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PHASE DEPENDENCE AND POPULATION CYCLES IN A LARGE-MAMMAL PREDATOR–PREY SYSTEM

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Abstract. Specialized enemies, such as predators and parasitoids, play an important role in the population cycles of small animals by generating delayed density dependence. We investigated the role of predation in population cycles in an undisturbed large-mammal system using long-term data on the sustained density fluctuations of wolves and moose on Isle Royale (Michigan, USA). Nonlinear time-series analysis revealed that wolves display phase-dependent dynamics with stronger density dependence during the decline phase than during the increase phase. This phase dependence was also reflected in predation rates: the number of moose killed daily by wolves was greater during the wolf increase phase than during the wolf decline phase. Accordingly, moose displayed multi-annual cycles generated by an interaction between weak self-regulation and strong delayed density dependence during periods of wolf increase, and strong self-regulation with negligible delayed density dependence during periods of wolf decline. This constitutes, to our knowledge, the first formal documentation of population cycles in large mammals. By making use of long-term data at both trophic levels, as well as data on predator behavior, this analysis may shed light on the mechanisms through which predators contribute to population cycles of prey in other taxa.

Key words: *cycles; density dependence; Isle Royale, (Michigan, USA); moose–wolf system; phase-dependent population dynamics; population cycles in large mammals; predation, role in population cycles; wolves.*

INTRODUCTION

Population cycles are a familiar and geographically widespread feature of the dynamics of small mammals in northern environments (Keith 1963, Bulmer 1974, Krebs 1996, Framstad et al. 1997, Stenseth 1999), but are atypical of large mammals (Caughley and Krebs 1983, Sæther 1997). In contrast to the decades of empirical, theoretical, and statistical research devoted to describing and explaining the multi-annual cycles of, for example, microtine rodents (Stenseth 1999), the comparatively few studies of undisturbed populations of large mammals have revealed no evidence of oscillatory behavior, but, rather, cases of persistent instability or stability (Grenfell et al. 1992, 1998, Clutton-Brock et al. 1997). We undertook an analysis of population cycles in moose (*Alces alces*) and wolves (*Canis lupus*) on Isle Royale (Michigan, USA), a system in which density fluctuations are well documented (Peterson et al. 1984, McLaren and Peterson 1994).

Population cycles may arise as a consequence of tensions between the stabilizing influence of self-regulation (direct density dependence) and the destabilizing influence of some population-extrinsic factor (May 1972) that produces delayed density dependence (May 1974, Turchin 1990, Stenseth et al. 1996, Stenseth 1999). The evidence from small-mammal studies and oscillatory forest insects suggests that the salient extrinsic factor contributing to density cycles in these species is likely specialist predation (Hanski et al. 1993, Krebs et al. 1995, Korpimäki and Krebs 1996, Stenseth 1999, Turchin et al. 1999), though parasites may fill this role in the absence of predators (Berryman 1996, Hudson et al. 1998, Forchhammer and Asferg 2000, Bjørnstad et al. 2001). The long-term data from Isle Royale (Fig. 1) present us with the advantage of being able to analyze herbivore population cycles with concurrent data on predator density in an undisturbed system. Here, we examine the dynamical properties of both trophic levels, and investigate patterns of delayed density dependence and population cycles at the herbivore level in relation to predator dynamics.

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METHODS

Predator–prey dynamics

Commonly, the starting point for investigating whether predation induces delayed density dependence, with consequences for population cycles, in herbivore populations is a set of bivariate equations describing the population dynamics of the predator (X) and the herbivore (Y), where (Royama 1992):

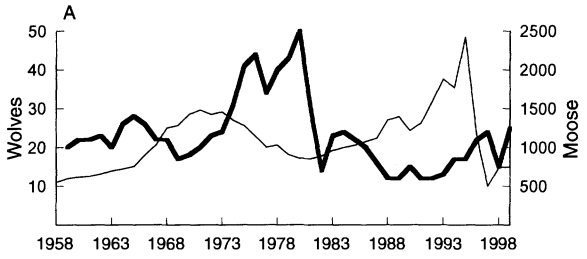

FIG. 1. Population dynamics of wolves (heavy line) and moose (thin line) on Isle Royale, Lake Superior, Michigan, USA, 1958–1999.

