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# Autocorrelated Rates of Change in Animal Populations and their Relationship to Precipitation

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**Abstract:** *I examined the prevalence of autocorrelation in mammalian, avian, and precipitation time series, how well autocorrelation in the environment translates into autocorrelation in animal populations, and length of the time series needed to accurately characterize the degree of autocorrelation. These are important questions because more-complex population models are incorporating autocorrelation terms in life-history characteristics and the intrinsic rate of increase. Including inaccurate or nonsignificant autocorrelation can alter the conclusions reached, providing either an unduly rosy or bleak picture of the likelihood of population viability and persistence. Using autocorrelation analysis in 175 vertebrate and 88 precipitation data sets, I found that 17.8% of the mammalian time series, 61.5% of the avian time series, and 97.7% of the precipitation data sets were autocorrelated. Carnivore populations were more likely than herbivore populations to show significant autocorrelation at lags of 2 or more years. I found only two cases of significant cross correlation between rate of population increase and local precipitation. This indicates that, although some environmental variables may be highly autocorrelated, it does not translate into autocorrelation in the resident animal populations. Based on subsampling of the precipitation and vertebrate data, I found that 15 years of data is sufficient to produce an autocorrelation not significantly different from one based on 100 years of data, although the variance continues to decrease with the length of the time series, as expected. My results suggest that, although some populations show temporal autocorrelation, it is not ubiquitous, and that environmental autocorrelation may not be a good predictor of autocorrelation in rates of increase. Population modelers should determine if autocorrelation exists in populations of interest prior to modeling their viability or probability of persistence because not all populations are equally influenced by autocorrelation.*

Tasas de Cambio en Poblaciones de Animales Autocorrelacionadas y sus Relaciones con la Precipitación.

**Resumen:** *Se examinó el predominio de la autocorrelación en series de tiempo de mamíferos, aves y precipitación; que tanto la autocorrelación ambiental se traduce en autocorrelación en poblaciones de animales, así como la longitud de las series de tiempo necesaria para caracterizar con precisión el grado de autocorrelación. Estas son preguntas importantes puesto que los modelos poblacionales mas complejos incorporan la autocorrelación en las características de la historia de vida y la tasa intrínseca de incremento. Aún la inexactitud o autocorrelación no significativa puede alterar las conclusiones obtenidas, proveyendo indebidamente una idea prometedora o poco prometedora de la probabilidad de viabilidad y persistencia de una población. Mediante el uso del análisis de autocorrelación en 175 juegos de datos de vertebrados y 88 de precipitación, encontré que un 17.8% de las series de tiempo de mamíferos, 61.5% de las series de tiempo de aves y un 97.8% de los datos de precipitación se encontraban autocorrelacionados. Las poblaciones de carnívoros fueron las mas viables a mostrar autocorrelación en lapsos de 2 o mas años que las poblaciones de herbívoros. Encontré solo dos casos de correlación cruzada significativa entre la tasa de incremento poblacional y la precipitación local. Esto indica que aunque algunas variables ambientales pueden estar altamente autocorrelacionadas, no se traduce en una autocorrelación en las poblaciones de animales residentes. Basado en un submuestreo de la precipitación y datos de vertebrados, encuentre que 15 años de datos es suficiente para producir una autocorrelación que no es significativamente diferente de aquella basada en 100 años de datos, aunque la varianza continua disminuyendo con la longitud de las series de tiempo a como es*

de esperarse. Mis resultados sugieren que aunque algunas poblaciones muestran autocorrelación temporal, esta no es evidente y la autocorrelación ambiental podría no ser un buen predictor de autocorrelación de tasas de incremento. Los modeladores de poblaciones deberán determinar si la autocorrelación existe en poblaciones de interés antes de modelar su viabilidad o la probabilidad de persistencia puesto que no todas las poblaciones son afectadas por la autocorrelación de la misma manera.

## Introduction

Conservation biology is becoming an increasingly complex discipline, especially in the models used to examine questions related to population persistence (Foley 1994). One complexity starting to be incorporated in models is the temporal autocorrelation of model parameters (Foley 1994; Ferson & Burgman 1995). Researchers are beginning to realize that autocorrelation in factors such as population growth (Foley 1994) and life-history parameters (Ferson & Burgman 1995) can greatly alter a model's prediction. For example, Foley (1994) found that incorporation of an autocorrelation term significantly increased the expected time to extinction of grizzly bears (*Ursus arctos horribilis*), checkerspot butterflies (*Euphydryas editha bayensis*), pumas (*Felis concolor*), and wolves (*Canis lupus*). Similarly, autocorrelation in an exogenous factor such as weather can result in false characterization of a population as experiencing delayed density dependence (Williams & Liebhold 1995).

