

# Population cycles are highly correlated over long time series and large spatial scales in two unrelated species: greater sage-grouse and cottontail rabbits

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**Abstract** Animal species across multiple taxa demonstrate multi-annual population cycles, which have long been of interest to ecologists. Correlated population cycles between species that do not share a predator–prey relationship are particularly intriguing and challenging to explain. We investigated annual population trends of greater sage-grouse (*Centrocercus urophasianus*) and cottontail rabbits (*Sylvilagus* sp.) across Wyoming to explore the possibility of correlations between unrelated species, over multiple cycles, very large spatial areas, and relatively southern latitudes in terms of cycling species. We analyzed sage-grouse lek counts and annual hunter harvest indices from 1982 to 2007. We show that greater sage-grouse, currently listed as warranted but precluded under the US Endangered Species Act, and cottontails have highly correlated cycles ( $r = 0.77$ ). We explore possible mechanistic hypotheses to explain the synchronous population cycles. Our research highlights the importance of control

populations in both adaptive management and impact studies. Furthermore, we demonstrate the functional value of these indices (lek counts and hunter harvest) for tracking broad-scale fluctuations in the species. This level of highly correlated long-term cycling has not previously been documented between two non-related species, over a long time-series, very large spatial scale, and within more southern latitudes.

**Keywords** *Centrocercus urophasianus* · *Sylvilagus* sp. · Indices · Generalized additive models · Conservation

## Introduction

Multi-annual animal population cycles have long been of interest to ecologists and population biologists (Elton 1924), and remain an important aspect of many ecological questions (Berryman 2002a). The cyclic nature of some populations is a fundamental component of population regulation and can profoundly affect research results and management plans for cyclic wildlife species. It is necessary to account for natural population cycles when assessing impacts of new ecosystem stressors such as climate change or human development. Upward or downward abundance trends caused by cycling could impact conclusions or confound studies with short temporal investigations or with those lacking proper controls.

Population cycles within a single species (Moss and Watson 2001) or correlated cycles among closely related species (Hanski and Henttonen 1996) are common. Many excellent examples also exist of predator and prey populations that demonstrate highly correlated population cycles (Boutin et al. 1995; Bulmer 1974; Hanski et al. 2001). Many factors can influence population cycles,

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including parasites, predators, and weather. The hypotheses associated with each of these factors fall into two general categories: exogenous and endogenous. Exogenous cycles are caused by the action of an independent external driving variable(s) (weather: Kausrud et al. 2008). Endogenous cycles are the result of delayed negative feedback loops (predator effects, pathogen, food resources: Huitu et al. 2003; Klemola et al. 2000; Krebs et al. 1995). Cycles can also be influenced by interactions between both endogenous and exogenous factors (Seivwright et al. 2005).

One of the more fascinating aspects of population cycles is that unrelated species without a predator–prey relationship can also demonstrate highly correlated cycles (Bety et al. 2002; Blomqvist et al. 2002; Boutin et al. 1995; Wilmshurst et al. 2006). The correlations of population cycles among unrelated species can be caused by exogenous factors (e.g., weather: Ranta et al. 1999) or endogenous factors (e.g., competition for resources: Boutin et al. 1995; Schmidt and Ostfeld 2003; shared predators: Bartel and Knowlton 2005; Bety et al. 2002; Blomqvist et al. 2002; Korpimäki et al. 2005; Wilmshurst et al. 2006). Boutin et al. (1995) documented correlations among numerous unrelated species over one population cycle at several study sites in northern Canada and speculated that these correlations were primarily due to cycling hare populations in the region. However, northern populations tend to have more pronounced population cycles that can collapse further to the south (Bjornstad et al. 1995; Turchin and Hanski 1997), which has been attributed to more generalist predators in the south (Hanski et al. 1991; Klemola et al. 2002). What remains unclear is whether correlated population cycles can exist in unrelated species over multiple population cycles, in relatively southern latitudes, and over large spatial scales.

We investigated the potential for correlated population cycles in two unrelated species, greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) and cottontail rabbits (*Sylvilagus* sp.), that share habitat and, potentially, parasites and predators. We investigated multiple population cycles (26 years) across the entire state of Wyoming (~25.3 million ha) using standard time-series analysis. We suspected that population cycles were correlated between sage-grouse and cottontail rabbits, due to competition for similar resources, predation, parasitism, or weather. We wanted to examine if this correlation can be maintained across large spatial scales and time periods. We quantified the degree of spatial synchrony to provide insight into mechanisms. We used all this information to explore predictions of multiple competing hypotheses for endogenous and exogenous factors to explain the observed patterns. This research has potentially significant political ramifications for the sagebrush (*Artemisia* spp.) ecosystem

with regards to sage-grouse, a candidate species for listing under the US Endangered Species Act.

