Sub-harmonic resonance and multi-annual oscillations in northern mammals: a non-linear dynamical systems perspective

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Abstract

We conjecture that the well-known oscillations (3- to 5-yr and 10-yr cycles) of northern mammals are examples of subharmonic resonance which obtains when ecological oscillators (predator-prey interactions) are subject to periodic forcing by the annual march of the seasons. The implications of this hypothesis are examined through analysis of a bare-bones, Hamiltonian model which, despite its simplicity, nonetheless exhibits the principal dynamical features of more realistic schemes. Specifically, we describe the genesis and destruction of resonant oscillations in response to variation in the intrinsic time scales of predator and prey. Our analysis suggests that cycle period should scale allometrically with body size, a fact first commented upon in the empirical literature some years ago. Our calculations further suggest that the dynamics of cyclic species should be phase coherent, i.e., that the intervals between successive maxima in the corresponding time series should be more nearly constant than their amplitude – a prediction which is also consistent with observation. We conclude by observing that complex dynamics in more realistic models can often be continued back to Hamiltonian limits of the sort here considered. © 2000 Elsevier Science Ltd. All rights reserved.

1. Introduction

The multi-annual oscillations (Fig. 1) of northern mammals [1–7] are arguably among ecology’s most celebrated patterns. Recently, Norrdahl [8] proposed a general explanation: the cycles result from the interaction of specialist predators and their victims, with the intrinsic time scale of the prey species setting the period of oscillation. This hypothesis is noteworthy on two counts. In the first place, as Norrdahl explains, it offers a spartan accounting of the principal empirical findings. To a reasonable approximation, it further articulates the conclusions to which one is led by considering seasonal predator–prey interactions from the viewpoint of non-linear dynamics. In the present paper, we enunciate these conclusions and sketch their derivation. In this regard, we observe that the mathematical formulation of Norrdahl’s hypothesis is that northern mammal cycles are ecological examples of sub-harmonic resonance. From this principal conclusion follow two subsidiary results: that cycle period should scale allometrically with body size; and that the intervals between successive maxima in the time series of cyclic species should often be more nearly constant.
than their amplitude. As evidenced by Fig. 1 and the literature [9] both predictions are consistent with empirical observation.

2. Resonance

Resonance [10,11] is the phenomenon, familiar to any parent who ever pushed a child on a swing, whereby an oscillator (the swing) subject to periodic forcing (the pushing), vibrates at a frequency which is rationally related to that of the forcing. In the case of the child on the swing, the two frequencies are usually the same. This is called 1:1 or “harmonic” resonance, and it is the case most familiar to population biologists [12]. Other possibilities include sub-harmonic resonance, in which instance, the frequency of the resonant vibrations is lower than that of the forcing, and superharmonic resonance, in which instance, the resonant frequency is greater.

In the case of northern mammal cycles, the presumptive oscillator is a predator–prey interaction, while periodic forcing is imposed by the annual march of the seasons. That seasonality is an essential component to any mechanistic model of cyclic species follows from the animals’ natural history. In the majority of cases, reproduction is confined to the spring and summer with the consequence that population densities decline during the winter. In short, there is “phase-locking” between the seasonal zeitgeber and the ecological oscillator. From this biologically pedestrian observation follow unexpected consequences.

3. A bare bones model

The essential phenomenology of seasonal predator–prey systems can be captured by straightforward generalization of the well-known model of Volterra [13]. Following [14], we write

\[
\begin{align*}
\frac{dx}{dt} &= \mu_x (1 + \epsilon \sin 2\pi t - e^v), \\
\frac{dy}{dt} &= \mu_y (e^v - 1),
\end{align*}
\]

(1)

where \(x\) and \(y\) are the natural logarithms of the densities of victims and predators. Of the three parameters, \(\epsilon\) is the magnitude of seasonality – assumed to act on the victims’ per capita rate of increase – while \(\mu_x\) and \(\mu_y\) specify the two species’ intrinsic time scales. These are the “size-related” rates of increase to which Norrdahl refers. The derivation of these equations from a more traditional formulation of Volterra’s equations is described in the footnote 1.