$$X_t = f(X_{t-1}, Y_{t-1}) + \varepsilon_t^{(X)} \quad (1a)$$

$$Y_t = g(Y_{t-1}, X_{t-1}) + \varepsilon_t^{(Y)} \quad (1b)$$

in which X and Y are $\log_e$-transformed predator and herbivore densities, respectively, and the ε_is represent random stochastic variation (i.e., white noise). Under the assumption of a linear relationship between population growth rate and log density (Bjørnstad et al. 1995, Stenseth et al. 1996), Eq. 1 can, in the simple linear system, be approximated as (Royama 1992)

$$X_t = a_0 + a_1X_{t-1} + a_2Y_{t-1} + \varepsilon_t^{(X)} \quad (2a)$$

$$Y_t = b_0 + b_1Y_{t-1} + b_2X_{t-1} + \varepsilon_t^{(Y)}. \quad (2b)$$

In the coupled predator–prey system, numerical tracking of herbivore density by predator density will result in delayed density dependence at the herbivore level. To realize this mathematically, we can incorporate the predator equation (Eq. 2a) into the herbivore equation (Eq. 2b). First, we solve Eq. 2b for X_{t-1}, and then insert it into Eq. 2a. Setting $t = t - 1$ in the resulting equation and inserting it back into Eq. 2b, we arrive at a univariate equation for herbivore dynamics in delay coordinates (see Post and Forchhammer [2001] for a detailed exposition of this approach):

$$Y_t = (a_0 + b_0) + (a_1 + b_1)Y_{t-1} - (a_1b_1 - a_2b_2)Y_{t-2} + \varepsilon_t. \quad (3)$$

Note that in this model of herbivore dynamics, the coefficient of delayed density dependence $(a_1b_1 - a_2b_2)$ quantifies the reciprocal influences of predator and prey on each other. Note also that Eq. 3 is equivalent to the statistical linear second-order autoregressive (AR(2)) model (see Royama 1992):

$$Y_t = \beta_0 + (1 + \beta_1)Y_{t-1} + \beta_2Y_{t-2} + \varepsilon_t \quad (4)$$

in which ε_t is additive stochastic variation (but not necessarily white noise).

Because the coefficient of the lag-two autoregressive term derives from trophic (or density) interactions between the herbivore and predator (Stenseth et al. 1996), the significance of delayed density dependence in the herbivore time series implies a role for predation when actual data on predator density are not available (Stenseth 1995, Stenseth et al. 1996). However, empirical demonstration of delayed density dependence in the herbivore time series would not alone be convincing evidence of the influence of predation, because other factors (e.g., a high degree of generational overlap or interactions with other trophic levels) might also contribute to delayed density dependence (Royama 1992).

Analysis of stability and cyclicity

Because the strengths of direct and delayed density dependence influence cyclicity in population dynamics (May 1972, Royama 1992), we used autoregressive (AR) analysis to quantify the coefficients of density dependence at each trophic level (Fig. 1A). We used maximum-likelihood (ML) estimation in the AUTOREG procedure in SAS version 6.0 (SAS Institute 1996) to estimate the coefficients of density dependence; as opposed to ordinary least squares, maximum-likelihood regression provides unbiased estimates of coefficients when there is significant autocorrelation in the error terms (i.e., non-white noise). We fit a first-order autoregressive [i.e., AR(1)] model to the wolf time series and a second-order autoregressive (AR(2)) model to the moose time series.

The choice of these models builds on recent process-oriented modeling of the Isle Royale system, which revealed that the most parsimonious model of wolf dynamics is an AR(1) model that includes as covariates pack size for the current and previous years, while the most parsimonious model of moose dynamics is an AR(2) model with pack size as a covariate (Post and Forchhammer 2001). Pack size reflects, among other processes, important variation in predation because pack kill rates (moose kills per pack per day) increase with pack size (Post et al. 1999); pack size also incorporates social structure and associated nonpredatory behavior that could affect dynamics of both wolves and moose (Vucetich et al. 1997).

The single-species model of wolf dynamics, with pack size as a covariate, provides a significantly better fit to the observed dynamics than does a multi-species model that includes moose density (i.e., Eq. 2a) (Post and Forchhammer 2001), although such a multi-species model does provide a good description of wolf dynamics (Vucetich et al. 1997, Peterson et al. 1998). It should be noted that the first-order model of wolf dynamics does not imply that wolf population fluctuations are insensitive to variation in moose density; indeed, the pack size covariate captures trophic interactions with moose (Post and Forchhammer 2001). The wolf time series modeled previously covered 1959–1988. Here, we analyzed an extended wolf time series (covering the period 1959–1999) with the same model, with the exception that the current-year predation term has been dropped because there is a significant lag-zero correlation between pack size and wolf density for this period.