## Materials and methods

Sage-grouse are a gallinaceous species native only to western semiarid sagebrush landscapes (Schroeder et al. 1999). Loss and degradation of native vegetation has impacted much of the sagebrush ecosystem and associated wildlife (Connelly et al. 2004; Knick et al. 2003). Previously widespread, sage-grouse have been extirpated from nearly half of their original range in western North America (Schroeder et al. 2004), with a range-wide population decline of 45–80% and local declines of 17–92% (Connelly et al. 2004). Over 70% of Wyoming is included within the distribution of sage-grouse, and there is high overlap between sage-grouse and rabbit distributions.

Sage-grouse have a lek mating system, in which males congregate at display grounds during the breeding season. Counts of males attending leks in the spring are one of the primary methods of monitoring sage-grouse populations. Male lek count data appear useful for assessing change, particularly at broad scales (Connelly et al. 2004; Walker et al. 2007). However, several authors have criticized the efficacy of lek counts to assess population change (Beck and Braun 1980; Walsh et al. 2004). Nevertheless, other studies suggest that male lek counts can be viewed as useful indices of population trends (Connelly et al. 2004; Johnson 2008; Johnson and Rowland 2007; Williams et al. 2004).

The state of Wyoming contains a significant portion of sagebrush habitat and is predicted to remain one of the few strongholds for sage-grouse populations (Knick et al. 2003). Furthermore, Wyoming has one of the longest-running lek monitoring programs with data collected as early as 1948 (Connelly et al. 2004), with counts on over 2,000 leks. These data are collected primarily by professionals from several agencies, and are collated and managed by the Wyoming Game and Fish Department (WGFD). Leks are counted during the peak of the breeding season in an effort to capture the maximum number of males attending a lek. We used these data to estimate the number of males attending a lek site in a given year. If a site was counted more than once within a year, we chose the maximum number for that year. The average number of sites surveyed within a year was  $513 \pm 140$  (SD).

Cottontail rabbits are widely distributed across the United States and are a popular small game animal in Wyoming. Both Desert cottontail (*S. audubonii*) and Nuttall's cottontail (*S. nuttallii*) distributions include most of Wyoming (Feldhamer et al. 2003). Eastern cottontails (*S. floridanses*) occupy a small portion of southeastern

Wyoming, outside the sage-grouse distribution. Cyclic tendencies in North American leporids have been documented numerous times in the past (Keith 1963) and Boutin et al. (1995) documented correlated cyclic population trends between hares and ptarmigan. Likewise, Hornfeldt (1978) documented correlated cycles among mountain hare (*Lepus timidus*), willow ptarmigan (*Lagopus lagopus*), black grouse (*Tetrao tetrix*), capercaillie (*Tetrao urogallus*), hazel grouse (*Bonasa bonasia*), red fox (*Vulpes vulpes*), and tularemia in Sweden.

Cottontails inhabit a wide variety of habitats and have a varied diet throughout North America. However, cottontails in Wyoming share many habitat needs with sage-grouse including food and cover requirements. During the summer, cottontails consume primarily grasses and forbs and forbs are particularly important in the autumn (Orr 1940). Cottontails and sage-grouse share predators (e.g., coyotes *Canis latrans*, foxes *Vulpes vulpes*, bobcats *Lynx rufus*, and raptors such as the golden eagle *Aquila chrysaetos* and great-horned owls *Bubo virginianus*). Disease and parasites also play a role in cottontail population regulation (Woolf et al. 1993).

The WGFD conducted hunter surveys via harvest questionnaires mailed to a random sample of small and upland game bird hunters each year. In Wyoming, rabbits are considered small game and hunters provide information on how many days they hunted and how many rabbits they harvested during that time. The WGFD managed small game populations based upon 36 ecologically-based management units since 1982. Prior to 1982, small game hunter information was tabulated, based upon political county boundaries. We therefore tabulated total harvest and total hunter day information from WGFD annual reports starting in 1982 and used the ecologically-based small game management units as our 36 sampling units. Cottontail season lengths varied slightly between years, but generally started in early September and lasted through February, with rabbits harvested after the first of the year being counted with fall hunting totals. Thus, a time lag of 1 year between sage-grouse lek counts conducted in April related to rabbits that were harvested anywhere between 1 and 6 months prior. As an example, 2006 data for sage-grouse were collected during the lek season in spring of 2006 and the 2006 data for cottontails were collected during the fall 2006 through January and February 2007. Hunter surveys effectively treat Desert and Nuttall's cottontails as a single species. Our index of population trends for cottontails by year was calculated for each game management unit as: total cottontail harvest/total hunter days. From 1982 to 2007, there were 2.44 million cottontails harvested (94,086 avg/year  $\pm$  99,945 SD) in 1.07 million hunter days (41,298 avg/year  $\pm$  29,039 SD). The average number of cottontails harvested per hunter-day was approximately 2.

