evropský sociální fond v ČR
EVROPSKÁ UNIE
MINISTERSTVO ŠKOLSTVÍ, MLÁDEŽE A TĚLOVÝCHOVY
OP Vzdělávání pro konkurenceschopnost

INVESTICE DO ROZVOJE VZDĚLÁVÁNÍ

„Propojení výuky oborů Molekulární a buněčné biologie a Ochrany a tvorby životního prostředí“

CZ.1.07/2.2.00/28.0032

Zápis z kurzu KBB/POS3

Název akce: KBB/POS3

Datum: 19. 11. 2014

Místo konání: Učebna SE – E2

Počet účastníků: viz seznam studentů

Program:

Rozbor odborného článku a diskuse na téma:
Europe-Wide Dampening of Population Cycles in Keystone Herbivores

Cornulier T., Yoccoz N.G., Bretagnolle V., Brommer J.E., Butet A., Ecke F. (201): **Europe-Wide Dampening of Population Cycles in Keystone Herbivores.** Science 430: 63 - 66

Přednášející:
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Příloha: uvedený článek

experimentally determined compositions of each of the three mixed-metal oxide films were in excellent agreement with the corresponding solution stoichiometries. These collective features indicate that the films consist of a homogeneous distribution of metal ions throughout the solid. Unlike what may arise with conventional metal oxide formation schemes (e.g., thermal decomposition, coprecipitation), the low-temperature PMOD process does not appear to lead to phase segregation.

Both *a*-CoO$_x$ and *a*-NiO$_x$ were, as expected, better OER catalysts than *a*-Fe$_2$O$_3$ (Fig. 3, C to F). Cyclic voltammetry (Fig. 3C) revealed additional electron-transfer processes that occur before water oxidation for all three mixed-metal oxide films. The current spike indicating catalytic water oxidation began between 1.41 and 1.44 V (η = 0.18 to 0.21 V) for the three materials. Moreover, Tafel slopes between 24 and 33 mV dec^{-1} enabled these materials to reach 0.5 mA cm^{-2} at potentials as low as 1.48 V (η = 0.25 V). Steady-state electrochemistry measurements on the mixed-metal films highlight an improvement in kinetics of water oxidation compared to those displayed by each of the monometallic amorphous phases (Fig. 3D). Although the onsets of linearity were similar for *a*-NiO$_x$, *a*-CoO$_x$, and each of the mixed-metal oxides, the mixed-metal compositions containing Fe were characterized by a lower Tafel slope and are therefore more efficient electrocatalysts at higher current densities (table 1) (*26*). The stabilities of the films, which are inherently sensitive to film composition, are also reasonably high at a current density of 1 mA cm^{-2} (e.g., a mere 6- and 30-mV increase in electrode potential was required to maintain a constant current density for *a*-NiO$_x$ and *a*-Fe$_2$O$_3$, respectively; fig. S9) (*20*). Each mixed-metal composition in this first generation of OER catalysts produced by PMOD exhibits catalytic parameters that approach those of the most active catalysts in the literature (Table 1). Given the broad applicability of this approach and the acute stoichiometric control of the metal compositions, we contend that the PMOD technique opens an entirely new parameter space for discovery and optimization of heterogeneous electrocatalysts.

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Acknowledgments: We thank Natural Sciences and Engineering Research Council of Canada, Mitacs, and FireWater Fuel Corp. for financial support. C.P.B. also thanks Canada Research Chairs and the Alfred P. Sloan Foundation for support. This research used facilities funded by the University of Calgary and the Canadian Foundation for Innovation. We thank R. Marr for running XRD experiments. S.T. and C.P.B. proposed the concept, designed the experiments, and supervised the project. R.D.L.S. and M.S.P. carried out electrochemical, structural, and optical characterization. Z.Z., P.A.S., and M.K.J.S. conducted preliminary experiments. R.D.F. carried out microscopy experiments. The authors declare competing financial interests: intellectual property pertaining to the technology described in this Report is protected by patent application PCT/CA2012/050609.