Temporal autocorrelation is the correlation between a variable at time period  $t$  and the same variable in another time period. For example, Fig. 1 shows the intrinsic rate of increase,  $r$ , for a Carolina Chickadee (*Parus carolinensis*) population (Christmas bird count data from Ehrlich & Roughgarden 1987; Fig. 1a) and its corresponding autocorrelation (Fig. 1b). A significant negative autocorrelation is found at a lag of 1 (Fig. 1b), indicating that the direction of the rate of change will most likely be in the opposite direction between any two time points  $t$  and  $t + 1$ , (Fig. 1a). Similarly, there is a significant positive autocorrelation at a lag of 6 (Fig. 1b), and Fig. 1a shows that the rate of change is most often in the same direction when it is six steps apart. From this, it can be seen that a positive autocorrelation term between time period  $t$  and  $t + 1$  will increase the likelihood that a trend will continue through time. Conversely, a negative autocorrelation decreases the probability that a trend will occur.

I examined autocorrelation in the intrinsic rate of increase for several mammal and bird species. Because autocorrelation is a statistical measure, it does not distinguish if the factor producing the autocorrelation in  $r$  is due to intrinsic factors, extrinsic factors, or both. I am, however, mainly concerned with intrinsic factors, such as autocorrelations produced by feedback from the population, not factors imposed on the population by envi-

ronmental trends. Thus, prior to estimating the autocorrelation, I removed environmental trends (Royama 1996). Because conservation biologists often don't have long-term data with which to estimate a population's autocorrelation function, I also investigated how similar the local precipitation's autocorrelation structure is to a resident population's autocorrelation. I used precipitation for two reasons: (1) it has been linked to primary productivity (Went 1948; Went 1949; Tevis 1958a; Tevis 1958b; Rosenzweig 1968), which has been shown to be linked to reproductive output, especially in arid-land organisms (e.g., Beatley 1969; Brown et al. 1979); and (2) it is one of the few variables for which long-term data exist.

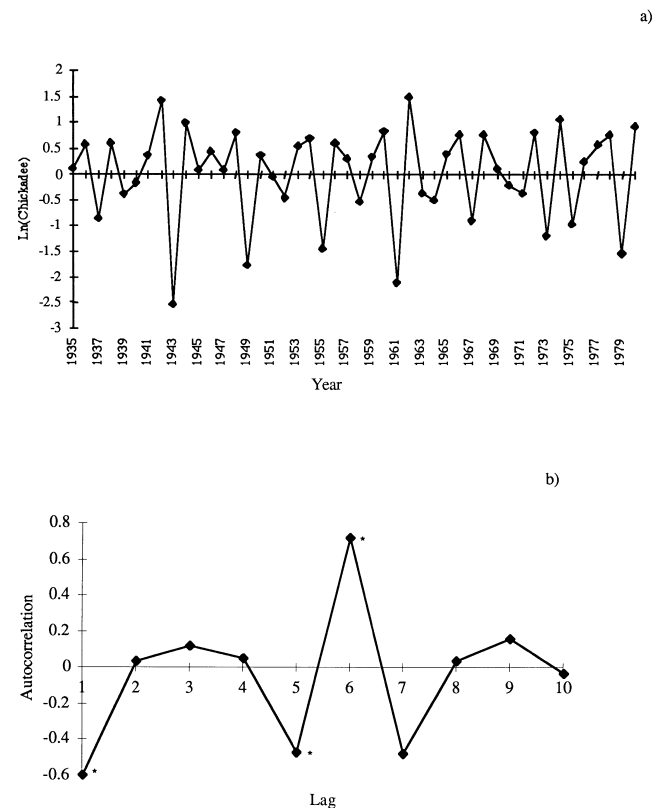


Figure 1. Time series plot (a) and autocorrelogram (b) of  $\ln$ -transformed and detrended population data for Carolina Chickadee. An asterisk indicates significant autocorrelation ( $p < 0.05$ ).

Trends in the autocorrelation function (ACF) also need to be removed to produce a statistical estimate using only one term; if the ACF changes with time, it is necessary to index the temporal component of the ACF with a second variable (Brockwell & Davis 1991). If the trend is environmental (i.e., extrinsic) in nature, failure to remove it would result in incorporating the environmental component twice: once in the population growth rate and again in the autocorrelation term. Several methods exist for detrending a time series, such as differencing and least squares regression (Brockwell & Davis 1991; Royama 1996). Statistical removal of an environmental trend does not mean that the environment does not influence a population. Indeed, environmental factors can override the autocorrelation within the population, producing a trend opposite to that of the autocorrelation. For example, a population with a negatively autocorrelated rate of change, indicating a high probability that the population size should change in the opposite direction than it did during the last time period, could show a continual decrease in population size during that time period due to an environmental trend that reduced habitat quality. It is still important to know what the intrinsic autocorrelation is, because the environmental conditions may not always be strong enough to counteract the intrinsic aspects. Removing environmental trends (Royama 1996) or evaluating the relationship between population size or intrinsic rate of increase and environmental variables should prevent erroneous classification of an environmental trend as intrinsic autocorrelation.

