Life-history speed, population disappearances and noise-induced ratchet effects

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1. Introduction

Life history is a fundamental axis of variation within nature. Researchers have argued cogently that this variation tends to follow a ‘slow–fast’ continuum where slow life histories have small population growth rates (low $r$), large body sizes and long generation times while fast life histories have high population growth rates, small body sizes, and short generation times [1–4]. Indeed, empirical work has found remarkably consistent relationships that suggest body size is a key attribute of life-history speed (figure 1a; [7]). These covarying traits along the ‘slow–fast’ continuum can impact many ecological processes and properties including population growth, ecosystem productivity and stability [1,8]. Given the changing nature of abiotic variation under climate change [9,10] and the increasing propensity for fast life histories under global change [11,12], understanding how life-history speed governs the ability for organisms and whole communities to persist (i.e. retain densities well above zero) is critical.

Theory has begun to unpack how population life-history ‘speed’ may tie into stability, with initial findings of fast and slow life histories amplifying or muting noise, respectively. Specifically, research has found that because of their high population growth rates, faster life-history organisms tend to produce overcompensatory dynamics (i.e. overshoot the equilibrium) and instability compared to slower organisms [13,14]. By contrast to fast organisms, slow organisms, with longer lives, buffer noise and thus maintain high stability. Consistent with this, empirical research has found negative correlations between population variability (one measure of stability) and both body size and generation time, and positive correlations between population variability and growth rates across multiple
taxa and kingdoms [15–18]. Taken altogether, larger and slower organisms appear capable of buffering noise better than small and fast organisms.

Nonetheless, while large slow-growth organisms may be able to buffer perturbations, this same potentially stabilizing slow-growth response can be destabilizing when perturbations are large enough to push population densities far away from the equilibrium [19,20]. Once a slow-growth species is pushed away from the equilibrium, the species becomes subject to the vagaries of different nonlinear dynamics (hereafter referred to as non-local nonlinear dynamics, see box 1) that can fundamentally alter the outcome of the system, including taking the dynamics close to zero or local extinction [19,20]. On the other hand, small fast-growing species may be less likely to be pushed far away from equilibrium because their rapid growth responses can keep them closer to equilibrium and local dynamic properties. These results suggest complex slow–fast life-history stability responses such that some aspects of life-history speed are beneficial (e.g. large and slow can buffer a perturbation) but also produce costs (e.g. large and slow growth can be detrimental once the population is pushed away from local equilibrium dynamics). Consequently, more research is required to understand how stability manifests along the slow–fast life-history continuum.

Another related factor that will impact stability along the slow–fast continuum is the colour of the stochastic noise (see box 1 for definition). Climate change is known to be reddening environmental noise by increasing the spatial and temporal autocorrelation of climate variables [9,10] which then can act to lengthen periods of suboptimal conditions for organisms [28]. Under extended suboptimal conditions, populations can be driven to smaller and smaller numbers, thus often hastening local extinction [28]. In a sense, these extended suboptimal conditions are akin to large perturbations (although each individual noise event is small). By pushing an organism’s dynamics far from an equilibrium, red noise is then also likely to cause non-local nonlinear dynamics. In this latter case, although not well explored, these autocorrelated perturbations could even lead beneficial perturbations to drive strong nonlinear effects that eventually produce local extinction (e.g. consumer increases in a consumer–resource interaction can lead to overshoot and dangerously low densities).

Figure 1. (a) The empirical relationship between body size and population growth rate ($r_{max}$) shows the existence of slow–fast life histories (e.g. Savage et al. [1]). (b) In our consumer–resource model, we use the parameter $\varepsilon$ to scale the consumer’s growth rate to replicate the empirical relationship between body size and growth rate. $\varepsilon$ scales the consumer equation such that the consumer growth rate decreases with increasing $1/\varepsilon$, producing a fast to slow life-history continuum. This method simultaneously holds the isocline arrangement constant and so is an experiment that changes ‘life-history speed’ in and of itself. (c) To explore the impacts of life-history speed, we will examine how slowing the consumer’s life history through $1/\varepsilon$ impacts the stability of the C–R interaction (using coefficient of variation (CV)). Stochastic perturbations, from white to reddened, will be added to the consumer. Because we know that the underlying deterministic skeleton interacts with noise in different ways [5,6], we will manipulate the consumer energy flux via the efficiency parameter ($e$) to produce the non-excitatory (i.e. real eigenvalues, monotonic dynamics) and excitable (i.e. complex eigenvalues, oscillatory decay dynamics) deterministic skeletons.
Box 1. Key terms and definitions.

Deterministic skeleton: The deterministic skeleton mathematically describes the processes of interest in the system being modelled. These are usually a dynamical system (e.g. ordinary differential equation or difference equations) and are effectively the model without stochastic processes [21].

Noise/Stochasticity: In ecology, noise is considered to be whatever we do not understand in the system [21,22]. Modellers add stochastic (random) noise to the deterministic skeleton. The interaction between the deterministic skeleton and noise can generate radically different dynamical responses, providing key insights into ecological phenomena (see review by Coulson et al. [22]).