Consistent with the predictions of the predator–prey

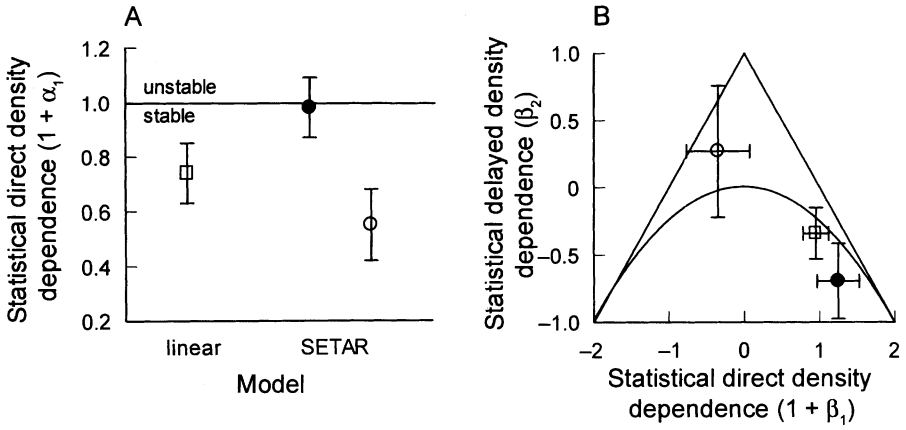

FIG. 2. Phase plots of the model coefficients estimated with linear and nonlinear time-series analysis. (A) Plot of the stability boundary for the first-order autoregressive skeleton model $X_t = \alpha_0 + (1 + \alpha_1)X_{t-1}$, after Royama (1992). Above the horizontal line, the dynamics are unstable, while below it they are stable in the region $-2 \leq (1 + \alpha_1) < 1$; see Royama (1992) for a full exposition of the model. The linear autoregressive model of wolf population dynamics is shown with an open square, the lower regime (i.e., increase phase) of the SETAR (self-excitatory threshold autoregressive) model is shown with a solid circle, and the upper regime (i.e., decline phase) of the SETAR model is shown with an open circle. (B) The phase plane of the linear second-order autoregressive model showing the relation between direct and delayed density dependence and periodicity of moose population dynamics (Royama 1992). Within the triangle, dynamics are characterized by stability (above the parabola) or cyclicity (below the parabola); outside the triangle, dynamics are chaotic. The linear autoregressive model is shown with an open square, while the circles depict the segments of the piecewise linear model of moose dynamics estimated with the SETAR approach according to the wolf decline phase (open circle) and the wolf increase phase (solid circle). Bars indicate ± 1 SE.

system of Eqs. 2, 3, and 4, the most parsimonious linear model of moose dynamics for the period 1958–1988 included direct and delayed density dependence, with previous-year pack size as a covariate (Post and Forchhammer 2001). Here, we used the same model to estimate the coefficients of direct and delayed density dependence in the linear scenario, and during phases of wolf increase and decline, during the period 1958–1999. We used the extended moose time series to increase sample size, but note that the data beyond 1988 have been estimated by aerial census while the estimates before 1988 have been adjusted by cohort reconstruction (Post et al. 1999). The parameter estimates for the full and truncated time series are similar (see *Results and discussion: Stability and cyclicity*, below), suggesting that the dynamical properties of the two time series are comparable.

Although our assessment of cyclicity focuses mainly on using statistical models to estimate the strength of density dependence at each trophic level (sensu Royama 1992), we also used spectral analysis (Warner 1998) to quantify periodicity of the time series at both trophic levels. We computed a g statistic to test the significance of the largest peak in the periodogram produced using a Tukey-Hamming window with a span of 5 for each population. In this test, g is calculated as the proportion of the total variance that is accounted for by the largest periodogram component, and is compared to critical values in Warner (1998).

