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125 October 2017
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9Schmidt et al: Weather-driven variation in cycles

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11Weather-driven change in primary productivity explains variation in the amplitude of two

12herbivore population cycles in a boreal system

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25**Abstract**

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2Author Contributions: EAR designed the vole study and EAR and MJF collected the vole data. CLM designed the
3hare project and collected the hare data. JHS analyzed the data and wrote the manuscript. All authors contributed
4to the conceptual integration of the datasets, discussed the results, and made substantive comments on the
5manuscript.

26Vertebrate populations throughout the circumpolar north often exhibit cyclic dynamics, and

27predation is generally considered to be a primary driver of these cycles in a variety of herbivore

28species. However, weather and climate play a role in entraining cycles over broad landscapes

29and may alter cyclic dynamics, although the mechanism by which these processes operate is

30uncertain. Experimental and observational work has suggested that weather influences primary

31productivity over multi-year time periods, suggesting a pathway through which weather and

32climate may influence cyclic herbivore dynamics. Using long-term monitoring data, we

33investigated the relationships among multi-year weather conditions, measures of primary

34productivity, and the abundance of two cyclic herbivore species: snowshoe hare and northern

35red-backed vole. We found that precipitation (rain and snow) and growing season temperatures

36were strongly associated with variation in primary productivity over multi-year time horizons. In

37turn, 4-fold variation in the amplitude of both the hare and vole cycles observed in our study area

38corresponded to long-term changes in primary productivity. The congruence of our results for

39these two species suggests a general mechanism by which weather and climate might influence

40cyclic herbivore population dynamics. Our findings also suggested that the association between

41climate warming and the disappearance of cycles might be initiated by changes in primary

42productivity. This work provides an explanation for observed influences of weather and climate

43on primary productivity and population cycles and will help our collective understanding of how

44future climate warming may influence these ecological phenomena in the future.

47**Introduction**

48Extensive effort has been directed towards understanding the mechanisms responsible for

49initiating and driving the cyclic population dynamics of vertebrates in the circumpolar north

50(Keith et al. 1984, Boonstra et al. 1998, Krebs et al. 1995, 2001a, Krebs 2011, 2013). In North

51America, predation is thought to be the dominant force driving the 10yr snowshoe hare [*Lepus*

52*americanus*] cycle observed across Canada and Alaska (Krebs et al. 2001a,b, 2013, 2014b, Krebs

532011), although some form of food limitation has also been implicated (Keith and Windberg

541978, Bryant 1981, Bryant et al. 1985, Krebs et al. 1995, 2014b, Hodges et al. 2001). Many

55species of microtine rodents also exhibit cycles at northern latitudes (Stenseth et al. 1999, Krebs

562013), however these cycles generally occur every 3-5yrs and are less commonly observed in

57North America (Boonstra and Krebs 2012, Krebs 2013). Populations of microtine rodents are

58also regulated in part by finite food resources (Boonstra et al. 2001, Huitu et al. 2003, 2007,

59Krebs et al. 2010, Johnson et al. 2017) and grazing-induced changes in food plants (Seldal et al.

601994, Reynolds et al. 2012, Wieczorek et al. 2014), though food limitation alone may be

61insufficient to cause the observed cycles (Krebs et al. 1995, Hodges et al. 2001, Krebs et al.

622001b, Krebs 2013, Prevedello et al. 2013). Similar to the case of snowshoe hares, top-down

63control through predation is generally thought to play a dominant role in microtine cycles

64(Hanski et al. 1993, Korpimaki and Krebs 1996, Korpimaki et al. 2002, 2004, Therrien et al.

652014, Fauteux et al. 2015b, Ginzburg and Krebs 2015).

66   In addition to the effects of food resources and predation, weather and climate patterns

67are implicated in cyclic dynamics. Seasonality and severe winter conditions may be necessary

68for the existence of cycles in general (Hansen et al. 1999, Yoccoz and Ims 1999, Stenseth et al.

692003, Bierman et al. 2006), and microtine rodents in particular are reliant on the insulative

70properties of snow for survival during extended winter periods (Reid and Krebs 1996, Korslund

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71and Steen 2006, Bilodeau et al. 2013, Terraube *et al.* 2015). Additionally, climate processes

72influence cycle synchronicity across broad landscapes (Stenseth et al 1999, 2002, Krebs et al.

732001b, 2002, 2013 Kausrud et al. 2008, Hone et al. 2011, Yan et al. 2013), and recent changes in

74climate have been linked to the collapse of cycles in some areas (Hornfeldt 2004, Hornfeldt et al.

752005, Ims and Fuglei 2005, Ims et al. 2008, Cornulier et al. 2013). There is also some evidence

76that the impacts of weather and climate conditions on cycles may accrue over multiple years,

77possibly through changes in predator efficiency (Yan et al. 2013), however, the mechanisms by

78which weather and climate influence cycles remain uncertain. One possible mechanistic

79pathway is through weather or climate induced changes in vegetation quantity and/or quality, and

80hence forage for herbivores.

81   The role of weather conditions in altering primary production has received comparatively

82little attention in the population cycles literature, although research in other areas suggests a

83strong link. Experimental work in high latitude systems has shown that early snow-melt and

84warmer and wetter conditions during the growing season result in increased plant productivity

85through time, in part through increased soil nutrient turnover (Wipf and Rixen 2010, Natali et al.