Red & white noise: Noise from time points close together that are similar to each other (positive autocorrelation) is classified as red noise. Red noise is the opposite of blue noise, where noise from time points close together are completely different (negatively autocorrelated). White noise lies between red and blue noise, that is, noise from time points close together are neither always similar nor always different (i.e. neither positively nor negatively autocorrelated).

Stability: Here, we define stability in terms of persistence where increasing the lower limit of population density away from zero increases stability/persistence (general stability in McCann [23]). Notably, the lower a population’s density is the greater the likelihood that a stochastic process can push it to local extinction. The coefficient of variation (CV) is a common theoretical and empirical metric that normalizes standard deviation relative to the mean and so is a good metric for general stability (see figure 1c and [24,25]). A high standard deviation relative to a low mean means that the population necessarily attains a very low density where risk of collapse is high.

Non-local nonlinear dynamics: Nonlinear dynamics occur in systems that react disproportionately to initial conditions or a small perturbation. These dynamics can include chaos and limit cycles. In this study, we differentiate between local and non-local nonlinear dynamics. Local nonlinear dynamics are dynamics when system trajectories are close to the equilibria in phase space. Non-local nonlinear dynamics are dynamics when system trajectories are far from equilibria.

Quasi-cycle: Quasi-cycles are a type of dynamic behaviour that occur when stochasticity resonates with damped oscillations surrounding an interior equilibrium [5,21,26]. Frequencies in the stochastic noise that most closely resemble the period of the damped oscillations are amplified. Thus, a power spectrum would show all frequencies with the frequency of the damped oscillations having the highest power [5].

Quasi-canard: Quasi-canards are another type of dynamic behaviour that occur when stochasticity induces a pattern similar to a deterministic canard. A deterministic canard occurs when a system’s solution follows an attracting state space area (manifold), passes over a critical point along this manifold, and then follows a repelling manifold [27]. In the C–R model, the canard solution slowly follows the resource isocline (the attracting manifold) until the maximum point of the isocline is reached (the critical point), then the solution quickly jumps to the consumer axis before slowly following the consumer axis (the repelling manifold). Finally, the solution quickly jumps back to the resource isocline and repeats the canard cycle. When stochasticity is introduced, trajectories combine both small oscillations around the equilibria and large relaxation oscillations qualitatively similar to deterministic canards. Generally, these patterns are called mixed mode oscillations [27]. However, we use the term quasi-canards in this study to evoke the importance of stochastic noise similar to the importance of stochastic noise in quasi-cycles.

collective theoretical results suggest a complex range of dynamical responses that demand further understanding.

Towards understanding the complex responses of stochastic models, Higgins et al. [29] pointed out that the dynamics of an underlying deterministic model are critical to understanding the full stochastically forced model. Through decomposing a stochastic population model of Dungeness crab into a deterministic model (the deterministic skeleton, see box 1) and a stochastic process, Higgins et al. [29] found that empirical observations matched the novel responses produced from the interaction of the density-dependent dynamics and stochasticity. Similarly, the qualitatively different dynamics of the deterministic consumer–resource (C–R) model can explain the qualitatively different stochastic dynamics. For example, weakly interacting deterministic C–R models are known to produce non-excitable monotonic dynamics (i.e. the deterministic equilibrium is stable with real eigenvalues) that when perturbed tend to simply produce noisy equilibrium dynamics [5,6]. As the stochastic dynamics suggest, the monotonic deterministic skeleton is aptly named ‘non-excitable’. By contrast, as the C–R interactions are strengthened, the deterministic equilibrium begins to show excitable dynamics with decaying cycles to the equilibrium (i.e. the deterministic equilibrium is stable with complex eigenvalues). Here, stochastic perturbations now tend to excite the underlying density-dependent frequencies of the deterministic C–R skeleton, producing stochastic cycles or quasi-cycles [6]. Again, the dynamics of the underlying deterministic skeleton is critical to understanding the full stochastic model.

Here, toward synthesizing the responses of slow–fast life histories to perturbations, we examine how stability (i.e. defined as the coefficient of variation (CV) [24,25]) is influenced by life-history speed along the slow–fast continuum. Specifically, we examine the C–R interaction—a fundamental building block of whole communities—because it has been well described by allometric arguments that are conducive to slow–fast theory [30,31]. We alter the consumer’s life-history speed using a common mathematical scaler ($\varepsilon$) employed for the analysis of slow–fast mathematical systems [32,33]. The parameter, $\varepsilon$, allows us to mimic known variation in growth rates (figure 1a,b) and to alter the life-history speed while maintaining the underlying qualitative dynamical conditions (i.e. the isocline geometry of the C–R model is preserved when changing $\varepsilon$ alone). We employ this model over a range of white to
red noise perturbations (figure 1c). Finally, we vary the C–R interaction strength (i.e. energy flux via consumer conversion efficiency, \(e\)) to explore both the non-excitable and the excitable deterministic skeletons (figure 1c). In doing so, we cover a broad range in the underlying deterministic skeleton and seek a general answer to the role that slow–fast life histories play in stability. Overall, we show that life-history speed drives a range of stability responses to noise. In particular, slow life histories are especially sensitive to non-local nonlinear dynamics and population disappearances when perturbed by reddened noise.