Eq. (1) omit biologically important considerations such as predator satiation and victim self-limitation. These omissions notwithstanding, Eq. (1) nonetheless constitute the dynamical birthing place wherein originate the periodic behaviors of more realistic models [14,15]. The latter include a detailed representation [16] of snowshoe hare demography which can reproduce the cycle’s “natural” period and amplitude as well as its response to experimental manipulation [7]. In short, there are reasons to believe that analyzing Eq. (1) can contribute to our understanding of multi-annual oscillations in nature.

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1 Derivation of Eq. (1): A more traditional formulation of Volterra’s model may be written as follows:

\[
\begin{align*}
\frac{dP}{dT} &= P(\beta kV - d), \\
\frac{dV}{dT} &= V(r(T) - kP).
\end{align*}
\]

Here \(V\) and \(P\) are the densities of predators and victims, \(k\) is the per predator kill rate, \(\beta\) converts harvested victims into baby predators and \(d\) and \(r(T)\) are (respectively), per capita rates of predator mortality and victim reproduction. To model the effects of seasonality, we set \(r(T) = r_0(1 + \epsilon \sin 2\pi \omega T)\), where \(\omega\) is the frequency, 1 y\(^{-1}\), of seasonal variations in victim reproduction and \(\epsilon\) indexes their magnitude. Now define dimensionless densities, \(v = V'/V^*\) and \(p = P/P^*(0)\), where \(V^* = d/\beta k\) is the equilibrial density of victims, and \(P^*(0) = r/k\) is the corresponding density of predators when \(T = 0, 1, 2, \ldots\). Further define dimensionless time, \(t = \omega T\). Substituting these quantities into Eq. (0) yields Eq. (1), where \(\mu_x = (r_0/\omega)\), \(\mu_y = (d/\omega)\) and \(t = \omega T\).
Following Norrdahl, we focus on the inherent time scales of the interacting species and consider the effects of $\mu_x$ and $\mu_y$ on the periods of resonant oscillations induced by Eq. (1). Without loss of generality, we introduce new parameters, $\bar{\mu}$ and $\epsilon_\mu$, such that

$$\mu_x = \bar{\mu}(1 + \epsilon),$$
$$\mu_y = \bar{\mu}/(1 + \epsilon).$$

Thus, $\bar{\mu}$ is the geometric mean of $\mu_x$ and $\mu_y$, i.e., $\bar{\mu} = (\mu_x\mu_y)^{1/2}$, while $\epsilon_\mu$ quantifies their disparity. The utility of this substitution will become apparent shortly.

### 4. The non-seasonal case

Ecologists have long been familiar [13,17] with non-seasonal versions of Eq. (1). In this case, $\epsilon = 0$, and the $x$-$y$ phase plane is densely populated by closed, neutrally stable solution curves surrounding the center at the origin (Fig. 2). The period, $T$, of these cycles increases monotonically, and without bound, as one moves outward from the origin. Close to the origin,

$$T \approx T_{min} = 2\pi/\bar{\mu}.$$  

### 5. Computing an orbit’s rotation number

It is convenient to think of the solution curves in Fig. 2 as degenerate tori and to associate with each of them a rotation number, $\rho$. We do this by sampling solution curves at intervals equal to the period of the forcing which is imposed once $\epsilon$ exceeds 0. Such a construction is called a “stroboscopic map”. This accomplished, we select an orbit and compute its rotation number as indicated in Fig. 3. Specifically, we assign an angle, $\theta_i$ to each point, $i = 1, 2, 3, \ldots$ on the orbit. Then $\rho$ is calculated according to the formula

$$\rho = \lim_{N \to \infty} (1/N) \sum_{i=0}^{N}(\theta_{i+1} - \theta_i).$$
From a biological point of view, \( q \) can be viewed as the inverse of an orbit’s “average period”, i.e., the mean interval between successive maxima in the associated time series. More fundamentally, the concept allows us to divide the degenerate tori into classes according to whether \( q \) is rational or irrational. The significance of this distinction, as we next discuss, is that it allows us to comprehend the consequences of introducing seasonality.