Nonlinear time-series analysis of phase dependence

To analyze the potential contribution of phase-dependent predation to density cycles in the moose population on Isle Royale, we applied a self-excitatory threshold autoregressive (SETAR) (Framstad et al. 1997, Stenseth et al. 1998*a*) approach to modeling wolf and moose dynamics. The analysis of phase dependence builds upon recent, nonlinear time-series analyses of other predator–prey systems that have revealed phase dependence in the dynamics of predators (Stenseth et al. 1998*b*, 1999). Moreover, phase dependence has been suggested in earlier analyses of wolf dynamics on Isle Royale (Peterson and Page 1988, Peterson et al. 1998).

The SETAR model is a piecewise linear autoregressive model that assumes that the strength of density dependence will differ between the two regimes defined by the threshold (Framstad et al. 1997, Grenfell et al. 1998, Stenseth 1999). That is, even though population density may be identical at some point in the increasing and declining phases of the population cycle, the strength of density dependence may differ between the two population phases. Hence, the SETAR model is useful in identifying such disparities in the strength of density dependence during different phases of the population cycle.

The SETAR approach requires defining a population threshold, θ, that separates the population dynamics into phases of increase and decline (Framstad et al. 1997) or regimes of high and low density (Grenfell et

al. 1998). Because we are interested in quantifying the strength of density dependence in the dynamics of the wolf population during periods of increase and decline, we set the threshold, θ, in R_t, where R_t is the population growth rate of wolves [$\ln(N_t/N_{t-1}) = X_t - X_{t-1}$]. As opposed to a threshold density model, in which θ is defined as the density at which the strength of density-dependent population limitation changes (Grenfell et al. 1998), the model in R_t represents a true phase-dependence model (Framstad et al. 1997, Stenseth 1999). In the phase-dependent scenario of the SETAR approach, therefore, the most parsimonious linear model of wolf dynamics, including previous year's pack size ($\omega_1 PS_{t-1}$) (Post and Forchhammer 2001) may be rewritten as

$$X_t = \begin{cases} \alpha_{1,0} + (1 + \alpha_{1,1})X_{t-1} + \omega_{1,1}PS_{t-1} + \varepsilon_{1,t} & \text{if } \theta \leq 0 \\ \alpha_{2,0} + (1 + \alpha_{2,1})X_{t-1} + \omega_{2,1}PS_{t-1} + \varepsilon_{2,t} & \text{if } \theta > 0. \end{cases} \quad (5)$$

Hence, the two growth-rate regimes refer to different phases of the cycle, as opposed to different density levels (Framstad et al. 1997, Stenseth et al. 1998*a*). We set θ = 0 to examine wolf dynamics during strict periods of decline (the upper regime in Eq. 5) and increase (the lower regime in Eq. 5), as well as to examine the role of phase-dependent wolf dynamics in moose population cycles. The coefficients of direct density dependence in wolves, and direct and delayed density dependence in moose, were estimated for each of the wolf phases separately using maximum-likelihood estimation in the AUTOREG procedure in SAS (SAS Institute 1996).

Results and Discussion

Stability and cyclicity

Phase plots of the model coefficients estimated with linear time-series analysis support the inference that wolves exhibit stable (i.e., exponentially dampened) fluctuations (Fig. 2A: open square; see also Fig. 1A), while moose display proper multi-annual cycles (Fig. 2B: open square). The coefficients of the moose model differ slightly between the full time series (95% confidence intervals (CIs)) are ($1 + \beta_1$): 0.61, 1.29; and β_2: −0.57, 0.11) and the subset covering 1958–1988 (95% CIs are ($1 + \beta_1$): 1.24, 1.92; β_2: −0.99, −0.31). However, the overlap of the 95% CIs indicates that they do not differ significantly (Bjørnstad et al. 1995), and the similarity of their positions in the parameter plane (cf. the estimates plotted in Fig. 2B with those in Post and Forchhammer [2001]) indicates that the periodicity and the stability features of the full and truncated time series are similar.

Spectral analysis of the wolf time series revealed a major peak at 41.7 yr ($g = 2.31$, $P < 0.01$), which, given the length of the time series, warrants skepticism. The wolf series also displayed a significant period of 20.5 yr ($g = 1.74$, $P < 0.001$), while for moose, there was a single major peak at 21 yr ($g = 3.24$, $P < 0.001$). Although a 41-yr time series may be too short to reliably estimate a period on the order of 20 yr, the estimates are plausible and concord with Fig. 1. This constitutes, to our knowledge, the first formal documentation of multigeneration population cycles in an undisturbed large-mammal system.