2. Methods

(a) Model

In this study, we used the classic Rosenzweig–MacArthur consumer–resource (C–R) model

\[
\frac{dR}{dt} = R \left( 1 - \frac{R}{K} \right) - \frac{aRC}{1 + aR},
\]

and

\[
\frac{dC}{dt} = aRC \left( 1 + aR \right) - mC,
\]

where \(r\) is the intrinsic growth rate of the resource (\(R\)), \(K\) is the carrying capacity of the resource, \(a\) is the attack rate of the consumer (\(C\)), \(e\) is the efficiency or conversion rate of consumed resources into new consumers, \(h\) is the handling time and \(m\) is the consumer mortality.

Previous exploration has illustrated the multiple bifurcations and different dynamics of this model [16,34]. The bifurcations are dictated by the ratio of energy entering and exiting the consumer (the relative energy flux of the consumer as defined by [16]). This energy flux can be shown as an equation:

\[
d_{ae} = \frac{kae}{m}.
\]

As the energy entering the consumer increases relative to the energy exiting the consumer (the numerator of (2.3) increases relative to the denominator), the first bifurcation is a transcritical bifurcation (switching of stable points) creating a stable interior equilibrium (see figure 1b). As first, this equilibrium is monotonic but it then exhibits damped oscillations. The next bifurcation is a Hopf bifurcation (the stable interior equilibrium becomes unstable) leading to periodic cycling. The mathematics underlying the shift from monotonic to damped oscillations for the stable interior equilibrium is a shift in eigenvalues from real (no imaginary part) to complex (with an imaginary part). Gellner et al. [6] termed these two regions the non-excitable region and the excitable region respectively (see figure 1c). In all analyses below, we vary energy flux by manipulating \(e\) while keeping \(k\), \(a\), and \(m\) constant.

Now, to manipulate the life history of the consumer, we added the parameter \(e\) to the consumer equation. The consumer is fast when \(e \sim 1\) and slow when \(e \ll 1\).

\[
\frac{dC}{dt} = e \left( \frac{aRC}{1 + aR} - mC \right).
\]

Because \(e\) scales the consumer’s intrinsic growth rate (\(e\eta_{\text{max}} - m\) where \(\eta_{\text{max}}\) is \(1/h\); see electronic supplementary material, Section ‘Scaling of the consumer growth rate by \(e\)’ but preserves the isoline geometry of the C–R model, we can manipulate the life history of the consumer along a slow–fast continuum (relative to the resource) (figure 1a,b) while controlling the underlying deterministic skeleton.

For all analyses, \(r = 2.0\), \(k = 3.0\), \(a = 1.1\), \(h = 0.8\) and \(m = 0.4\).

(b) Stability along the slow–fast continuum

We used the CV to measure stability as the consumer’s life history was varied from fast to slow (1/\(e\) was varied from 1.0 to 1000). We used a flow–kick approach to add stochasticity (versus a stochastic ordinary differential equation approach) [35]. In this flow–kick approach, we kick the consumer variable every unit of time and let the model flow (integrate) without noise until the next kick. The kick is generated from normally distributed noise (with mean 0.0 and standard deviation 0.01). For each value of 1/\(e\), we ran 50 simulations of 24,000 time units (package DifferentialEquations.jl v. 6.20.0, Algorithms: Vern7 & Rodas4 with automatic stiffness detection [36]). From these simulations, for each value of 1/\(e\), we calculated the average CV after removing the first 2000 time units. We did this for the efficiency values (\(e\) of 0.5 (non-excitable deterministic dynamics with real eigenvalues) and 0.71 (excitable deterministic dynamics with complex eigenvalues)). Note, any simulations that landed on the axis solution were removed from the average CV calculation. The axis solution is where the resource isoline intersects the consumer = 0 axis or in other words, where the consumer goes extinct and the resource is at its carrying capacity.

To unpack the CV result as the consumer’s life history is slowed, we examined the dynamical behaviours that drove the change in CV. Three general dynamical behaviours occur depending on whether the C–R interaction is excitable (complex eigenvalues) or non-excitable (completely real eigenvalues; see figure 2a). The first dynamical behaviour is quasi-cycling and occurs only when the C–R interaction is excitable (see box 1 and figure 2b). Quasi-cycling occurs when stochastic perturbations resonate with the excitability of the C–R model to extend the range of cyclic dynamics (see box 1 and [5,6]). Compared to the deterministic limit cycles, these quasi-cycles generally do not threaten persistence because quasi-cycles exhibit small variation. Nevertheless, because slowing the consumer’s life history reduces the excitability of the C–R interaction (see electronic supplementary material, Section ‘Slowing the consumer decreases excitability’), we may see an impact of slowing the consumer’s life history on the stability (CV) of the C–R interaction. The second dynamical behaviour is quasi-canards which can happen for both excitable and non-excitable C–R interactions (see box 1 and figure 2b). A quasi-canard is similar to a deterministic canard, which is a type of relaxation oscillation. This deterministic canard occurs after the Hopf bifurcation (i.e. at a phase plane position to the left of the resource isoline maximum) and does not require stochastic noise [33]. By contrast, a quasi-canard occurs before the Hopf bifurcation (i.e. at a phase plane position to the right of the resource isoline maximum) and requires stochastic noise (see box 1). The stochastic noise combined with the slow life history increases the occurrence of visits to the relaxation oscillator. Because quasi-canard trajectories are quite large, stability will decrease markedly (i.e. CV will increase). The third dynamical behaviour is what we term stretched wandering and occurs for non-excitable C–R interactions only (see figure 2b). The dynamics are stretched along the resource isoline with no obvious cycling.

