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Noisy Clockwork: Time Series Analysis of Population Fluctuations in Animals

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for four time intervals: Late Pleistocene (before humans arrived in the Americas), Holocene (when only aboriginal populations were present), pre-1983 (before the mass mortality of *Diadema antillarum*), and post-1983 (after the *Diadema* mortality).

115. We dedicate this paper to the memory of Mia

Tegner who died while diving after this paper was submitted. This work was conducted as part of the Long-Term Ecological Records of Marine Environments, Populations and Communities Working Group supported by the National Center for Ecological Analysis and Synthesis (funded by NSF grant DEB-0072909, the University of California, and the

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REVIEW

# Noisy Clockwork: Time Series Analysis of Population Fluctuations in Animals

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Both biotic interactions and abiotic random forcing are crucial influences on population dynamics. This frequently leads to roughly equal importance of deterministic and stochastic forces. The resulting tension between noise and determinism makes ecological dynamics unique, with conceptual and methodological challenges distinctive from those in other dynamical systems. The theory for stochastic, nonlinear ecological dynamics has been developed alongside methods to test models. A range of dynamical components has been considered—density dependence, environmental and demographic stochasticity, and climatic forcing—as well as their often complex interactions. We discuss recent advances in understanding ecological dynamics and testing theory using long-term data and review how dynamical forces interact to generate some central field and laboratory time series.

The century of studies in population ecology has been dominated by a nested set of debates regarding the importance of various dynamical forces. The first controversy concerned the relative impact of biotic versus abiotic control of population fluctuations. The key question was the relative importance of “noise” (small-scale, high-frequency stochastic influences) versus climatic forcing (larger-scale, often lower-frequency signals) versus nonlinear interactions between individuals of the same or different species. The second question concerned the impact of intrinsic (i.e., intraspecific) processes, as opposed to extrinsic or community-level interactions, an argument that has been particularly heated with reference to population cycles. A third debate, nested within the latter, concerns the “dimensionality” of population fluctuations; given that most populations are embedded in rich communities and affected by numerous interspecific interactions, can simple (low-dimensional) models involving one or a few species capture the patterns of fluctuations? All these questions have been studied through a number of detailed analyses of specific systems in which theoretical models are linked with

long-term studies (often 10 or more generations) through time series analysis.

There has been much parallel and intertwined development of these three dynamical themes, and history testifies to a succession of popularity of the various positions (1). Crudely summarized, early focus on extrinsic influences was replaced by the “density-dependent paradigm” (2) in the 1950s and 1960s. This accelerated in the late 1970s, with May’s *cri de coeur* (3) about the potential of dynamical complexity even in simple models, leading to a focus in the 1980s on nonlinearity and the detection of deterministic chaos (Taken’s embedology, Lyapunov exponents, etc.). Research has focused on two fronts in the past decade: (i) the impact of large-scale climatic forcing, coinciding with the rise in popularity of climate change studies through the early 1990s, and (ii) stochastic nonlinear models that combine the nonlinear deterministic and (largely) linear stochastic theories. The goal in synthesizing these approaches in recent years is to understand how population fluctuations arise from the interplay of noise, forcing, and nonlinear dynamics. The comparable importance of deterministic and stochastic forces makes ecological dynamics unique. In particular, the interaction between noise and nonlinear determinism in ecological dynamics adds an extra level of complexity compared with the largely stochastic dynamics of, say, economic systems or the largely deterministic dynamics of many physical and chemical processes.

The dynamics of marine stocks serve as an illustration of the current paradigm. Most commercial fish stocks vary greatly in abundance and the associated time series exhibit complex spectra, with combinations of high-frequency oscillations and longer term trends (4, 5) (Fig. 1). High-frequency oscillations are thought to arise from environmental variability particularly affecting reproduction [through expatriation of eggs, temperature-induced mortality, etc. (4)], as well as interactions between individuals (competition and cannibalism) or between species (fish-fish or plankton-fish interactions). The low-frequency oscillations and trends are usually related to external forcing such as overfishing, climatic changes, and decadal, supra-, or super-decadal oscillations in climate. The most recent studies that combine theoretical modeling with time series analysis indicate that the full variability in marine stocks can only be explained by considering the interaction between nonlinear dynamics and stochastic forcing (5, 6), often in the face of strong human influences (7, 8) and obscured by measurement error (5, 7).

