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Resource Management Cycles and the Sustainability of Harvested Wildlife Populations

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Constant harvest policies for fish and wildlife populations can lead to population collapse in the face of stochastic variation in population growth rates. Here, we show that weak compensatory response by resource users or managers to changing levels of resource abundance can readily induce harvest cycles that accentuate the risk of catastrophic population collapse. Dynamic system models incorporating this mix of feedback predict that cycles or quasi-cycles with decadal periodicity should commonly occur in harvested wildlife populations, with effort and quotas lagging far behind resources, whereas harvests should exhibit lags of intermediate length. Empirical data gathered from three hunted populations of white-tailed deer and moose were consistent with these predictions of both underlying behavioral causes and dynamical consequences.

One of the most central problems in ecology is what causes some harvested populations to collapse, whereas others are able to withstand exploitation (*1–4*)? Population collapses in many fisheries have encouraged substantial theoretical work on the challenging problem of optimal harvesting policy in response to demographic and environmental stochasticity (*1–8*). This has led to several sophisticated optimal harvest models supporting constant harvest mortality rates, threshold harvesting policies, or no-take reserves. Although these policies are sometimes feasible, in reality many management agencies have limited ability to control the number of resource users or harvest effort. This is particularly true of recreational harvesting, because of the open-access philosophy underlying sport fisheries and wildlife hunting. Even when harvest levels are directly set by regional managers, such control is often in the form of ad hoc quotas that vary from year to year. Modern harvesting theory is based on coupling harvest with dynamic variation in resource abundance. Here we show that weak compensatory response by harvesters or resource managers can itself generate cyclic variation in resources, exacerbating the risk of collapse. Weak harvest regulation contributes to the problem rather than providing an acceptable management solution to resource fluctuation.

To consider this issue, we developed a dynamical system model in discrete time (*9*), based on simple intuitive assumptions about human behavior, combined with mass action principles commonly applied in ecological models (*10–16*). The model assumes that harvesting is open access, meaning that there is no governmental restriction of harvest effort, but annual quotas are used to constrain the maximum harvest. Harvesters share information about their experiences during hunts or fishing trips, just as people talk about other important aspects of their lives. Mass action principles accordingly guide the sharing of social information, based on the probability of communication among networking members of a finite population of potential harvesters. Hence, we predict that the rate of change in effort from year to year should be a positive function of resource abundance but a negative function of current effort (*9*).

We assume that a similar mix of positive and negative feedbacks influences quota levels set by resource managers. High levels of resource abundance should encourage increasing quotas if managers are sensitive to meeting the rising expectations of harvesters, whereas declining resource levels should encourage the opposite response. Our model assumes that managers make such responses in incremental fashion, applying small percentage increases or decreases to the previous year's level in making their an-

Fig. 1. Predicted time series for the proposed dynamic harvest-effort-quota system, for a locally stable set of parameters ($a = 0.3$, $K = 4$, $q = 0.0001$, $c = -0.1$, $w = 0.2$, $u = 0.00002$, $f = -0.05$, $i = 0.15$, $j = 0.1$) (*9*) (**A**) without any environmental stochasticity and (**B**) with the standard deviation in environmental stochasticity (ε) = 0.20. To simplify plotting on a single set of axes, variables were normalized by dividing yearly values by equilibrium values.
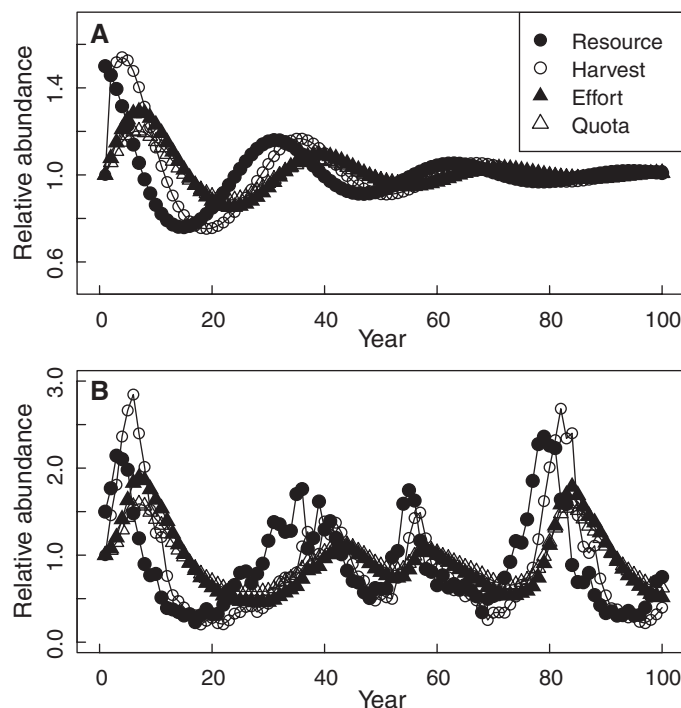
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nual modification of quotas. Our model also assumes that managers are reluctant to exceed quota levels experienced in the past, leading to a negative feedback on rates of quota change (9).

