.81 | 0.78 |
|                                | 1.5  | 1.06                          | 1.02 | 0.97 | 0.93 | 0.89 | 0.84 | 0.80 | 0.75 | 0.75 | 0.71 |
|                                | 1.75 | 1.06                          | 1.00 | 0.95 | 0.90 | 0.85 | 0.80 | 0.75 | 0.70 | 0.70 | 0.64 |
|                                | 2    | 1.05                          | 0.99 | 0.93 | 0.87 | 0.81 | 0.75 | 0.70 | 0.64 | 0.64 | 0.58 |
|                                | 2.25 | 1.04                          | 0.98 | 0.91 | 0.84 | 0.78 | 0.71 | 0.64 | 0.58 | 0.58 | 0.51 |
|                                | 2.5  | 1.04                          | 0.96 | 0.89 | 0.81 | 0.74 | 0.67 | 0.59 | 0.52 | 0.52 | 0.44 |
|                                | 2.75 | 1.03                          | 0.95 | 0.87 | 0.79 | 0.70 | 0.62 | 0.54 | 0.46 | 0.46 | 0.38 |
| 3                              | 1.02 | 0.94                          | 0.85 | 0.76 | 0.67 | 0.58 | 0.49 | 0.40 | 0.40 | 0.31 |      |

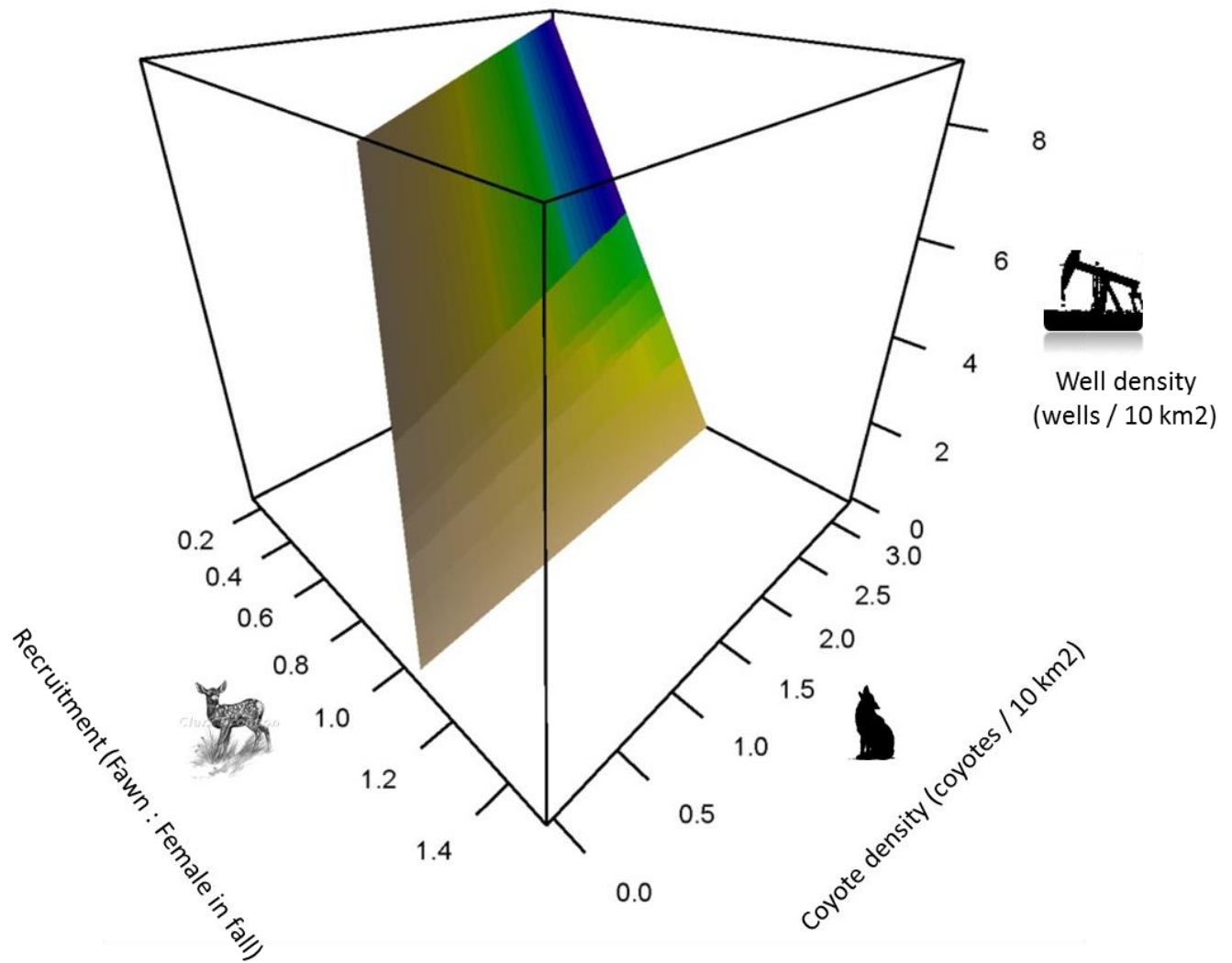
Particularly mild winters (average min winter temperature -9.2 Celsius degrees)



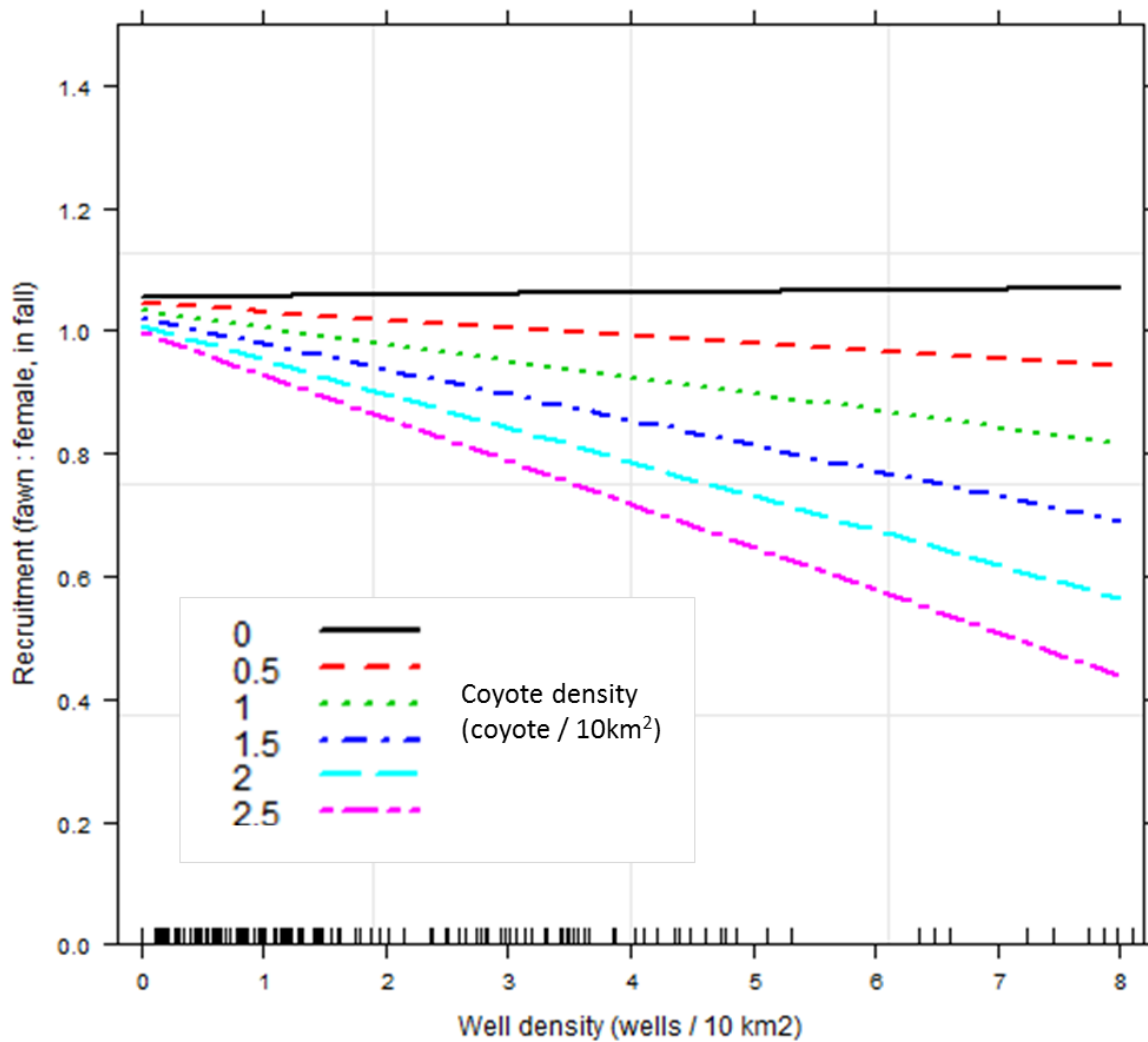
**Fig 2.1.** Effects of average min temperatures recorded during the winter prior to births on fall fawn recruitment (fawn:female ratio) in the North Dakota badlands (1962-2012).