The relative importance of different components of ecological dynamics differs somewhat between systems—notably between terrestrial versus marine, vertebrate versus invertebrate, simple versus complex life-cycle, etc. However, evidence is mounting that all components contribute and interact at particular spatial and temporal scales in most systems. Here we review the current understanding of the different forces that drive ecological dynamics.

*Simple density-dependent interactions.* Nonlinear, density-dependent interactions can potentially stabilize or promote fluctuations in abundance because such interactions can either result in stable equilibria (point attractors, namely “the carrying capacity”) or cyclic or chaotic attractors, associated with strongly overcompensatory density dependence (3). About 25 years ago, Hassell *et al.* (9) and Gurney *et al.* (10) took the bold step of insisting that the then-qualitative, strategic theory ought to be testable by analyses of

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time series of abundance. The research agenda was thereby focused on apportioning variability in abundance.

Initially, time series were used to test for density dependence in population growth. The idea is that density dependence, which implies a negative relation between per capita population growth rates and population density, should produce a discernible signature in time series data. Technical exploration to test for this signature uncovered numerous pitfalls (confounding correlation with causation, for instance) and causes of spurious results (measurement error and environmental correlation are notable culprits). However, since the advent of robust and unbiased tests (11, 12), evidence of density dependence in population growth is often observed in long-term studies. Variations on this line of inquiry noted that age- or stage-structured populations may exhibit density dependence that acts with a time lag, reflecting the developmental period. With multiple interacting stages or age classes, density-dependent feedbacks may also act with several lags simultaneously. Therefore, the methodology has been extended to test for number of lags (called the "order of density dependence") as well as for regulation in multi-species systems against the null hypothesis of purely stochastic variation (11, 13, 14).

**Stochastic variation.** Because of the inherent discreteness of individuals, populations will fluctuate even in the absence of nonlinear interactions or environmental variability. Such demographic stochasticity was initially investigated by the early statistical demographers (15, 16). According to this theory, stable populations should fluctuate around the carrying capacity according to a Poisson or negative binomial distribution. Variance in such fluctuations will increase with abundance, but the importance of demographic stochasticity scales inversely with carrying capacity in the sense that the coefficient-of-variation (SD divided by the mean) decreases with density (15–17). An early analysis to test these distributional predictions studied numerous time series and used the fact that the slope of log variance versus log mean should be between one and two (but strictly smaller than two) for fluctuations arising from demographic stochasticity (18). This study revealed fair agreement; however, it and other analyses of abundance time series of animals in the wild have uncovered several instances of "extra-demographic" variability.

The most obvious cause of extra-demographic variation is environmental stochasticity: random fluctuations in the environment that induce temporal variation in per capita growth rates. The consequences of such environmental fluctuations are that population size will be distributed according to a gamma or log-normal distribution around equilibrium

(19, 20). The slope of log variance plotted against log mean is exactly two for such distributions. Therefore, populations affected by environmental stochasticity will be more variable, and the coefficient-of-variation is independent of carrying capacity. The direct consequence of environmental stochasticity is that demographic rates are not constant through time, but are distributed according to some distribution.

Stochastic population fluctuations will represent a mixture of demographic and environmental variability. Recent work on apportioning stochastic variability to each of these components uses diffusion approximations to the birth-death process (20). According to this, the variance in the per capita growth rate,  $r(x)$ , is approximately (as long as abundance,  $x$ , is not too low and density dependence is not overcompensatory) given by  $\text{var}[r(x)] = \sigma_d^2/x + \sigma_e^2/x^2$ , where  $\sigma_d^2$  is the demographic variance and  $\sigma_e^2$  is the environmental variance (20, 21). The magnitude of each of these components as well as the strength of density dependence,  $b$ , in the growth rate can then be estimated on the basis of a time series of data by considering that  $r(x_t) \equiv \log(x_{t+1}/x_t) \sim N(a - b x_t, \sigma_d^2/x_t + \sigma_e^2/x_t^2)$  (21). Here " $\sim N(\mu, \nu)$ " is the shorthand notation for "is normally distributed with mean  $\mu$  and variance  $\nu$ ." This technique was applied to long-term data on passerine birds to test how the two sources of stochastic variability scale with abundance. The study confirmed that both environmental and demographic variability are significant in a wild population, and that demographic stochasticity declines with population size (21).