(c) Quasi-cycles

To examine how slowing the consumer’s life history impacted quasi-cycles, we ran 100 simulations each of the C–R model with 1/\(e\) values of 1 and 10 and where, again using the flow–kick approach, the consumer variable was perturbed every time unit with normally distributed noise (with mean 0.0 and standard deviation 0.01) (package DifferentialEquations.jl v. 6.20.0, Algorithms: Vern7 & Rodas4 with automatic stiffness detection [36]). To examine the initial decrease in CV as the consumer’s life history was slowed, we chose 1/\(e\) values of 1 and 10. We calculated the autocorrelation of the last 1000 time units of each simulation for lags between 0 and 40 (function autocor, package StatsBase v.0.33.13; see https://github.com/JuliaStats/StatsBase.jl). The lag is the number of time
units that the original time series is shifted to calculate the autocorrelation. We then calculated the average autocorrelation value for each lag across the 100 simulations for each set up with a different $1/e$ value. We did this for the efficiency values ($e$) of 0.5 (non-excitable) and 0.71 (excitable). As suggested by Pineda-Krch et al. [5], we used autocorrelation to identify the occurrence of quasi-cycles. An autocorrelation function (ACF) generated from quasi-cycles would show pronounced amplitude oscillations that decrease in amplitude with increasing lags. No oscillations in the ACF indicate that quasi-cycles are not occurring and constant ACF oscillations indicate noisy period cycling. An ACF with smaller damped oscillations indicates that the periodicity of the quasi-cycles is being removed. Note that in our ACF figures, the mean of each time series was removed from each time point value. Thus, our ACF figures look different (our ACF scale goes from 0.95 to 1) whereas the scale used by Pineda-Krch et al. [5] goes from 0.95 to 1. Our method makes spotting the damped oscillations easier.

(d) Quasi-canards

To examine how slowing the consumer’s life history impacted quasi-canards, we examined the prevalence of quasi-canards in stochastically perturbed simulations of the C–R model with varying $e$ and efficiency values. First, we examined the prevalence of quasi-canards under white noise stochasticity. We ran 1000 simulations with 24,000 time units for each value of $1/e$ varied from 6.667 to 1000, where, using the flow–kick approach, the consumer variable was perturbed every time unit with normally distributed noise (with mean 0.0 and standard deviation 0.01) (package DifferentialEquations.jl v. 6.20.0, Algorithms: Vern7 & Rodas4 with automatic stiffness detection [36]). We used an autoregressive model of order 1 (AR1) to create reddened noise with autocorrelation varying from 0 (white noise) to 1 (red noise). We scaled the variance of the noise to the variance from the original white noise using the technique in Wichmann et al. [37] where the ratio of white noise to red noise variances scales individual noise values in the red noise sequence.

All analyses were done using julia v. 1.7.0. [38]

3. Results

(a) Stability along the slow–fast continuum

When the C–R model is non-excitable ($e = 0.5$), slowing the consumer’s life history increases the CV (figure 3). Slowing

![Figure 2](http://example.com/figure2.png)

Figure 2. (a) Table of dynamical behaviours when the C–R interaction is non-excitable and excitable and when the consumer’s life history is fast or slow. (b) Phase diagrams and time series of quasi-cycles (yellow), quasi-canards (purple) and stretched wandering (green). The orange and blue curves in the top row are the consumer and resource isoclines, respectively. Dashed vertical lines in the phase diagrams denote where the deterministic Hopf bifurcation occurs. Note, the standard deviation of the noise was increased to 0.05 to help emphasize what quasi-cycles, quasi-canards and stretched wandering look like.
the consumer's life history changed the dynamical behaviour from stretched wandering to quasi-canards. When the C–R is highly excitable (ε = 0.71), slowing the consumer's life history initially decreases then increases the CV (figure 3). Reducing life-history speed is first modestly stabilizing, in effect removing the oscillatory potentials of the underlying excitable model. Further slowing of life history generates large increases in CV that likely produce population disappearances (R ≈ 0 during trajectories) due to quasi-canards.

(b) Quasi-cycles

When the C–R model is non-excitable (ε = 0.5), quasi-cycles are never found regardless of how slow the consumer's life history is (figure 4a,e,f). By contrast, when the C–R model is highly excitible (ε = 0.71) quasi-cycles are found when 1/ε = 1.0 (figure 4b,d). With a slowing of the consumer's life history (now 1/ε = 10), the average autocorrelation function (ACF) line flattens out, indicating reduced manifestation of quasi-cycles (figure 4b,f).

