# Synchronous Variation and Long-Term Trends in Two Populations of Black Rat Snakes 

P. J. WEATHERHEAD,*§ G. BLOUIN-DEMERS, $\dagger$ AND K. A. PRIOR $\ddagger$<br>*Department of Biology, Carleton University, Ottawa, Ontario, K1S 5B6, Canada<br>$\dagger$ Department of Evolution, Ecology and Organismal Biology, Botany and Zoology Building, The Ohio State University, 1735 Neil Avenue, Columbus, OH 43210-1293, U.S.A.<br>$\ddagger$ Endangered Species Division, Canadian Wildlife Service, Hull, Quebec, K1A 0H3, Canada


#### Abstract

Synchronous variation among animal populations affects the vulnerability of endangered species and is relevant to understanding population fluctuation generally. We analyzed data collected over 18 years from two populations of black rat snakes (Elaphe o. obsoleta), a species of conservation concern in Canada, to determine whether the populations varied synchronously. Because the populations were 30 km apart and genetically distinct, synchrony should be attributable to common stochastic environmental factors, the Moran effect. Syncbronous variation in annual estimates of population size, survival probability, recruitment, and age structure all provided evidence of a Moran effect. However, opposite trends in age structure through time suggested that the internal dynamics of the two populations were different. The conservation implication of synchrony is that this population of rat snakes is vulnerable to stochastic environmental phenomena because all subpopulations could become rare simultaneously. Evidence of different population processes in the two populations suggests, however, that local factors may be of more immediate relevance to conservation than regional phenomena. More generally, these results indicate that evidence of synchronous variation in population size and similar long-term population trends-both populations appeared to be declining-are not necessarily indicative of common underlying population dynamics.


#### Abstract

Variación Sincrónica y Tendencias a Largo Plazo en Dos Poblaciones de Culebras Ratoneras Negras Resumen: La variación sincrónica entre poblaciones animales afecta la vulnerabilidad de especies en peligro $y$ es relevante para el entendimiento de las fluctuaciones poblacionales en general. Analizamos datos obtenidos durante 18 años de dos poblaciones de culebras ratoneras negras (Elaphe o. obsoleta), una especie de interés para la conservación en Canadá, para determinar si las poblaciones variaban sincrónicamente. Debido a que las poblaciones estaban separadas 30 km y eran genéticamente distintas, la sincronía debería atribuirse a factores ambientales estocásticos comunes (el efecto Moran). La variación sincrónica en estimaciones anuales del tamaño poblacional, probabilidad de sobrevivencia, reclutamiento y estructura de edades proporcionó evidencia de un efecto Moran. Sin embargo, las tendencias contrarias de la estructura de edades a lo largo del tiempo sugirieron que las dinámicas internas de las dos poblaciones eran diferentes. La implicación de la sincronía en la conservación es que esta población de culebras ratoneras es vulnerable a fenómenos ambientales estocásticos porque todas las subpoblaciones podrían volverse raras simultáneamente. Sin embargo, la evidencia de procesos poblacionales diferentes en las dos poblaciones sugiere que los factores locales pueden ser de mayor relevancia inmediata para la conservación que los fenómenos regionales. Más generalmente, estos resultados indican que la evidencia de variación sincrónica en el tamaño de la población y las tendencias a largo plazo similares (ambas poblaciones parecían en declinación) no necesariamente eran indicadores de dinámicas poblacionales internas comunes.


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## Introduction

A central theme in animal ecology has been the description and explanation of population fluctuations (Ranta et al. 1997; Hudson \& Cattadori 1999). Much of the historical interest has focused on the factors that synchronize population cycles. However, populations can vary synchronously even though they do not fluctuate cyclically (Ranta et al. 1997). Thus, recent interest has focused on the cause of synchronous variation among populations, a phenomenon that appears to be widespread (Ranta et al. 1995; Hudson \& Cattadori 1999). Synchrony among populations is of particular relevance to conservation (Ranta et al. 1995; Koenig 1998; Hudson \& Cattadori 1999). If subpopulations of a rare species vary asynchronously, a subpopulation that goes extinct can be "rescued" by dispersal from neighboring subpopulations. If all subpopulations vary synchronously, however, the potential for extinction of the entire population is much greater, because all subpopulations can decline simultaneously. We used 18 years of census data for two populations of black rat snakes (Elaphe o. obsoleta) to look for evidence of synchrony and considered the implications of our results for the conservation of this threatened species.