Classic examples of autocorrelation are cyclic populations and populations experiencing Allee effects. Cyclic populations (Fig. 2), such as insects (Berryman 1978; 1991; Turchin 1990), lynx (*Felis lynx*; Keith 1963), and red fox (*Vulpes vulpes*; Swanson 1993) show positive autocorrelations at time lags equal to the period of the cycle and negative autocorrelations at time lags equal to half the period length. Populations experiencing Allee effects have reduced rates of population growth at low population levels (Fig. 3). By definition then, populations undergoing Allee effects have an autocorrelated rate of increase because low populations lead to lower rates of increase, forming a positive feedback loop wherein the population continues to get smaller and the rate of increase continues to decrease.

Models that incorporate temporal autocorrelation often assume that (1) significant autocorrelation exists in environmental factors, (2) significant autocorrelation exists in rates of change in population size, and (3) change in population size is correlated with environmental change. These assumptions arise from the considerable work that exists on invertebrate population dynamics, showing that populations often are both autocorrelated and correlated with climate (Berryman 1978; 1991; Turchin 1990; Hanski & Woiwod 1991; Woiwod & Hanski

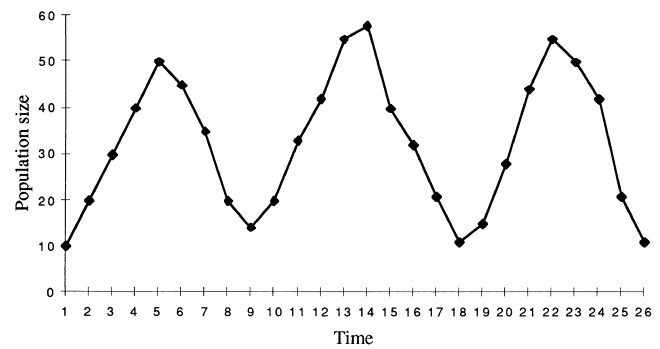


Figure 2. Hypothetical autocorrelogram of a cyclic population showing positive autocorrelation in the intrinsic rate of increase at lags equal to 1, the period of the cycle, and negative autocorrelation at lags equal to half the period of the cycle.

1992). Less research, however, has examined the long-term population data of vertebrates or the relationship of population size to climate. This is due partly to the difficulties in collecting long-term vertebrate data, although these data sets are becoming more commonplace (Sinclair et al. 1993; McLaren & Peterson 1994; Saucy 1994; Boutin et al. 1995; Ranta et al. 1995).

I investigated four questions: (1) How common is autocorrelation in mammalian and avian populations? (2) How common is autocorrelation in the environment, specifically yearly precipitation? (3) Does autocorrelation in an environmental variable translate into autocorrelation in avian or mammalian populations? (4) How long does a time series need to be in order to provide a good approximation of the autocorrelations? Answering these questions provides insight into the population processes that need to be incorporated into models of population viability and persistence, as well as into the quantity of data needed to make accurate estimates for inclusion in models.

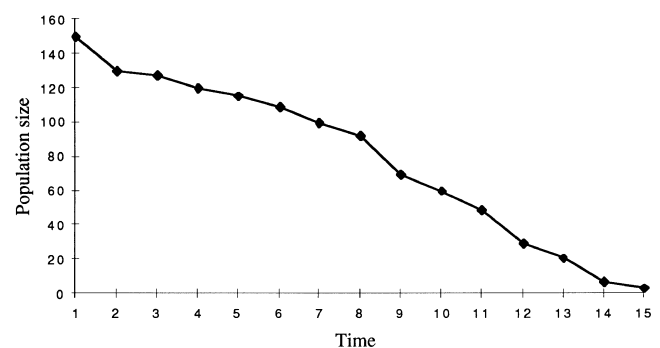


Figure 3. Hypothetical autocorrelogram of a population showing positive autocorrelation in the intrinsic rate of increase due to Allee effects.