**Fig 2.2.** Effects of the interaction of spring coyote density (coyote / 10 km<sup>2</sup>, x-axis) with oil and gas well density (wells / 10 km<sup>2</sup>, different scenarios corresponding to different plots) on fall fawn recruitment (fawn:female ratio, y-axis) in the North Dakota badlands (1962-2012).



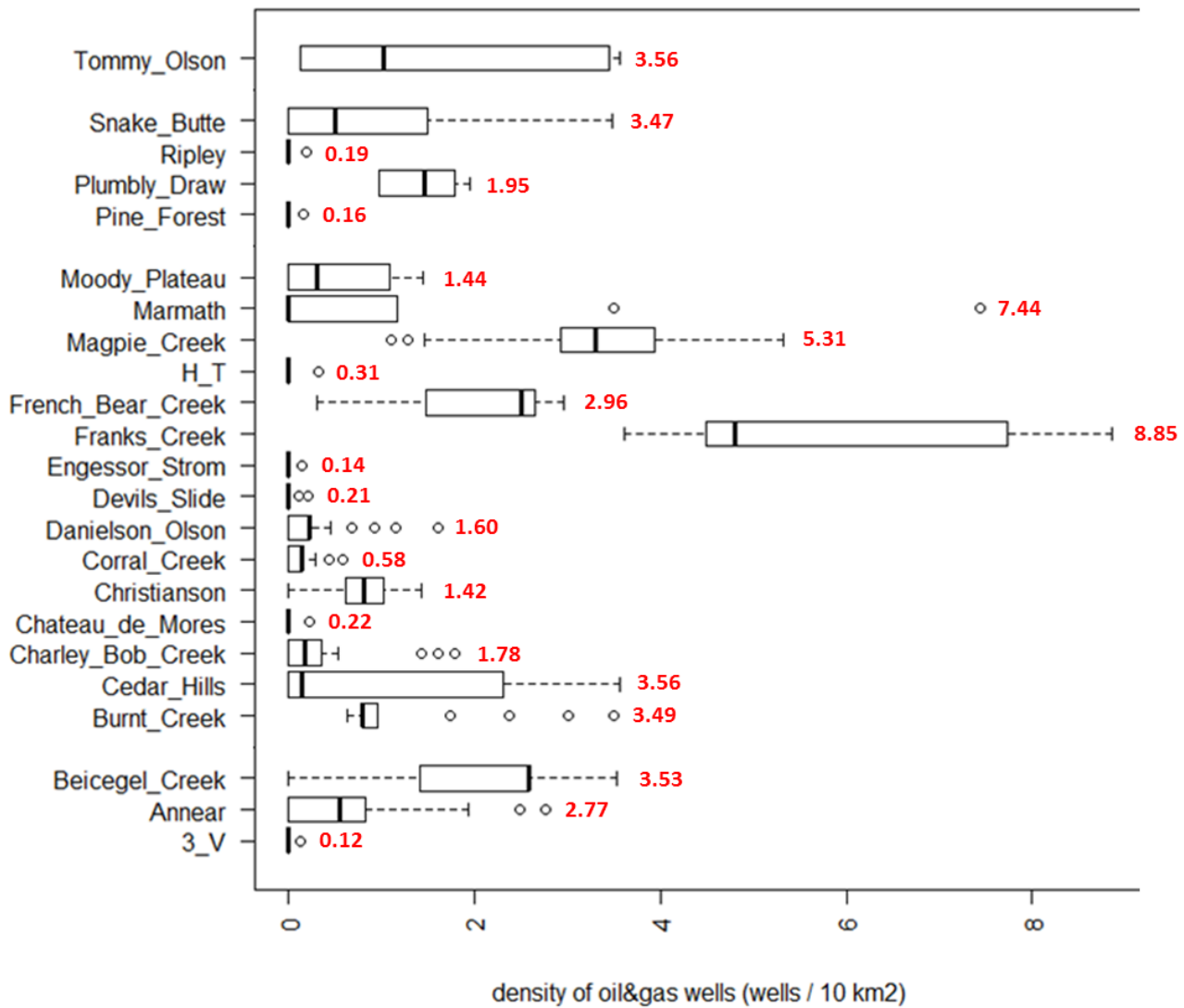
**Fig 2.3.** Effects of the interaction of spring coyote density (coyote / 10 km<sup>2</sup>, x-axis) with oil and gas well density (wells / 10 km<sup>2</sup>, z-axis) on fall fawn recruitment (fawn:female ratio, y-axis) in the North Dakota badlands (1962-2012).



**Fig 2.4.** Effects of the interaction of oil and gas well density (wells / 10 km<sup>2</sup>, x-axis) and spring coyote density (coyote / 10 km<sup>2</sup>, different lines correspond to different density thresholds) on fall fawn recruitment (fawn:female ratio, y-axis) in the North Dakota badlands (1962-2012).