(c) Quasi-canards

When the C–R model is non-excitible (ε = 0.5), quasi-canards can be found under white noise but require a very slow consumer life history (figure 5a). When the C–R model is highly excitible (ε = 0.71), quasi-canards can be easily found along the gradient of fast to slow consumer life histories (figure 5b). Reddening the noise increases the likelihood of finding both quasi-canards and the axial solution regardless of the consumer's life history (figure 5c,d,e,f). Note that for a highly excitable C–R interaction, landing on the axial solution is less likely than for a non-excitible C–R interaction because there is more phase space that the dynamics must traverse through. Slowing the consumer's life history down increases the likelihood of the highly excitible C–R interaction landing on the axial solution.

4. Discussion

Using the simple technique of changing the time scales within the Rosenzweig–MacArthur consumer–resource (C–R) model, we set up a biologically motivated mathematical experiment exploring the stability of faster and slower consumer life histories under white to red stochastic noise. Here, we experimentally manipulated the consumer's intrinsic growth rate while maintaining the underlying qualitative dynamical conditions. When the energy flux is high, we find that initially slowing the consumer's life history increased stability through reduced manifestation of quasi-cycles (alternatively, when energy flux is low, slowing the consumer's life history always decreased stability). However, further slowing the consumer's life history decreased stability through increasing the likelihood of quasi-canards and population disappearances. Furthermore, we found that increasing the autocorrelation of noise tended to increase the likelihood of quasi-canards and population disappearances. Finally, Yodzis & Innes's [30] biologically plausible C–R model similarly exhibits quasi-canards (see electronic supplementary material, Section 'Biologically plausible parameters' & electronic supplementary material, figure S5). Consequently, our results are general and suggest that such instability ought to occur under increasingly reddened perturbations arising from climate change.

Our results illuminate a gradient in stability along the slow–fast life-history continuum that is dependent on energy flux. If the C–R interaction is highly excitible, initial slowing of the consumer's life history can increase stability. Stability increases because slowing the consumer reduces the excitability of the C–R interaction, which reduces the manifestation of the quasi-cycles (see electronic supplementary material, Section 'Slowing the consumer decreases excitability'). If the C–R interaction is non-excitible or moderately excitible, initial slowing of the consumer's life history decreases stability (although slowing the consumer's life history does reduce quasi-cycles for the moderately excitible C–R interaction). Here, perturbations push a slow growth consumer away from the equilibrium and thus the CV continually increases. For all types of C–R interaction, when the consumer's life history is sufficiently slow, additional perturbations multiply the effect of each perturbation, resulting in a consumer biomass that is 'far from equilibrium' and prone to the distant nonlinear effects of the C–R dynamics (i.e. the quasi-canard). Overall, there appears to be a gradient in stability along the slow–fast life-history continuum that is mediated by energy flux.

The combination of life history and red noise significantly increased the opportunities for non-local nonlinear dynamics to be expressed. Reddening the noise in our C–R model increased the likelihood of quasi-canards (and landing on the axial solution) for both fast and slow organisms. Furthermore, the onset of quasi-canards occurred with less autocorrelation for faster organisms. To understand this pattern, we must examine the relative time scales of the autocorrelation and the system population processes [21]. Slowing the life history is effectively increasing the time scale of the population response processes, and thus the system will stay for longer in the phase space region that the system was pushed into after a perturbation. Increasing the autocorrelation increases the time scale of the perturbations, and thus the perturbations are effectively magnified over time.

To unpack the idea of the magnification of the perturbations, we can use similar research on how multiple discrete disturbances can kick dynamics out of basins of attraction to produce different dynamical outcomes (flow–kick dynamics: Meyer et al. [35]). In the flow–kick framework,
models are kicked at discrete time points and are allowed to flow (integrate) without kicks in between the discrete time points. Meyer et al. [35] found that rare but large disturbances can have the same effect as frequent and small disturbances. Reddened noise is technically lots of frequent and small disturbances (the kicks in flow–kick dynamics). But because of the autocorrelation pushing dynamics far from their attracting equilibria, reddened noise has the same effect as a large disturbance. Furthermore, slowing life histories reduces the relative time available for organisms to respond to the disturbances (the flow in flow–kick dynamics), thus pushing dynamics far from their attracting equilibria.