These compensatory responses can be readily incorporated into a modified version of the Rosenzweig-MacArthur model of consumer-resource interactions (11, 12). We consider a discrete time formulation to be more realistic than a continuous formulation for several reasons: (i) most fish and wildlife species of interest have a single birth-pulse breeding season each year, (ii) harvesting is typically confined to a short season each year, and (iii) license sales and quota levels are usually set in advance of the harvest season. We accordingly structured our discrete time model by assuming that harvesting is followed by density-dependent recruitment according to the Ricker logistic formulation, with negative feedbacks on the exponential rate of population growth dictated by post-harvest resource abundance (9). For subsequent analyses of the deterministic form of the discrete time model, we re-scaled state variables to make them dimensionless. Local stability analysis (9) was used to compare the range of stable versus unstable parameter combinations, to determine whether damped oscillations characterize the response to local perturbations from equilibria and to estimate the period length of such damped oscillations (13–16).

In the absence of environmental stochasticity, our model predicts that equilibria are locally stable for a restricted set of parameter combinations, whereas stable limit cycles are the norm for other parameter combinations, a pattern often seen in ecological models (12–16). Deterministic instability is particularly likely when resource carrying capacity is high, the maximum rates of increase in effort or quotas are particularly high, or the rate of decline in effort or quotas at low resource abundance is particularly low (fig. S1). Even in stable systems, however, our model predicts that the approach to stability after perturbation will be extremely slow, characterized by damped oscillations over time (Fig. 1A). The return time for such damped cycles depends on intrinsic growth rates, but for many large-bodied species, including most mammals, birds, and sport fish, it may take decades for perturbed populations to recover their former abundance (fig. S2).

In the real world, populations are invariably subject to substantial levels of environmental and/or demographic stochasticity (17, 18). Damped oscillations in the deterministic system coupled with stochastic variation in population growth rates leads to quasi-cyclic fluctuation (15, 16) (Fig. 1B), with similar periodicity as that seen in simpler perturbed systems (Fig. 1A). In other words, dynamic variation in harvest effort and/or quotas, coupled with environmental or demographic stochasticity, should often lead to wildlife population cycles regardless of other ecological interactions.

