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Irregular timing of population cycles

Jonathan E. Rubin¹, David J. D. Earn², Priscilla E. Greenwood³, Todd L. Parsons⁴, and
Karen C. Abbott⁵

¹Department of Mathematics, Center for the Neural Basis of Cognition, University of
Pittsburgh, Pittsburgh, PA, USA

²Department of Mathematics & Statistics, McMaster University, Hamilton, Ontario,
Canada

³Department of Mathematics, University of British Columbia, Vancouver, British
Columbia, Canada

⁴Laboratoire de Probabilités, Statistique et Modélisation (LPSM), Sorbonne Université,
CNRS UMR 8001, Paris, France

⁵Case Western Reserve University, Cleveland, Ohio, USA

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Abstract

1
2 Despite considerable study of population cycles, the striking variability of cycle periods in many
3 cyclic populations remains largely unexplained. Mathematical models of cyclic population
4 dynamics seem to exhibit much greater regularity in cycle periods than many real populations,
5 even when accounting for environmental stochasticity. We contend, however, that recent
6 advances in understanding the origins of long transient dynamics point the way to a previously
7 unrecognized means by which environmental stochasticity can create cycle period variation.
8 Specifically, consumer-resource cycles that bring the populations near a saddle point (a
9 combination of population sizes toward which the populations tend, before eventually
10 recovering away) may be subject to a slow passage effect that has been dubbed a saddle crawlby.
11 In this study, we illustrate how stochasticity that generates variability in how close predator and
12 prey populations come to saddles can result in substantial variability in the durations of
13 crawlbys and, as a result, in the periods of population cycles. Our work suggests a new
14 mechanistic hypothesis to explain a significant factor in the irregular timing of population
15 cycles and provides a basis for understanding when environmental stochasticity is, and is not,
16 expected to generate cyclic dynamics with variability across periods.

Introduction

17

18 Recurrent population cycles – eruptive increases and crashes in population size – are
19 widespread (Kendall et al. 1999, Barraquand et al. 2017). Consumer-resource and host-enemy
20 interactions are famously known to promote cycles (Turchin and Hanski 2001, Myers 2018), but
21 models of these interactions predict a far more regular cycle period than is observed in many
22 real cyclic populations (Dwyer et al. 2004). The more irregular timing of some cycles is difficult
23 to explain. While it is tempting to implicate environmental stochasticity, the intrinsic period of
24 ecological cycles appears to be surprisingly robust to noise. Past theoretical studies have shown
25 that although white noise readily generates variance in cycle amplitudes, it has little effect on
26 the regularity of the cycle period (Dwyer et al. 2004, Greenman and Pasour 2011). As such,
27 other mechanisms, such as chaos, stochastic transitions between alternative attractors, and
28 resonance between intrinsic cycles and seasonal forcing, have been invoked to explain the
29 irregular timing of some population cycles (Dwyer et al. 2004, Nguyen and Rohani 2007, Ives
30 et al. 2008, Greenman and Pasour 2011, Benincà et al. 2015). These alternative ideas are
31 convincing and no doubt play an important role in some ecological systems. Still, the ubiquity
32 of environmental stochasticity makes it appealing as a parsimonious and perhaps more general
33 explanation for other, unexplained instances of cycle period variability. Though we know from
34 counter-examples (e.g. Dwyer et al. 2004, Greenman and Pasour 2011) that environmental
35 stochasticity *may* not cause significant variance in cycle period, we do not know that it *cannot*
36 cause such variance, so we contend that it deserves a closer look.

37 In this paper, we reconsider the possibility that the irregular timing of population cycles can
38 originate from the interaction between density-dependent consumer-resource interactions and
39 certain forms of parametric noise, motivated by recent advances in the understanding of
40 ecological transient dynamics (Hastings et al. 2018), which suggest a particular mechanism that
41 may strongly influence cycle timing. In addition to being prone to limit cycles,
42 consumer-resource models generally share another feature: the presence of saddle points at the
43 origin and at the resource carrying capacity in the absence of consumers (Murdoch et al. 2003).

44 If the consumer-resource cycle brings the population trajectory close enough to these saddle
45 points, then a long transient during which the populations remain near the saddle will result
46 (for an introduction to this role of saddle points, see e.g. Abbott 2020); this effect has been
47 termed a *saddle crawlby* (Hastings et al. 2018). The duration of the crawlby scales with the
48 distance from the saddle (Cushing et al. 1998, Jäger et al. 2008, Morozov et al. 2020). Therefore,
49 we conjecture that stochasticity that results in more variability from cycle to cycle in how close
50 the populations get to these saddles will produce higher variability in cycle timing. To explore
51 this possibility, we partition variance in the total duration of a cycle into variance in the
52 duration of its constituent parts, with particular interest in the times spent passing by and
53 moving between the saddles.

54 Our contributions come from acknowledging two important features of ecological dynamics.
55 The first is the potential role of saddle crawlbys in cycle period variation. Second, a frustrating
56 problem in population ecology is that there are many different aspects of an underlying
57 ecological process that may be influenced by stochasticity, but different stochastic models can
58 lead to very different dynamics (Allen and Allen 2003, Nisbet and Gurney 2003, Coulson et al.
59 2004, Vadillo 2019). With this in mind, we seek to understand whether environmental
60 stochasticity in different demographic parameters causes different levels of cycle period
61 variability, and whether any approach the degree of variability seen in real cyclic populations.