Overall, we can use the analogy of a rusty ratchet to understand how slow life histories and reddened noise interact. White noise is akin to a ratchet that can spin in any direction (without a pawl), and red noise is akin to a ratchet with a pawl that can spin in only one direction for a period of time (figure 6). Because the reddened noise has a tendency to produce similar values for a period of time, reddened noise consistently pushes the dynamics of the C–R model far from the local area around the stable equilibrium. Whereas the fast life history is akin to oil in the ratchet, the slow life history is akin to rust in the ratchet that slows the spinning speed and thus increases the time required for trajectories to return to the local area around the equilibrium. To describe this process, we use the term 'noise-induced ratchet effects' inspired by the rate-induced critical transition literature [39,40]. In a rate-induced critical transition, canards can be produced when the equilibrium shifts at a slow rate. The dynamics enter non-local nonlinear dynamics because the equilibrium has been pulled from under the dynamics. For the quasi-canard, the dynamics enter non-local nonlinear dynamics because the dynamics have been pushed by the noise (thus quasi-canards are noise-induced critical transitions). When slow life histories are combined with red noise, we get noise-induced ratchet effects.

Our finding that slow life histories with stochasticity can exhibit sudden population disappearances is a further example of how stochasticity is immensely useful in ecological research to understand the full nonlinear dynamics of

![Figure 4](https://example.com/figure4.png)
First, stochasticity can act to uncover underlying processes (Boettiger [21] coined the phrase noise the informer for this phenomenon). Similar to quasi-cycles where stochastic resonance is visible in advance of a Hopf bifurcation, the quasi-canards also occur in advance of the Hopf bifurcation after which deterministic canards occur. Although noise has the same effect of uncovering an imminent Hopf bifurcation leading to either deterministic cycles or canards, the mechanisms producing the quasi-cycles and quasi-canards are different. The quasi-cycles are created from stochasticity interacting with local nonlinear dynamics (excitability). The quasi-canards are created from slow life histories plus reddened noise pushing dynamics towards non-local nonlinear dynamics.

Second, stochasticity can cause different stability outcomes from what our normal linear stability analysis would predict. Indeed, linear stability analysis would not have predicted the highly destabilizing behaviour of slow consumers that we found. One method to reveal these differences in stability is through using the mathematical tools of the potential function or quasi-potential, which can be simplified conceptually to the ball and cup analogy [41]. In this analogy, the state of a system is the position of the ball rolling around a surface (the cup) with minima being attractors. The potential

![Figure 5](https://royalsocietypublishing.org/doi/10.1098/rspb.2022.2149)

**Figure 5.** (a,b) Proportion of 1000 simulations under white noise per value of $1/\varepsilon$ that exhibited quasi-canards with constant efficiency values of 0.5 (non-excitable) and 0.71 (excitable), respectively. Vertical dashed lines correspond to log$_{10}(1/\varepsilon)$ values used in (c,d,e,f). (c,d) Proportion of 1000 simulations per value of log$_{10}(1/\varepsilon) = 1.1$ that exhibited quasi-canards or axial solution or neither with constant efficiency values of 0.5 and 0.71, respectively, and with noise correlation (AR$_1$ process) varied from 0.0 to 0.9. (e,f) Proportion of 1000 simulations per value of log$_{10}(1/\varepsilon) = 2.4$ that exhibited quasi-canards or axial solution or neither with constant efficiency values of 0.5 and 0.71, respectively and with noise correlation (AR$_1$ process) varied from 0.0 to 0.9.

![Figure 6](https://royalsocietypublishing.org/doi/10.1098/rspb.2022.2149)

**Figure 6.** Illustration of simplified trajectories with white noise (top) and reddened noise (bottom) together with the consumer and resource isoclines and vector field when the consumer’s life history is slow ($1/\varepsilon$ is large). We use the analogy of a rusty ratchet to illustrate the interaction of slow life histories with reddened noise. White noise is similar to a ratchet wheel without the pawl (it can spin in any direction) and reddened noise is similar to a ratchet with the pawl (it can spin in only one direction for a period of time). Slow life history is akin to rust in the ratchet, which slows the spinning speed.

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and quasi-potential are the cup. The potential function can be found for any system that exhibits solely fixed point attractors (gradient systems). Quasi-potentials can be found for gradient and non-gradient systems (the C–R model is a non-gradient system because it exhibits cycling). The quasi-potentials for our model show the stretching of the quasi-potential along the resource isoline due to stochasticity with low efficiency and a fast consumer life history, then the quasi-canard shape when efficiency is large enough, and finally the flattingen of the quasi-potential quasi-canard shape with a slow consumer life history (see electronic supplementary material, figure S6). Linear stability analysis would solely focus on the tiny region around the intersection of the consumer and resource isolines. By contrast, the flattened quasi-potentials reveal other possible dynamics (quasi-canards) in addition to the stable interior equilibrium. Overall, stochasticity can reveal dynamical outcomes not predicted by normal linear stability analysis.

5. Conclusion
By varying growth rates along the slow–fast life-history continuum within the classic Rosenzweig–MacArthur model, we have shown that life history has interesting stability consequences for the system. Slowing the life history can initially increase stability up to a point in the face of many tiny perturbations, but further slowing can dramatically decrease stability and increase the potential for highly variable dynamics and population disappearances. Noise-induced ratchet effects occur when positively correlated noise is added to an already slowed consumer. This noise-induced ratchet effect is another mechanism that selects against slow life histories leading to greater proportions of species with fast life histories. Our study examines a single C–R interaction, which is a fundamental component of food web theory. Moving forward, the interaction of many more organisms with varying life histories is required for a more comprehensive understanding of life history and stability. Furthermore, other examples of non-local nonlinear dynamics should be explored, especially in the context of slow life histories and reddened noise. Taken together, we have shown how life history along the slow–fast life-history continuum can impact the stability of systems and shown how human-caused reddened noise will disproportionately impact slow living organisms through noise-induced ratchet effects and population disappearances.