## Statistical analysis

We examined the long-term trends in both species using several approaches to explore how robust the relationships were to our analytical approach and model parameters. The analysis of long-term population trends (or indices of population trends) can be approached by several different analysis paradigms (Thomas 1996). At the coarsest level and simplest approach, we compared the averages of our indices over time for both species. For sage-grouse, we calculated the maximum number of birds attending each surveyed lek. We then calculated the annual average of that number. For cottontails, we calculated the overall average number of individuals shot per hunter-day for each year. We also followed the approach developed by Fewster et al. (2000) to address many of the statistical challenges of modeling long-term trends because it is more statistically robust, flexible, and capable of detecting and describing nonlinear trends. For these reasons, and others, generalized additive models have been used to describe the population trends of many species (Atkinson et al. 2006; Fonseca et al. 2009; Siriwardena 2004).

Male peak lek count time-series (hereafter lek count) and rabbit hunter-harvest data were compiled as a continuous time-series across Wyoming over 26 years (1982–2007). Indices of male sage-grouse and rabbit hunter-harvest were investigated using an abundance index (Fewster et al. 2000) based on generalized additive models (GAMs; Hastie and Tibshirani 1990). Fewster et al. (2000) defined the abundance index for year  $t$  relative to an arbitrarily chosen base year. We chose the first year of data (1982) as the base year because this is the first year in the WGFD rabbit database that had ecologically-defined small-game management boundaries. Therefore, we defined the abundance index ( $I$ ) for year  $t$  as:

$$I(t) = \frac{\text{total predicted count for year } t}{\text{total predicted count for 1982}} = \frac{\exp(\hat{s}(t))}{\exp(\hat{s}(1982))}$$

Thus, the index was a ratio of exponentially transformed year effects calculated as a smoothed function of  $t(\hat{s})$ . We modeled the expected peak male sage-grouse lek counts and rabbit hunter-harvest in each year applying a generalized additive model with Poisson error distribution and logarithmic link function (Fewster et al. 2000). We modeled trends as a nonlinear function of time by estimating the components of the index using GAMs. The amount of 'smoothing' applied to a GAM is determined by the degrees of freedom ( $df$ ) selected. We used the same degrees of freedom for both species using the recommended  $0.3T$  rounded to the nearest integer ( $T = 26$ ; Fewster et al. 2000). Models were fitted in the GAM R-package procedure (R-package mgcv) and code was modified slightly from that provided by Fewster and outlined in Fewster et al. (2000).

The degrees of freedom applied to a GAM model influence the level of ‘smoothness’ the model will allow. Past studies have developed a convention of using  $0.3T$  *df* (Fewster et al. 2000; Fonseca et al. 2009; Hewson and Noble 2009; Robinson et al. 2005; Spinola and Gates 2008; Wright et al. 2009). This value tends to represent a good tradeoff between forcing linearity and the ‘smoothness’ of the trend line. We used  $0.3T$  *df* for the majority of our analyses. However, to ensure the resiliency of the relationship between sage-grouse and cottontails, we explored a range of alternative degrees of freedom (2, 4, 8 or  $0.3T$ , and 25).

Annual correlations between sage-grouse and rabbit hunter-harvest index values were examined using Pearson correlations. We examined correlations between the two species at annual time lags out to 5 years.

The duration of the multi-annual cycles were examined using the GAM model index values with  $0.3T$  *df* (Fewster et al. 2000) and using autocorrelation functions to a time lag of 16 years (ACF). The sage-grouse data demonstrated a trend (i.e. overall downward slope) as well as the cyclic component. Thus, for the sage-grouse autocorrelation analysis, we used first-differencing of the index values to mitigate the effects of the trend. First-differencing modifies the time series so that each new value represents the difference between successive original values. We assessed confidence intervals using Bartlett’s criterion  $2\sqrt{\eta}$ , where  $\eta$  is the length of the series (e.g., 26 years; Box et al. 2008).