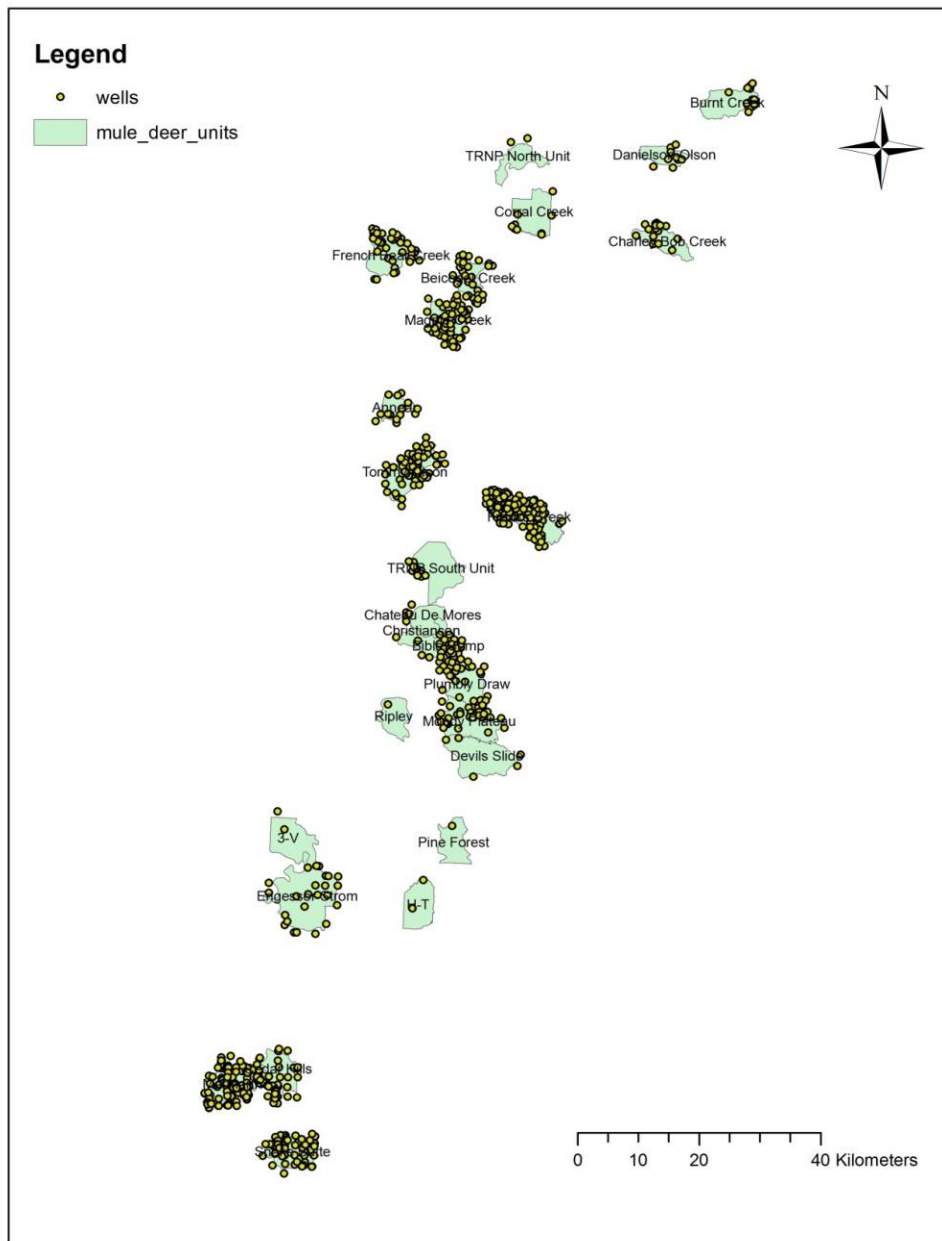


1962-2012

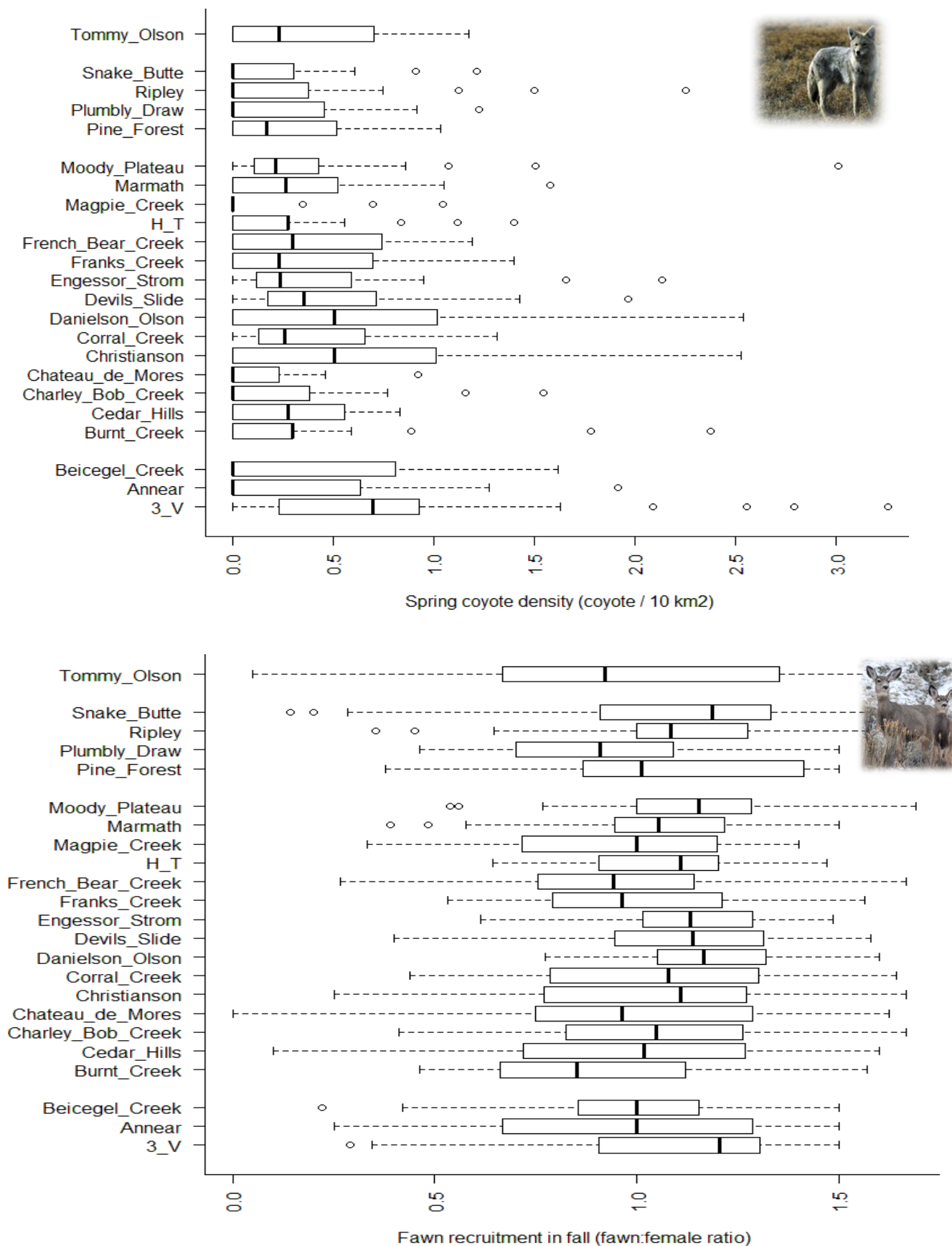


**Fig S1.** Density of active oil and gas wells recorded in the mule deer study sites (inside and outside considering a buffer of 1000 m) over the period 1962-2012. Max density values are indicated in red

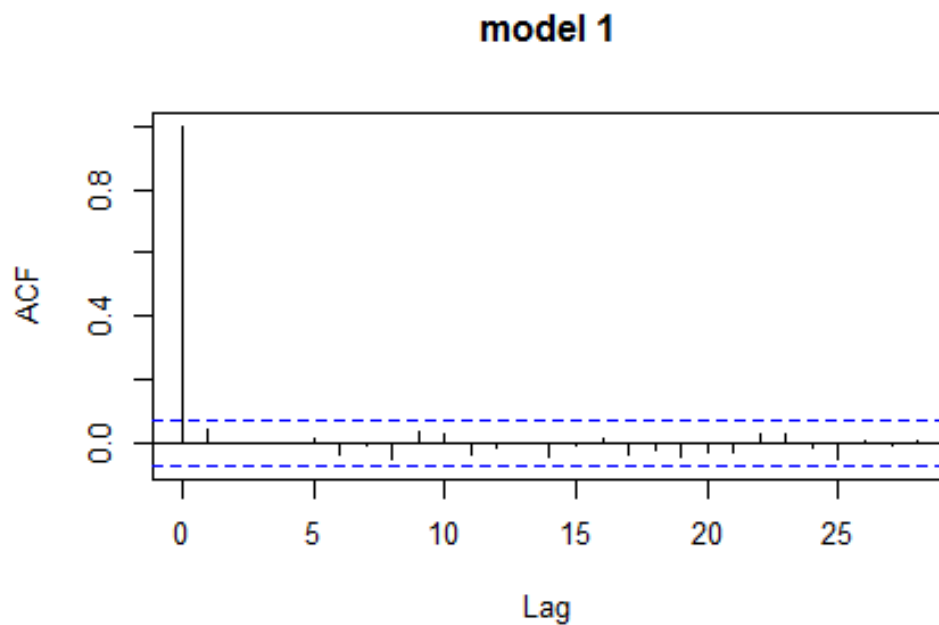
**Fig S2.** *Active oil and gas wells recorded in the mule deer study sites (inside and outside considering a buffer of 1000 m) over the period 1962-2012.*