Three factors are thought to be responsible for producing synchrony among populations (Bjørnstad et al. 1999; Koenig 1999). First, individuals can move between populations so that the two "populations" are not actually independent. Second, predators or parasites can move between populations, with variation in predator or parasite abundance causing synchronous variation in the prey or host population. Third, randomly occurring stochastic perturbations can affect populations over a wide area (Ranta et al. 1995; Hudson \& Cattadori 1999). When fluctuations in size of two separate populations become synchronized through exposure to common environmental perturbations, the phenomenon is referred to as the Moran effect (Moran 1953). The commonly observed weakening of synchrony with distance is consistent with each of these three factors having a synchronizing effect (Koenig 1999). However, synchrony among populations for which dispersal between populations is not possible indicates that the Moran effect alone can play a major role in population dynamics (e.g., Grenfell et al. 1998).

Snakes seem likely to exhibit the Moran effect. First, variation in temperature affects all aspects of snake ecology (Huey \& Kingsolver 1989), so populations should be vulnerable to stochastic environmental variation. The rat snake populations we studied seemed particularly likely to exhibit a Moran effect because they were within 50 km of the northern limit of the species' distribution (Prior et al. 1997). At this latitude, 6 months of hibernation (Weatherhead 1989; Blouin-Demers et al. 2000) allows the snakes limited time to feed and repro-
duce. Second, snake populations, including black rat snakes, appear to be genetically structured at a scale of only a few kilometers (Lougheed et al. 1999; Gibbs \& Weatherhead 2001). Thus, movement of individuals between populations is restricted, making even nearby populations independent. Our two study populations were approximately 30 km apart and separated by the St. Lawrence River and a major four-lane highway. Thus, our study sites were too far apart and isolated for movement of snakes or predators between populations, but they were close enough to be influenced similarly by climatic variation.

Our first goal was to determine the extent to which the two populations varied synchronously. Our second goal was to determine whether trends in demographic processes (recruitment, mortality) or in demographic components (sex ratio, age structure) were correlated with population trends. If two populations vary synchronously, then it should be possible to identify which demographic processes underlie that synchrony. Within populations, trends in demographic processes should reveal something about the cause of the population trend (e.g., a population decrease might be related to declining recruitment, declining survivorship, or both).

## Methods

## Study Species and Areas

Demographic analysis of the black rat snake population we studied indicated that individuals can live as long as 30 years (Blouin-Demers et al. 2001). Both male and female rat snakes mature at a minimum snout-vent length (SVL) of approximately 1050 mm , which equates to a mean age of 9 years for males and 10 years for females (Blouin-Demers et al. 2001). Young snakes recruit to communal hibernacula at a mean age of approximately 8 years and thereafter remain highly faithful to the same hibernaculum. Their hibernation patterns prior to joining communal hibernacula are unknown.

The current range of black rat snakes in Canada is limited largely to a disjunct population in the Frontenac Axis of eastern Ontario. The virtual disappearance of rat snakes from the rest of their historic range in Ontario led to the species' designation as threatened in Canada (Prior \& Weatherhead 1998). Both our study populations were within the Frontenac Axis, the first located at the Queen's University Biological Station (lat. $44^{\circ} 34^{\prime} \mathrm{N}$, $76^{\circ} 19^{\prime} \mathrm{W}$ ) and the second 30 km south on Hill Island in St. Lawrence Islands National Park.

The biology station study site was $1.8 \mathrm{~km}^{2}$ in area. The mixture of second-growth, mixed deciduous-coniferous forest, old field, pasture, lawn, wetland, and gravel roads (Weatherhead \& Charland 1985) continued well beyond the study site. There were few permanent homes but ap-
proximately 30 summer residents in the area. Hill Island is a $5.6-\mathrm{km}^{2}$ island in the St. Lawrence River with habitat similar to that at the biology station. The study area ( $2.0 \mathrm{~km}^{2}$ ), located east of a two-lane, paved highway that divides the island, contained approximately 30 seasonal and permanent residences, primarily along the shores of the island. We expected the rat snake populations at both sites to be doing well. The presence of the biology station and the national park should have minimized human malfeasance as a problem for the snakes, and there were no obvious changes in the habitat at either site over the course of the study.

## Population Monitoring

Snakes were captured every year from 1981 to 1998 at the biology station and from 1982 to 1997 at Hill Island. Most captures from both sites came from visiting hibernacula during spring emergence (approximately midApril through May; Blouin-Demers et al. 2000) and searching the ground and trees. No record of search effort was kept, and with one exception we have no reason to expect that search effort varied systematically. The exception was that one of the two hibernacula at each site was fenced each spring to enhance capture success, beginning in 1987 at Hill Island and in 1992 at the biology station, and continuing thereafter. The other hibernaculum at each site was in terrain too rough to fence. When interpreting our data, we assessed the possibility that fences increased the proportion of snakes captured. At both study areas snakes were also captured opportunistically away from the hibernacula during the remainder of the active season. Although we could not quantify search effort for opportunistic captures, we again have no reason to expect systematic variation over the course of the study.