862012, Schaeffer et al. 2013, Sistla et al. 2013). The role of multi-annual weather patterns on

87plant productivity in the boreal forest has also been demonstrated empirically through long-term

88observational studies (Krebs et al. 2009, Roland et al. 2014, Nicklen et al. 2016). While annual

89variation in primary productivity might not be expected to induce cycles, climate-driven changes

90in primary production may provide a mechanistic explanation for lagged relationships between

91population cycles and climate (e.g., Yan et al. 2013). There has been some exploration of the

92direct effects of weather on cycle amplitude (e.g., Krebs et al. 2014a), but we are not aware of a

93direct assessment of multi-annual changes in weather and climate as drivers of variation in

94herbivore population cycles through the influence on primary productivity.

95   We used long-term monitoring data to investigate the effects of weather-induced

96variation in primary productivity on the cyclic dynamics of 2 herbivore species occurring in

97Denali National Park and Preserve (hereafter Denali): northern red-backed voles [*Myodes*

98*rutilus*], and snowshoe hares (hereafter voles and hares, respectively). We hypothesized that

99multi-year weather conditions may drive variation in primary productivity, in turn, influencing

100the vole and hare cycles observed in our study area. Our primary objectives were to: 1) assess

101the relationship between multi-year weather conditions and corresponding indices of primary

102productivity, and 2) assess the relationship between measures of primary productivity and

103variation in cyclic dynamics in voles and hares. If a sequential link between weather, primary

104productivity, and herbivore cycles were established, it would provide a common mechanism by

105which climate factors could drive variation in 2 cyclic herbivore populations in North America.

106**Materials and methods**

107*Study area*

108Our study area encompassed 2522 km^2 in the northern foothills of the Alaska Range within

109Denali in interior Alaska, USA (see McIntyre and Schmidt 2012; Fig. 1). The study area

110encompassed boreal-montane ecosystems including conifer and mixed conifer and deciduous

111forests in the lowlands ranging upwards into subalpine shrublands then through an alpine tundra

112zone into barren rock and ice in the highest elevations (Roland et al. 2013). The topography

113ranged from rugged mountainous terrain to broad glacial valleys and floodplains, as well as

114rolling upland areas. Elevations ranged from ~400m-1400m. The area experienced long, cold,

115dry winters and short, warm summers. Historically, the average annual temperature was -3°C,

116with an average high of 20°C and an average low of -22°C (Shulski and Wendler 2007).

117Average annual precipitation was 38.1cm (Shulski and Wendler 2007). Annual snowfall

118averageed 206cm, which is usually concentrated in the months of November and December

119(Sousanes 2008).

120*Field Methods*

121We summarized weather data from the climate station located at Denali headquarters within our

122study area (Fig. 1). We used temperature records to calculate the number of growing degree

123days (GDD; base temperature 5° C) accumulated between April-August for each year of our

124study. We also obtained the total recorded precipitation for the same period (PPT) and

125calculated the average snow depth over the previous winter (Oct 15-April 1) as an index of

126winter snow conditions (SNOW). We selected these measures because they broadly represent

127weather factors associated with major sources of variation in plant productivity and nutrient

128turnover (e.g., Wipf and Rixen 2010, Natali et al. 2012, Schaeffer et al. 2013, Sistla et al. 2013,

129Roland *et al.* 2014). We also developed a binary early winter severity index to represent

130potentially thermally stressful conditions for voles that could cause increased early winter

131mortality (i.e., Reid and Krebs 1996), possibly lowering their abundance in the subsequent year.

132The early winter severity index (freeze) was a binary variable indicating years with >5 days in

133early winter (October-December) with snow depths <15 cm and daily minimum temperatures <-

13417.8°C. To provide an annual measure of primary productivity, we calculated the average

135annual maximum Normalized Difference Vegetation Index (NDVI), based on satellite imagery

136(AVHRR; 1km^2 pixels), across the study area from 1990-2013 (values were not available prior to

1371990). Due to the small size of the vole study site relative to the spatial grain of the satellite

138imagery, we used measures of NDVI based on the larger snowshoe hare study area for the vole

139analysis. We assumed that measures of NDVI over this larger scale would reflect conditions at

140the local scale of the vole study site and expected that the results based on measures of NDVI at

141a larger scale would be more conservative (i.e., less likely to detect an effect) due to local scale

142variation in productivity that would be averaged over the larger area. These weather and primary

143productivity variables were then used as covariates for analysis.

144   We sampled the vole population on 4 plots at a site in Denali centered on (63º 43' 47" N,

145longitude 148º 58' 52" W) during August from 1992-2014 (Fig. 1). Each plot consisted of a 10 x

14610 grid of Sherman live traps spaced 10 m apart over 0.81 ha. Two plots were located along the

147Rock Creek riparian zone (riparian plots) and 2 were located approximately 500 m away on a

148forested ridge (forest plots). One forest plot and one riparian plot were sampled annually, a

149second forest plot was sampled 1997-2014 (except 2004), and a second riparian plot was

150sampled during 1992-1993 and 1997-2014. Each trap contained bedding material and was baited

151with sterilized sunflower seeds. Trapping sessions were 4-5 days long with 3 trap checks per

152day, resulting in 10-15 sampling occasions per plot per year. Captured individuals were

153identified to species, scanned with a passive integrated transponder (PIT) tag reader to identify

154previously captured individuals, injected with a uniquely identifiable PIT tag if unmarked, and

155then released. The final dataset consisted of 2277 capture histories over the 23 year period.