Instability in our model traces from asynchrony in the dynamic responses of either harvesters or their regulating agencies to changes in resource
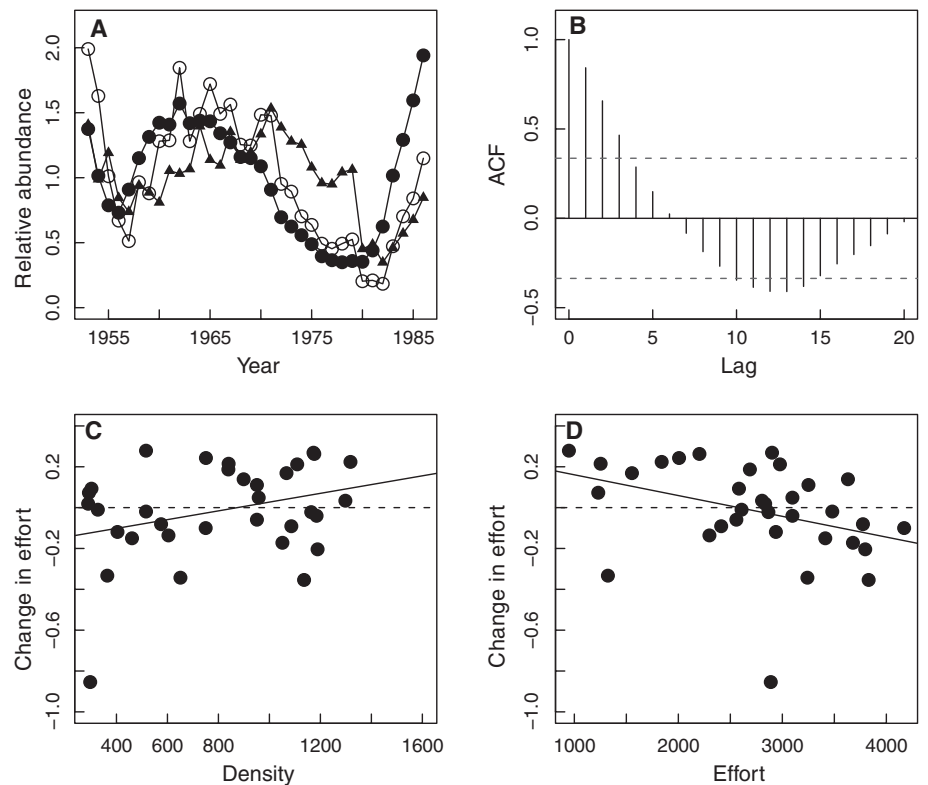
levels. Social adjustments in effort or regulatory adjustments in quotas occur at discrete, annual intervals because of short harvest season lengths. As a consequence, even locally stable systems would require a long time to equilibrate. In a realistically noisy world, such slow equilibration would translate into quasi-cycles of extended length, typically on the order of decades. The propensity for quasi-cyclic fluctuations is more pronounced for species with low intrinsic growth rates and modest levels of environmental stochasticity, such as large mammals, than it is for species with faster life histories or those subject to high variation in environmental conditions.

Our model suggests that harvested species are regulated by either harvester behavior or management policy, but not both. The structure of the model is such that either effort or quotas fully determine system equilibria, depending on which regulatory process supports the higher level of resources at equilibrium. Because both processes respond to changes in resource abundance, however, time dynamics of effort and quotas in unstable systems should become synchronized (Fig. 1B). Our model makes a number of testable predictions: (i) rates of change in effort and quotas should be positively associated with resource levels,

but negatively related to current levels of effort or quotas; (ii) harvested populations should often fluctuate with return times on the order of decades; and (iii) both effort and quotas should fluctuate in unison, but each should be far out of phase with resources, whereas harvest should have a lag of intermediate length.

As a proof of concept, we evaluated our model using three different populations of hunted ungulates (Canadian white-tailed deer and Norwegian moose) that had at least 20 years of continuous time series data available on population density, harvest, effort, and quota. Moose data for the Troms and Vest Agder Districts in Norway were provided by the National Moose-Monitoring Program (19). For the purposes of this paper, population abundance was estimated using moose seen per hunter day. Data on harvest level and hunter effort came from hunter questionnaires with high response rates. Data for white-tailed deer came from the Canonto District of Ontario. Deer harvests during 1953–1987 were limited to a 1- to 2-week period during the autumn. Access to the site was limited to two roads, both of which were closely monitored by wildlife personnel, who interviewed every hunter leaving the area to estimate hunt-

Fig. 2. Harvest data are illustrated for white-tailed deer from the Canonto District of Ontario, Canada. (**A**) Annual estimates of resource abundance (solid circles), harvest (open circles), and effort (solid triangles). To simplify plotting on a single set of axes, variables were normalized by dividing yearly values by the mean for the entire time series. Autocorrelation functions for resource abundance are shown in (**B**). All sample autocorrelation function values that exceed the horizontal bars are statistically significant ($P < 0.05$). The bottom two plots show rates of change in hunting effort (z) in relation to resource density (x) (**C**) and current effort (y) (**D**) ($z = 0.0706 + 0.000305x - 0.000104y$, $F_{2,30} = 5.51$, $P = 0.009$, $R^2 = 0.271$).