## Methods

I used trapping records (pelt returns) of 30 Hudson's Bay Company posts in Ontario as an estimate of population size for beaver (*Castor canadensis*), ermine (*Mustela erminea*), fisher (*Martes pennanti*), marten (*Martes americana*), mink (*Mustela vison*), and muskrat (*Ondatra zibethica*). Most data sets ran from 1916 to 1938, although the data sets varied between 15 and 23 years in length. Statistical power in autocorrelation depends on the length of the time series, so no data set was used if the total number of consecutive data points fell below 15. An approximate 15-year minimum length appears to provide enough power to detect autocorrelation (Turchin 1990; Holyoak 1993; Saucy 1994; Ranta et al. 1995). This resulted in different sets of posts being used for each species.

I also examined population indices (see individual citations for methods of population estimates) from Merriam's kangaroo rat (*Dipodomys merriami*; Brown & Harney 1993), the silky pocket mouse (*Perognathus flavus*; Brown & Harney 1993), elephants (*Loxodonta afri-*

*cana*; Broten & Said 1995), ostriches (*Struthio camelus*; Broten & Said 1995), waterbucks (*Kobus ellipsiprymnus*; Broten & Said 1995), warthogs (*Phacochoerus aethiopicus*; Broten & Said 1995), giraffes (*Giraffa camelopardalis*; Broten & Said 1995), elands (*Tragelaphus oryx*; Broten & Said 1995), wild dogs (*Lycaon pitus*; Burrows 1995), lions (*Leo leo*; Hanby et al. 1995), and dwarf mongooses (*Helogale parvula*; Waser et al. 1995). All time series ran for at least 14 years except for the mongoose data set, which required interpolation of one data point.

Avian population indices (Table 1) were collected for the Downy Woodpecker (*Picoides pubescens*), Carolina Chickadee (*Parus carolinensis*), Tufted Titmouse (*Parus bicolor*), White-breasted Nuthatch (*Sitta canadensis*), Northern Cardinal (*Cardinalis cardinalis*), and Northern Flicker (*Colaptes auratus*) from Christmas bird counts at Buckeye Lake Park, Ohio (Ehrlich & Roughgarden 1987). Population size estimates for male Indigo Buntings (*Passerina amoena*), Gray Catbirds (*Dumetella carolinensis*), Eastern Wood-peewees (*Contopus sordidulus*), Red-eyed Vireos (*Vireo olivaceus*), and

**Table 1.** Number of populations (*n*) of each species that showed significant autocorrelation (ACF) at the given lag and whether the populations showed significant cross correlation with local nontransformed or transformed (differenced) precipitation data.

| Species ( <i>n</i> )        | Length of time series (years) | Populations with significant ACF at the given lag |       |              | Significant correlation with precipitation* |             |
|-----------------------------|-------------------------------|---------------------------------------------------|-------|--------------|---------------------------------------------|-------------|
|                             |                               | No lag                                            | Lag 1 | Lag $\geq 2$ | Nontransformed                              | Transformed |
| Beaver (30)                 | 15-23                         | 24                                                | 6     | 0            | n/a                                         | n/a         |
| Eland (1)                   | 14                            | 1                                                 | 0     | 0            | no                                          | no          |
| Elephant (1)                | 14                            | 1                                                 | 0     | 0            | no                                          | no          |
| Ermine (26)                 | 15-23                         | 17                                                | 2     | 7            | n/a                                         | n/a         |
| Fisher (20)                 | 15-23                         | 16                                                | 2     | 2            | n/a                                         | n/a         |
| Giraffe (1)                 | 13                            | 1                                                 | 0     | 0            | no                                          | no          |
| Grizzly bear (1)            | 50                            | 0                                                 | 0     | 1            | no                                          | yes         |
| Lion (1)                    | 16                            | 1                                                 | 0     | 0            | no                                          | no          |
| Marten (23)                 | 15-23                         | 15                                                | 6     | 1            | n/a                                         | n/a         |
| Merriam's kangaroo rat (1)  | 14                            | 1                                                 | 0     | 0            | no                                          | no          |
| Mink (26)                   | 15-23                         | 25                                                | 1     | 0            | n/a                                         | n/a         |
| Mongoose (1)                | 13                            | 1                                                 | 0     | 0            | no                                          | no          |
| Muskrat (27)                | 15-23                         | 26                                                | 0     | 1            | n/a                                         | n/a         |
| Silky pocket mouse (1)      | 14                            | 1                                                 | 0     | 0            | no                                          | no          |
| Waterbuck (1)               | 14                            | 1                                                 | 0     | 0            | no                                          | no          |
| Warthog (1)                 | 14                            | 1                                                 | 0     | 0            | no                                          | no          |
| Wolf (1)                    | 18                            | 1                                                 | 0     | 0            | no                                          | no          |
| Downy Woodpecker (1)        | 47                            | 1                                                 | 0     | 0            | no                                          | no          |
| Carolina Chickadee (1)      | 47                            | 0                                                 | 1     | 0            | no                                          | no          |
| Tufted Titmouse (1)         | 47                            | 0                                                 | 1     | 0            | no                                          | no          |
| White-breasted Nuthatch (1) | 47                            | 0                                                 | 1     | 0            | no                                          | no          |
| Cardinal (1)                | 47                            | 0                                                 | 0     | 1            | no                                          | no          |
| Flicker (1)                 | 47                            | 0                                                 | 1     | 0            | no                                          | no          |
| Gray Catbird (1)            | 24                            | 1                                                 | 0     | 0            | no                                          | no          |
| Indigo Bunting (1)          | 37                            | 0                                                 | 1     | 0            | no                                          | no          |
| Eastern Woodpeewee (1)      | 41                            | 0                                                 | 1     | 0            | no                                          | no          |
| Red-eyed Vireo (1)          | 33                            | 0                                                 | 1     | 0            | no                                          | no          |
| Wood Thrush (2)             | 26                            | 2                                                 | 0     | 0            | yes                                         | no          |
| Ostrich (1)                 | 14                            | 1                                                 | 0     | 0            | no                                          | no          |
| Total (184)                 |                               | 147                                               | 24    | 13           | 1                                           | 1           |