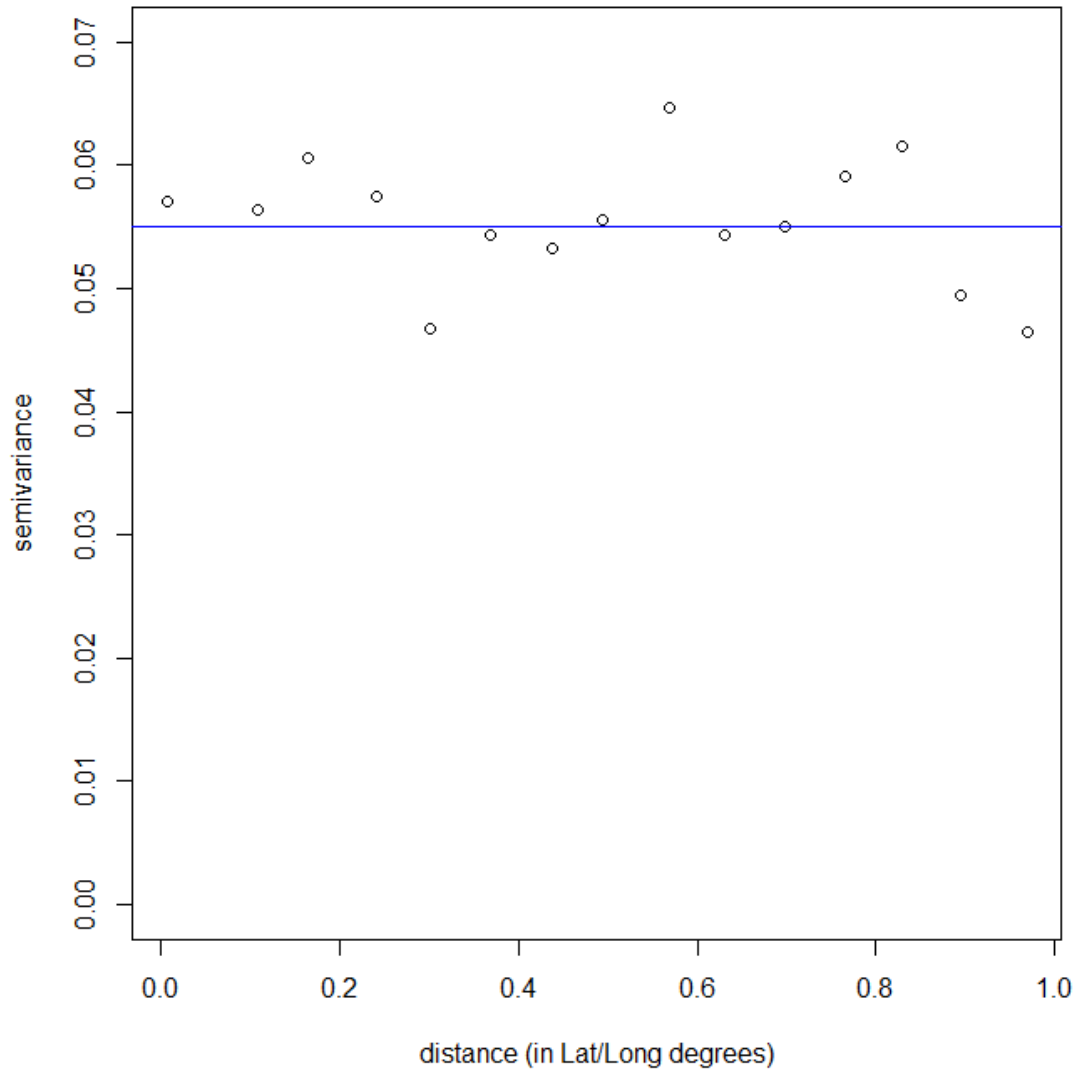
**Fig S3.** Boxplot indicating spring coyote density (upper panel) and fawn recruitment (lower panel) recorded in the mule deer study sites over the period 1962-2012.



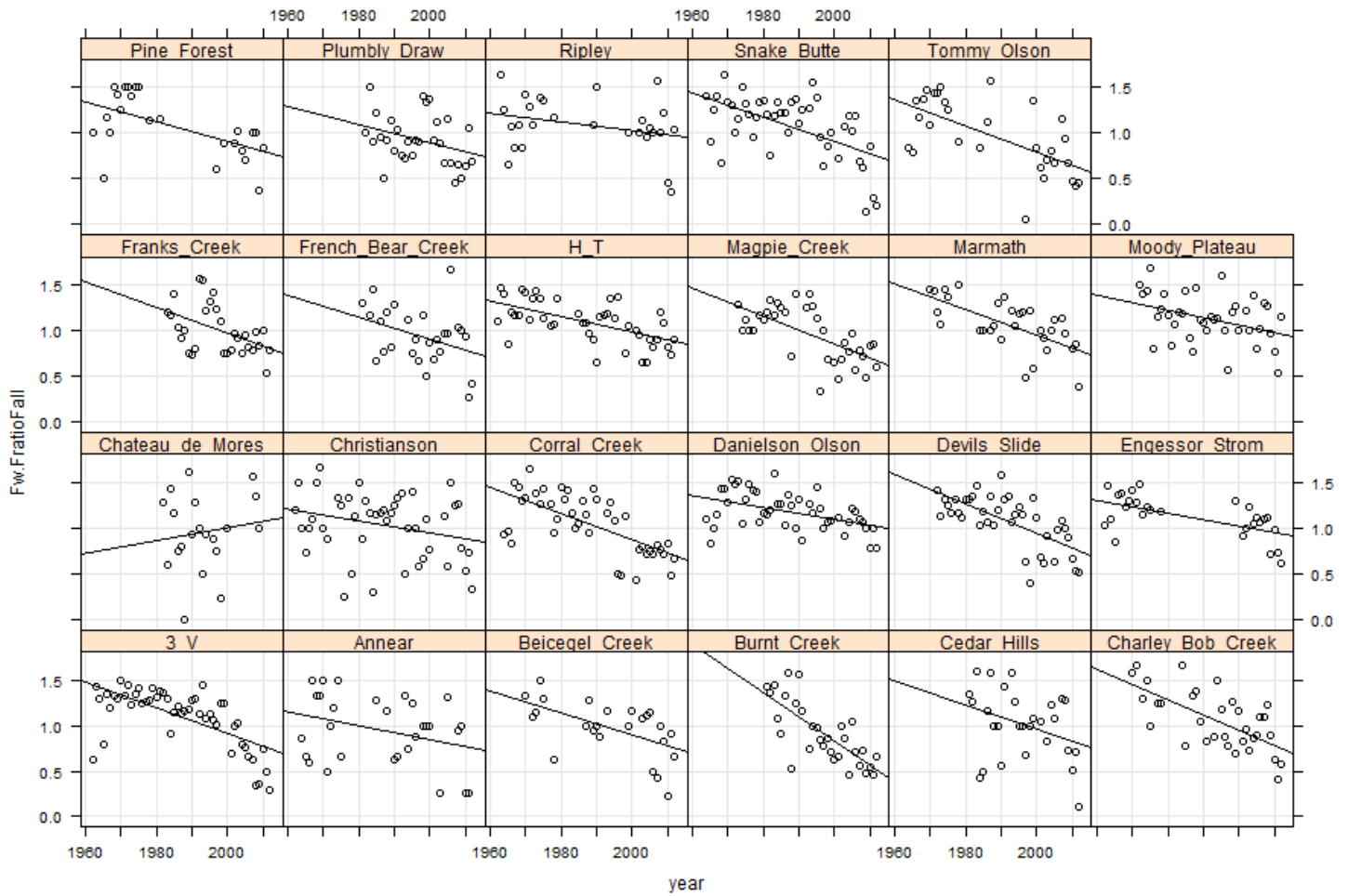
**Fig S4.** Autocorrelation plot for the residuals of top ranked model predicting fawn recruitment in the North Dakota badlands (1962-2012). ACF values (auto-correlation function) are plotted against time lag (x-axis, year).