6. Consequences of seasonality

Implicit in much of the ecological literature is the assumption that the effect of seasonality is to replace equilibrial dynamics with annual cycles which vary from year to year only to the extent that one year’s weather, and hence mean rates of reproduction and mortality, differs from the next. In fact, as shown in Fig. 4a, the dynamical consequences of seasonality are far more complicated. In particular, we note the following:

1. For small values of \( \epsilon \), the irrational tori are unaffected, save that they are no longer degenerate. Motion on the irrational tori is quasi-periodic, i.e., the associated time series evidence oscillations modulated by a second, incommensurate frequency.

2. Whereas the irrational tori survive the imposition of infinitesimal seasonality, their rational counterparts are destroyed. In their stead, one observes complicated structures called “island chains”. Each chain is...
organized about a pair of periodic orbits, the rotation number of which equals that of the rational torus it replaces. One of these cycles is neutrally stable, while the other has the stability character of a saddle.

3. Associated with the saddle cycles are chaotic orbits. For small values of $\epsilon$, these orbits are bounded by irrational tori and consequently confined to thin, so-called “stochastic” layers.

4. Surrounding the neutrally stable cycles are secondary tori which themselves are surrounded by additional island chains. In fact, the island chains are self-similar, i.e., the primary island chains are surrounded by secondary chains which themselves are surrounded by tertiary chains, etc. This fact is a consequence of the Poincaré–Birkhoff theorem [18].

With increasing seasonality, the irrational tori also begin breaking down in a sequence determined by their rotation numbers [18]. As a result, chaotic orbits, heretofore confined to thin layers, now wander more widely, eventually merging to form regions of macroscopic chaos referred to as the “stochastic sea”. For small values of $\epsilon$, the sea is kept far from the origin by surviving irrational tori (Fig. 4b). For larger values of $\epsilon$, the stochastic sea laps closer to the origin (Fig. 4c). At the same time, the island chains also begin to disappear, with the outermost chains being the first to suffer destruction.

These results exemplify the transition from “integrable” to “non-integrable” dynamics in Hamiltonian systems as described by the KAM theorem [10,11,18,19] and, as such, they are very general. In such cases they provide a realistic description of real-world phenomena. By contrast, the relevance of Hamiltonian dynamics to ecology depends on the fact [14–16] that a number of ecological models possess Hamiltonian limits and that the dynamics to be found therein can be continued into biologically plausible regions of parameter space. Fundamentally, the apparent ubiquity of Hamiltonian limits in ecology reflects two facts. The first is that energy flows up the trophic ladder; the second, that predator–prey interactions, at their core, are essentially glorified pendula.

7. Progenitrix of cycles

In Section 6, we observed that an infinite number of cycles and, hence, the island chains organized about them, are created when $\epsilon$ is varied away from zero by an arbitrarily small number. Of course, an infinite number of cycles does not correspond to all possible cycles. Indeed, we already know from Eq. (3) that the cycles thus created have rotation numbers, $\rho < \bar{\rho}/2\pi < 1/T_{\text{min}}$. It follows that increasing $\bar{\rho}$ results in the creation of additional cycles. Where do these cycles come from? The answer is surprisingly simple. All of the cycles emerge from the annual cycle which corresponds to the central fixed point of the stroboscopic map.

In the case of the period-2 island chain, the chain’s origination is a two step process involving super- and sub-critical period-doublings that occur at different values of $\bar{\rho}$. Analogous complications attend the origins of the period-3 and period-4 chains [20–22]. The remaining sub-harmonics are created by single bifurcations. This process is illustrated in Fig. 5 wherein we show the birth of cycles of rotation numbers $\rho = 1/5, 1/6$ and $1/7$. These are, of course, but three of an infinite number of cycles which arise on the range of $\bar{\rho}$ values depicted. For example, between $\bar{\rho} = \mu_{1/5}$ (birth of the $1/5$ cycle) and $\mu_{1/6}$ (birth of the $1/6$ cycle),
is $\mu_{2/11}$ (birth of the 2/11 cycle); between $\mu_{1/5}$ and $\mu_{2/11}$, is $\mu_{3/16}$, etc. This enumeration can be continued \textit{ad infinitum}, with the consequence that on any interval, $\bar{\mu} = [\mu_1, \mu_2]$, there arise an infinite number of orbits with periods ranging from $2\pi/\mu_1$ to $2\pi/\mu_2$. These orbits are born as imperceptible modulations of the annual cycle and thereafter increase in amplitude (Fig. 6).