Fig. 3. Predicted probability of population collapse (to 10% of the equilibrium density) in a model system with constant effort (open circles) compared to one with weak compensatory changes in effort (solid circles), based on 5000 Monte Carlo replicates for each level of environmental stochasticity. Constant effort and quota levels were set at equilibria for the dynamic system. Simulations were based on the same locally stable set of parameters shown in Fig. 1 ($a =$ 0.3, $K = 4$, $q = 0.0001$, $c = -0.1$, $w =$ 0.2, $u = 0.00002$, $f = -0.05$, $i = 0.15$, $j = 0.1$) with the standard deviation in environmental stochasticity ε ranging between 0.00 and 0.25.
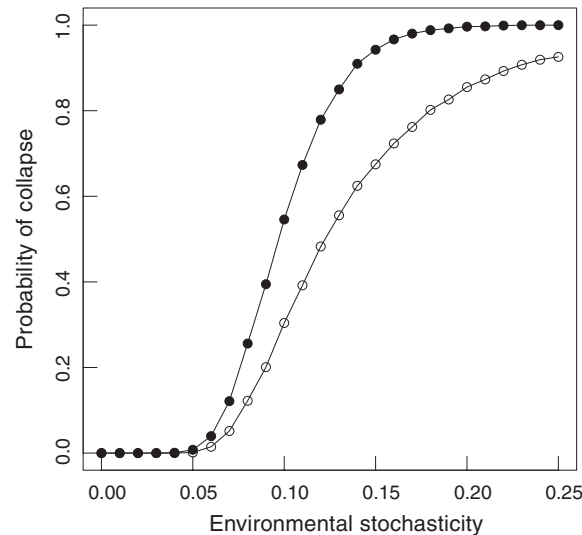
ing effort (days) and harvest. Deer population density in the 230-km² study area was estimated with virtual population analysis (20). For all study populations, exponential rates of increase in effort and quotas were estimated by $y_t = \ln(x_{t+1}/x_t)$, where y is the exponential rate of change, x is the response variable (either effort or quota), and t is time, measured in years. Linear regression was used to test whether rates of increase in effort and quotas were significantly related to resource abundance and current levels of either effort or quota. Standard time series analyses (autocorrelation and cross-correlation functions in the statistical software R, version 2.4) were applied to each data set to evaluate statistical support for recurrent versus damped oscillations and lag length for harvest, effort, and quotas relative to resource abundance (15). Although complete understanding of the population dynamics of long-lived species is enhanced by age-specific data on demographic rates (21), simpler nonstructured models, such as the Ricker equation used here, can often be used to capture the most salient dynamical features (15, 22). Simpler models have the added benefit of allowing the full range of analytical tools needed to evaluate the stability of complex dynamic systems.

All of the populations exhibited diagnostic patterns that were remarkably consistent with our model (Fig. 2 and figs. S3 and S4). Population abundance varied considerably over time, with the smallest range of variation recorded in moose in the Troms District (twofold) and the highest variability recorded in white-tailed deer (fivefold). In each population, autocorrelation functions provided evidence of phase-forgetting (damped) oscillations in resource abundance, with period lengths of 8, 24, and 30 years. Cross-correlation functions indicated a pronounced lag (2 to 6 years) between fluctuations in resource abundance and effort, a modest lag between harvest and effort, and little lag between quotas and effort (fig. S5). Changes in effort were pos-

itively related to resource abundance but negatively related to current levels of effort. Rates of change in quotas were also positively related to resource abundance but negatively related to quota level (fig. S6). All of these time series characteristics were predicted by the model.

Alternatively, changes in harvesting pressure can induce generational cycles in long-lived species by perturbations of the stable age distribution (21–23). We tested this possibility by time series analysis of the proportion of deer and moose young through time. Although strong cohorts were identified in all three study populations, autocorrelation functions showed no evidence of cyclic fluctuation in age structure that could explain the observed oscillations in overall population abundance (figs. S7 and S8). Thus, although it is theoretically possible that temporal variation in age structure can interact with harvest dynamics and population abundance to amplify unstable dynamics, generation cycles do not explain the observed oscillations in the abundance of white-tailed deer and moose.