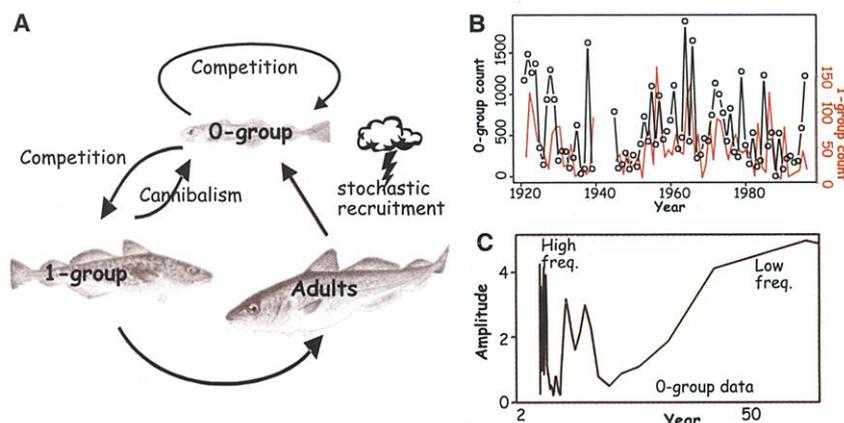
**Environmental forcing.** Large-scale climatic fluctuations are characteristically autocorrelated, showing a dominance of multianual or decadal variability [e.g., the El Niño–

Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO)]. Linking animal dynamics or demography to these climatic features has become something of an industry in recent years. The link between time series of abundance of planktonic copepods in the North Sea and the NAO, via phytoplankton productivity, provides a mechanistically well-understood example (22). We further discuss climatic forcing in the case studies.

**Complex dynamics.** Stochasticity and density-dependent feedbacks play a role in all ecological systems. However, additional issues arise whenever delayed or overcompensatory density dependence drives complex dynamics. Significant progress has recently been made in testing a range of more complex theoretical predictions:

1) Dimensionality of interactions. Specialist enemies are predicted to induce delays in regulation of the host, and thereby increase the dimensionality of host dynamics [see, for example, (14)]. From a dynamical systems point of view, this delay comes about because of the (one-way) equivalence between the state-space representation (i.e., the model considering predators and prey simultaneously) and the delay-coordinate representation (i.e., the model of delayed feedbacks in only one of the species) (11, 14). On the ecological side, this is an important correspondence because it allows us to understand lags in the density-dependent feedbacks. Statistically this equivalence also helps us test theory because the order can be estimated even without knowing the details of the ecological interactions (23).

The prediction of increased dimensionality of host dynamics in the presence of specialist enemies has been tested by adding a parasitoid and a virus to laboratory populations of the Indian Meal moth, *Plodia inter-*

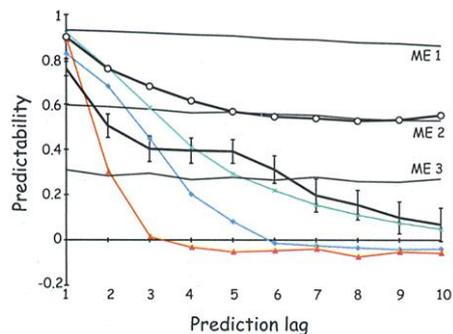


**Fig. 1.** (A) The age-structured dynamics of coastal Atlantic cod populations are shaped by competition and cannibalism in the juvenile classes and by stochastic reproduction due to expatriation and starvation of eggs and larvae. (B) The abundance index from scientific census of young of the year ("O-group": circles and black lines, left axis) and 1-year-old ("1-group": circles and red lines, right axis) along the Norwegian Skagerrak coast (57) exhibits erratic fluctuations. (C) The periodogram reveals that the dynamics are dominated by both high-frequency oscillations and long-term low-frequency trends (5).

*punctella* (14). The predictions of lags in regulation and a significant increase in dimensionality of the system's dynamics in the presence of the parasitoid were confirmed in the experimental time series (14).