In the course of this evolution, each cycle is destabilized by period-doubling, and there follows a period-doubling cascade (Fig. 7). The cascades accumulate, i.e., the interval of $\bar{\mu}$ values between successive dou-
blings diminishes [23], so that for each value of \( q \), there is a range of parameter values for which cycles of that rotation number are neutrally stable. As shown in Fig. 8, this range depends on both \( l \) and the degree of seasonality, \( \epsilon \).

These observations allow us to associate a range of available periods (Fig. 9) with a given \( \overline{\mu} - \epsilon \) pair. The shortest is \( T_{\text{min}} = 2\pi/\overline{\mu} \); the longest corresponds to the accumulation point of the above-mentioned period-doubling cascade. To summarize: the effects of parametric variation are to down-shift the range of available periods in response to increasing \( l \) and to narrow the range in response to increasing \( \epsilon \).

From a deterministic point of view, it is the destabilization of the cycles and their period-doubled descendants which sets the maximum value of \( \overline{\mu} \) consistent with observable motions of a particular rotation number. In real-world systems, an equally important determining factor is that with increasing values of \( \overline{\mu} \) minimum population densities become so small that the biological expectation is extinction. Happily, both mechanisms work in the same direction.

8. Asymmetry in time scales

Thus far, we have assumed that the intrinsic time scales of the two species are the same. Energetic considerations dictate that this will often be roughly true, i.e., as a generality, really large predators do not subsist on really small prey. There are, however, exceptions, in which instances, the parameter \( l \) in Eq. (2) will differ from zero by a significant amount. The consequence of this complication is to narrow the range of available periods – principally by moving the period-doubling curves to the left.

9. Mathematical basis of resonance and self-similarity

Mathematically, the birth of sub-harmonics can be understood in terms of the eigenvalues (also called Floquet multipliers) of the annual cycle when viewed stroboscopically. At \( \overline{\mu} = 0 \), both eigenvalues equal 1. Thereafter, they separate and move to the left along the unit circle in the complex plane. With each value of \( \overline{\mu} \), one can therefore associate an angle, \( \theta_\mu \). With increasing \( \overline{\mu} \), \( \theta_\mu \) increases from 0 to \( \pi \), thereby passing through an infinite number of values rationally related to \( 2\pi \). At each such value, a pair of cycles is emitted from the central periodic orbit. Eventually, the eigenvalues remerge at \( -1 \), at which point the period-2 sub-harmonic is born. This explains the origination of the primary island chains as shown in Fig. 5.

If we now consider the eigenvalues of the cycles about which the primary island chains are organized, we see that the foregoing process is repeated. With increasing values of \( \overline{\mu} \), the eigenvalues of the various sub-harmonics move along the unit circle, again passing through an infinite number of values rationally related to \( 2\pi \). At these points, secondary island chains are produced. By the same mechanism, the secondary sub-harmonics give rise to tertiary island chains, which, in turn give rise to fourth order chains, etc. This explains the self-similarity of the island chains. Each of the period-doubled cycles also emits its own set of secondary island chains, which then give rise to higher-order chains. In short, a single mechanism gives rise to all possible sub-harmonics.