\*Populations for which precipitation data were not available are indicated by n/a.

Wood Thrush (*Hylocichla mustelina*) were examined from a 24-ha woodlot in Illinois (Brawn & Robinson 1996), and a second Wood Thrush data set came from a small (15-ha) woodlot in Delaware (Roth & Johnson 1993).

People have criticized the use of Christmas bird count data and harvest records as unreliable. But fur prices in Ontario were not related to harvest number in any species during this time period (D. R. Johnson & B. J. Swanson, unpublished data). Thus, harvest provides an adequate approximation of population size. Similarly, the results from the Christmas bird count data do not vary from population data taken with more rigorous methods in this study.

Because the duration of several of the avian time series was much greater than that of the mammalian time series, I subsampled all avian data sets that exceeded 30 years in 15-year, non-overlapping subsamples. I also analyzed the subsamples with autocorrelation analysis and used paired *t* tests to determine if the subsampled ACFs differed from the ACFs of the entire time series.

Total annual precipitation data in 11 states, spanning 99 years (1895–1993; Table 2), were extracted from the National Climate Data Center (NCDC). The Center subdivides each state into smaller areas based on climate, and precipitation data is averaged from weather stations within each subdivision (Table 2). Five of the states examined were chosen because they corresponded to the locations of the animal data sets; the remainder were chosen randomly. A 102-year precipitation data set from the Konza prairie in Kansas was also used.

Analysis of time series data requires a stationary mean and variance to produce accurate estimates of the autocorrelation (Royama 1996). I transformed all the data sets with natural logarithms prior to analysis in order to induce stationary variance (Brockwell & Davis 1991; Royama 1996) and then differenced ( $N_{\text{difference}} = \ln(N_t) -$

$\ln(N_{t-1})$ ) them to produce a stationary mean (Royama 1996). This transformation also converts the population size data to intrinsic rates of increase, *r*. Based on regression analysis, none of the data sets were found to have a significant trend following the transformation (all *ps* > 0.10). I performed autocorrelation analysis on all 248 data sets, examining all lags up to 7 or 15 years, depending on the length of the data sets. For shorter data sets there was not enough power to investigate lags greater than 7 years, and effects from lags greater than 15 years do not seem biologically probable.

I examined how subsampled data sets approximated the autocorrelation estimated from the entire data set to determine the length of time series needed for an accurate estimate of the ACF. I subsampled precipitation data from three randomly chosen states (Arizona, Arkansas, and Wyoming) and those vertebrate data sets with at least 30 years of data into non-overlapping periods of 5, 10, 15, 25, and 50 years. I combined subsamples based on data type (precipitation or taxa) and duration of the subsample (5, 10, 15, etc.) and compared them to the full length time series ACF using paired *t* tests. I then used regression analysis to evaluate the accuracy of the subsamples. Ideally, the subsamples would explain 100% of the variance and produce a slope of 1, indicating that the subsamples were perfect estimators.

Finally, I calculated cross correlations between the transformed data sets of population size and transformed and untransformed precipitation to determine if autocorrelation in precipitation could serve as a substitute estimate of autocorrelation when population data are of insufficient length. Cross correlation analysis examines the correlation between one factor at time *t* and another factor at time lags of various lengths *t* + *i*. Cross correlations at a lag of zero (*t* + 0) are simply the traditional Pearson's correlation.