2) Cycles and chaos. A second theoretical prediction is that interactions between stages or age classes can result in stable, cyclic, or chaotic fluctuations, depending on the strength of the interactions (24). Cyclic time series can easily be distinguished from other types of fluctuations through spectral analysis (25). Separating chaotic fluctuations (characterized by exponential sensitivity to initial conditions) from simple stochastic fluctuations is much more difficult and is a focus of continuous methodological debate and refinement (Fig. 2). However, an important qualitative difference between the two is that chaotic fluctuations paint complex geometric objects in phase-space, whereas simple stochastic fluctuations do not. Considerations of the "spatial distance" (in state-space) between observed time series and theoretical attractors is a most promising avenue for testing hypotheses of chaotic fluctuations (26). Such considerations also promise a robust criterion for estimating model parameters (27).

The transition from stable to cyclic and chaotic dynamics, predicted by a detailed



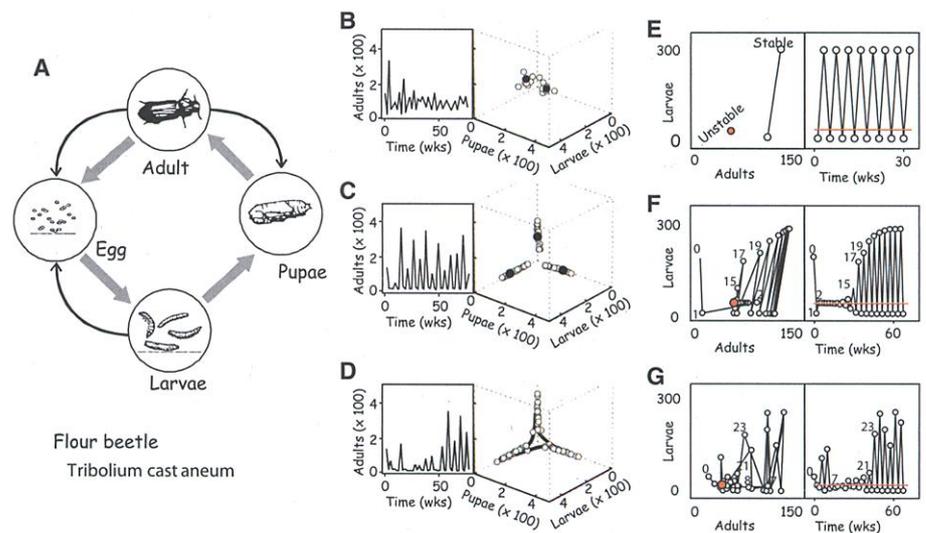
**Fig. 2.** Nonlinear forecasting to distinguish measurement error from ecological signal. The Ricker model (with parameters tuned to a limit cycle) was subjected to stochasticity in the growth rate, and clothed by three different levels of sampling error (67). Measurement error induces variability in the data that resembles dynamic variability, a resemblance that is superficial because sampling variability is not inherent to the system, and does not have consequences for the underlying dynamics. The figure shows  $k$ -step ahead prediction profiles (23, 68) for the model as follows: blue diamond, chaos; red triangle, environmental stochasticity; light blue cross, demographic stochasticity. The prediction profiles for the first half of Nicholson's blowfly data (10) (open circle), and the average profile for 14 lynx time series (38) (solid line) is also included for comparison (the error bars for the Lynx represent standard errors). Thus, measurement errors result in lower 1-step ahead prediction, but the predictability does not decline with prediction interval. This is in stark contrast to dynamic variability (whether stochastic or chaotic).

consideration of the geometry of state-space, was recently confirmed through manipulations of between-stage cannibalism rates in laboratory populations of flour beetles (*Tribolium* spp.). Cannibalism rates were manipulated by physically segregating stages or by subsidizing or diminishing recruitment into each stage class (28, 29). In particular, dynamics are predicted and observed to shift from stable to cyclic or chaotic, depending on the rate of cannibalism of pupae by adults. The laboratory experiments beautifully recreated the predicted bifurcation cascade (Fig. 3, B through D).

3) Coexisting attractors. A third theoretical prediction is that both stage-structured and trophic interactions can lead to coexisting attractors (30, 31). That is, depending on the initial conditions, different realizations of a process can exhibit qualitatively distinct dynamics because trajectories may lock onto alternative dynamic regimes. For instance, the trophic interaction between *Daphnia* and their algal food-source is predicted to have two coexisting attractors (30, 31). These predictions have also been tested in laboratory populations and have been confirmed through qualitative and quantitative consideration of the time series of abundance using a state-space perspective (Fig. 4).