We sexed each snake by probing for the presence of hemipenes and measured its snout-to-vent length (SVL) to the nearest millimeter. From 1981 to 1991 we marked snakes by heat-branding the caudal scutes in a unique pattern. After 1991 we implanted passive integrated transponder (PIT) tags. We released snakes at their capture location within 24 hours. All protocols were approved by the Carleton University Animal Care Committee.

## Data Analysis

We used the Jolly-Seber capture-recapture model to derive annual estimates of population size, survival rate, and recruitment for each study area (Pollock et al. 1990; Lebreton et al. 1992). According to this model recruitment was an estimate of new individuals joining the population and involved no assumptions about their reproductive status. We used the software Jolly (Pollock et al. 1990). Of the models available, we used model A because it is a conservative estimator, allowing for both
death and immigration (Pollock et al. 1990). We also calculated two other population parameters directly from the capture data. For each year at each site, we calculated the percentage of individuals that were mature and the percentage that were males. In all calculations, we included each individual only once each year.

We log-transformed all population parameters to normalize their distributions (Koenig 1998) and reduce correlation between the variance and mean (Koenig \& Knops 1998; Koenig 1999). To determine whether there were significant temporal trends in the time series of population parameters at each study site, we regressed each population parameter on year at each site and tested for a significant slope (Meyer et al. 1998). To determine whether each population parameter fluctuated in synchrony at the two sites, we used the Pearson moment correlation between the two time series (Grenfell et al. 1998; Koenig \& Knops 1998; Bjørnstad et al. 1999). Instead of using the log-transformed raw data directly in our correlation calculations, we used the difference between the logs of two successive observations. Detrending the data in this fashion puts the emphasis on synchrony between annual variation at each site, which reflects regional phenomena and not potential apparent synchrony arising from common long-term trends caused by global phenomena such as habitat degradation or climate change (Koenig \& Knops 1998; Bjørnstad et al. 1999). Failure to control for long-term trends in this fashion could indicate evidence of synchrony where none existed if the trends in both populations are the same. We assumed a time lag of zero years in all our correlation calculations.

Time series of population parameters from a given site are strongly serially dependent (Ranta et al. 1995; Grenfell et al. 1998; Bjørnstad et al. 1999). Therefore, we obtained significance values for the slope estimates (in the case of trends) and for the Pearson moment correlation estimates (in the case of synchrony) from the distribution of the statistic of interest obtained by 5000 randomization trials. In each trial we randomized the order of the variable on the x-axis (years in the case of trends and first-difference time series for one population in the case of synchrony), kept the order of the variable on the $y$-axis constant, and calculated the slope or correlation. We then compared the slope or correlation for the data in their true order to the family of values obtained from the 5000 randomization trials. For the analysis of trends in population parameters obtained from the Jolly-Seber model, we did not attempt to take into account the variance associated with the estimates in the randomization trials. We used a similar approach to derive $95 \%$ confidence intervals (CI) for the statistics of interest from the distribution of 5000 bootstrap estimates (Manly 1997; Simon 1998). Development of methods to assess synchrony is ongoing (Buonaccorsi et al. 2001), but the approach we followed avoids the serious pitfalls.

We used Resampling Stats 5.0 for MacIntosh (Resampling Stats 1999) to conduct statistical analyses. All means are reported as $\pm 1 \mathrm{SE}$.

## Results

We captured 305 individual snakes 654 times at the biology station and 212 individual snakes 388 times at Hill Island (Table 1). The population at the biology station declined significantly, whereas at Hill Island the population decline was not significant (Table 2). There was no jump in estimated population sizes coincident with the onset of fencing hibernacula in 1987 and 1992 at Hill Island and the biology station, respectively (Fig. 1). Annual variations in population size estimates were positively correlated ( $r=0.539,95 \% \mathrm{CI}=0.319-0.787$, $p=0.027$; Fig. 1), indicating that the two snake populations varied synchronously.