156   We indexed annual hare abundance from 1988-2014 as the average number of adults

157observed per day during routine fieldwork from mid-April to late June as part of a larger project

158(see McIntyre and Adams 1999, McIntyre and Schmidt 2012). All observations were made and

159recorded by the same individual (C. McIntyre) using a standardized approach for the entire

160period (McIntyre and Schmidt 2012). While the annual indices could not be converted to true

161abundance, we were confident that this measure accurately represented relative abundance

162between years and the frequency and relative amplitude of the hare cycle in Denali (McIntyre

163and Schmidt 2012, Krebs et al. 2013). Our hare index was in general agreement with an

164assessment of the hare cycle in nearby areas (Arthur and Prugh 2010, Krebs et al. 2013), further

165supporting our assertion that our data accurately represented the relative abundance and phase of

166the hare cycle in Denali.

167*Statistical Analysis*

168<u>Primary productivity</u>

169Measures of NDVI provide a meaningful annual index of primary productivity at large scales

170(Kerr and Ostrovsky 2003), however, we wanted to explore the relationship between weather

171conditions and changes in primary productivity over multi-year windows. We hypothesized that

172primary productivity may be a function of weather patterns that influenced growing conditions

173over time (e.g., Wipf and Rixen 2010, Natali et al. 2012, Schaeffer et al. 2013, Sistla et al. 2013),

174presuming plant growth may increase when the weather is warmer, wetter, and less snowy.

175Therefore, we fit a series of models to running averages of NDVI over the previous 1-5 years

176using corresponding running averages of GDD, PPT, and SNOW as covariates. All variables

177were standardized to have a mean = 0 and SD = 1 to improve convergence and allow direct

178comparisons of effect sizes among covariates. The general model can be written as:

179$NDVI_i = \beta_1 GDD_i + \beta_2 PPT_i + \beta_3 SNOW_i$

180where *i* represents the running average *i* in 1…5 years. We used the adjusted R^2 value as a

181measure of model fit and selected the most appropriate value of *i* based on the vole and hare

182analyses (see below).

183<u>Voles</u>

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184To estimate vole abundance and density, we used spatially-explicit capture-recapture models

185(Royle and Dorazio 2008, Efford et al. 2009, Borchers 2012, Efford and Fewster 2013) fit in a

186Bayesian hierarchical framework (e.g., Royle and Young 2008, Gardner et al. 2009, 2010, Royle

187et al. 2009). Spatially-explicit capture-recapture approaches utilize the locations of recaptures to

188estimate the activity center of each individual, while also addressing the decline in detection

189probability with distance of the activity center from each trap (Royle and Young 2008, Gardner

190et al. 2009, Efford and Fewster 2013). This straightforward combination of the process and

191detection models allows the direct estimation of abundance or density within the sampling area

192without requiring the concept of the somewhat ambiguous effective trapping area (Efford and

193Fewster 2013). Data augmentation (Royle et al. 2007) was employed to address the problem of

194an unknown number of activity centers within the sample area (Gardner et al. 2010).

195   We used the spatial mark-recapture model presented by Gardner et al. (2009) to estimate

196the number of individuals, *N*, with activity centers within the sampling area, *S*. Density was

197defined as *N/S*. We investigated the importance of multiple covariates by formulating a model

198for the inclusion probability, *psi*. This is the probability that an individual from the augmented

199data list is a member of the population (Gardner et al. 2009). This allowed us to assess the

200influence of covariates on population size. We allowed capture probability to vary by year, and

201included an individual random effect to account for heterogeneity in capture probability among

202individuals in addition to variation due to the locations of each activity center. We included a

203plot by year random effect in the model for *psi* to account for differences between plots and

204years that were not explained by the covariates.

205   Prior to conducting the Bayesian analysis, we used an exploratory analysis of the raw

206capture data to identify potentially useful covariates. We used this approach due to the

207prohibitively long run times that would be required for model selection in a Bayesian framework.

208We fit generalized linear models to the average number of unique captures in each year to (i.e.,

209raw data) using sine and cosine terms with 2, 3, or 4 year periodicity to address cyclic patterns in

210abundance. This range of values was selected after an inspection of the auto-correlation

211function. Although we could have used other time series approaches to address cycle periodicity

212(e.g., threshold autoregressive modeling; Stenseth et al. 1998), we chose to employ a fixed cyclic

213pattern for simplicity and because our primary questions were related to variation in cycle

214amplitude. Our approach to modeling the basic cyclic pattern was expected to have no impact on

215our assessment of the factors affecting cycle amplitude. After using AIC to select the best model

216describing the basic cycle, we explored the potential relationship between vole abundance and

217the early winter severity index (freeze) and the range of running averages (i.e., 1 to 5 years) for

218NDVI for our study area. Based on this exploratory analysis, we selected $NDVI_5$ as the most

219informative predictor of variation in vole abundance for final model fitting (see results). We

220then fit the model to the data in a Bayesian framework to assess whether the apparent

221relationships from the exploratory step held under formal analysis. The most general model for

222the probability of a potential individual being included in the population, ψ, can be written as:

223$logit(\psi) = \int + \beta_1 \sin\left(\left(\frac{2\pi}{L}\right) * t_i\right) + \beta_2 \cos\left(\left(\frac{2\pi}{L}\right) * t_i\right) + \beta_3 NDVI_5 + \beta_4 freeze + e_{ij}$

224where int is the intercept, the β_k are parameters, L is the cycle period length (i.e, 2, 3, or 4 years),

225t_i is the annual time step (years 1-23), and e_{ij} is a random effect adjustment term for each year, i,

226and site, j. For the 1992-1994 period, when $NDVI_5$ values were not available, we used the

227longest running average possible (i.e., 2, 3, and 4 years respectively). Post-hoc analysis using

228only data from 1995-2014 produced nearly identical results, suggesting the use of slightly shorter

229NDVI averages for the first 3 years of our series did not materially affect our results. Therefore,

230we only present results based on the full 1992-2014 dataset. Models were fit using program R

231(v. 2.14.2, R Development Core Team 2012) and OpenBUGS (Thomas et al. 2006).