Supplementary Materials

www.sciencemag.org/cgi/content/full/science.1233638/DC1
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4 December 2012; accepted 16 January 2013
Published online 28 March 2013;
10.1126/science.1233638

Europe-Wide Dampening of Population Cycles in Keystone Herbivores

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Suggestions of collapse in small herbivore cycles since the 1980s have raised concerns about the loss of essential ecosystem functions. Whether such phenomena are general and result from extrinsic environmental changes or from intrinsic process stochasticity is currently unknown. Using a large compilation of time series of vole abundances, we demonstrate consistent cycle amplitude dampening associated with a reduction in winter population growth, although regulatory processes responsible for cyclicity have not been lost. The underlying syndrome of change throughout Europe and grass-eating vole species suggests a common climatic driver. Increasing intervals of low-amplitude small herbivore population fluctuations are expected in the future, and these may have cascading impacts on trophic webs across ecosystems.

Small cyclic herbivores such as voles, lemmings, moths, and grouse are keystone prey for predators in many temperate and arctic ecosystems (*1*, *2*). There are concerns that multiple instances of population cycle collapses documented in rodents could have profound effects on predators, alternative prey, and forage plants (*3*–*6*). Current evidence on the extent of the phenomenon mostly relies on a reasonably large but qualitative collection of anecdotes (*4*). The lack of a systematic and quantitative characterization of the patterns, however, makes generalization and prediction difficult. Quantitative analyses of changes in vole dynamics have invoked local explanations, such as changes in land use (*7*) or climate (*8*, *9*). However, without adequate temporal and spatial coverage, correlational studies have little power to distinguish between deterministic processes caused by large-scale environmental change and transient patterns caused by random environmental perturbations. A major challenge is to understand whether the patterns of cycle collapse and their underlying processes are local or more general phenomena (*10*).

Prevailing models for rodent population dynamics assume that cycles are mostly determined by delayed density dependence (a reduction of population growth rate by, for example, specialist predators, plant anti-herbivore defenses, or pathogens responding to past vole density), whereas direct density dependence (negative effect of current density through, for example, competition for resources) has a more limited contribution (*11*). In this setting, theory suggests three broad, nonexclusive pathways by which high-amplitude population cycles can fade out. First, in the presence of large environmental noise, quasi-cycles models commonly produce transient periods lacking visible cycles, without change in intrinsic population growth rates or density-dependent processes (pathway 1) (*4*). Second, sustained environmental change may affect seasonal, density-independent population growth rates, affecting cycle amplitude (pathway 2). Third, sustained environmental change may weaken interactions with biotic agents responsible for delayed density dependence (*12*), affecting the population's propensity to fluctuate cyclically (pathway 3) (*8*). We analyzed time series of vole population dynamics from a range of ecosystems across Europe in order to investigate which of these three pathways are empirically supported.

Identifying a common syndrome of change between populations would signify a shared environmental driver. We looked for such coherent changes in the time series parameters, focusing on population growth rates and direct and delayed density dependence estimated statistically by using log-linear autoregressive (AR) models. Whereas wavelet analysis (*10*) decomposes amplitude and frequency variation in time series, AR models decompose series into deterministic and stochastic components, including observation error, environmental noise, intrinsic population growth rate, and density dependence. Pathways of change can therefore be directly mapped to changes in AR model parameters. We used an extension of the seasonal AR model that has been used to describe temporal variation in population regulation around a given point in time (*9*, *13*, *14*).

Most vole-monitoring schemes in Europe involve some degree of spatial replication, with up to more than 50 sampling sites per study area. In most cases, however, data have been aggregated before analysis and publishing. Spatial aggregation of time series can introduce artificial dampening and distort estimates of population growth rate and density dependence (*15*). We collated raw data for a large proportion of the long-term (>18 years) time series available across Europe, sampled biannually and with known sampling effort, taking advantage of the spatial replication to improve parameter estimation.

Cycles in vole communities are understood to result from two-way trophic interactions involving large-sized, mostly grass-eating vole species (*Microtus spp.*) and in some cases *Myodes rufocanus*, whereas fluctuations of competitively inferior species (such as *Myodes glareolus* and *M. rutilus*) are entrained by shared natural enemies (*16*–*18*). For our analysis, we selected the large and dominant species in each site. We left moss-eating lemmings out because they are present only in Fennoscandia and assumed processes underpinning density dependence are different (*19*, *20*).