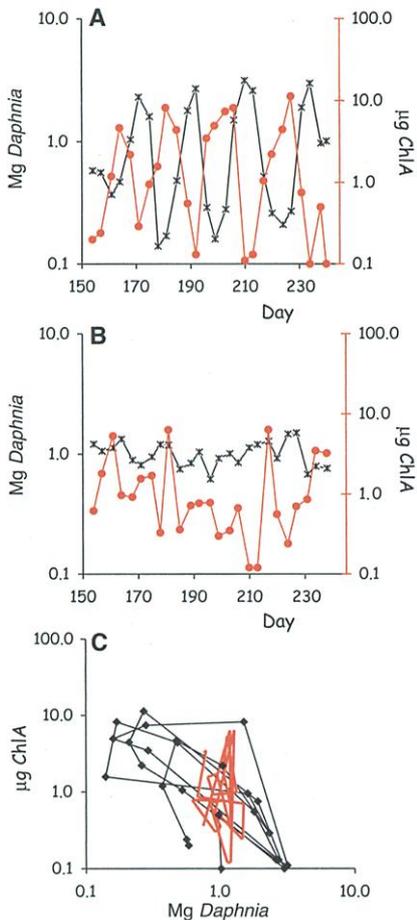
These slowly accumulating laboratory-

based verifications of the components of ecological theory are very promising. Populations in the wild, of course, are subject to the whole spectrum of forces acting in concert. This sets two linked challenges for theoretical ecology. The first is to build models that incorporate low- and high-frequency stochasticity as well as nonlinear interactions. The second is to describe and understand how determinism and noise interact. Essentially, the interactions result from stochastic perturbations "probing" a system, revealing dynamical behavior not readily apparent in the deterministic dynamics. For example: (i) Deterministically stable systems often exhibit phase-forgetting cycles when affected by environmental stochasticity (25). (ii) In addition to attractors (Figs. 3 and 4), there is the possibility of unstable equilibria (representing saddles) (32) (Fig. 3E) and unstable invariant sets ("repellers") (33). Small stochastic disturbances can push populations onto different coexisting attractors or close to unstable equilibria (or repellers) where the trajectories will linger (Fig. 3F). If the unstable invariant sets are complex, stochastic dynamics may be entirely unrelated to any individual stable attractor (33). (iii) In age-structured populations that deterministically exhibit a stable or cyclic attractor, dynamics can appear to be superimposed on long-term trends because stochastic reproduction is temporally "echoed" by life-cycle interactions



**Fig. 3.** (A) The transition rates (gray arrows) in the stage-structured dynamics of the flour beetle (*Tribolium castaneum*) are governed by competitive and cannibalistic interactions (black arrows). The dynamics of the system depends on the pupal cannibalism by adults. Manipulating the cannibalism rates is predicted and observed to induce chaotic fluctuations and limit cycles (69). (B through D) The observed dynamics (lines and open circles) and predicted attractors (solid circles or thick black lines) for time series of adult abundance (left) and coordinates in state-space (right) for three different cannibalism rates ( $\mu_p$ ) and attractors. Reprinted by permission from *Ecology* (68), copyright 2001, Ecological Society of America. (B) Two cycle,  $\mu_p = 0$ . (C) Three cycle,  $\mu_p = 1$ . (D) Invariant loop,  $\mu_p = 0.35$ . (E) The model predicts that a stable two-cycle attractor (open circle) coexists with an unstable equilibrium (red circle) for control populations (32). Long-term deterministic dynamics follow the stable attractor. (F) Stochastic or transient dynamics of the model may intermittently trace the unstable equilibrium. (G) Laboratory populations linger around the predicted unstable equilibrium before locking on to the stable two-point cycle as predicted by stochastic theory (32).

through a cohort-resonance effect (5). (iv) Chaotic attractors make forecasting ability very restricted because of sensitivity to initial conditions (3, 34) (Fig. 2). When chaotic systems are affected by stochasticity the “global” deterministic properties becomes unimportant because the complex phase-space often contains saddle nodes, repellers, and multiple attractors. However, locally any stochastic influences will be increased or shrunk depending on the exact geometry. Local Lyapunov exponents measure whether stochastic variation diverges or contracts at each specific location in phase-space (35). We sketch out each of these interactions in more details in the Web material (36).