232Hares

233We log-transformed the annual hare index and used linear models to describe the cycle and

234select among covariates. We first inspected the autocorrelation function based on the time series

235data to assess the period length of the cycle. Based on these findings, we then fit models

236containing sine and cosine terms with a 9, 10, or 11 year period to assess whether cyclic terms

237were supported and to identify the appropriate period length. After selecting the best

238approximating model describing the basic cycle, we considered the covariates GDD_i, PPT_i, and

239$SNOW_i$ as proxies for $NDVI_i$. We used the weather data in this case because the hare dataset

240began 7 years prior to the availability of NDVI for our study area. Our objective was to assess

241whether these proxies for NDVI would predict variation in hare numbers. We did not consider

242the winter severity term as we did not expect hares to be as dependent as voles on snow cover for

243thermal protection during early winter. The most general model describing each index of

244abundance, *index*, can be written as:

245$$\log(index)=\int +\beta_1 \sin\left(\left(\frac{2\pi}{L}\right)*t_j\right)+\beta_2 \cos\left(\left(\frac{2\pi}{L}\right)*t_j\right)+\beta_3 GDD_i+\beta_4 PPT_i+\beta_5 SNOW_i \text{where } int \text{ is}$$

246the intercept, β_k β_k are parameters, L is the period length (9, 10, or 11 years), and t_j is the annual

247time step (i.e., 1-27 years). We first used AIC to select the appropriate terms describing the

248cycle (i.e., sine and cosine terms) and period length. We then used AIC to identify whether the

249weather covariates improved model fit. We also conducted a post-hoc exploratory analysis using

250only the 1995-2014 data, replacing the three weather covariates with $NDVI_i$, to confirm that any

251relationships were consistent and increase our confidence in the results.

252**Results**

253*Primary productivity*

254NDVI$_i$ was highest in multi-year periods that were warmer, wetter, and less snowy,

255corresponding to conditions in the mid-2000's (Fig. 2). Model fit improved as the length of the

256moving average increased, and the 3 weather variables (GDD$_5$, PPT$_5$, SNOW$_5$) explained nearly

257all of the variation in NDVI$_5$ between 1995 and 2014 (R^2 = 0.94; Fig. 2). This result indicated a

258direct link between average weather conditions over the previous 5 years and average NDVI over

259the same time period. We present the results for NDVI$_5$ because this variable was the best

260predictor for variation in vole cycle amplitude.

261*Voles*

262The average annual number of unique captures per plot varied from 6 to 81. We found strong

263support for the inclusion of both sine and cosine terms with period length = 3, indicating the vole

264population in our study area cycled regularly every 3 years (Table 1, Figs. 3, 4B). As predicted,

265in years following those with severe early winter conditions, abundance was reduced, suggesting

266a reduction in survival in early winter in those years (Table 1, Fig. 4B). Model selection results

267indicated that the model containing NDVI$_5$ fit better than versions containing NDVI$_4$ (ΔAIC =

2682.6) or NDVI$_3$ (ΔAIC = 4.7), and there was little support for NDVI averaged over shorter time

269periods (i.e., ΔAIC >15). The best approximating model indicated that cycle amplitude varied 4

270fold in direct relation to NDVI$_5$ (Fig. 4). Estimated densities based on the Bayesian model

271ranged from 2.2/ha during the 1994 low to 36.6/ha during the 2008 peak. The strong relationship

272between NDVI$_5$ and vole cycle amplitude suggests that variation in vole densities was directly

273related to primary productivity throughout the 3 yr cycle. The period length of the cycle

274remained consistent through time despite variation in both winter severity and primary

275productivity.

276*Hares*

277Our index of hare abundance ranged from 0.3 to 40.6 during our 27yr study. The hare cycle was

278best represented by sine and cosine terms with a period length of 10 (Table 2, Fig. 3). Models

279containing 4 and 5 year running averages of the 3 weather variables received equal support and

280outperformed averages over shorter intervals. For consistency with the vole results, we present

281estimates from the model containing 5 year running averages of GDD_5, PPT_5, $SNOW_5$.

282Although the period of the hare cycle (10 years) was longer than that of voles (3 years), the

283population-level response to these predictors of primary productivity was similar (Fig. 4C).

284Although $NDVI_5$ values did not exist for the early years of the hare dataset, the model containing

285weather conditions identified as the primary drivers of $NDVI_5$ predicted variation in the

286amplitude of the hare cycle well (R^2=0.82). An exploratory analysis using a subset of the data

287for the period when $NDVI_5$ was available produced very similar results, supporting these

288conclusions (results not shown). There was little support for a model lacking the weather

289variables ($\Delta AIC = 20.7$) and the fit of the reduced (i.e., cyclic terms only) model was lower

290(adjusted R^2=0.44), indicating strong support for a link between long-term weather and hare

291abundance. The third hare peak was 4 fold higher than the previous two and was synchronous

292with a peak in vole densities of similar magnitude (Fig. 4). Both peaks also corresponded with

293the period of highest $NDVI_5$. Thus, although hares and voles cycled at much different rates and

294exhibit different life history characteristics, they shared a contemporaneous relationship with

295primary productivity.