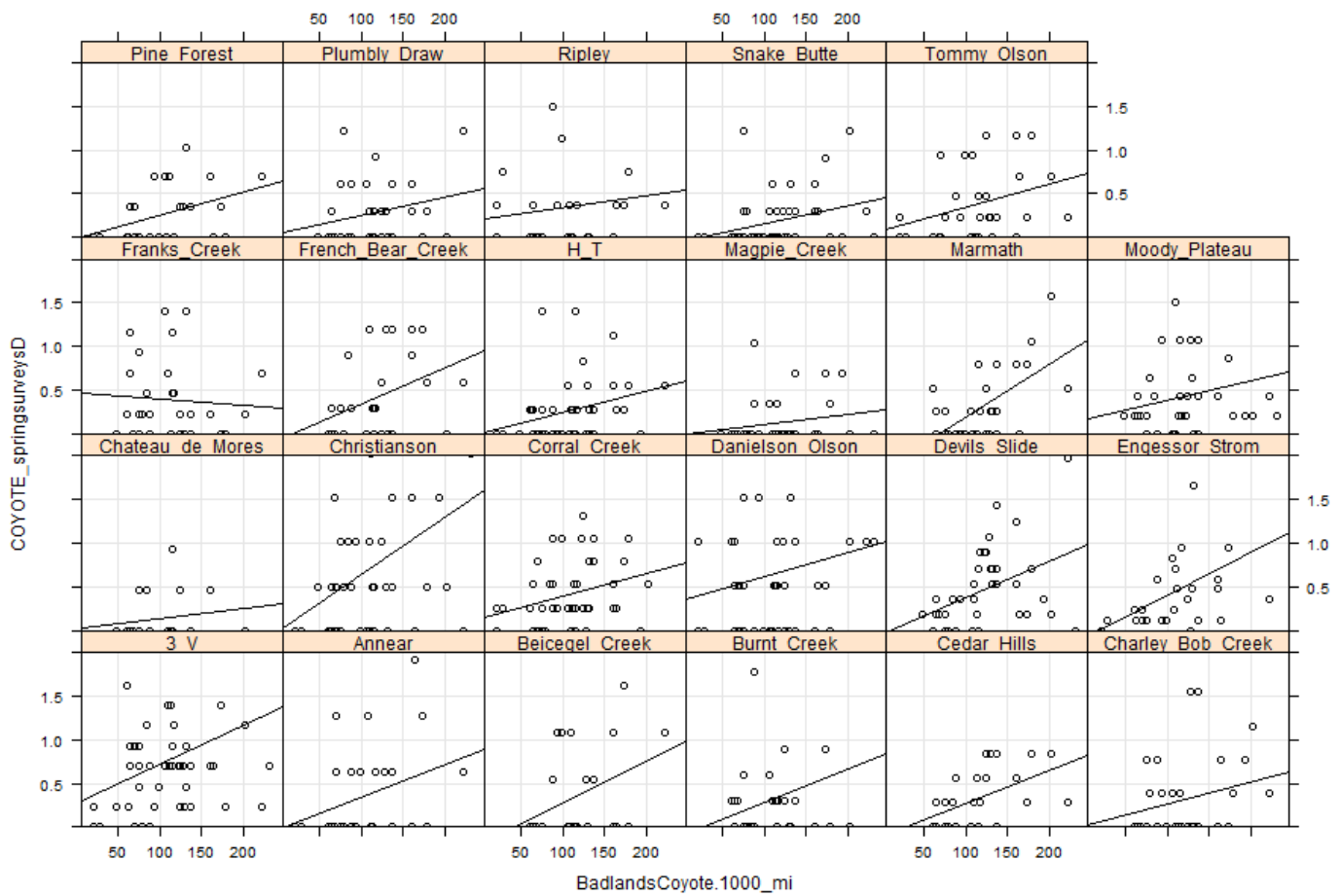
**Fig S5.** Lack of spatial autocorrelation patterns in the residuals of models predicting fawn recruitment in the North Dakota badlands (1962-2012); 0.1 degrees correspond to 11 km in latitudinal distance or 7 km in longitudinal distance.



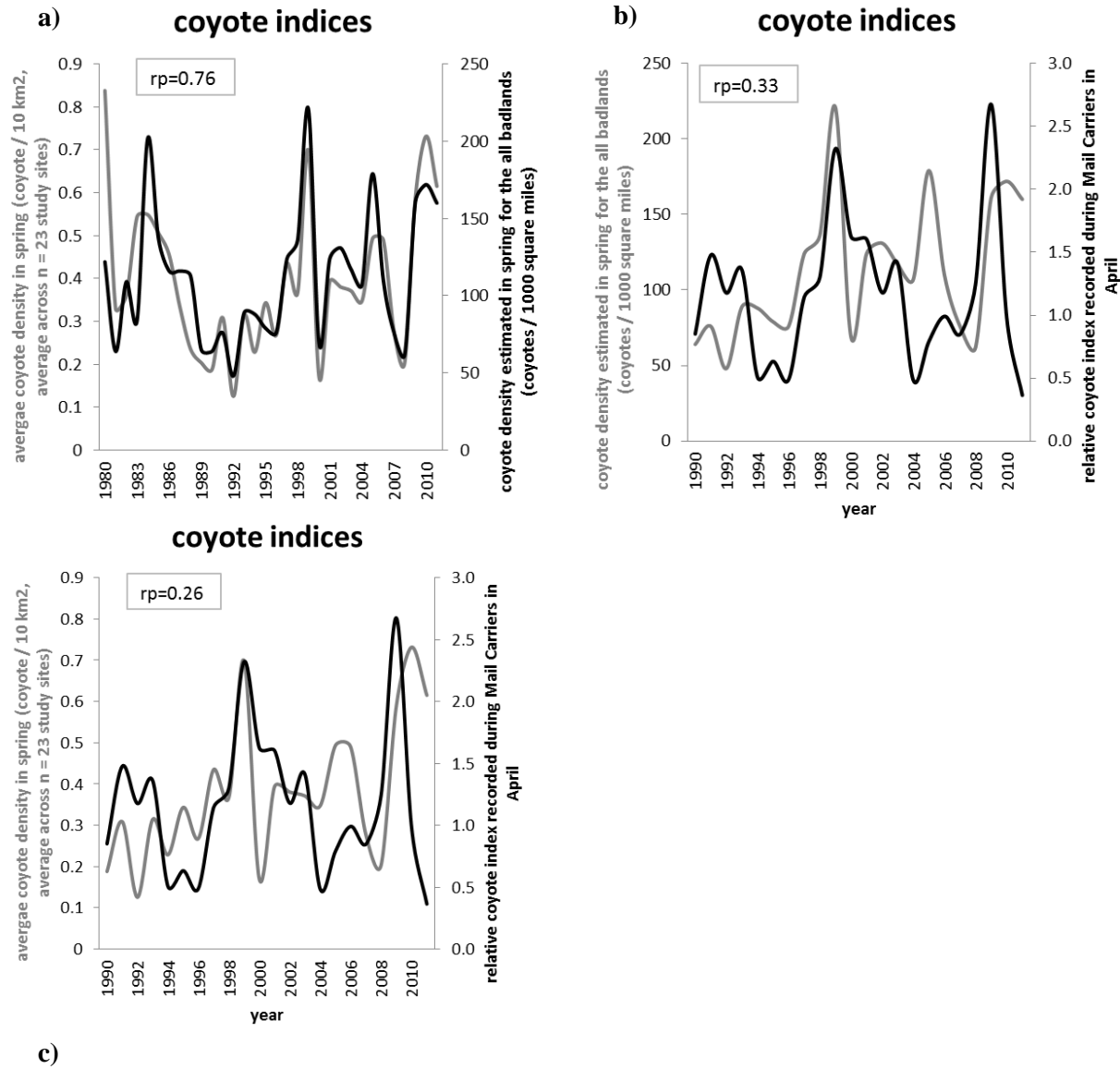
**Fig S6.** Recruitment rates (Fawn: female ratios, y-axis) in the North Dakota badlands over the period 1962-2012 (x-axis). Each plot corresponds to a different mule deer study site. Linear regression fits were added to increase readability.