Our results show that out of our panel of 12 populations (Fig. 1), 10 (83%) underwent at least a twofold decline in cycle amplitude in spring, and eight populations (67%) did in both spring and autumn. In most of Europe, declines were most marked in spring, and series displayed low amplitudes around 1995 to 2005, thus generalizing patterns reported from northern Fennoscandia and the United Kingdom (*9*, *21*). The *Microtus* populations in Eastern Germany and Poland are the only exceptions to the general pattern of cycle dampening.

Winter population growth rate trajectories declined in a way that is consistent with the declines in spring amplitude (Fig. 2A), the only exception being *Myodes rufocanus* at Pallasjärvi, North Finland (site-specific results are available in fig. S1). Summer growth rates showed trends opposite to winter (Fig. 2B) but in a way weakly related to amplitude (absolute correlation ≤ 0.34) (fig. S4). Changes in direct density dependence were inconsistent and of small magnitude, typically equivalent to a 1-year change in cycle period length (Figs. 1 and 2C).

The strength of delayed density dependence fluctuated in most populations but largely independently of amplitude (Fig. 2D). Although local changes in delayed density dependence were in some cases large enough to suggest the loss of intrinsic cyclicity, these were neither coherent between populations nor consistent over time (Figs. 1 and 2D). Loss of delayed density dependence—and hence of cycles—was therefore not necessary for amplitude dampening to occur, which is inconsistent with pathway 3.

Previous system-specific correlative studies have tried to explain shifts between cyclic and noncyclic vole population dynamics (*8*–*10*, *12*, *21*). However, strong causal inference or the ruling out of purely random fluctuations (pathway 1) has been hampered by the models fitted (supplementary text VII) and lack of sufficient independent spatial or temporal replication to make general inference. If caused by intrinsic process stochasticity, a transient loss of cycles would be expected to occur independently in different systems (*18*). Across Europe, however, parallel declines in spring amplitude and in winter population growth rates occurred broadly at the same time for different species in farmlands, forests, and alpine and boreal habitats across a large range of latitudes with very different local climates, which is inconsistent with pathway 1.

Uncertainty about the temporal changes in parameters is large and likely to remain so for any single data series. Only through use of the type of meta-analysis we present here can we get the large-scale insight and sufficient power to isolate change in winter population growth rates (pathway 2) as a parsimonious proximal process, thus providing strong support for the hypothesis of extrinsic cyclic dampening. Our results broaden the processes contributing to the pattern of variation in vole cycles to include not only the prevailing delayed density dependence paradigm (pathway 3) but also the maximal seasonal population growth rate. This unifies the understanding of population dynamics of voles with that of insects and lemmings, for which cycle dampening has been associated with access to resources (*12*, *22*, *23*). General vole cycle dampening is therefore possible, even though the processes responsible for cycles may be local. However, pattern coherence suggests that global explanations involving large-scale environmental changes are more likely than local ones (such as snow hardness or habitat fragmentation) to explain the reduction in winter population growth rates.

Although climatic forcing is a natural candidate for explaining changes occurring at the scale of Europe and across highly different ecosystems, research is now required to identify the precise variable (or variables) affecting seasonal population growth rates in voles. It is difficult with fixed census dates to infer whether large-scale variation in seasonal growth rates relates to phenological changes (overall annual growth unchanged but shifting with respect to census dates) or changes in the mean without change in timing. Invoking phenological changes in reproduction to explain declines in winter population growth rate would imply a later average onset of reproduction, which is opposite to global

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patterns. Neither empirical evidence nor hypothetical mechanisms exist for this. Increasingly negative winter population growth rates (stronger winter declines) reduce population densities at the onset of the next breeding season, thus limiting the incremental growth of the population over several years (*21*). This may, for instance, involve a degradation of wintering conditions affecting survival (*24*). New theoretical research is needed to explain how contrasts in seasonal growth rates (*25*) affect vole population dynamics (*26*). Spatial gradients provide some evidence that snow-melt patterns affected vole cycles in Fennoscandia (*2*); however, these would not account for cycle dampening in temperate, essentially snow-free areas such as the Atlantic West of France and northern England. Quantifying short- and long-term variation in vole