Partial autocorrelation functions (PACF) out to 10 years were used to detect the order of the time-series (Box et al. 2008). The GAM index values with  $0.3T$  *df* were also used for this analysis and we used first-differencing of the sage-grouse values. Confidence intervals were calculated as  $1/\sqrt{\eta}$  where  $\eta$  = the number of lags.

We estimated the spatial extent of inter-specific synchrony by examining the correlations between sage-grouse and cottontail trends within individual small game management units. We used the same GAM based approaches as outlined above with  $0.3T$  *df*. We estimated trends for sage-grouse and cottontails for each unit and then calculated the correlation between those trends over time. Fedy and Aldridge (in review) used similar GAM approaches on sage-grouse lek data from 1965 to 2008 and found the number of lek sites included in the analyses can impact the accuracy of the models. Based on their findings, we examined small game management units that contained a minimum of 50 lek sites.

We examined the extent of spatial synchrony among population trends across Wyoming because the presence of distance decay in correlated cycles would lend insight into potential mechanisms. We investigated the extent of spatial synchrony in sage-grouse trends across the state. We chose sage-grouse instead of cottontails because of the finer

resolution of the data. We calculated the correlation among sage-grouse trends for small game management units with  $\geq 50$  lek sites. We determined the distance between management units by measuring the Euclidean distance between the centroid of each management unit using ArcGIS 9.3 software. We used a scatter plot and linear regression to describe the relationship between the Euclidean distance among management units and the correlation of sage-grouse trends among those units. Correlations between species indices, ACF, and PACF analyses were conducted in STATA ver. 10.1.

## Results

The strongest correlations of sage-grouse and cottontail annual trends using multiple approaches (averages and GAM index values) and varying the model parameters (*df*) ranged from  $r = 0.68$  to  $0.99$  from the same year, and a lag of 1 year (Table 1). The highest  $r$  value with  $0.3T$  ( $df = 8$ ) was  $r = 0.77$ . The correlations were the strongest at time  $t$  and time  $t - 1$  regardless of the method used. The sage-grouse lek data were collected in spring each year and the rabbit data were collected during each fall hunting season. Therefore, a sage-grouse count in one spring correlated most strongly with the rabbit harvest data of the previous and subsequent fall seasons. Sage-grouse and cottontails in Wyoming had closely paralleled multiannual cycles over 26 years with similar cycle lengths and amplitudes (Figs. 1, 2).

Autocorrelation function analyses revealed that both species cycle over similar multiannual time frames. Sage-grouse positive autocorrelation was highest and was significant at a lag of 8 years. Cottontail positive autocorrelation neared significance at lag year 8 (Fig. 3a).

Partial autocorrelation function (PACF) results for both species were also very similar. The presence of negative feedback gives rise to a negative PACF therefore, only negative correlation coefficients need to be considered (Berryman 2002a, b). For both sage-grouse and cottontails the highest and most significant lag was at 2 years (Fig. 3b).

Seventeen of the 36 small game management units had  $\geq 50$  sage-grouse leks. Thirteen of the 17 units demonstrated significant ( $P \leq 0.05$ ) positive correlations between sage-grouse and cottontail indices. The average  $r$  value for the units significant at  $P \leq 0.05$  was  $0.63 \pm 0.16$ . Across all management units, the average  $r$  value was  $0.51 \pm 0.27$ .

The correlation matrix testing for distance decay among sage-grouse trends between 17 management units resulted in 136 pair-wise correlation values (Fig. 4). The average pair-wise correlation between sage-grouse trends in different

**Table 1** Pearson’s correlation ( $r$ ) and associate  $P$  values ( $P$ ) between greater sage-grouse (*Centrocercus urophasianus*) and cottontail rabbit (*Sylvilagus* sp.) indices in Wyoming

Lag (years)	Average	df 2	df 4	df 8	df 17	df 25	
0	$r$	0.68	<b>0.99</b>	<b>0.94</b>	<b>0.77</b>	<b>0.69</b>	<b>0.68</b>
	$P$	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
1	$r$	<b>0.69</b>	0.98	0.87	<b>0.77</b>	0.68	0.67
	$P$	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
2	$r$	0.40	0.87	0.68	0.49	0.42	0.40
	$P$	0.05	<0.01	<0.01	0.01	0.04	0.05
3	$r$	-0.06	0.66	0.39	0.00	0.01	0.01
	$P$	0.77	<0.01	0.06	0.99	0.98	0.96
4	$r$	-0.42	0.40	0.08	-0.42	-0.32	-0.32
	$P$	0.05	0.06	0.73	0.05	0.15	0.15
5	$r$	-0.53	0.14	-0.22	-0.54	-0.42	-0.42
	$P$	0.01	0.55	0.35	0.01	0.06	0.06