Data accessibility. All code to reproduce the above analyses and figures is publicly available on GitHub and has been archived on Zenodo (version 2.0).

Supplementary material is available online [42].

References

1. Savage VM, Gillooly JF, Brown JH, West GB, Charnov EL. 2004 Effects of body size and temperature on population growth. Am. Nat. 163, 429–441. (doi:10.1086/381872)
2. Gaillard J-M, Yoccoz NG, Lebreton J-D, Bonenfant C, Réale D, Garant D, Humphries MM, Bergeron P, Ollason B, Pintelon D, Allaine D. 2005 Generation time: A reliable metric to measure life-history variation among mammalian populations. Am. Nat. 166, 119–123. (doi:10.1086/40330)
3. Réale D, Garant D, Humphries MM, Bergeron P, Caneu V, Montégier P-O. 2010 Personality and the emergence of the pace-of-life syndrome concept at the population level. Phil. Trans. R. Soc. B 365, 4051–4063. (doi:10.1098/rstb.2010.0208)
4. Healy K, Ezard THG, Jones DR, Salguero-Gómez R, Buckley YM. 2019 Animal life history is shaped by the pace of life and the distribution of age-specific mortality and reproduction. Nat. Ecol. Evol. 3, 1217–1224. (doi:10.1038/s41559-019-0938-7)
5. Pineda-Krch M, J. Blok H, Dieckmann U, Doebeli M. 2007 A tale of two cycles – distinguishing quasi-cycles and limit cycles in finite predator–prey populations. Oikos 116, 53–64. (doi:10.1111/j.2006.0030-1299.19494.x)
6. Gellner G, McCann KS, Hastings A. 2016 The duality of stability: towards a stochastic theory of species interactions. Theor. Ecol. 9, 477–485. (doi:10.1007/s12080-016-0303-2)
7. Peters RH. 1984 The ecological implications of body size. Cambridge, UK: Cambridge University Press.
8. Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. 2004 Toward a metabolic theory of ecology. Ecology 85, 1771–1789. (doi:10.1890/03-900)
9. Lenten TM, Dakos V, Bathiany S, Scheffer M. 2017 Observed trends in the magnitude and persistence of monthly temperature variability. Sci. Rep. 7, 5940. (doi:10.1038/s41598-017-06382-x)
10. Di Cecco GJ, Gouhier TC. 2018 Increased spatial and temporal autocorrelation of temperature under climate change. Sci. Rep. 8, 14850. (doi:10.1038/s41598-018-33217-0)
11. Audzijonyte A et al. 2016 Trends and management implications of human-influenced life-history changes in marine ectotherms. Fish Fish 17, 1005–1028. (doi:10.1111/faf.12156)
12. Cout J, Marjäkangas E-L, Santangeli A, Kääls JA, Lindström Å, Lehtikalais A. 2022 Short-lived species move uphill faster under climate change. Oecologia 198, 877–888. ( doi:10.1007/s00442–021–05094–4)
13. Stone L. 1993 Period-doubling reversals and chaos in simple ecological models. Nature 365, 617–620. (doi:10.1038/365617a0)
14. Gellner G, McCann KS. 2016 Consistent role of weak and strong interactions in high- and low-diversity trophic food webs. Nat. Commun. 7, 11180. (doi:10.1038/ncomms11180)
15. Gaston KJ, Lawton JH. 1988 Patterns in body size, population dynamics, and regional distribution of bracken herbivores. Am. Nat. 132, 662–680. (doi:10.1086/284881)
16. Rip JM, McCann KS. 2011 Cross-ecosystem differences in stability and the principle of energy flux. Ecol. Lett. 14, 733–740. (doi:10.1111/j.1461-0248.2011.01636.x)
17. MäkJévová M, de Bello F, Dalečal J, Lepš J. 2014 Plant functional traits as determinants of population stability. Ecology 95, 2369–2374. (doi:10.1890/13-1880.1)
18. Röpke C, Pires THS, Zuanon J, Freitas CEC, Hernandes MC, Souza F, Amadio S. 2021 Growth–reproduction trade-off and fecundity regulate population stability in Amazon floodplain fishes. Freshwater Biol. 66, 1101–1109. (doi:10.1111/fwb.13702)
19. Saether B-E et al. 2013 How life history influences population dynamics in fluctuating environments. Am. Nat. 182, 743–759. (doi:10.1086/673497)
20. Gamelon M, Gimenez O, Baubet E, Coulson T, Tuljapurkar S, Gaillard J-M. 2014 Influence of life-
history tactics on transient dynamics: a comparative analysis across mammalian populations. *Am. Nat.* **184**, 673–683. (doi:10.1086/677929)