Wildlife harvesting of species such as moose, elk, deer, bears, bobcats, and cougars is often conducted in a manner consistent with our model. In many jurisdictions, virtually anyone is eligible to apply for a hunting permit. There are often regional quotas on harvest, however, facilitated via telephone hotlines. Although there can be special restrictions on the age, sex, or location of harvested animals, regulatory procedures for a given species often tend to be fairly consistent across different wildlife agencies.

As a result of the open-access philosophy typically underlying wildlife harvest management (that is, employing few restrictions on participation in hunting, instead changing quotas on an annual basis), large-scale fluctuations in abundance are to be expected. A scattering of published papers in the literature are consistent with the unstable scenario we have drawn (1, 24–27), suggesting that quasi-periodic fluctuations in resources, exploitation rate, and quotas may be

much more common than previously realized. If we are correct in asserting that asynchronous dynamics of harvested resources, effort, and quotas often occur, due to delayed human behavioral responses to changing conditions, then conservation and management agencies might well benefit from more frequent reassessment of quota levels in response to undesirable changes in population levels occurring over the course of the hunting season, or from the institution of more conservative, temporally stable policies. Future harvest policies should aim to minimize variation in resource mortality risk by maintaining constant effort, setting quotas proportionate to current resource abundance, or shifting to threshold or proportional threshold approaches. Reconciling these alternative management options with open-access policies will no doubt prove challenging.

Weak harvest regulation should be particularly worrisome in populations with high levels of demographic or environmental stochasticity or with pronounced Allee effects due to predation, disease transmission, or reduced probability of breeding (28–30). Our simulations suggest that the risk of population collapse could be dramatically higher in systems with dynamic effort and quota levels (Fig. 3), simply because of extreme population excursions caused by quasi-periodic dynamics resulting from even mild levels of environmental stochasticity. When resource abundance is regulated by dynamic management responses via quotas, unstable systems are often vulnerable to extinction, even in the absence of Allee effects or stochastic variation in growth rates. These findings suggest that it is unwise to neglect dynamic patterns of change in both harvest effort and quotas in assessing long-term strategies for sustainable resource use.

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31. This work was supported by Discovery Grants to J.M.F. and K.M. from the Natural Sciences and Engineering Research Council of Canada, and NSF Grants for Long-Term Research in Environmental Biology and Biocomplexity to C.P. The contributions by B.E.S. and E.J.S. were funded by the Directorate for Nature Management and the Norwegian Research Council (Changing Landscapes, Lanskap i Endring, and project

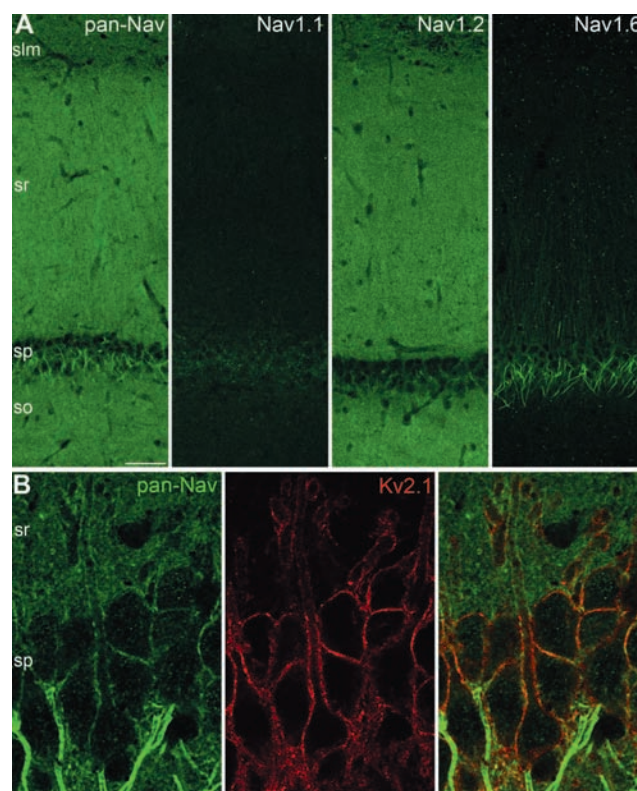# Molecular Identity of Dendritic Voltage-Gated Sodium Channels