## Results

The majority of the mammalian data sets (*n* = 133; 82.2%) did not show significant autocorrelations at any lag (Table 1), whereas 5 of the 13 avian data sets (38.5%) did not show any significant autocorrelations (Table 1). Significant autocorrelations at a lag of 1 were found in 53.8% of the avian populations (*n* = 7) and 10.4% of the mammalian populations (*n* = 17). A total of 7.4% of the mammalian data sets (*n* = 12) and 7.7% (*n* = 1) of the avian data sets (Table 1) showed only higher-order dynamics (significant autocorrelations at lags of ≥2). Autocorrelation was found to occur significantly more frequently in the avian data sets than the mammalian data sets ( $\chi^2 = 14.27$ , *p* < 0.0001). Trophic breakdown of the mammalian data sets revealed no difference in the number of herbivore (*n* = 6; 11.1%) and carnivore (*n* = 11; 22.4%) data sets that were significantly autocorrelated

**Table 2.** Number of National Climate Data Center precipitation data sets that showed significant autocorrelation at no lags, lag of 1 year, and lags of 2 or more years.

| State      | n  | Significant autocorrelation lag |        |          |
|------------|----|---------------------------------|--------|----------|
|            |    | None                            | 1 year | ≥2 years |
| Arizona    | 7  | 1                               | 6      | 0        |
| Arkansas   | 9  | 0                               | 9      | 0        |
| California | 7  | 0                               | 7      | 0        |
| Delaware   | 2  | 0                               | 2      | 0        |
| Idaho      | 7  | 0                               | 7      | 0        |
| Illinois   | 7  | 0                               | 7      | 0        |
| Indiana    | 10 | 0                               | 10     | 0        |
| Kansas     | 1  | 0                               | 1      | 0        |
| Ohio       | 10 | 0                               | 10     | 0        |
| Michigan   | 7  | 0                               | 7      | 0        |
| Washington | 11 | 0                               | 10     | 1        |
| Wyoming    | 10 | 0                               | 10     | 0        |

at a lag of 1 year ( $\chi^2 = 2.6, p > 0.1$ ). A significantly greater ( $\chi^2 = 50; p < 0.001$ ) number of carnivore data sets ( $n = 11$ ; 91.7%) was autocorrelated at lags of 2 or more years than herbivore data sets ( $n = 1$ ;  $p = 8.3\%$ ). There was no significant difference ( $\chi^2 = 0.3, p > 0.75$ ) in the number of Neotropical migrants (50%) and nonNeotropical populations (28.6%) that exhibited autocorrelation.

The majority (81.8%) of the 15-year subsamples of the avian time series had significant ACFs (all  $ps < 0.05$ ). No significant difference ( $t_{df = 21} = 1.354, p = 0.2$ ) was found between the mean ACF for the entire time series (mean  $\pm$  SD,  $-0.582 \pm 0.076$ ) and the 15-year subsamples ( $-0.549 \pm 0.134$ ).

Analysis of the precipitation data showed that significant autocorrelation occurred in 97.7% ( $n = 86$ ) of the data sets at a lag of 1 (Table 2). One of the 88 (1.1%) precipitation data sets showed significant autocorrelation at lags greater than 1, and 1 (1.1%) had no autocorrelation.

As expected, subsampling of the precipitation data showed that longer subsamples produced better approximations of the ACFs of the total series. The autocorrelations of the 5-year subsamples (mean  $\pm$  SD,  $-0.303 \pm 0.263$ ) were significantly greater ( $t = 6.75, p < 0.0001$ ) than the ACFs ( $-0.457 \pm 0.046$ ) of the full-term precipitation data sets. Similarly, the regression analysis of the 5-year subsamples' autocorrelations on the entire time series was nonsignificant ( $F = 0.192, p = 0.66$ ), and none of the variance was explained (adjusted  $r^2 = 0.0$ ). Autocorrelations from subsamples of 10 years ( $-0.316 \pm 0.213$ ) were also significantly greater ( $t = 6.2, p < 0.0001$ ) than the autocorrelations for the total time span and produced a nonsignificant regression ( $F = 1.158, p = 0.28$ ) that explained less than 1% of the variance (adjusted  $r^2 = 0.001$ ). But neither the mean autocorrelation from the 15-year subsamples ( $-0.432 \pm 0.175$ ), the 25-year subsamples ( $-0.433 \pm 0.161$ ), nor the 50-subsamples ( $-0.468 \pm 0.121$ ) was significantly different ( $t = 1.82, p = 0.08$ ;  $t = 1.502, p = 0.14$ ;  $t = 0.838, p = 0.41$ , respectively) from the entire series mean. The regression of the 15-year subsamples was significant ( $F = 8.456, p = 0.004$ ), although it explained just over 4% of the variance (adjusted  $r^2 = 0.046$ ). The regression lines of the 25-year and 50-year subsamples were also significant ( $F = 4.27, p = 0.04$ ;  $F = 7.45, p = 0.009$ , respectively), although very little of the variance (adjusted  $r^2 = 0.03$ , adjusted  $r^2 = 0.13$ , respectively) was explained in either model.