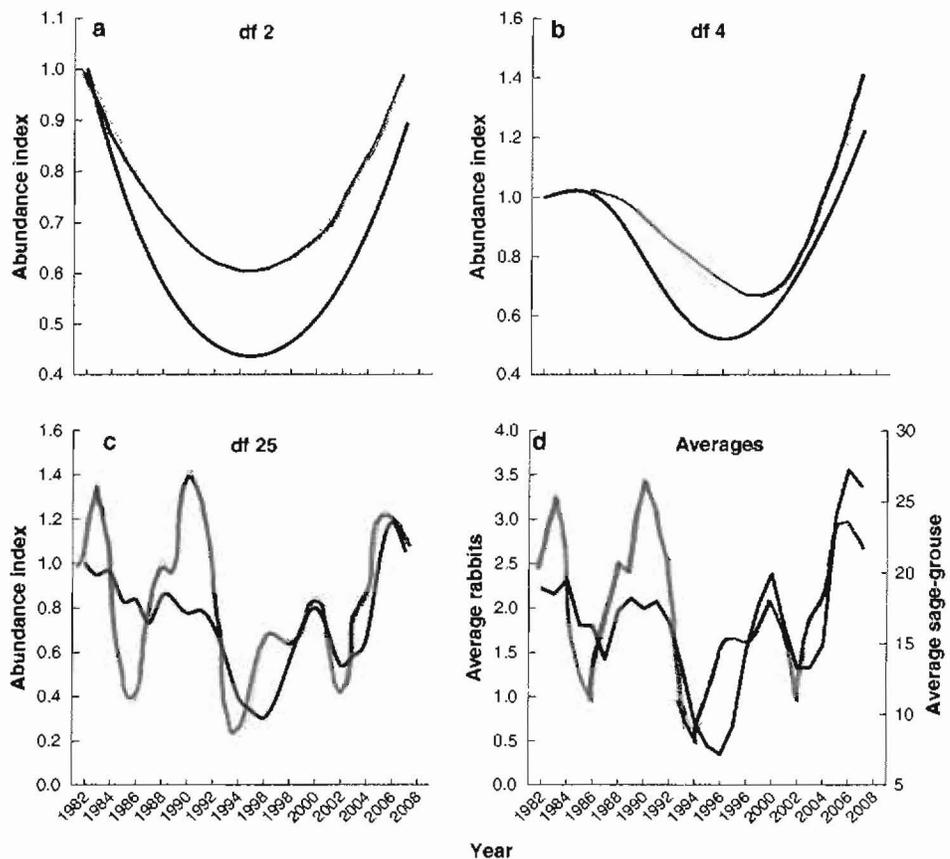
Annual correlations were calculated among sage-grouse indices at time ( $t$ ) and cottontail indices at time ( $t$ ) through multiple lags to time ( $t - 5$ ). We present correlations over the time series among the average values for both species and for multiple iterations (various  $df$ ) using the generalized additive models approach (see “Materials and methods” for more details). The lag with the highest correlation for each trend model is highlighted in bold

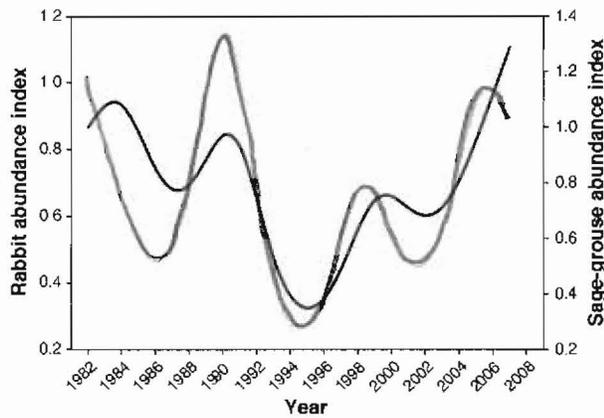
management units was  $0.47 \pm 0.29$ . The linear coefficient between correlation and distance was slightly negative ( $-0.0005 \pm 0.0002$ ;  $P = 0.05$ ), but weak. We estimated the correlation among sage-grouse trends would decline  $r = 0.04$  for every 100 km in distance between management units (Fig. 4). The regression explained very little of the variation ( $r^2 = 0.03$ ) and model estimated  $r$  values varied little over the range of distances with high predicted  $r$  values (approximately  $r = 0.40$ ) at over 500 km. We show high positive correlations between sage-grouse separated by 100–500 km (Fig. 4).