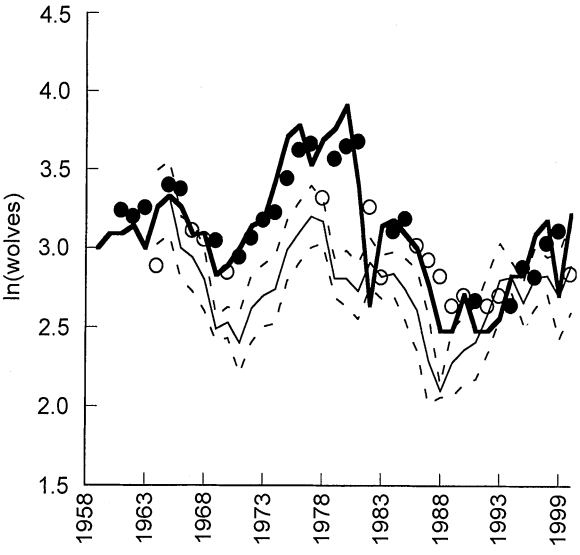

FIG. 3. Fit of the SETAR (self-excitatory threshold autoregressive) model (Eq. 5) to the observed wolf dynamics (heavy line). The thin line represents the mean of 1000 runs of the model (dashed lines are 95% confidence bands), using the first six years of observed data as seed values and noise sampled from a distribution identical to that of the residuals in each of the regimes in Eq. 5. Six years of data were the minimum necessary to provide the model with at least two years of data in each regime. Note that Eq. 5 includes lagged pack size. To include a pack-size effect in the model, we substituted the time series on observed pack-size dynamics with a lag-one density term divided by 3, because annual pack size equals the number of wolves divided by the number of packs on the island, which averages three packs for the period 1959–1999. Circles represent one-step-ahead predictions of density during the increase (●) and decline (○) phases. The correlation between the simulated (thin line) and observed (heavy line) time series, with seed values omitted, is $r = 0.67$, $P < 0.001$.

Phase dependence

The SETAR (self-excitatory threshold autoregressive) model of wolf dynamics provides a substantially better fit than does the linear autoregressive model, supporting the inference of phase dependence in the wolf dynamics. Corrected Akaike information criterion (AIC_c; Sakamoto et al. 1986) scores for the wolf models are: linear = 4.3, and SETAR = −33.7. Goodness of fit measures are: linear $R^2 = 0.65$; SETAR $R^2_{\text{increase}} = 0.90$, $R^2_{\text{decline}} = 0.82$. The SETAR model reproduced the observed dynamics of wolves reasonably well, although it in some years underestimated actual densities (Fig. 3).

Direct density dependence in wolves is significantly

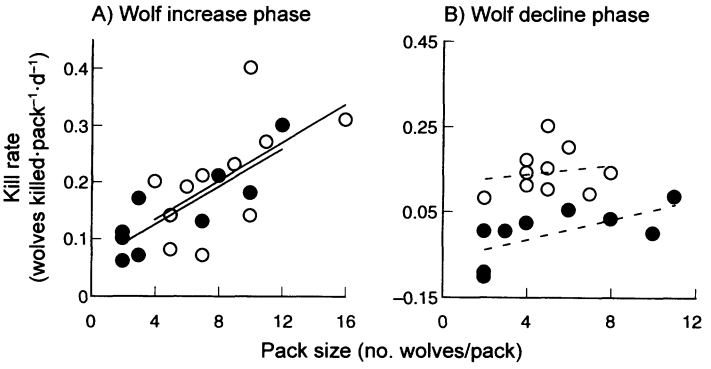

FIG. 4. Wolf pack kill rates in relation to pack size during (A) the wolf increase phase and (B) the wolf decline phase. Open circles are data from the East pack (EP), and closed circles are from the West pack (WP) (Post et al. 1999). During the increase phase, kill rates increase significantly with pack size for both packs (EP, $R^2 = 0.37$, $P = 0.049$; WP, $R^2 = 0.72$, $P = 0.004$). During the decline phase, kill rate is not significantly related to pack size for the East pack ($R^2 = 0.03$, $P = 0.63$); for the West pack, kill rate is significantly related to wolf density (partial $r = -0.59$, $P = 0.02$), but not to pack size (partial $r = 0.68$, $P > 0.10$, df = 4 after adjusting for first-order autocorrelation).