Cross correlation analysis found a significant relationship between the transformed precipitation data and  $r$  only for the grizzly bear at lags of  $-3, -4$ , and  $-5$  (all  $ps < 0.05$ ). No other species showed any significant (all  $ps > 0.05$ ) cross correlation between  $r$  and precipitation at any lag. Comparing the untransformed precipitation data and  $r$  also revealed only one significant cross correlation—for the Wood Thrush at lags of  $-1$  and  $-3$  ( $p < 0.05$ ). No other cross correlations at any lags were significant.

## Discussion

These results show that significant autocorrelation at a lag of 1 year often occurs in avian populations (53.8%), is less common in mammals (10.4%), and is very common in precipitation (97.7%) (Table 2). But the lack of significant autocorrelation in 82.1% of the mammalian data sets and 38.5% of the avian data sets argues that autocorrelation in the rate of change is not a ubiquitous phenomenon and should be examined on a case-by-case basis. This is especially surprising because it suggests that the rate of population change does not depend on the previous year's population size. Alternatively, the lack of autocorrelation in the mammalian populations could be an artifact of the relatively short duration of the data sets compared to those of the avian populations. It seems unlikely that time series duration is the underlying mechanism because subsampling down to 15 years altered neither the results of the avian nor the precipitation time series. In addition, significant autocorrelations were detected in red fox (Swanson 1993) and lynx (D. R. Johnson & B. J. Swanson, unpublished data) populations from the same group of posts with equal-length time series, as well as in insect populations of similar lengths (Turchin 1990). The results could be due to sampling over an improper scale for some of the populations. In species for which multiple populations were examined (Table 1), no observable pattern was evident between the presence or absence of autocorrelation and area. Nevertheless it is prudent to consider scale if the estimate of autocorrelation and the population it will be applied to are different.

Trophic level analysis found differences only in populations that exhibited autocorrelation at lags of 2 or more years in the mammalian data sets. This relationship may be due to carnivores often exhibiting a numerical response to prey conditions rather than a function response, causing an expected delay of 2 years.

Only 2 of the 88 precipitation data sets (2.3%) failed to show significant autocorrelation at a lag of 1, which can be ascribed to chance based on the large number of data sets examined. Williams and Liebhold (1995) showed that an exogenous autocorrelated variable, such as weather, can produce significant but spurious second-order dynamics (delayed density dependence). Given the high percentage of precipitation data sets that showed significant autocorrelation, researchers should be careful when concluding that a population is exhibiting delayed density dependence. But because so few data sets showed significant second-order dynamics or a relationship between precipitation and population change, spurious second-order dynamics due to autocorrelated precipitation are probably uncommon in mammalian or avian populations.

Only two cross correlations between rate of population increase and precipitation were significant (grizzly

bear and transformed precipitation [Table 1; Fig. 4] and Wood Thrush and nontransformed precipitation [Table 1]), showing that precipitation is not often a good predictor of changes in vertebrate populations and thus not an adequate substitute for population autocorrelation. This seems non-intuitive, because precipitation is related to primary productivity (Went 1948, 1949; Tevis 1958a, 1958b; Rosenzweig 1968) and primary productivity has been linked to reproductive output in some species (Beatley 1969; Brown et al. 1979). These results suggest that there is a decoupling of the relationship between precipitation, primary productivity, and population dynamics. Alternatively, the larger scale at which most of the precipitation data was gathered compared to that of the population data could smooth over local variation that would more closely correspond to local population dynamics.

Obviously, the longer the data series, the more precise the autocorrelation estimate. Long data sets (several decades) are often not available however, which raises the question of how long is long enough. The mean autocor-

relation of the subsamples ceased to differ from the mean of the total series with 15 years of data (Table 3). But the estimates continually improved with increased length of the time series (i.e., increasing  $r^2$ ). Regression analysis showed that, despite the low amount of variation explained by the regressions, their performance did improve with increased length of the time series based on the slope's approach to 1 (Table 3). The consistently low  $r^2$  values are representative of how noisy the data are and not a function of sample size. Although the coefficient of variation was still large with 50-year subsamples, it did vary inversely with the length of the time series. These results do not suggest that we should stop collecting data after 15 years, only that 15 years of data should allow a reasonable prediction of the ACF.