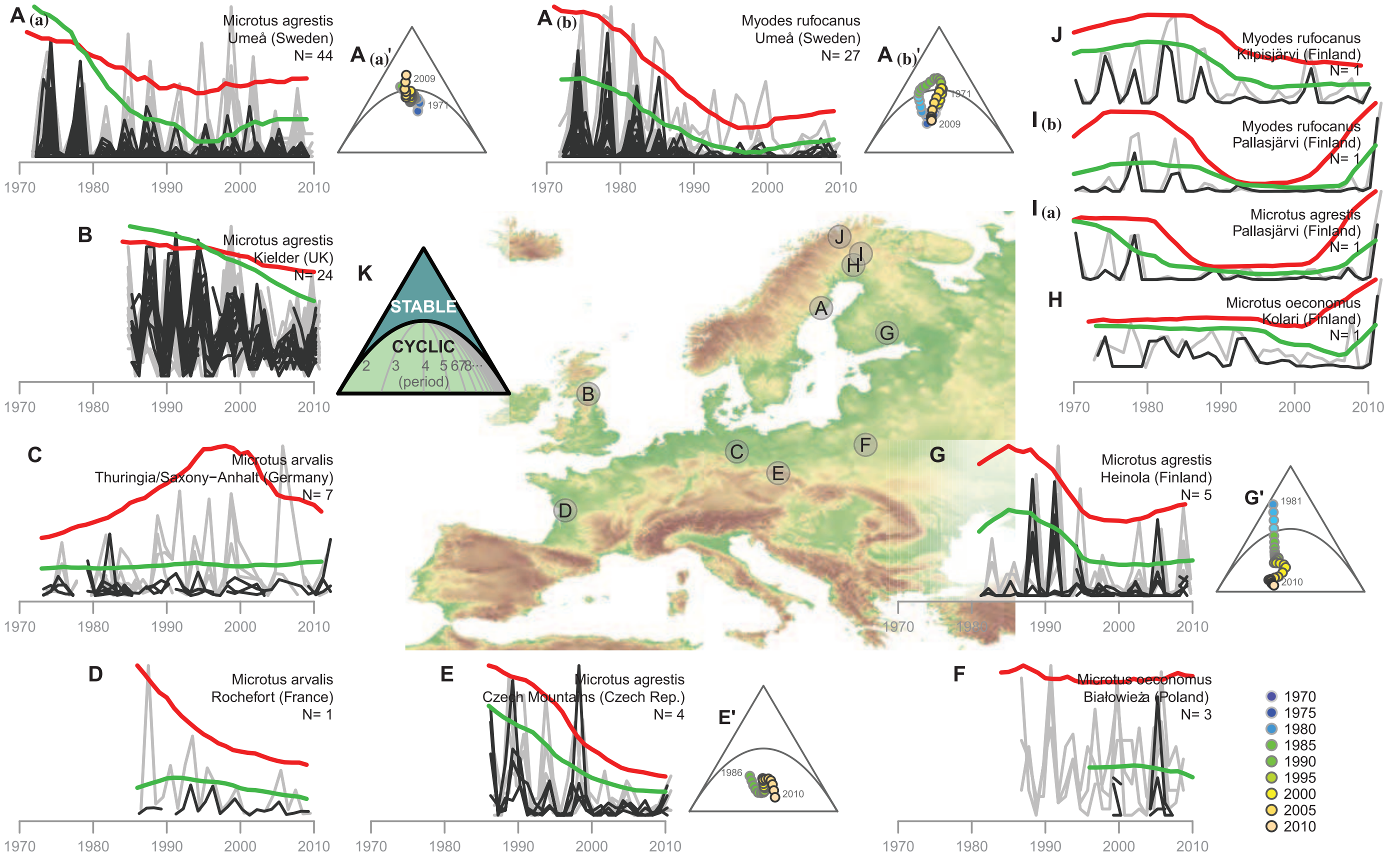

Fig. 1. Changes in grass-eating vole population dynamics in Europe. (**A** to **J**) Time series of vole abundance indices for spring (dark gray) and autumn (light gray). The origin of the series is shown on the central map. [Source: European Environment Agency] Green (spring) and red (autumn) curves show variation in the amplitude of fluctuations by using kernel-smoothed 90% quantiles. (**K**) Parameter plane of the log-linear auto-regressive model (*30*) (*x* axis, direct density dependence; *y* axis, delayed density dependence). The triangle defines regions producing stationary dynamics, either stable (top) or with multiannual cycles (bottom). (A$_{(a)}$'), (A$_{(b)}$'), (E'), and (G') illustrate examples of inconsistent temporal changes in the trajectories of the density dependence regulation parameters despite similar declines in amplitude. *N* indicates the number of spatial replicates of time series per data set.