21. Boettiger C. 2018 From noise to knowledge: how randomness generates novel phenomena and reveals information. *Ecol. Lett.* **21**, 1255–1267. (doi:10.1111/ele.13085)

22. Coulson T, Rohani P, Pascual M. 2004 Skeletons, noise and population growth: the end of an old debate? *Trends Ecol. Evol.* **19**, 359–364. (doi:10.1016/j.tree.2004.05.008)

23. McCann KS. 2000 The diversity-stability debate. *Nature* **405**, 228–233. (doi:10.1038/35012234)

24. Garibaldi LA, Aizen MA, Klein AM, Cunningham SA, Harder LD. 2011 Global growth and stability of agricultural yield decrease with pollinator dependence. *Proc. Natl Acad. Sci. USA* **108**, 5909–5914. (doi:10.1073/pnas.1012431108)

25. Hsieh C, Reiss CS, Hunter JR, Beddington JR, May RM, Sugihara G. 2006 Fishing elevates variability in population growth: the end of an old debate? *Science* **313**, 1431–1435. (doi:10.1126/science.1137.1431)

26. Hastings A, Abbott KC, Cuddington K, Francis TB, Lai Y-C, Morozov A, Petrovskii S, Zeeman ML. 2021 Stochastic dynamics and deterministic skeletons: population behavior of dangerous crab. *Science* **376**, 1431–1435. (doi:10.1126/science.376.5317.1431)

27. Touboul J, Krupa M, Desroches M. 2015 Noise-induced canard and mixed-mode oscillations in ecological time. *SIAM Rev.* **57**, 2017. (doi:10.1137/140990528)

28. Schwager M, Johst K, Jeltsch F. 2006 Does red noise increase or decrease extinction risk? Single extreme events versus series of unfavorable conditions. *Am. Nat.* **167**, 879–888. (doi:10.1086/503609)

29. Higgins K, Hastings A, Sarvela JN, Botsford LW. 1997 Stochastic dynamics and deterministic skeletons: population behavior of dangerous crab. *Science* **276**, 1431–1435. (doi:10.1126/science.276.5317.1431)

30. Yodzis P, Innes S. 1992 Body size and consumer-resource dynamics. *Am. Nat.* **139**, 1151–1175. (doi:10.1086/285380)

31. Brose U, Williams RJ, Martinez ND. 2006 Allometric scaling enhances stability in complex food webs. *Ecol. Lett.* **9**, 1228–1236. (doi:10.1111/j.1461-0248.2006.00978.x)

32. Hsu T-H, Wolkowicz GSK. 2020 A criterion for the existence of relaxation oscillations with applications to predator-prey systems and the existence of canard solutions. *J. Math. Biol.* **80**, 39–60. (doi:10.1007/s00285-019-01337-4)

33. Poggiale J-C, Aldebert C, Girardot B, Kooi BW. 2020 Analysis of a predator-prey model with specific time scales: a geometrical approach proving the occurrence of canard solutions. *J. Math. Biol.* **80**, 39–60. (doi:10.1007/s00285-019-01337-4)

34. Rosenzweig ML. 1971 Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* **171**, 385–387. (doi:10.1126/science.171.3969.385)

35. Meyer K, Hoyer-Leitzel A, Iams S, Klasky I, Lee V, Ligtenberg S, Bussmann E, Zeeman ML. 2018 Quantifying resilience to recurrent ecosystem disturbances using flow-kick dynamics. *Nat. Sustain.* **1**, 671–678. (doi:10.1038/s41893-018-0106-2)

36. Rackauckas C, Nie Q. 2017 Differentialalequations.jl—a performant and feature-rich ecosystem for solving differential equations in Julia. *J. Open Res. Software* **5**, 15. (doi:10.5334/jors.151)

37. Wichmann MC, Johst K, Schwager M, Blasius B, Jeltsch F. 2005 Extinction risk, coloured noise and the scaling of variance. *Theor. Pop. Biol.* **68**, 29–40. (doi:10.1016/j.tpb.2005.03.001)

38. Beznosov J, Edelman A, Karpinski S, Shah VB. 2017 Julia: A fresh approach to numerical computing. *SIAM Rev.* **59**, 65–98. (doi:10.1137/141000671)

39. Siteur K, Eppinga MB, Doelman A, Siero E, Rietkerk M. 2016 Ecosystems off track: rate-induced critical transitions in ecological models. *Oikos* **125**, 1689–1699. (doi:10.1111/oik.03112)

40. Vanselow A, Wieczorek S, Feudel U. 2019 When slow is too fast - collapse of a predator-prey system. *J. Theor. Biol.* **479**, 64–72. (doi:10.1016/j.jtbi.2019.07.008)

41. Nolting BC, Abbott KC. 2016 Balls, cups, and quasi-potentials: quantifying stability in stochastic systems. *Ecology* **97**, 850–864. (doi:10.1890/15-1047.1)

42. Greyson-Gaito CJ, Gellner G, McCann KS. 2023 Life-history speed, population disappearances and noise-induced ratchet effects. *Figshare*. (doi:10.6084/m9.figshare.c.6460983)