296**Discussion**

297Our results demonstrate that multi-year weather patterns were directly related to variation in

298measures of primary productivity at the landscape-scale in our boreal study system, which were

299in turn positively related to the dynamics of two widely distributed cyclic herbivore species,

300hares and voles. These findings establish sequential relationships between long-term weather

301patterns, primary productivity, and cyclic dynamics, thereby increasing our collective

302understanding of the processes underlying these important phenomena. Weather and climate

303patterns have been identified as important factors in the dynamics of many cyclic species, but the

304mechanism through which they influence these populations had heretofore been elusive

305(Stenseth et al. 1999, Watson et al. 2000, Cattadori et al. 2005, Kausrud et al. 2008, Hone et al.

3062011, Yan et al. 2013). The establishment of these linkages provides a potential mechanistic

307explanation for the observed diminution of some cycles (Hornfeldt 2004, Hornfeldt et al. 2005,

308Ims and Fuglei 2005, Ims et al. 2008, Cornulier et al. 2013) through climate-induced changes in

309primary productivity.

310*Weather and primary production*

311Our results suggest that primary productivity in Denali varies at the landscape-scale in response

312to annual precipitation (both rain and snow) and summer temperatures, and that these responses

313operate over multi-year time spans. That is, annual time-steps may not always be the appropriate

314temporal window for considering the relationships among weather variables and primary

315productivity in this region. The positive influence of warmer, wetter, and less snowy conditions

316we found were not surprising given other studies that have demonstrated similar links between

317annual metrics of broad-scale productivity (as measured by NDVI) and annual climate in high

318latitude regions (e.g. Goetz et al. 2005, Verbyla 2008, Berner et al. 2013). Specifically, shrub

319tundra areas (that occur over a large portion of our study area) showed increasing NDVI trends in

320response to increasing summer warmth (Verbyla 2008, Berner et al. 2013), some interior lowland

321boreal forest areas showed decreasing NDVI trends at least in part in response to drought (Goetz

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322et al. 2005, Beck et al. 2011), and delayed green-up has been related to deep snows in spring

323(Pettorelli et al. 2005, Wipf and Rixen 2010).

324   Although the specific climate-productivity relationships we found in Denali are not

325necessarily surprising, it is noteworthy that our data suggest that some weather-vegetation

326interactions governing NDVI accrue over multi-year windows. Possible explanations for the

327strong association between multi-year weather conditions and NDVI include a variety of

328processes including increased rates of nutrient turnover in response to warm and/or wet periods

329(e.g. Hobbie 1996, Natali et al. 2012, Schaeffer et al. 2013, Sistla et al. 2013) that may stimulate

330increased plant growth over multiple years, and the possibility that the deepening of active layer

331depths over a series of years may induce productivity effects that manifest over multi-year time

332scales (e.g. Beck et al. 2015). For example, tree ring studies in interior Alaska (including

333Denali) routinely showed significant responses to previous years' weather (Lloyd et. al 2013,

334Walker and Johnstone 2014, Girardin et al. 2016, Nicklen et al. 2016). Further, a recent

335investigation into white spruce reproduction in Alaska revealed significant weather effects on

336seed production over a four-year period (Roland et al. 2014). Additionally, the impacts of

337extreme weather events showed delayed responses that may occur even two years later (Zona et

338al. 2014). Such relationships will not be apparent when using strictly annual metrics without

339utilizing lagged effects due to high interannual variability and the unquantified influence from

340previous annual time steps. While our current data cannot confirm the mechanisms behind the

341conspicuous association, a fertile area for future work may be the role of multi-year weather

342patterns in regulating long term trends in primary productivity.

343*Hare and vole cycles*

344Extended winter periods, such as those experienced in Denali, are often considered necessary for
345the existence of population cycles at high latitudes (Hansson and Henttonen 1985, Yoccoz and
346Ims 1999, Aars and Ims 2002, Stenseth et al. 2003, Hornfeldt et al. 2005, Bierman et al. 2006).
347While it is unlikely that food resources are limiting for either hares or voles during the growing
348season, our results suggest that primary production might play a role in limiting populations
349during the subsequent winter months (e.g., Huitu et al. 2003, 2007). The link between weather
350and primary productivity also suggests a mechanism by which changes in season length and
351productivity may result in the dampening or elimination of population cycles in some areas in
352association with climate change (Ims et al. 2008, Cornulier et al. 2013, Korpela et al. 2013).
353Although we did not observe a dampening of cycles in Denali, we speculate that the diminution
354or elimination of cycles in other areas might occur through a reduction in the limiting effects of
355winter through increased food resources, or alternatively, a general amelioration of the winter
356period (i.e., length or severity) sufficient to avoid population limitation. However, the specific
357causal variables and the sign of the relationships will likely vary among ecosystems, climatic
358regions, and/or geographic locations, and we expect future work in other areas may reveal
359additional relationships between climate and primary production.