**Fig S7.** Relationship ( $r_p = 0.27$ ,  $p < 0.001$ ) between coyote density estimated on a large scale for the all badlands (coyote / 1000 square miles, x-axis) and on the fine scale from mule deer spring surveys (y-axis, coyotes / 10 square km). Each plot corresponds to a different study site. Linear regression fits have been added to increase readability.

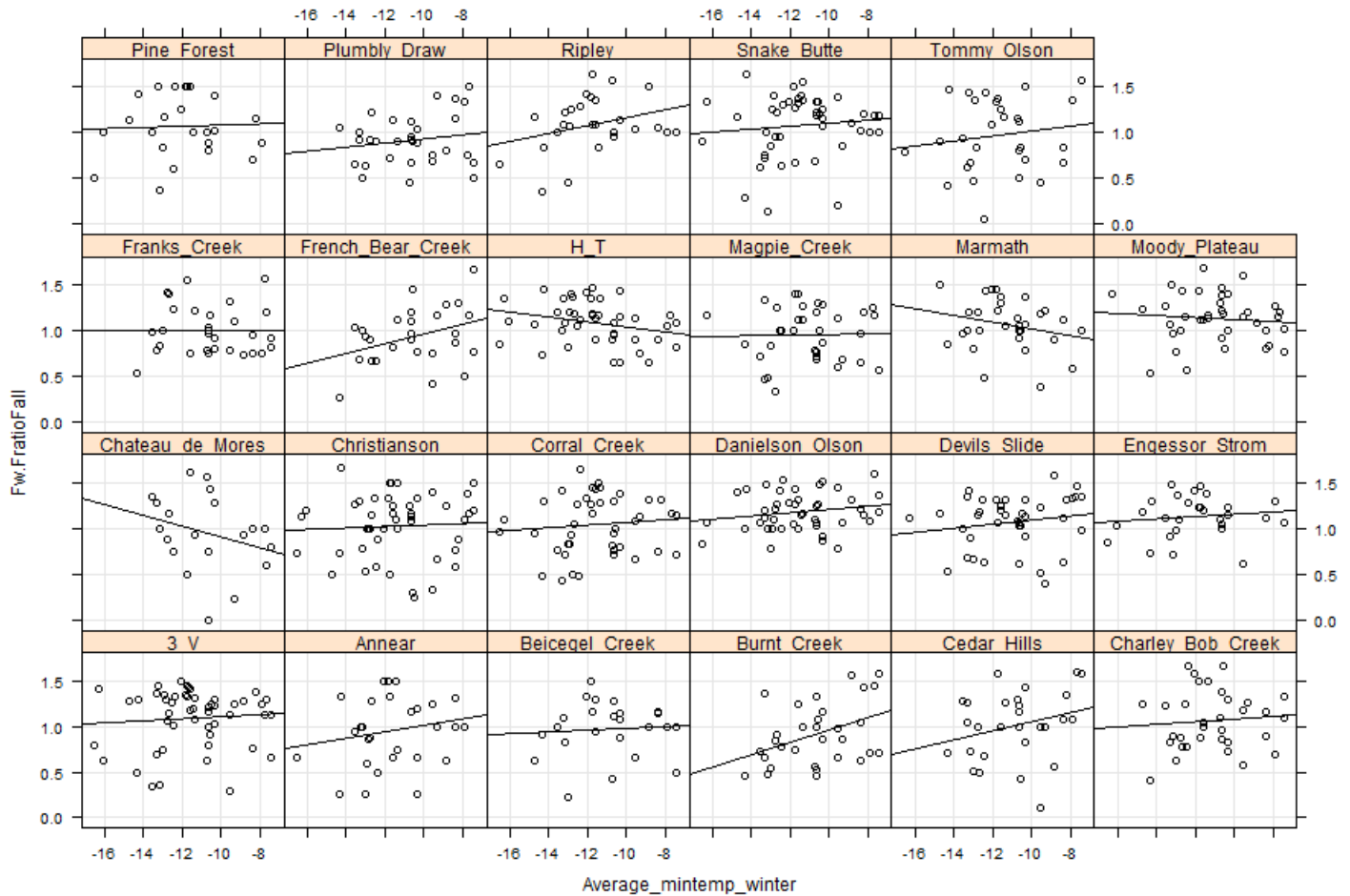


**Fig S8.** Relationship (Pearson correlation coefficients) between **a)** coyote density estimated on a large scale for the all badlands (coyote / 1000 square miles) and on the fine scale from mule deer spring surveys (coyotes / 10 square km), **b)** coyote density estimated on a large scale for the all badlands and relative coyote index presence estimated by Mail Carriers in April, and **c)** coyote density estimated on the fine scale from mule deer spring surveys and relative coyote index presence estimated by Mail Carriers in April.





**Fig S9.** Recruitment rates (Fawn: female ratios, y-axis) in the North Dakota badlands over the period 1962-2012 depending on average min temperature recorded during the winter prior to the birth season (x-axis). Each plot corresponds to a different mule deer study site. Linear regression fits were added to increase readability.



## Final remarks

*Simone Ciuti, William F Jensen, Scott E Nielsen, Mark S Boyce*

The mule deer is one of the most sought after game species in North Dakota. Every year approximately 10,000 hunters apply during the first drawing for about 2,500 antlered mule deer licenses. As a result the high level of interest in mule deer, the North Dakota Game and Fish Department is frequently questioned about the impacts of predation, winter weather, hunting pressure, range condition, and most recently energy development. Energy developments (**Fig R1-R3**) are indeed one of the most dramatic changes occurred to North Dakota landscapes and especially within the badlands, i.e., the primary habitat of mule deer, with exponential increases in energy development density recorded in several areas. As of 2010, about one quarter of the primary mule deer range in North Dakota has been moderately and highly impacted by oil wells. Much of this development has occurred over the past decade (**Fig R1-R3**). Over the past 40 years, it is estimated that the department has spent between \$800,000 and \$1,000,000 collecting aerial survey data, supported substantially by Pittman-Robertson funding. While these data have been vital for setting yearly harvests and managing the population, a retrospective review of this data set is now timely. With major landscape changes underway, we are at a point in mule deer management when the existing long-term mule deer data set needs to be evaluated before setting a new course for the future. This is the rationale behind the research effort described by this report, which we like to consider the beginning, rather than the end point, of a long-term assessment with the objective of anticipating mule deer population dynamics in this increasingly changing landscape. We are optimistic that future landscapes of North America can continue to support thriving populations of wildlife. But to ensure that this occurs we must understand how to reduce cumulative effects, apply best management strategies, and pay particular attention to key habitats and how they are likely to be affected by energy developments. After the first set of analyses conducted in 2005 by staff of the University of Alberta as a pro bono preliminary analysis (Nielsen and Boyce, unpublished), it became clear that additional analyses were required to evaluate the relative importance of oil and gas development on mule deer recruitment. The new set of analyses presented in this report identifies main factors affecting variation in fawn recruitment in the North Dakota badlands. Winter harshness prior to birth of fawns is clearly one of them. Indeed, stochastic weather events have major influence on recruitment and dynamics of many wildlife populations. However, we showed for the first time (Chapter 1) how Pacific-based indices, such as the North Pacific Pattern, can be a good proxy of climate in the North Dakota badlands, even in an area that hosts one of the mule deer populations most distant from the Pacific coast. These Pacific-based climate

indices are characterized by a certain degree of multi-year oscillation and predictability that could be better deployed to adjust mule deer management accordingly.