**Discussion**

Sage-grouse and cottontails in Wyoming demonstrated highly correlated long-term cycles and trends. This level of correlation ( $r = 0.77$ ) has not previously been documented between two non-related species, over a long time-series, and very large spatial scale with synchrony between units separated by up to 500 km. Boutin et al. (1995) documented a significant correlation between hares and ptarmigan. However, our study differs from theirs in several

**Fig. 1** Trend estimates for sage-grouse (*Centrocercus urophasianus*) male lek counts (black line) and cottontail (*Sylvilagus* sp.) hunter-harvest records (gray line) from 1982 to 2007 in Wyoming under different model parameters. **a–c** Model-estimated index values developed using generalized additive models (GAM). The value of the degrees of freedom influences the smoothing of the trend data when using GAM. **d** Coarsest estimates of trends overtime and presents the average number of cottontails shot per hunter day, and the average maximum number of males attending a lek. The correlation between sage-grouse and cottontail long-term trends were high, regardless of the model parameters (Table 1)

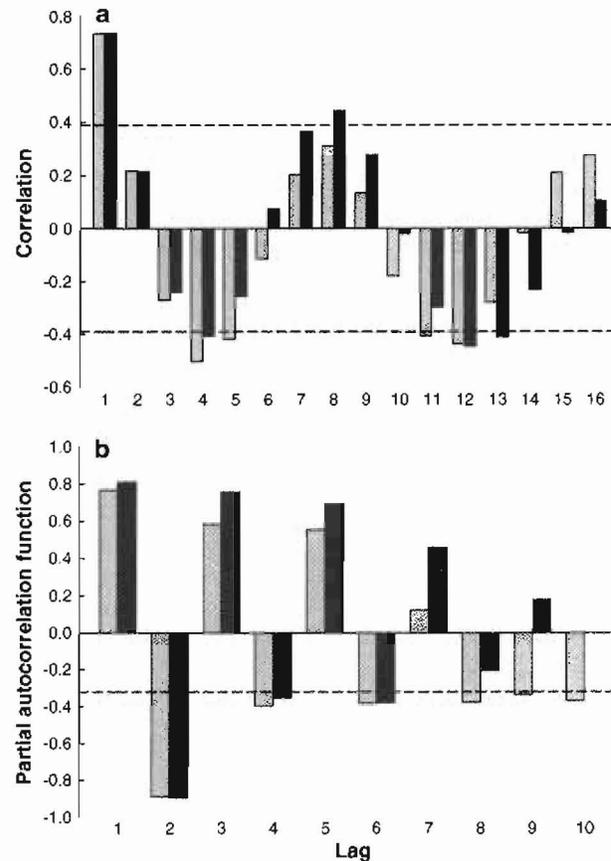




**Fig. 2** Trend estimates for sage-grouse male lek counts (black line) and cottontail hunter-harvest records (gray line) from 1982 to 2007 in Wyoming estimated using generalized additive models. The trend estimates presented here were generated using a value  $0.37 df$ . This value is conventionally used in studies that implement generalized additive models to describe long-term population trends, and represents a good tradeoff between the over-smoothing of linear approaches and the coarsest approach of using yearly averages

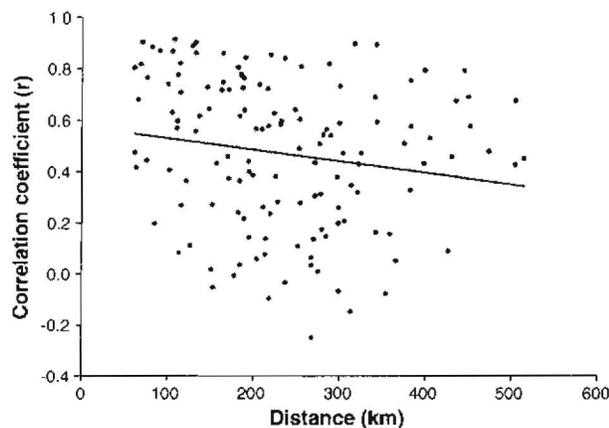
respects. Our study covered a much longer time frame (incorporating multiple cycles), was conducted at a larger scale, and occurred in a more southern location. These factors highlight the resilience of the correlation to varying analytic techniques and the long-term strength of the correlation. In general, sage-grouse and cottontails must be responding to similar cues in the system.