360   The 3 yr vole cycle we documented was unique for this species in North America
361(Boonstra and Krebs 2012, Boonstra et al. 2016), although the basic cyclic pattern was similar to
362that of populations in Fennoscandia and elsewhere in Eurasia (Stenseth et al. 1996, Stenseth
3631999). Existing studies in Alaska have provided limited information on long-term dynamics or
364evidence of cycles, although long-term datasets are uncommon (e.g., Whitney 1976, West 1982,
365Whitney and Feist 1984). We expect that cyclic dynamics may exist in other vole species (e.g.,
366Fauteux et al. 2015a), or in other portions of North America, however, an assessment of the scale

367and breadth of such cycles is dependent on the implementation of additional monitoring

368programs and further analysis of any existing datasets. Our results are consistent with past

369findings that microtine rodent populations at high latitudes are generally dependent on snow

370cover to mitigate the effects of extreme cold (Reid and Krebs 1996, Boonstra and Krebs 2006,

371Korslund and Steen 2006, Bilodeau et al. 2013, Fauteux et al. 2015b). Interestingly, severe

372winter conditions influenced vole cycle amplitude but had no apparent effect on periodicity,

373suggesting winter severity itself does not cause cycles directly. Instead, the link between

374primary productivity and amplitude throughout the cycle suggests food might be implicated as a

375limiting factor (Boonstra et al. 2001, Huitu et al. 2003, 2007, Previtali et al. 2009, Krebs et al.

3762010), presumably during the extended winter period when individuals are dependent on finite

377food resources.

378   A critical finding of our study was the discovery of an apparent relationship between

379long-term measures of primary productivity and abundance throughout both the 10yr hare and

3803yr vole cycles. Although only 3 hare peaks were observed during our study period, the nearly

381identical pattern of increased amplitude in the vole cycle during the same time frame strengthens

382our conclusion that primary productivity may limit cycle amplitude in both species. The

383importance of large-scale weather patterns on hare cycles has previously been identified

384(Stenseth et al. 1999, Yan et al. 2013), although the causal link remained unclear. The direct

385relationship between weather and primary productivity establishes a potential mechanism

386through which weather and climate could influence population cycles. We argue that the most

387parsimonious explanation for the 4-fold variation in cycle amplitude is that multi-year levels of

388primary productivity placed an upper limit on both the hare and vole cycles. This is consistent

389with the theory of bottom-up control which has been demonstrated in similar species (Flowerdew

390et al. 2017, Johnson et al. 2017). Our results suggest that variation in amplitude was driven by

391limited resources, with higher peak densities occurring during periods of high primary

392productivity when food resources are presumably more abundant. The congruency of our

393results, despite considerable differences in the spatial and temporal scales captured in each

394dataset, supports our conclusions.

395   There are two important mathematical properties that warrant further discussion in the

396context of interpreting our results. First, variation in cycle amplitude has an equal and opposite

397effect on opposing phases of the cycle (all else being equal), therefore, as amplitude increases,

398both the high and low phases become more extreme. This behavior resulted in a potentially

399counterintuitive finding that low-phase densities were lower when NDVI was higher. However,

400rather than being incongruent with our bottom-up hypothesis, these reduced low-phase densities

401were a direct consequence of increased cycle amplitude during periods of high NDVI. Second,

402population cycles differ from basic cyclic patterns (e.g., a sine wave) in that the low phase of

403population cycles is constrained to be ≥ 0 while the high phase has no upper bound. Due to this

404constraint, there is less potential for variation among low-phase densities as compared to peak

405densities. Together these explanations help clarify that our findings are consistent with our

406bottom-up hypothesis throughout both the hare and vole cycles, despite a few potentially

407unintuitive patterns.

408   Long-term, comprehensive monitoring programs (e.g., the Kluane project; Krebs et al.

4092001a), are responsible for much of what we know about population cycles in the boreal forest.

410One of the primary strengths of long-term studies across taxa and trophic levels is the ability to

411consider cyclic dynamics in the context of the larger system. The largest contributions of our

412work to the overall understanding of population cycles in the north are: 1) the establishment of a

413 direct link between weather conditions and primary productivity at the landscape-scale across

414 multi-year time-steps, and 2) the potential role of weather-induced variation in primary

415 productivity in controlling cycle amplitude in two disparate cyclic taxa. By extension, we

416 hypothesize that the apparent role of primary productivity in limiting cycle amplitude in hares

417 and voles suggests that bottom-up forces play a larger role in cycle dynamics than is currently

418 thought (e.g., Krebs et al. 2013, 2014ab, Therrien et al. 2014, Ginzburg and Krebs 2015). We

419 suspect the primary reason for our novel findings is that the multi-year nature of the links

420 between weather, primary productivity, and cycle amplitude were heretofore unidentified. In

421 light of our results, we suggest the reanalysis of existing datasets using indices of primary

422 productivity over multiple years to investigate the extent to which our findings might be

423 generalized to other systems. Such work should be relatively easy to conduct because NDVI

424 data are widely available for the last 2 decades, and weather data generally exist over long time

425 periods. Such work would directly assess the applicability of our findings to other areas and

426 would expand our understanding of the role of primary productivity in population cycles in the

427 north.

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675   5888

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676Table l. Parameter estimates from the Bayesian model (Eq. 2) describing variation in the density

677of voles in Denali National Park and Preserve, Alaska from 1992-2014.