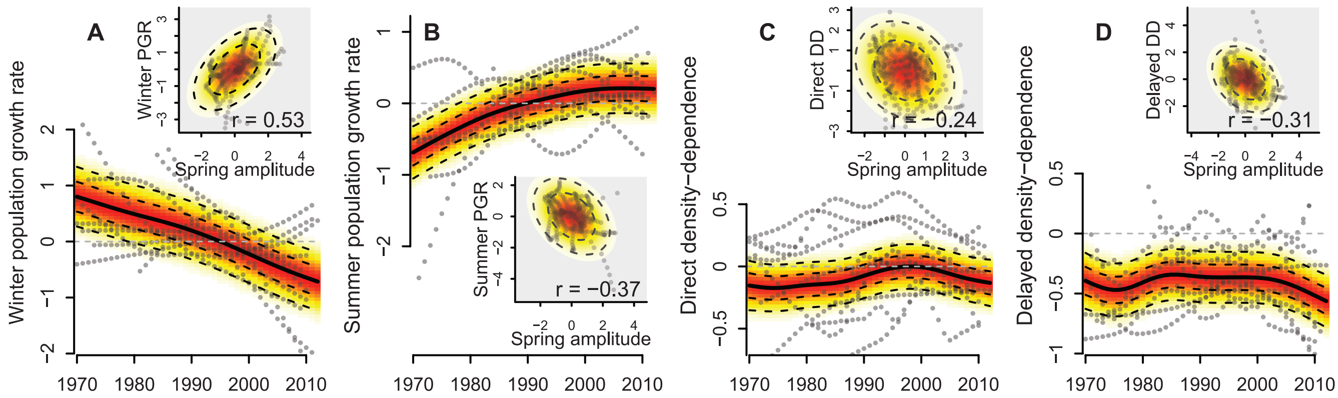

Fig. 2. Analysis of vole population dynamics parameters. (**A** to **D**) Temporal changes in the four main parameters of the seasonal autoregressive model across populations (solid lines). (Insets) Correlation ellipses between each parameter and the amplitude of vole fluctuations, both centered and scaled by population. Color gradients represent confidence, with dashes marking the 68% (1 SD) and 95% (2 SD) intervals for the trends and the 68 and 95% regions for the correlations (insets). Gray dots show annual estimates from each vole population (population-specific results are available in fig. S1). Only winter population growth rates (A) display a marked general change over time across populations and a strong correlation with cycle amplitude.

mortality or breeding phenology, including frequency of winter reproduction, should be part of future research, as should quantifying vegetation quality that could reflect, for example, continent-scale long-term variation in climate or nutrient deposition.

Irrespective of the proximate process (or processes) affecting winter population growth rate, the coherence of the changes coinciding with a period of ongoing global environmental change suggests increasingly frequent prolonged periods of low amplitude, although high-amplitude vole peaks—as seen in 2011 in northern Fennoscandia—may occasionally reappear. The loss of years of super-abundant voles could reduce zoonotic disease risk and crop damage (*27*). Continent-scale collapses in population cycles are likely to be deleterious for vole predators because for most, reproduction is modulated by vole density in spring, which is when the strongest and most consistent dampening occurs. Large impacts on vegetation (*6*) and predator populations (*1*, *28*) could see cascading effects on other compartments of the food webs (*3*, *29*) in ecosystems as diverse as farmland, forest, and arctic tundra.