Inspection of the autocorrelation function (ACF) and the partial autocorrelation function (PACF) can provide general insight into the cause of the oscillation and help distinguish between endogenous and exogenous factors (Berryman 2002a). The amplitude of the ACF for both sage-grouse and cottontails tends to get smaller with increasing time lag (Fig. 3a). This pattern in the ACF suggests the causal process is likely endogenous (Nisbet and Gurney 1982). Endogenous population cycles are the product of second-order feedback processes. Thus, the large negative correlation in the PACF at lag 2 in both sage-grouse and rabbits (Fig. 3b) suggested the dynamics of both species are dominated by second-order feedback (Berryman 2002a). The pattern in the PACF (declining) also suggests populations are declining, but we saw little evidence of declines in the cottontail dataset. However, the PACF values for the sage-grouse data are based on first-differencing of the original values which accounts for the downward population trend prior to calculating the PACF. ACF and PACF both suggest endogenous factors influence the dynamics of both species; however, these analyses cannot give us much information about the specific mechanisms driving the cycles, rule out the presence of exogenous factors, or determine whether the mechanisms involve intra- or interpopulation processes.



**Fig. 3** Autocorrelation (a) and partial autocorrelation (b) plots of greater sage-grouse indices estimated from lek counts (black bars) and cottontail rabbit indices estimated from hunter-harvest surveys (gray bars) from 1982 to 2007 in Wyoming. We plot Pearson's correlation ( $r$ ) between the index for 1 year and the index in another year at specified time lags for both sage-grouse (black bars) and cottontails (gray bars). Dashed lines represent the 95% confidence intervals that approximate significance

Our analyses provide insights into several mechanisms that may influence the cycling of sage-grouse and cottontails throughout Wyoming. First, direct competition between sage-grouse and rabbits could potentially explain the correlated cycles. However, the competition hypothesis predicts a negative relationship between lek counts and cottontail hunter-harvest. Our data show clear long-term positive correlations between both species, and therefore we can reject competition between the two species as a factor influencing the correlation of population cycles. Second, prey switching has been proposed as a mechanism to correlate cycles in other species with shared predators (Bety et al. 2002; Blomqvist et al. 2002) and could produce correlated cycles in sage-grouse and cottontails. If prey switching was occurring, we would predict a lag between the peaks of each species cycle (Wilmshurst et al. 2006). No lag, or a lag of 1 year, produced the highest correlations



**Fig. 4** Correlation coefficients among sage-grouse trends from management units with  $\geq 50$  lek sites. Trends were estimated using the GAM approach for sage-grouse within each individual management unit across the time series (1982–2008). We calculated the correlation coefficient between trends for each pair-wise comparison. These values are plotted against the pair-wise distance between the centroid of each management unit. The black line represents a linear regression model fit to the scatter

between the two species. This means the tightest correlation between sage-grouse and cottontail indices was the fall count of cottontails in a given year and the following year's spring count of males attending leks or the same year's spring sage-grouse count and fall cottontail survey. Either way, these counts are only separated by a few months and, therefore, there was essentially no lag between the peaks of each species' cycle. Thus, it seems unlikely that prey switching is influencing the correlated dynamics of the populations. The absence of a time-lag allows us to eliminate prey switching between sage-grouse and cottontails as a hypothesis; however, prey switching may occur among other species (e.g., ground squirrels *Spermophilus* sp.). Predation, in general, is another potential factor driving and correlating sage-grouse and cottontail population cycles in Wyoming as the species could be responding to shared predators. Finally, diseases such as tularemia in rabbits may influence population cycles in Wyoming as suggested in grouse, rabbit, and vole populations in Sweden (Hornfeldt 1978). It is important to note that endogenous and exogenous mechanisms can interact to influence population cycles (Seiwright et al. 2005)