678

Covariate	Mean	Lower 95%CrI	Upper 95% CrI
Intercept	0.26	0.06	0.41
Sine	-0.83	-1.10	-0.58
Cosine	-0.44	-0.73	-0.14
$NDVI_5$	0.35	0.13	0.57
Early winter	-0.61	-1.01	-0.22
severity			

679

680

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681Table 2. Parameter estimates from the top model (Eq. 3) describing variation in the hare

682population index over time in Denali National Park and Preserve, Alaska from 1988-2014. The

683sine and cosine terms assume an 10 year periodicity, GDD_5 represents the 5 year running average

684of growing degree days April-August, PPT_5 represents the 5 year running average of

685precipitation April-August, and $SNOW_5$ represents the 5 year running average of average snow

686depth in the previous winters. Estimates are presented as means with standard errors in

687parentheses.

688

Covariate	Hares
Intercept	1.39 (0.12)
Sine	0.90 (0.13)
Cosine	0.18 (0.15)
GDD_5	0.56 (0.09)
PPT_5	0.32 (0.12)
$SNOW_5$	-0.50 (0.15)

689

690

691Figure 1. The location of Denali National Park and Preserve within the state of Alaska (inset),

692the general location of the vole survey plots, and the location of the climate station within our

693study area are shown. The dashed line indicates the area from which the average maximum

694NDVI values were calculated and the snowshoe hare index data were collected.

695

696Figure 2. Plots of the five year running average of NDVI (NDVI$_5$; black), growing degree days

697(GDD$_5$; solid gray), summer precipitation (PPT$_5$; dashed gray), and average snow depth in the

698prior winter (SNOW$_5$; dotted gray) in Denali National Park and Preserve, Alaska from 1988-

6992014. Values have been scaled to have a mean = 0 and a SD = 1.

700

701Figure 3. Autocorrelation function (ACF) plots for vole density from 1992-2012 (a) and the hare

702abundance index from 1988-2012 (b) in Denali National Park and Preserve, Alaska. Vertical

703lines in the ACF plots that extend above the horizontal dashed lines indicate statistically
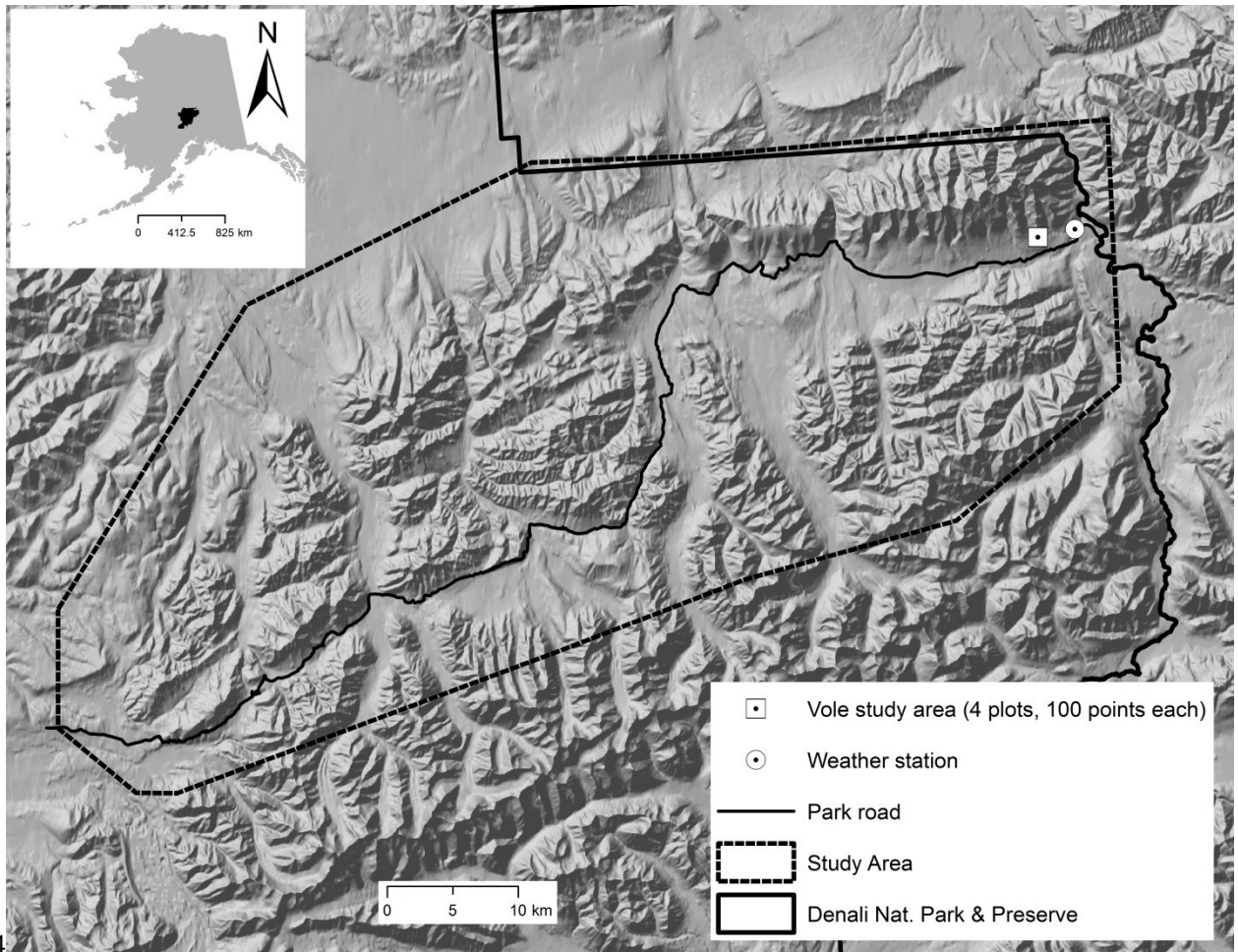
704significant autocorrelations.