**Fig. 4.** The trophic interaction between *Daphnia* and its resource is predicted to result in two coexisting attractors (a stable fix-point coexisting with a large-amplitude predator-prey cycle). The time series exhibiting the two types of dynamics are from replicate populations in identical environments (30). (A) Large-amplitude cycles. Cross, *Daphnia*; solid circle, chlorophyll. Left axis and black lines represent *Daphnia* abundance, Right axis and red lines represent algal abundance. (B) Small amplitude fluctuations. (C) The two types of dynamics superimposed on one another as coordinates in phase-space. Black lines represent large-amplitude cycles (A); red lines represent small-amplitude fluctuations (B). [Reprinted by permission from *Nature* (30), copyright 1999, Macmillan Magazines Ltd.]

**Confronting Theory with Data: Time Series of Wild Populations**

A justifiable critique of laboratory-based confirmation of ecological theories is the environmental and spatial simplicity of microcosms. Therefore, the ultimate test of theory needs to come from the field. Moving from laboratory to field studies adds extra complexities to the issues raised above. First, the measurement of population size in the field is usually done with error. Second, systems are usually only partially observed (not all state variables are tracked). Third, we frequently need to consider local and regional spatial heterogeneity; many key ecological time series are richly disaggregated over large spatial areas. Characterizing the resultant spatio-temporal patterns is, perhaps, the major challenge for ecological time series analysis and for mechanistic modeling. This topic is, however, outside the scope of the current review.

Many of our case studies are from cyclic populations, reflecting the major historical fascination of time series analysts in understanding the recurrent booms and busts of these systems. Population oscillations also give a particularly strong “signal” against which to investigate the balance of stochastic and deterministic forces. We focus on what a number of case studies have to say about the general theory outlined above, and, in particular, their bearing on: (i) environmental forcing and large-scale biogeographical variations; (ii) the ecological dimension of population interactions (Can dynamics in free ranging populations be low dimensional?), (iii) the interaction between nonlinearity and stochasticity in the wild, and (iv) the problem of partial observation and measurement error.

*The snowshoe hare and the lynx: Cyclicity and dimensionality.* By far the most analyzed time series in ecology are those of the snowshoe hare (*Lepus americanus*) and the Canadian lynx (*Lynx canadensis*) (11, 37, 38). These studies provide a tidy illustration of the practice of time series analysis in population dynamics. Initially, time series were used to test for the existence of population cycles (37); however, both the questions and methods applied to the time series have since advanced considerably. Considering first the relative impact of environmental drivers versus density-dependent structure, autoregression that corrects for autocorrelation in the observations shows that there is no direct causal relation between sunspot cycles and cycles in abundance (11). On the question of dimensionality: given that the hare is embedded in a rich community of plants, competitors, and predators, is it still possible to understand the dynamics in terms of a small number of key interactions? Order estimation testifies that the dynamics of the hare are three-dimensional (as would be expected from a tri-trophic interaction), whereas those of the lynx are approximately two-dimensional (as expected for a predator-

prey system) (38). The current consensus, gleaned from detailed field studies and field experiments (39) and supported through theoretical and statistical modeling of time series, is that the hare cycle can be represented as a tri-trophic interaction whose cycles are sustained through nonlinear interactions between the predator and prey. But the last word has still not been said—the influences of seasonality and space are crucial areas of ongoing research (40, 41).

*Rodent cycles: Roles of nonlinearity, stochasticity, and biogeographic variation.* In comparison to the long-term data on the lynx and hare, few ecological time series have been analyzed as extensively as those revealing vole and lemming cycles. Because of the numerous competing hypotheses (42), this provides an interesting illustration of how time series analyses have been used in the face of a hierarchy of uncertainties about mechanism: it is still unclear whether the lemmings’ chief dynamic role is as a “predator” on the vegetation or as a prey of weasels (43), and information on variables (predators or food biomass time series) is desperately lacking. This research also illustrates the continuing fascination with the search for chaos in ecological systems (44).