Among other factors responsible for variation in fawn recruitment in mule deer, we showed (Chapter 2) how the interaction between predator pressure (coyote) and energy development (well density) can have strong negative effects on fawn recruitment in the badlands. We found that oil and gas well density can have a strong negative impact on recruitment depending on the degree of predator pressure. We strongly recommend increased monitoring of mule deer and coyotes in those areas that are moderately to highly affected by energy developments to find ways to mitigate these effects. We also predicted different scenarios of fawn recruitment depending on predator pressure, winter harshness, and presence of energy developments that might be of use for management in those areas heavily impacted by oil extraction. Energy development has been shown to be responsible of direct (well pad surface) and indirect (2-3 km from the well site) habitat loss, as documented by recent research in Wyoming (Sawyer et al. 2002, Sawyer and Lindzey 2004, Sawyer et al. 2005, Sawyer et al. 2006, Sawyer et al. 2009). Our study adds a new piece to understanding this complex ecosystem, showing how coyote density and oil and gas development could have little effect when occurring as isolated factors, but can have marked negative consequences when occurring in an interacting and/or cumulative fashion. Habitat loss due to energy development could be responsible of a decreased spatial randomness of mule deer fawn bedding sites, which could be more predictable and localized away from well pads as a result of habitat fragmentation, as presented in Chapter 2. Our interpretation is that fragmentation and disturbance concentrate deer into more discrete secure patches that are more easily targeted by coyotes. Under such conditions, coyotes could be more effective predators on fawns. This could explain why the two factors negatively interact to affect mule deer recruitment. The concentration of mule deer by disturbance/developments could render the deer more vulnerable to coyotes. In a predator-prey system of the Canadian province of Alberta, Lingle et al. (2008) showed that mule deer (density = 7 deer / km<sup>2</sup>) and white tail deer (12 deer / km<sup>2</sup>) employ different anti-predator tactics (aggressive defense vs. flight) that result in contrasting patterns of age-dependent vulnerability in their probability of being captured when encountered by coyotes: shifting coyote hunt activity from summer to winter, or vice versa, alleviated annual mortality on one species and focused it on the other (Lingle et al. 2008). However, the ecological context in the North Dakota badlands is different, because white tail deer (density = 0.16 deer/ km<sup>2</sup>) occur at significantly lower density compared to mule deer (2.1 deer / km<sup>2</sup>). This makes coyote switching between alternative prey less likely. Understanding how the delicate predator-prey equilibrium can be altered by human developments is clearly one the priority of future research: this could allow better managing and protecting our human-modified landscapes. Characterizing the impacts of emerging energy development on wildlife with an eye

towards mitigation is the critical challenge of current days (Northrup and Wittemyer 2013). We think that the predation result is a proximal cause but that the ultimate mechanism relates to habitat fragmentation and concentration of deer into ever smaller pieces of habitat. This is likely a habitat issue, not one that can be fixed by coyote control. If we can ensure secure sizable blocks of habitat for mule deer, say adjacent to development sites, this might decrease the influence of coyote on mule deer recruitment in those areas heavily impacted by human developments. Further, if roads were configured to ensure adequate blocks of undisturbed landscape, we would expect a benefit to mule deer recruitment. Rowland et al (2000) clearly showed how road density can vary substantially whilst still ensuring some larger blocks of optimal habitat. Future road configuration might be crucial for mule deer habitat management. We will go on with our investigation using the data we gathered during this study. Moreover, targeted research (e.g. radiotracking) could shed light on the mechanism behind the interaction between coyote, human developments and deer recruitment. The decreased recruitment that we recorded in areas with high well densities and high coyote densities also could be the end result of cumulative factors. Indeed, previous research has indicated that coyote predation is compensatory (reviewed in Chapter 2), meaning that it has little effect on mule deer population fluctuations. However, recruitment can significantly decrease when coyote pressure and disturbance by energy development (e.g., mortality due to car collisions, habitat loss, and decreased body condition of animals using suboptimal habitats) are occurring simultaneously. The net cumulative effect of these factors is a loss in the resilience of the mule deer population to disturbances. We hope that the current mule deer radiotelemetry study in the North Dakota badlands will shed additional light on the mechanisms behind the interacting effect of energy developments and predator pressure on mule deer fawn recruitment.

Fig R1: Number of active wells (y-axis, all well typologies) recorded from 1956 to 2012 within and outside (1000 meters buffer area) mule deer study sites (n=26).

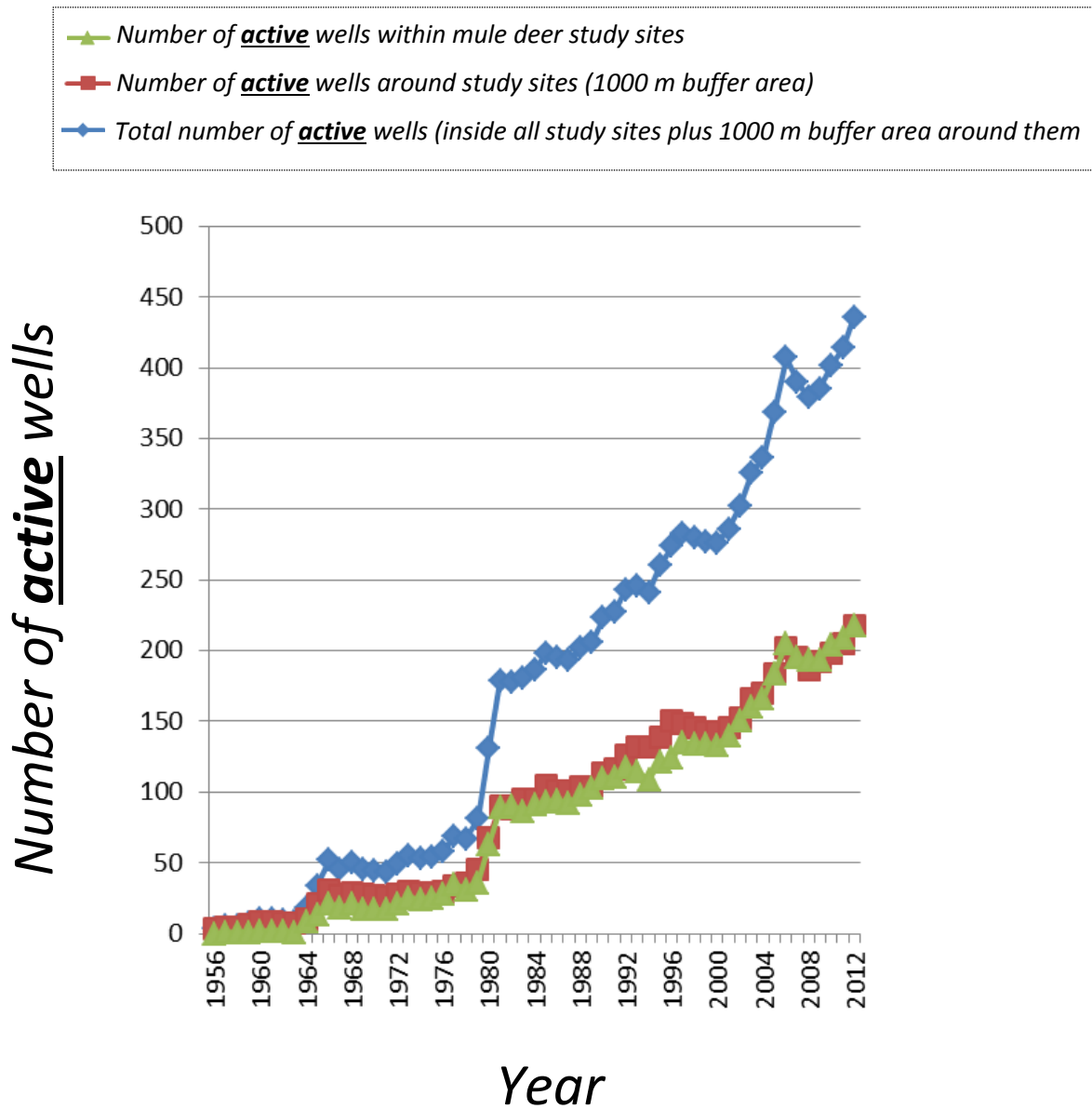


Fig R2: Number of active wells (dark grey, left y-axis, all well types) recorded from 1956 to 2012 within and outside (1000-m buffer area) mule deer study sites (n=26) compared to number of active wells in North Dakota during the same period (light grey, right y-axis, all well typologies)