stronger during the wolf decline phase ($[1 + \alpha_{1,1}] = 0.56 \pm 0.13$) than during the wolf increase phase ($[1 + \alpha_{1,2}] = 0.98 \pm 0.11$) ($t_{34} = 28.3$, $P < 0.001$), further indicating that the density dependence is phase dependent in wolves. Note that $(1 + \alpha_{i,j}) < 1$ indicates negative density dependence. The threshold may also be set in X_{t-1} (Framstad et al. 1997), in which case direct density dependence is still stronger in the decline phase (-0.06 ± 0.4) than in the increase phase (0.70 ± 0.14) ($t_{32} = 25.3$, $P < 0.001$); however, this approach results in a loss of degrees of freedom in the decline phase and a less parsimonious model ($AIC_c = 8.7$). While wolf dynamics fall in the stability region during the decline phase, the weakening of density dependence during the increase phase moves the dynamics to the brink of instability (Fig. 2A).

An examination of moose dynamics during the two wolf phases indicates the role of phase-dependent predation in moose cycles. During the wolf increase phase, moose dynamics are cyclic, with strong delayed density dependence and significant, though not overwhelmingly strong, self-regulation (Fig. 2B: solid circle). In contrast, during the wolf decline phase, there is a dramatic shift toward very strong self-regulation in moose and a weakening of delayed density dependence, resulting in the decay of multi-annual cyclicity to aperiodic dynamics (Fig. 2B: open circle) reminiscent of the 3–4 yr cycle characteristic of overcompensatory density dependence in Soay sheep (*Ovis aries*; Grenfell et al. 1992, 1998).

These phase plots are consistent with the hypothesis that wolf predation has a stronger effect on moose dynamics during the wolf increase phase than during the wolf decline phase, because delayed density dependence in moose is strong while wolves are increasing but weak while wolves are declining. Moreover, analysis of pack-specific kill rate data (1972–1998) (Post et al. 1999) indicates that wolf packs kill significantly more moose per day during the wolf increase phase than during the wolf decline phase. A general linear model of pack kill rates identified a significant influence of pack size ($F_{1,36} = 45.6$, $P < 0.001$) and a significant interaction between wolf phase and moose phase ($F_{1,36} = 8.24$, $P = 0.007$; total model $R^2 = 0.59$; $P = 0.003$; error df = 36), reflecting the fact that periods of wolf increase tend to overlap periods of moose decline, and vice versa (McLaren and Peterson 1994). Accordingly, we detected a difference in mean pack kill rates during periods of wolf increase and moose decline (0.20 ± 0.02 moose killed·pack^{-1}·d^{-1}) and periods of wolf decline and moose increase (0.15 ± 0.01 moose killed·pack^{-1}·d^{-1}) ($t_{28} = 6.25$, $P < 0.001$). As well, the number of moose killed per pack per day (Post et al. 1999) increases sharply with pack size during the wolf increase phase, but not during the wolf decline phase (Fig. 4). Together with the plot of the wolf SETAR model (Fig. 2A), these observations suggest to us that it is the wolf increase phase that drives the moose cycle.

CONCLUSION

The role of predation in generating population cycles in prey through delayed density dependence has long been emphasized in theoretical models (May 1972, 1974), recently demonstrated through statistical and experimental studies of small animals (Hanski et al. 1993, Krebs et al. 1995, Framstad et al. 1997, Stenseth et al. 1998*a*, Turchin et al. 1999), but never before revealed in large mammals. The Isle Royale data constitute the only long-term observational data on large-mammal, predator–prey dynamics in an undisturbed system, and this analysis suggests strongly that cyclicity in moose dynamics is dependent on the phase in wolf dynamics. During the wolf-decline phase, when wolves experience strong density dependence and their kill rates are lower, moose dynamics are acyclic and display strong direct density dependence. During the wolf-increase phase, however, when wolves experience weak density dependence and exhibit higher kill rates, moose dynamics are cyclic and display strong delayed density dependence. Hence, in this case, prey oscillations may arise from delayed density dependence induced by phase-dependent predation. Thus, the population cycles of wolves and moose on Isle Royale not only complement a rich literature on population cycles in small mammals, they also represent a singular example of multi-annual oscillations and phase dependence in large mammals.

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