Changes in population size could arise through changes in survivorship, recruitment, or both. Variation in survival estimates was high at both sites, and the increase in survival through time was not significant at either site (Table 2). However, annual survival estimates at the two sites were highly positively correlated ( $r=0.845,95 \% \mathrm{CI}=0.729-0.951$, $p<0.001$; Fig. 2). Estimated annual recruitment declined over the course of the study at the biology station and increased at Hill Island. Neither trend was significant, however, and the $95 \%$ CI of these trends overlapped (Table 2). Despite the different direction of these recruitment trends, annual variation in recruitment was positively correlated at the two sites $(r=0.562,95 \% \mathrm{CI}=0.189-0.830, p=0.043$; Fig. 2).

At the biology station, the relative abundance of mature snakes increased significantly through the study, whereas at Hill Island mature individuals declined significantly (Table 2). Once again, despite these opposing long-term trends, annual variation in the relative abundance of mature snakes was synchronous at the two sites $(r=0.556,95 \% \mathrm{CI}=0.187-0.797, p=0.016$; Fig. 2). Finally, the sex ratio did not change significantly over time at either site (Table 2). Annual variation in sex ratios differed from the other parameters in that the two populations tended to be negatively synchronous, although the trend was not significant $(r=-0.402,95 \%$ $\mathrm{CI}=-0.760-0.364, p=0.089$; Fig. 2).

## Discussion

The snake populations we studied were not selected because we had any a priori reason to expect particular trends. In fact, our expectation was that both populations should have been protected from some of the factors that seem likely to be responsible for the species' decline through much of its Canadian range. From a statistical perspective, the Hill Island population met this expectation, whereas the biology-station population declined over the study period. However, the similarity of the estimated slopes for the two populations and the overlap of the CI for those trends suggest that the Hill Island population may also be declining. The high variation in annual population estimates for Hill Island made the detection of a slow decline much more difficult than at the biology station.

Table 1. Number of individual black rat snakes (Elaphe obsoleta) captured at the Queen's University Biological Station and at Hill Island in the St. Lawrence Islands National Park, Ontario, Canada.

| Year | Biology station |  | Hill Island |  |
| :---: | :---: | :---: | :---: | :---: |
|  | captures (\% recaptures) | population size estimates (SE) | captures (\% recaptures) | population size (SE) |
| 1981 | 22 (0.0) | - | - | - |
| 1982 | 34 (32.4) | 42.8 (6.9) | 16 (0.0) | - |
| 1983 | 47 (25.5) | 98.8 (23.1) | 18 (11.1) | 52.8 (39.3) |
| 1984 | 47 (53.2) | 75.7 (10.7) | 7 (57.1) | 11.9 (2.7) |
| 1985 | 25 (52.0) | 96.6 (26.1) | 28 (10.7) | 161.9 (101.7) |
| 1986 | 30 (50.0) | 78.5 (16.6) | 15 (26.7) | 64.0 (27.5) |
| 1987 | 26 (50.0) | 77.1 (16.5) | 19 (42.1) | 46.5 (10.4) |
| 1988 | 42 (52.4) | 87.7 (16.3) | 30 (70.0) | 47.1 (7.1) |
| 1989 | 30 (60.0) | 69.1 (14.5) | 27 (55.6) | 53.5 (14.6) |
| 1990 | 21 (71.4) | 40.1 (6.4) | 12 (58.3) | 29.5 (9.1) |
| 1991 | 25 (60.0) | 40.8 (5.8) | 19 (42.1) | 33.9 (8.7) |
| 1992 | 49 (40.8) | 62.5 (6.8) | 24 (45.8) | 34.1 (6.2) |
| 1993 | 37 (78.4) | 47.1 (3.0) | 20 (80.0) | 20.0 |
| 1994 | 54 (53.7) | 66.2 (5.7) | 27 (0.0) | 27.0 |
| 1995 | 30 (70.0) | 63.0 (10.1) | 33 (33.3) | 70.8 (17.9) |
| 1996 | 34 (73.6) | 41.9 (3.2) | 32 (59.4) | 48.1 (8.6) |
| 1997 | 31 (61.3) | 56.0 (10.6) | 22 (72.7) | - |
| 1998 | 35 (57.1) | - |  |  |

Table 2. Slope of the regression of the $\log$ of the population parameters on year for black rat snakes from two sites.*

| Study site | Population parameter | Slope (95\% CI) | p |
| :--- | :---: | :---: | ---: |
| Hill Island | population size | $-0.009(-0.056-0.031)$ | 0.345 |
|  | survival probability | $0.011(-0.014-0.030)$ | 0.162 |
|  | recruitment | $0.044(-0.084-0.158)$ | 0.226 |
|  | \% mature | $-0.015(-0.021--0.008)$ | 0.002 |
|  | \% male | $-0.006(-0.019-0.006)$ | 0.213 |
| Biology station | population size | $-0.013(-0.027-0.001)$ | 0.050 |
|  | survival probability | $0.001(-0.005-0.007)$ | 0.247 |
|  | recruitment | $-0.027(-0.062-0.009)$ | 0.094 |
|  | \% mature | $0.013(0.006-0.024)$ | $<0.001$ |
|  | \% male | $-0.002(-0.010-0.004)$ | 0.375 |

*Significance was obtained by 5000 randomization trials and confidence intervals (CI) by 5000 bootstrap estimates.