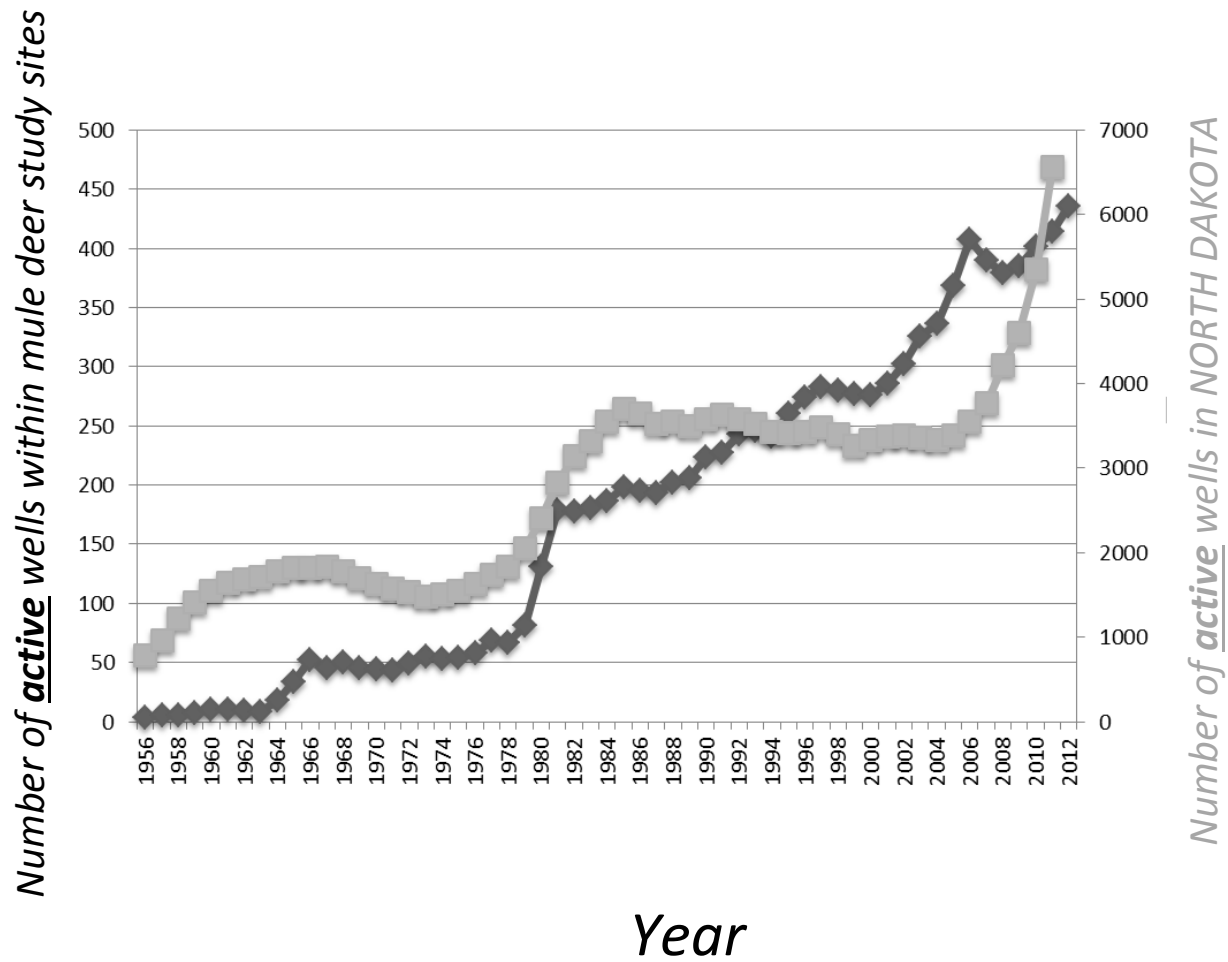
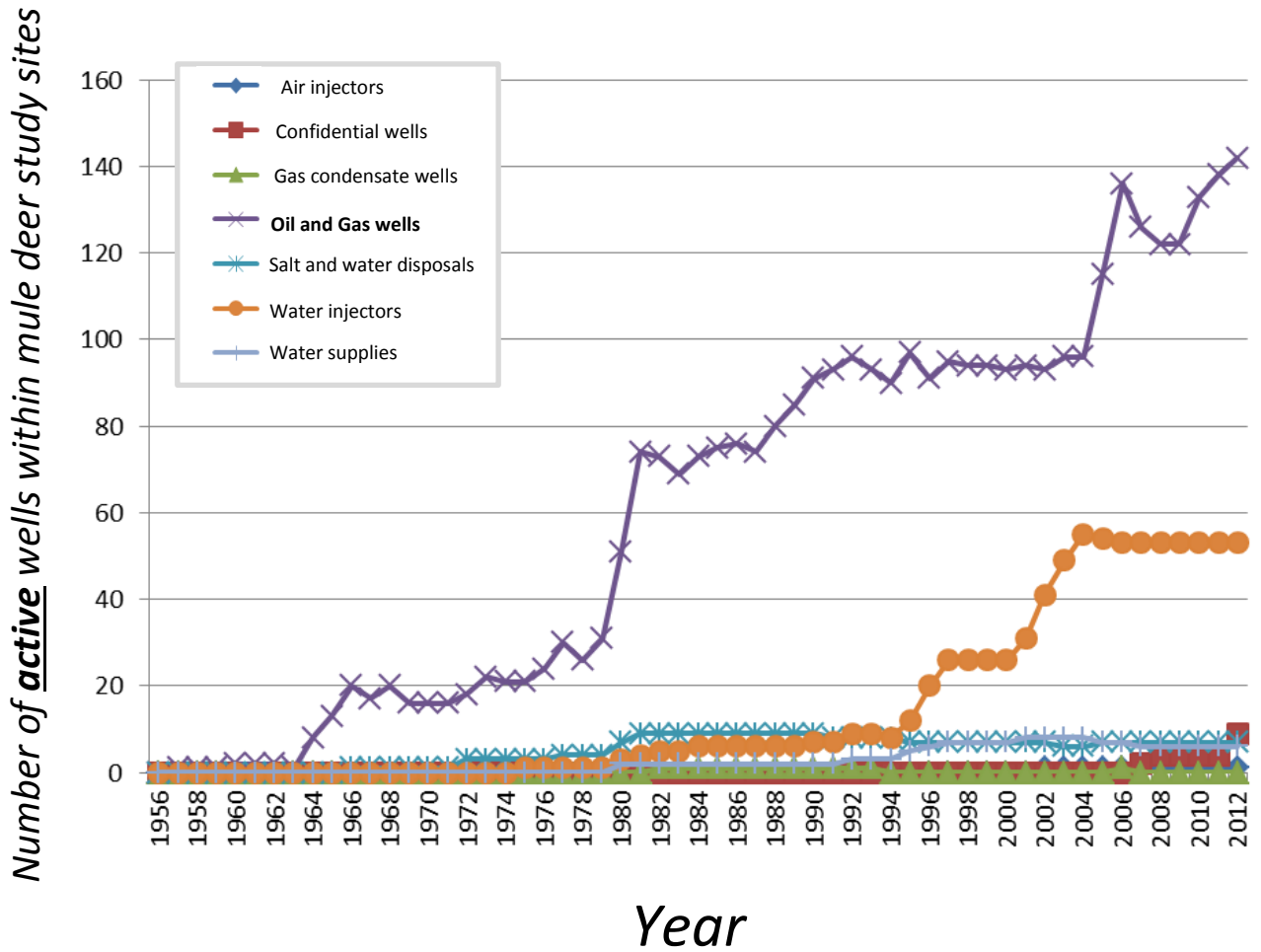


Fig R3: Number of active wells (y-axis, all well types) recorded from 1956 to 2012 within Mule Deer study sites (n=26). Wells are identified by well type.



## Literature cited

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