Fig. 9. A range of periods \([T_{\text{min}}, T_{\text{max}}]\) is associated with every \((\overline{\mu}, \epsilon)\) pair. \( T_{\text{min}} = 2\pi/\overline{\mu} \); \( T_{\text{max}} \) corresponds to the point at which the period-doubling sequence accumulates.
10. Allometric scaling of cycle period

Norrdahl’s view that cycle period is determined by the intrinsic time scales echoes a suggestion by Calder [9] that mammalian herbivores oscillate at periods which scale allometrically with body size. Calder observed that, if cycle period, $T$, is measured in years and body mass, $M$, in kg,

$$T = aM^b,$$

where $a$ ranges 6.5–7.7 and $b$ from 0.25 to 0.27. This result is based on data for 10 species, several of which evidence multi-annual cycles. ²

Our results suggest a simple explanation for this finding, subject to the important proviso that the populations in question participate in exploitative interactions. In this regard, we note that, for most species, the intrinsic per capita rate of increase, $r$, varies with body mass, $M$, according to

$$r = cM^{-d}$$

[24]. For homeotherms, when $r$ is measured in units of $y^{-1}$ and $M$ in kg, $c \approx 2.2$ and $d \approx 0.275$. This allows us to obtain a lower bound on cycle period by computing $T_{\text{min}}$. If we follow Norrdahl and equate $\pi$ with the victims’ per capita rate of increase, $r_v$, we obtain

$$T_{\text{min}} = 2\pi/r_v = 2\pi/cM^{-d} = 2.9M^{0.275},$$

which, on a log–log plot, gives the proper slope, but the wrong intercept. ³ Despite their utter simplicity, Eq. (1) thus give order of magnitude agreement with the empirical results.

11. From Hamiltonian to dissipative dynamics

What happens when Eq. (1) are perturbed in the direction of greater biological realism by addition of a finite victim carrying capacity, $K_v$, and predator satiation? This question was answered by King and Schaffer [15] who considered the system

$$\frac{dx}{dt} = \mu_x[g(t) - \alpha x^a - (1 - \alpha)f(x)e^t],$$

$$\frac{dy}{dt} = \mu_y[f(x)e^t - 1],$$

$$f(x) = (1 + \eta)/(1 + \eta e^t),$$

$$g(t) = 1 + \epsilon \sin 2\pi t.$$  

Here, $\alpha$ is the ratio of $V^*$, the equilibrium density of victims under predation in a constant environment, to $K_v$, and $\eta$ determines the rate at which per predator kill rate saturates with increasing numbers of victims.

If $\alpha = \eta = 0$, Eq. (8) collapse to (1), for which reason, we say that $\alpha = \eta = 0$ is a Hamiltonian limit, $\mathcal{H}$ . At this point, areas of the Poincaré map are preserved, and there exist the infinite numbers of regular and chaotic motions discussed above. For all other values of $\alpha$ and $\eta$, the so-called dissipative regime, areas of the Poincaré map either expand or contract. As a consequence, neutrally stable limit sets are no longer possible. Instead, one observes sinks, saddles and repellers. More specifically, the range of asymptotic states depends on the relative values of $\alpha$ and $\eta$. On varying these quantities, one observes the following:

² Subsequent attempts [25] to apply Eq. (5) to wider range of taxa were methodologically flawed – most of the populations for which cycle periods were reported evidenced little objective evidence of periodic behavior [26].

³ By this accounting, lemmings should cycle with periods on the order of a year, and the snowshoe hare, periods on the order of 3 years. These estimates are low by a factor of 3. They can be improved if we observe that predators are often somewhat larger than their victims and replace $r_v$ with $(\mu_x \mu_y)^{1/2}$. 

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1. If $x/\eta$ is sufficiently large, all initial states tend to the annual cycle which, on the Poincaré map, is a fixed point near the origin.
2. For smaller values of $x/\eta$, both the annual cycle and one or more sub-harmonic oscillations are stable.
3. For still smaller values of $x/\eta$, the annual cycle is unstable. Trajectories based at points in its vicinity spiral out to one or more attractors which may either be periodic or chaotic.
4. As $x/\eta$ is subjected to further reductions, the attractors, bey Qualcomm or chaotic, move ever outward from the origin, with the consequence that the average “period” of oscillation, i.e., the mean interval between successive peaks in the associated time series, increases.