We predicted that our rat snake populations were likely to exhibit a Moran effect, and the evidence was consistent with that prediction. Annual estimates of population size, recruitment, survival, and age structure all varied synchronously between the two populations. The only exception was variation in sex ratios, which tended to vary synchronously but did so negatively. Because we can think of no reasonable explanation for negative synchrony in annual sex-ratio variation and because the trend was not significant, we do not consider it further. Collectively, the synchrony between the populations in the other parameters suggest that a common factor such as regional weather patterns affected the two populations similarly.

Despite similar trends in population size over time and synchrony in most population parameters we examined, we found evidence that the two populations behaved differently in some respects. At the biology station, the
decrease in population size appeared to be a consequence of declining recruitment. Consistent with lower recruitment, the age structure of that population shifted toward proportionately more mature individuals, and stable survivorship over the study meant that the change in age structure was not caused by individuals living longer. At Hill Island the situation was less straightforward. Recruitment was erratic, although there was some indication that it was higher in more recent years. A significant decline in the proportion of mature individuals was consistent with improved recruitment. Despite the evidence of improved recruitment and stable survivorship, however, the combination of which should cause the population to increase, the population trend at Hill Island was negative. In his model of synchrony, Moran (1953) assumes the populations have identical dynamics. Deviation from that assumption dilutes the Moran


Figure 1. (a) Trends in the time series of estimated population size (log-transformed) from the Jolly-Seber model for black rat snakes at Hill Island and the biology station, and (b) the first-difference times series of annual population size (log-transformed) at Hill Island and the biology station.


Figure 2. The first-difference times series of log-transformed annual (a) survival probability, (b) recruitment, (c) percent mature individuals, and (d) percent males at Hill Island and the biology station.
effect. Our rat snake populations had some clear differences in dynamics, which reduced the degree of synchrony that was possible.

Our results have several implications for conservation. In the specific case of black rat snakes in Canada, evidence of declining populations in circumstances where rat snakes and their habitats were assumed "safe" is disquieting. The challenge for conservation biologists is to distinguish between declines that are natural negative fluctuations and those that represent a sustained decrease in a population (Reed \& Blaustein 1995; Gibbs et al. 1998). For long-lived species such as rat snakes, even an 18-year period of monitoring is insufficient to differ-
entiate between these alternatives. Although continued population monitoring should eventually clarify the situation, more focused research also seems warranted. Evidence of a population decline was clear at the biology station and appeared to be a consequence of declining recruitment. Thus, determination of whether the decline in recruitment is attributable to natural or anthropogenic factors should help indicate whether the population decline is a natural fluctuation or a sustained decline resulting from some human action.

The broader conservation implications involve our evidence of population synchrony in black rat snakes. Species with populations that vary synchronously over wide
areas are more vulnerable to extinction, because subpopulations cannot rescue each other through dispersal if they all decline simultaneously. Our evidence of synchrony in two black rat snake populations suggests that, at least within its Canadian range, this species is vulnerable to population-wide declines. If all of the population becomes reduced because of human-mediated factors such as habitat loss, the potential for widespread extinction would be even greater.

There is one caveat to our conclusion about the conservation implications of population synchrony. The synchrony we found appears to be attributable to a Moran effect because our two study populations were too far apart for the movement of individuals or predators between populations. Had we analyzed only population size, a reasonable interpretation of our results might have been that the dynamics of both populations were the same: annual variation in population size was synchronous and long-term trends were similar. This interpretation could lead to the conclusion that the same conservation strategy would be appropriate for both populations. The dynamics of the two populations were clearly different, however, with opposite long-term trends in age structure. Thus, a more appropriate interpretation is that, despite their overall similarities, the two populations are affected by different processes. The general caution that emerges is that synchrony in population size variation and similar trends in population size through time are not a sufficient basis on which to conclude that the underlying population dynamics are the same.

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[^0]:    §Current address: Program in Ecology, Evolution and Conservation Biology, University of Illinois, 606 E. Healey
    Street, Champaign, IL 61820, U.S.A., email pweather@uiuc.edu
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