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Acknowledgments: This research was funded by the national funders Natural Environment Research Council, Research Council of Norway, and Agence Nationale de la Recherche, part of the 2008 ERA-Net BiodivERsA call for research proposals. D.A.E. was funded by the Scottish Government. We thank R. B. O'Hara and F. Barraquand for useful methodological inputs and all the contributors to vole sampling over decades. General correspondence should be addressed to X.L. and specific requests to T.C. (cornulier@abdn.ac.uk). Raw data are available in supplementary text section IX). Authors declare no conflicts of interest. A.B., B.H., B.J., C.I., E.F., E.T., F.E., H.H., H.P., J.E.B., J.J., K.Z., O.H., S.J.P., V.B., and X.L. led the data collection; T.C., N.G.Y., R.A.I., A.M., and X.L. conceived the ideas for the paper and its structure; T.C., N.G.Y., D.A.E., and X.L. designed the analyses; T.C. and X.L. wrote the manuscript; and all authors discussed the results and commented on the manuscript.

Supplementary Materials

www.sciencemag.org/cgi/content/full/340/6128/63/DC1
Materials and Methods
Supplementary Text
Figs. S1 to S6
BUGS Code
Data
References (*31–47*)

17 August 2012; accepted 12 February 2013
10.1126/science.1228992

Detection and Learning of Floral Electric Fields by Bumblebees

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Insects use several senses to forage, detecting floral cues such as color, shape, pattern, and volatiles. We report a formerly unappreciated sensory modality in bumblebees (*Bombus terrestris*), detection of floral electric fields. These fields act as floral cues, which are affected by the visit of naturally charged bees. Like visual cues, floral electric fields exhibit variations in pattern and structure, which can be discriminated by bumblebees. We also show that such electric field information contributes to the complex array of floral cues that together improve a pollinator's memory of floral rewards. Because floral electric fields can change within seconds, this sensory modality may facilitate rapid and dynamic communication between flowers and their pollinators.

Flowers produce a diverse range of cues and attractants to pollinators and in doing so act as sensory billboards (*1*). The diversity of floral cues encompasses intricate color hues and patterns, petal texture, fragrant volatiles, local air humidity, and echolocation fingerprints (*1–4*). The impact of floral cues on pollinator behavior has been observed since Aristotle (*5*), yet new floral cues are still being discovered (*3*, *4*). Multimodal floral cues have been found to enhance both pollinator foraging efficiency and pollination (*6*), and thus facilitate increased seed and fruit set.

Flying insects, including pollinators like honeybees, usually possess a positive electric potential (*7–10*). Conversely, flowers often exhibit a negative potential (*7*, *11*). Electric fields arising as a result of this potential difference between flowers and insects promote pollen transfer and adhesion over short distances (*7*, *8*, *12*, *13*). Furthermore, these fields differ according to the pollination status of the flower, as the deposition of pollen and resulting pollination changes flower electric potential (*14*, *15*). However, the use of electric fields by pollinators as informative cues has not been investigated. In the complex world of plant-pollinator interactions, any cue that increases pollination and foraging efficiency should be mutually beneficial. Here, we report that bumblebees can detect and learn to use floral electric fields, and their structural variation, to assess floral reward and discriminate among flowers.

The electrical interactions between the bee and the flower arise from the charge carried by the bee and the potential of the flower in relation to the atmospheric electric field. To quantify bee charge, individual *B. terrestris* workers were trained to fly into a Faraday pail that contained a sucrose reward. The net charge q carried by the bee was measured from the induced voltage on a calibrated capacitor (methodology described in supplementary materials). Measured on 51 individuals, 94% of bees were positively charged and 6% negatively charged ($q_{\text{mean}} = 32 \pm 5$ pC, SD = 35pC) (Fig. 1A). These results corroborate previous measurements on the honeybee *Apis melifera* (*9*) and establish that the majority of bees flying in the arena carry a positive charge susceptible to transfer.

Electrical interaction between bee and flower was further explored by placing *Petunia integrifolia* flowers in an arena with free-flying foraging bees. The electric potential in *Petunia* stems was recorded to assess the electrical signature produced by the approach and landing of an individual charged bee. Charge transfer to the flower resulted in a positive change in electric potential recorded in the stem. The landing of 50 indi-

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Europe-Wide Dampening of Population Cycles in Keystone Herbivores

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Science **340**, 63 (2013);
DOI: 10.1126/science.1228992

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