These possibilities are illustrated in Fig. 10 which depicts the consequences of decreasing $x$ while holding $\eta$ fixed. In Fig. 10a, the fixed point near the origin and the 1:3 cycle are stable; in Fig. 10b, the fixed point has lost stability and initial conditions are attracted either to the 1:3 or to the 4:12 cycle which surrounds it. In Fig. 10c the stable cycles include 1:4, 3:12 and the 2:12 resonances. There is also a chaotic saddle [27] which can induce extended chaotic transients. Finally, in Fig. 10d, all of the cycles are unstable and motion is on a strange attractor.

12. Phase coherent character of multi-annual oscillations

Multi-annual cycles in nature are often characterized by the relative constancy of their period vis-a-vis their amplitude (Fig. 1) an observation to which attention has been called in the case of lynx cycle by Schaffer [28]. This property, called “phase coherence” in the dynamical systems literature, ⁴ is characteristic of the type of chaos first described by Otto Rössler [29]. Chaotic motions induced by Eq. (8) also possess this property [15] for the reason that the rotation numbers of the periodic orbits about which they are...

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⁴ The name reflects the fact that nearby initial conditions on a phase coherent attractor preserve their relative phase relations over extended periods even if the motion is chaotic. This results in a power spectrum with sharp peaks superposed on a noisy background [30].
organized decrease monotonically as one moves outward from the annual cycle. This geometry traces to the Hamiltonian limit, $\mathcal{H}$, and is therefore to be expected in systems which can be formulated as perturbations of such a limit. It is not, we emphasize, a characteristic of chaotic dynamics generally.

The topology responsible for phase coherence in chaotic solutions to Eq. (8) is worth displaying, and we do so in Fig. 11. Here, recurrent points are color-coded by the reciprocals of their rotation numbers. More precisely, we display points which return to a small neighborhood of themselves after 5–18 iterations of the Poincaré map. Color-coding is according to the sequence of colors in the visible spectrum: dark red corresponds to points for which $1/\rho = \tau_{\text{min}} < 5$; dark violet, to points for which $1/\rho = \tau_{\text{max}} > 9$. Two features of the diagram merit comment. The first is that there is an overall tendency for the color to change from red to violet as one moves outward from the attractor’s inner margin. This reflects the aforementioned ordering of the saddle cycles. The second is that swirls of red spread out from the inner margin while swirls of violet spread inward from the outer margin. To understand why this is the case, we recall that the cycles about which the attractor is organized have the stability character of saddles, with the consequence that recurrent points will be on or near the stable manifold of such a cycle. What our construction thus reveals is the tangled structure of the manifolds, which is the geometric basis of chaotic behavior. From the viewpoint

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5 Chaotic attractors are organized about infinite numbers of saddle periodic orbits in the sense that the latter are “dense on the attractor.” By this it is meant that every point on such an attractor is arbitrarily close to a periodic orbit.
of the biology, what is important, of course, is not the tangling, but the fact that motion on the resulting attractor is an amalgamation of nearly periodic motions representing a circumscribed range of frequencies.

13. Relation of the present model to three-trophic level models of the lynx–hare cycle

Thus far, our discussion has focused on predator–prey interactions. In fact, recent opinion regarding the genesis of multi-annual cycling in nature has tended to emphasize the importance of resource limitation as well as predation. This perspective is most strongly supported by field experiments of Krebs and his associates [7] on snowshoe hare (*Lepus americanus*) populations in the Canadian Yukon. Principally, these authors showed that supplemental feeding of hares dramatically increased their maximum density and prolonged the peak phase of the cycle. At the same time, excluding mammalian, but not avian, predators, slowed the post-peak decline. In other words, the experiments suggest a three-trophic-level system. Statistical analysis [31] of historical data points to the same conclusion: hare population cycles appear to be determined by two factors whereas explication of lynx time series requires but a single factor. This result has been interpreted to indicate that the hare is limited both by its food supply and by predation, lynx population growth rates depend only on the abundance of the hare which is its principal food species. Elsewhere [16], we have shown that a three trophic level model of snowshoe hare demography is, in fact, compatible not only with the available census data, but also with the experimental results noted above. The present analysis, of course, makes no mention of herbivore forage and it is therefore worthwhile, we believe, to enquire as to what relationship the dynamics of Eq. (1) might bear to those of a more expansive scheme.