Overall, we cannot say for certain if the processes driving population cycles in both species are endogenous or exogenous. The ACF and PACF analyses suggested the population cycles were influenced by endogenous factors. However, the hypothesis that both species are responding to a common exogenous factor, such as weather (Ranta et al. 1999), predicts that population responses will be simultaneous and their highs and lows will correspond. The high correlation between the two species is consistent with

the prediction that populations are responding to a common external cue (e.g., weather), that may synchronize the population patterns without any interaction between the two species. It is important to note the large spatial scales addressed in this research because they are unique and can lend insights into the mechanisms influencing the correlations among species. Previous studies documenting mechanisms of population cycling such as predation and disease have been conducted at smaller spatial scales (predators: Bartel and Knowlton 2005; Bety et al. 2002; Blomqvist et al. 2002; Korpimäki et al. 2005; Wilmshurst et al. 2006; disease: Seiwright et al. 2005; Hornfeldt 1978). The broad spatial distribution of the correlations in this study at the individual management unit level (i.e. 100–500 km) demonstrated that correlations are not an isolated phenomenon in Wyoming and lend support to a broad-scale causal influence (e.g., climate). Correlations were typically positive and were significant ( $P \leq 0.05$ ) for more than half the units. Our analysis of spatial synchrony in sage-grouse across the state suggested the level of correlation between trends was not strongly influenced by distance (Fig. 4). Units with significant positive correlations were distributed fairly evenly across sage-grouse distributions in Wyoming from the northeast to the southwest corners of the state. This is further support of a broad-scale causal influence for the trend patterns. However, other factors may be important at smaller scales than we could assess with the available data. More work is needed to determine conclusively what factors are driving the highly correlated cycles of sage-grouse and cottontails in Wyoming.

There are two other general points highlighted by our research: (1) the value of indices and (2) the role of cycles in the management of species of conservation interest. Our analyses are based on indices: sage-grouse male lek counts, and cottontail hunter-harvest records. The usefulness and accuracy of indices are often criticized (e.g., Anderson 2001, 2003; Ellingson and Lukacs 2003; MacKenzie and Kendall 2002; Norvell et al. 2003; Rosenstock et al. 2002; White 2005). For sage-grouse in particular, several authors have argued that lek counts do not represent true population trends (Walsh et al. 2004), though lek counts have been used to examine cycling dynamics in other species (Williams et al. 2004) and for valuable insights into sage-grouse populations (Connelly et al. 2004; Walker et al. 2007; Garton et al. 2010). The high correlation between sage-grouse and cottontail indices over several cycles makes a compelling case that these two indices are fairly robust to monitoring methods and function as valid indices of broad-scale fluctuations in the species. We were interested in broad-scale patterns and had access to extensive datasets. Therefore, the usefulness of these indices for our study was clearly influenced by the scale of our analysis and the statistical property of data, in that the importance of sampling error decreases as you

increase sample size. The decreased importance of sampling error is only violated if you have a systematic and consistent bias in the error. The data for each species were collected using very different sampling approaches, and it is difficult to imagine a situation in which the sampling biases in both approaches would result in the long-term correlations we present here. Though we cannot quantify the probability of sampling error causing two unrelated species to correlate strongly through three cycles with a duration of 7–8 years for each cycle, reason suggests it is infinitesimal. Our analyses support Johnson (2008) who argued against the wholesale rejection of indices to population size and the many valuable studies that have been published using index data such as the Breeding Bird Survey (Eglington et al. 2010; Robbins et al. 1986; Sauer et al. 2008), Christmas Bird Counts (Dunn et al. 2005), and Common Bird Census (Taylor 1965; Williamson and Homes 1964). We have shown that two very different indices (lek counts and hunter-harvest) are capable of tracking biologically meaningful fluctuations within the system.

Population cycles have long been of interest to ecologists (Elton 1924); however, their relevance to the management of wildlife populations appears to receive little attention. The explicit consideration of long-term population cycles can make important contribution to species management. One of the most common types of research studies conducted on wildlife involves determining responses to habitat treatments intended to increase populations under the framework of adaptive management or assess affects of a novel land use change such human development. In both cases, wildlife responses are often assessed under the assumption (explicit or implicit) that populations are on a flat trajectory. Furthermore, most studies are not long enough to encompass an entire cycle. Our research highlights the need for explicit consideration of where a population is on the cycle, if they exist, because failing to account for population trends could confound conclusions. For example, if a potential population perturbation is introduced while the population is increasing, and monitoring to determine impact is shorter than the cycle length (i.e. 3 or 4 years), researchers may conclude there was no impact, or even a positive relationship between the perturbation and the population. Likewise, managers may conclude that specific habitat treatment effects were either beneficial or detrimental in an adaptive management framework without adequate monitoring of control populations because of larger scale population processes such as cycling. Our research is another clear example of the need for control populations in both adaptive management and impact studies because mechanisms which are regulating demography are often lacking, as was the case with cyclic population trends in sage-grouse and cotton-tail rabbits in Wyoming. The explicit consideration

of long-term population cycles can have profound implications to wildlife research even if the exact mechanisms causing the cycling are unknown.

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