Incorporating autocorrelation in population models where no significant autocorrelation exists, or using environmental autocorrelations, could result in either an unduly rosy or bleak prediction of a species' future, depending on the sign and strength of the autocorrelations. Including spurious positive autocorrelations would increase the probability of a series of either positive or negative  $r$  values. Alternatively, including unnecessary negative autocorrelation terms would reduce the probability of the model producing a positive or negative trend in  $r$  and population size. Two cases are particularly worrisome. Including an unnecessary positive autocorrelation term could indicate a false increasing trend, overestimating the actual time to extinction. Similarly, including a spurious negative autocorrelation could hide a true negative trend, also overestimating time to extinction. The converse of each case would result in underestimating the time to extinction.

This study suggests that although autocorrelation is commonplace in one environmental measure, precipitation, it does not necessarily translate into autocorrelation in animal populations; thus, researchers should

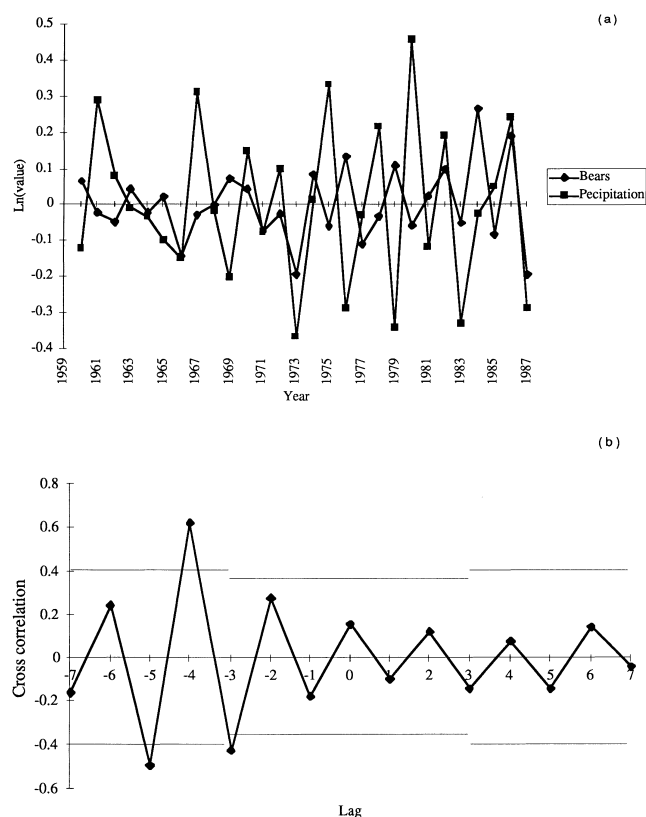


**Figure 4.** Time series plots (a) for the grizzly bear and precipitation data from Yellowstone National Park. Cross correlation results (b) between grizzly bear and precipitation data (solid lines indicate 95% confidence intervals). Significant negative cross correlations occur at lags of -3, and -5, and a significant positive cross correlation occurs at a lag of -4.

**Table 3.** Mean autocorrelation (ACF) of the subsampled National Climatic Data Center precipitation data sets, standard deviation (SD), coefficient of variation (CV), slope, and adjusted  $r^2$  for the subsampled time series.

| Length of subsampled precipitation time series (years) <sup>a</sup> | Mean ACF            | SD    | CV    | Slope              | Adjusted $r^2$ |
|---------------------------------------------------------------------|---------------------|-------|-------|--------------------|----------------|
| 5                                                                   | -0.303 <sup>b</sup> | 0.263 | 0.868 | 0.276              | 0.0            |
| 10                                                                  | -0.316 <sup>b</sup> | 0.213 | 0.674 | 0.624              | 0.001          |
| 15                                                                  | -0.432              | 0.175 | 0.405 | 0.863 <sup>c</sup> | 0.05           |
| 25                                                                  | -0.433              | 0.161 | 0.372 | 0.707 <sup>b</sup> | 0.03           |
| 50                                                                  | -0.468              | 0.121 | 0.227 | 0.951 <sup>b</sup> | 0.13           |
| Total                                                               | -0.457              | 0.046 | 0.101 |                    |                |

<sup>a</sup>Subsampling was performed by taking non-overlapping periods of 5, 10, 15, 25, and 50 years from the precipitation data sets.

<sup>b</sup> $p < 0.05$ .

<sup>c</sup> $p < 0.01$ .

gauge the appropriateness of substituting environmental autocorrelation for population autocorrelation. I have also shown that autocorrelation is relatively rare in mammals but more common in birds. Researchers predicting population changes and the probability of extinction should therefore try to determine if significant autocorrelation occurs in a population prior to including it in models, because incorporation of autocorrelation structure can drastically alter modeling results (Ferson & Burgman 1995).

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