Interestingly, the nature of this relationship turns out to hinge on the dynamics of the forage. In the case of the snowshoe hare, the limiting resource is winter browse consisting of the terminal twigs of woody plants [5]. Essentially, there are two qualitatively distinct ways in which one can model browse dynamics. On the one hand, one can suppose that consumption of browse has a minimal effect on the plants’ photosynthetic abilities. This leads to an equation of the form

\[ \frac{dB}{dt} = r_B(t)(K_B - B) - F_B(H, t)B. \]  

Here \( B \) and \( H \) are the densities of browse and hares, \( r_B(t) \) is the seasonally-dependent rate of browse production, \( K_B \), the maximum abundance of browse and \( F_B() \), the hare’s functional response which is assumed to depend on both hare abundance and on the time of year.

An alternative approach is to assume that browse consumption has a significant effect on the plants’ photosynthetic abilities. This leads to a browse renewal equation of the form

\[ \frac{dB}{dt} = r_B(t)B[(1 - B/K_B) - F_B(H, t)B]. \]  

The differences between (9) and (10), while they would appear slight, have important implications. With browse renewing according to Eq. (9), the hare and its food supply cannot oscillate in the absence of predators. As a result, the oscillations of the three level system trace to a Hamiltonian limit which corresponds to Eq. (1). In this fundamental sense, the oscillations are predator–prey cycles, and it is interesting, therefore, that the model of King and Schaffer, which seems capable of giving a good accounting of the empirical observations, caricatures browse dynamics according to Eq. (9).

In contrast, the use of Eq. (10) makes for the possibility of multiple Hamiltonian limits [15]. One of these is an herbivore–vegetation system; another, a predator–prey interaction. In this case, explicating the dynamics of the three level model may require consideration of both limits and therefore all three state variables. In passing, we remark that the possibility of multiple Hamiltonian limits raises fascinating, and, as yet unexplored, questions regarding the interaction of invariant motions emanating therefrom.

14. Ubiquity of Hamiltonian limits in ecological models

Our approach to the dissipative dynamics of Eq. (8) is motivated by the fact that non-integrable Hamiltonian limits can be found in a variety of ecological models. We emphasize this point because it is so
completely at variance with the conventional wisdom [17,32]. The latter holds that Hamiltonian models by virtue of their structural instability [11] are irrelevant to the behavior of non-Hamiltonian schemes which attempt to a more faithful representation of biological reality. In fact, structural stability is a mathematical concept which is less relevant to the dynamics of non-linear systems than is often supposed [15].

In addition to Eq. (8), non-integrable Hamiltonian limits have been observed in the following instances:

1. Periodically forced chemostat (double Monod) models in which holozoic protozoan predators consume heterotrophic bacteria.
2. Periodically forced three-level food chains in which the vegetation renews logistically [15].
3. The snowshoe hare model mentioned above [16].
4. $N \geq 2$ species systems consisting of two or more predator–prey pairs coupled by overlapping predator diets in non-seasonal environments.

The final example merits comment in that it is autonomous (constant parameter values) and therefore illustrates the general principle [10] that coupling two non-linear oscillators is fundamentally equivalent to subjecting a single oscillator to periodic forcing. An example – two predators, two prey – is shown in Fig. 1 wherein we display what is called a two-dimensional “surface of section” of the full four-variable system. To our knowledge, Fig. 12 is the first observation of the fieldmarks of non-integrable Hamiltonian dynamics in ecological models. It suggests that there may be merit in revisiting the statistical mechanical models of Kerner and Leigh (see [17] for review) of $n$-species ecological associations from a modern dynamical point of view.

In conclusion, we note that the apparent ubiquity of Hamiltonian limits in ecological models reflects the fact that embedded in predator–prey interactions are the non-integrable dynamics of the frictionless pendulum. It is a surprising result, suggesting as it does an unsuspected unity among disparate scientific disciplines.

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