About half the hypotheses involve trophic interactions. Therefore, an early use of time series analysis tested for delayed density dependence (and “second order” dynamics) as a general probe for the consistency of trophic hypotheses. This has been done using a variety of linear and nonlinear time series tools (45, 46). In a similar spirit, the biogeographic transition in community structure (generalist predators are more abundant in the south) thought to give rise to the transition from multiannual cycles to seasonal cycles in Scandinavian rodents was converted to the hypothesis that the coefficient of direct, but not delayed, density dependence should vary clinally in space. A meta-analysis of the time series across the gradient in dynamics supported this prediction (47).

These studies provided important information about general strategic models. In recent years, however, there has been a shift toward including more explicit and detailed mechanism. This has been very successfully pioneered for noncyclic rodents for which density-dependent age-structured dynamics interacting with climatic forcing appears to be the key issue (48, 49) (we discuss this class of models in more detail in the next section). Mechanistic modeling has also been attempted for cyclic rodents, but a significant difficulty here is the absence of time series data on plants and predators. Two different routes have been taken to deal with this problem of “partial observation.” One is to rewrite the model in delay coordinates of the observed variable (46). The other is to reconstruct the unobserved variables as part of the estimation, considering these as a sequence

of unknown parameter to be estimated (50). Both of these avenues pose many conceptual and technical challenges for future work. Despite this, all the recent time series analyses add to the evidence that predation is an important component of the vole cycle. There are still controversies about whether a key feature of the cycle—the regular period but variable amplitude [also seen in many other cyclic populations (41)]—is best understood in terms of highly nonlinear interactions with modest influence of environmental stochasticity or weakly nonlinear interactions with strong stochastic forcing (50, 51).

*Island laboratories: The dynamics of Soay sheep.* Island populations, where the mainland food web and spatial dispersal of populations are reduced, may be seen as an intermediate environment between the laboratory and the wild. Island populations have provided the basis of extensive long-term studies in vertebrate population dynamics (52–54). The most detailed time series studies have concerned the feral Soay sheep of the St. Kilda archipelago. A time series for the main island Hirta has been logged since the 1950s (augmented by detailed individual-based demographic studies since 1985) and reveals recurrent population crashes in which up to half the population can die during the winter. Because the sheep are free of predators, the cause of these fluctuations lie in density-dependent interactions with food availability, modified by weather and, to some extent, parasitism.

The time series of this system reflects the technical and conceptual transition seen in population dynamics in general. Correlational studies (using key factor analysis) emphasized the importance of overcompensatory density dependence arising from food limitation at high density (53). Deterministic models confirmed that these strong nonlinearities could potentially drive recurrent deep population crashes (50). Attention then turned to explaining irregularities in the pattern of crashes using the semi-mechanistic threshold autoregressive model to quantify the balance between density dependence, environmental forcing, and other sources of process noise (54). The significant correlation between isolated sheep populations in adjacent islands in the archipelago was used to highlight the great impact of environmental forcing on the dynamics (54). Recently, a more fully mechanistic age- and sex-structured model has been developed (55) that reveals that the observed dynamics arise from an interaction between density dependence, weather (including climatic oscillations), and the age structure of the population. Harsh winters kill young and old individuals, but only in high-density years. This synthetic model derives from new statistical mark-recapture methods applied to the individual-level data. Thus, understanding the overall dynamics depends on detailed knowledge of demography at the individual level and

how that, in turn, is affected by environmental fluctuations [see also (48, 49, 56)].

*Coastal cod: Age structure, stochastic reproduction, and measurement error.* Quantifying the magnitude of stochastic influences requires models that account for measurement error in the time series. To estimate the variance in reproductive rates and strength of within- and between-cohort interactions in Atlantic cod (Fig. 1), a hierarchical time series model was fit to 75-year-long time series of Atlantic cod (5). The dynamics was assumed to follow a stochastic age-structured model with interactions among the cohorts. Superimposed on that, the observational process was assumed to follow a Poisson counting-process. The analysis verified significant within- and between-cohort density-dependent mortality as well as stochastic variation in reproduction (5). The stochastic fluctuations in reproduction were further shown to be “echoed” temporally by the age-structured interaction (57). Thus, the coastal cod provides a particularly clear example of the inability of purely stochastic or purely deterministic models to capturing the qualitative dynamics.