705

706Figure 4. Plots showing the temporal relationship between NDVI$_5$ (a) and the northern red-

707backed vole (b) and snowshoe hare (c) cycles in Denali National Park and Preserve, Alaska from

7081988-2014. Plots of observed (solid lines) and predicted (dashed lines) values are included as a

709visual assessment of model fit. Fine dotted lines on panel (b) indicate years with severe early

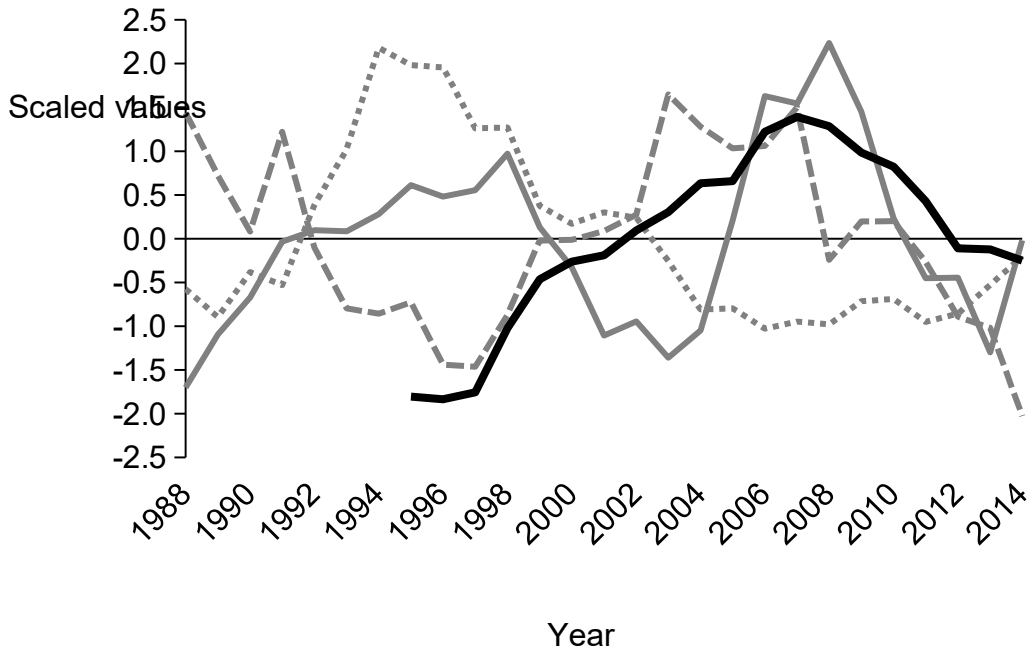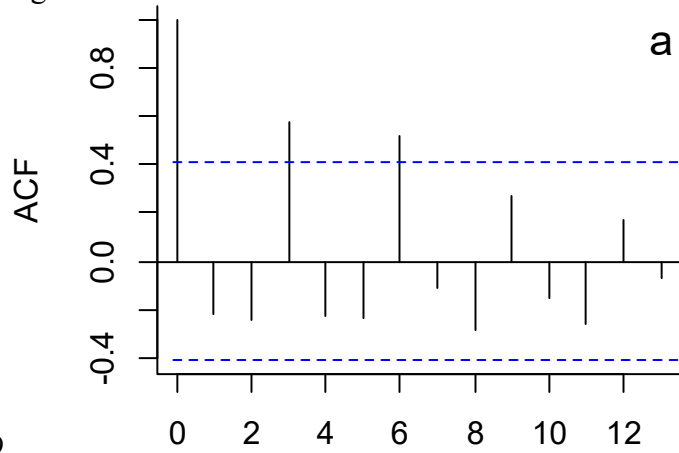710winter conditions. Values have been scaled to have a mean = 0 and a SD = 1.
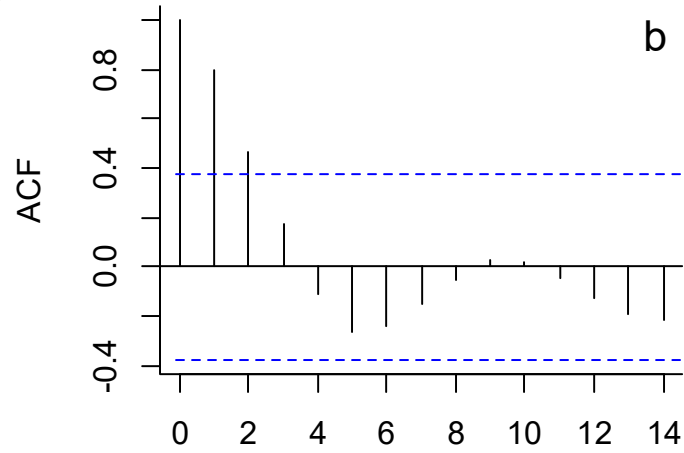
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Schmidt et al.

713Fig. 1.

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Schmidt et al.

715 Fig. 2.

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717
                                    Year

Schmidt et al.

718Fig. 3.

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721 Fig. 4.

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Year