Andrea Lorincz* and Zoltan Nusser*

Active invasion of the dendritic tree by action potentials (APs) generated in the axon is essential for associative synaptic plasticity and neuronal ensemble formation. In cortical pyramidal cells (PCs), this AP back-propagation is supported by dendritic voltage-gated Na$^+$ (Nav) channels, whose molecular identity is unknown. Using a highly sensitive electron microscopic immunogold technique, we revealed the presence of the Nav1.6 subunit in hippocampal CA1 PC proximal and distal dendrites. Here, the subunit density is lower by a factor of 35 to 80 than that found in axon initial segments. A gradual decrease in Nav1.6 density along the proximodistal axis of the dendritic tree was also detected without any labeling in dendritic spines. Our results reveal the characteristic subcellular distribution of the Nav1.6 subunit, identifying this molecule as a key substrate enabling dendritic excitability.

Associative synaptic plasticity in cortical pyramidal cells (PC) is the most widely accepted cellular model of learning. An essential prerequisite of the model is that input synapses, which are distributed over an enormously large dendritic tree, must be capable of sensing the precise timing of the output signal. The most likely mechanism for this is the active invasion of the dendritic tree by fast sodium action potentials (APs) initiated in the axon initial segment (AIS). Modification of back-propagating APs therefore holds tremendous potential for altering synaptic plasticity and forming of neuronal representations. Voltage-gated Na$^+$ (Nav) currents have been detected in hippocampal and neocortical PC dendrites, where they not only support AP back-propagation but also underlie nonlinear synaptic integration and dendritic sodium spike generation [(1–6) and reviewed in (7–10)]. Patch-clamp experiments demonstrate that axonal and somatodendritic Nav currents differ in their activation and inactivation properties (11, 12), indicating either different Nav subunit compositions or distinct posttranslational modifications of identical subunits (12–14). However, the lack of subunit-specific drugs precludes the unequivocal identification of the subunit composition of the axosomatodendritic Nav channels using

functional approaches. Immunohistochemistry with subunit-specific antibodies offers an alternative experimental approach to address this issue. Nav1.1, Nav1.2, and Nav1.6 are the Nav subunits expressed in adult brains (15, 16). They have been

detected in nodes of Ranvier, AISs, and preterminal axons using immunofluorescence localization (17–22). Unfortunately, this method has so far failed to visualize any of these Nav subunits in somatodendritic compartments, most likely due to its insufficient sensitivity. We modified the immunofluorescence technique to increase its sensitivity and employed a highly sensitive, quantitative electron microscopic (EM) immunogold method [SDS-digested freeze-fracture replica-labeling (SDS-FRL)] (23–25) to identify the Nav subunit content of the somatodendritic plasma membranes of CA1 PCs.

In conventional immunofluorescence localization techniques, the tissue is usually fixed with a phosphate-buffered fixative containing paraformaldehyde, resulting in a fixation that masks antigens in many subcellular compartments, including, for example, postsynaptic densities and AISs (26). The visualization of antigens in some of these compartments might be possible after antigen retrieval, such as microwave irradiation or pepsin digestion (27, 28). We used a low-pH–

Fig. 1. Somatodendritic localization of voltage-gated sodium channels. (**A**) Immunofluorescence localization of the pan-Nav, Nav1.1, Nav1.2, and Nav1.6 subunits in the CA1 area. (**B**) Double immunofluorescence reaction shows weak pan-Nav immunolabeling along the Kv2.1 subunit immunoreactive somatodendritic plasma membrane of CA1 PCs. Note the much higher labeling intensity of the AISs. slm, stratum lacunosum-moleculare; sr, stratum radiatum; sp, stratum pyramidale; so, stratum oriens. Scale bars: (A), 50 μm; (B), 10 μm.

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