### Conclusions

Like many “new syntheses,” the proposal that “everything (nonlinearity, noise, etc.) is important” is not new (1). However, the recent blend of modern statistical approaches with mechanistic biological ingredients is shedding new light on the subject; ironically, adding technical and methodological complexities greatly clarifies our biological understanding. Another area of population biology where the dialogue between theory and time series data has been almost exactly replicated is the population dynamics of infectious diseases (16, 58). An interesting contrast between childhood disease time series and the systems reviewed here is that demographic stochasticity has been much more studied “in the wild” in the former and has been shown to be of palpable importance. Whether this is an intrinsic difference, or whether the animal systems have not been studied at the right scale to detect demographic stochasticity in the troughs between peaks or outbreaks, is not clear. We suspect, as indicated by recent theoretical studies (59, 60), that the latter is true. If so, it will be important to develop non-Gaussian models that encompass demographic stochasticity and discreteness of individuals and to perform field studies at finer spatial resolution.

During our survey, we have come across several other areas where technical developments are needed. First, we need to add statistical models for measurement error to the current crop of nonlinear time series models. Initial progress in this direction has been promising (5, 61, 62), but more general protocols need to be developed. In this and many other areas, Markov chain Monte Carlo and related approaches appear to provide a powerful method-

ology (5, 21, 61, 62). Second, more mechanistic models are required for the impact of environmental forcing. Such developments appear to depend on having individual-level data on responses to environmental conditions (48, 49, 55). Third, seasonality is too frequently ignored; this goes hand-in-hand with a desperate need for methods to fit ecologically realistic continuous-time models (that include stochasticity and climatic forcing) to time series. Initial progress in this area is also very promising (63), but this scientific area is still open. Fourth, although methods have been developed to estimate the dimension of ecological interactions, they have mostly been applied to laboratory time series. Estimating effective dimension in the field is a much tougher task. Fifth, continued developments of techniques to “reconstruct” unobserved variables, coupled to semi-mechanistic approaches, and better methods for model comparison (64, 65) will always be important, because we will never be able to measure all variables affecting free-ranging populations. Lastly, probably the biggest challenge—and opportunity—lies in understanding spatio-temporal dynamics. Apart from the intrinsic problems of developing methods and amassing suitable data, adding the spatial dimension subsumes the above problems. Two issues, in particular, are (i) to estimate the extent and pattern of spatial coupling between dynamical units and (ii) to quantify how spatial pattern feeds back on temporal dynamics.

For population ecology, the wedding of long-term studies with theory forces scientists to juggle two apparently incompatible aims: To understand any system, we need to appreciate its idiosyncrasies; to encompass broad patterns, we need to extract generalities. The current challenge to time series analysis and ecological theory is, thus, to simultaneously accommodate and transcend the details of natural history. However, theoretical developments can only build on continuing and new collection of high-quality and long-term data, ideally involving field experimentation (39, 66).

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REVIEW

# Complex Species Interactions and the Dynamics of Ecological Systems: Long-Term Experiments

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Studies that combine experimental manipulations with long-term data collection reveal elaborate interactions among species that affect the structure and dynamics of ecosystems. Research programs in U.S. desert shrubland and pinyon-juniper woodland have shown that (i) complex dynamics of species populations reflect interactions with other organisms and fluctuating climate; (ii) genotype x environment interactions affect responses of species to environmental change; (iii) herbivore-resistance traits of dominant plant species and impacts of "keystone" animal species cascade through the system to affect many organisms and ecosystem processes; and (iv) some environmental perturbations can cause wholesale reorganization of ecosystems because they exceed the ecological tolerances of dominant or keystone species, whereas other changes may be buffered because of the compensatory dynamics of complementary species.

Throughout the 20th century, most theoretical and empirical research attempted to understand the structure and dynamics of populations, communities, and ecosystems by identifying the components and studying their relations in isolation from the complicating influences of larger systems. This research strategy was suc-

cessful in elucidating fundamental ecological processes: responses to stresses of extreme abiotic conditions; limiting resources of food, water, and inorganic nutrients; and the biotic interactions of competition, mutualism, predation, parasitism, and disease. It was less successful in revealing the complex patterns of

temporal and spatial variation in the abundance, distribution, and diversity of species or the complicated roles of species in ecosystems. By the 1980s, it was becoming apparent that more holistic, synthetic approaches were needed (1–4). To understand realistically complex ecological systems, it is necessary to study how the components affect and are affected by the larger, more complicated systems in which they are embedded.

Especially valuable insights have come from decades-long studies that combine experimental manipulations of selected species

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