62 In this paper, we study the stochastic Rosenzweig-MacArthur predator-prey model
63 (Rosenzweig and MacArthur 1963) to understand the roles of saddle crawlbys and different
64 sources of environmental noise in generating variably timed population cycles. We find that
65 when stochasticity enters via a parameter that affects how close the cycle passes to saddle points
66 (e.g., the half saturation constant of the predator's functional response), the result is substantial
67 variation in how close the populations come to the saddle points in each cycle, leading to
68 variation in the duration of saddle crawlbys and thus variation in overall cycle period. In
69 contrast, stochasticity in parameters with no direct bearing on the proximity to saddles (e.g., the
70 prey's intrinsic population growth rate) tends to yield much more regular cycles. Our detailed
71 study of the effect of saddle crawlbys on cycle period leads both to a new proposed explanation

72 for irregularly timed cycles observed in nature and to an understanding of why past work has
73 seen little effect of stochasticity on cycle period variability.

74

Methods

75

Basic properties of cyclic populations

76 While a complete meta-analysis of cycle period variation is well beyond the scope of this study,
77 we do need a reasonable expectation for what levels of variation are realistic. Following Dwyer
78 et al. (2004), we measure cycle period variability by its coefficient of variation (CV). Dwyer et al.
79 (2004) report cycle period CVs ranging from 0.16 to 0.67 for a range of outbreaking forest
80 insects. We supplement these data with our own analysis of ecological time series from the
81 Global Population Dynamics Database (GPDD; NERC Centre for Population Biology 1999).
82 Beginning with the 664 GPDD time series analyzed by Sibly et al. (2007), we found that 459 had
83 at least 2 local maxima and showed some evidence of periodicity (the peak in true wavelet
84 power spectrum exceeded the average observed in 100 bootstrap trials). Of these 459, 47 (10.2
85 %) showed perfectly regular cycle periods (CV = 0). The remaining cycle period CVs ranged
86 from 0.10 to 0.98. Overall, the cyclic GPDD data had a mean cycle period CV of 0.30. This
87 analysis confirms that the cycle period CVs reported for forest insects in Dwyer et al. (2004) are
88 representative of other taxa as well.

89

Model formulation

90 We study cycles in a stochastic version of the Rosenzweig-MacArthur predator-prey model. The
91 underlying deterministic model is

$$\begin{aligned}\frac{dx}{dt} &= rx \left(1 - \frac{x}{K}\right) - \frac{axy}{x+h} \\ \frac{dy}{dt} &= \frac{abxy}{x+h} - my,\end{aligned}\tag{1}$$

92 where x is prey population density and y is predator population density. The prey population
93 grows at maximum rate r and would equilibrate to carrying capacity K in the absence of

94 predation. Predation occurs according to a Type 2 functional response (Holling 1965) with
95 maximum attack rate a and handling time whose effect is described by the half-saturation
96 constant, h . Predator population growth occurs at a rate proportional (described by b) to its
97 prey consumption rate, and predator death is density independent with rate m .

98 Our baseline parameter values are listed in Table 1. The implied time unit is most easily
99 interpreted via the mean predator lifetime, which is $1/m \simeq 1.67$ time units. These values result
100 in a limit cycle featuring close, but not too close, passage to the $x = 0$ and $y = 0$ axes and thus
101 to the saddle points of system (1) at $(x, y) = (0, 0)$ and $(K, 0)$. Close passage sets the stage for
102 saddle crawlby. To enforce a degree of biological realism, though, we omit from our analyses
103 any simulated cycles in which prey and/or predator dropped to very low densities. Although
104 models such as (1) allow recovery from infinitesimally small population densities, we recognize
105 that real populations below a certain size will almost certainly go extinct before recovering. We
106 used 10^{-5} times the prey carrying capacity as the extinction threshold, and chose our baseline
107 parameter set to achieve a low rate of crossing of this threshold unless the noise amplitude was
108 quite high. Imposing this extinction threshold ensures that crawlby effects that we observe in the
109 model are not merely artifacts of letting the system drop to unrealistically low population sizes.

110 To model different possible ways for environmental stochasticity to affect this interaction,
111 we replace individual parameters with a Cox-Ingersoll-Ross stochastic processes. That is, we
112 make any parameter p (where p is a stand-in for r, h, \dots) stochastic by modeling it as

$$dp = \gamma(\bar{p} - p)dt + \sigma\sqrt{\bar{p}}dW, \quad (2)$$

113 where W is a Wiener process and \bar{p} is the mean (i.e. baseline) value for the parameter. This
114 formulation prevents parameters from becoming negative and has been shown in past work to
115 have various mathematically desirable and biologically reasonable properties: it is
116 mean-reverting and has a positive temporal autocorrelation that decays exponentially (Allen
117 2016).

118 Although we have explored effects of noise in each of the parameters (results not shown),
119 we focus here on contrasting the effects of a noisy prey growth rate, r , versus a noisy predator

120 handling time, reflected by noise in h . This pair of parameters spans many interesting contrasts
121 (i.e. appearance in a linear versus only in a nonlinear term, a multiplier versus a denominator, a
122 rate in one species' equation versus both) and thus serves well to illustrate the impacts of
123 different sources of noise. We recognize that natural species interactions are not characterized
124 by a single stochastic demographic parameter, but modeling one parameter at a time as
125 stochastic allows us to isolate different putative effects of noise. Modeling noise only in r
126 approximates the situation where the prey's intrinsic growth rate is more sensitive to
127 environmental perturbations (e.g., fluctuations in temperature) than other processes. Noise in h
128 represents a situation where predator behavior or physiology (e.g., digestion rate) is the system
129 feature most sensitive to perturbations.

130 *Analyses*

131 We study our model numerically to answer a series of questions about the genesis of cycle
132 period variation. First, we study the deterministic model (equation (1)) to characterize the
133 impact of different model parameters on the cycle period. We do this by starting with the
134 baseline parameter set and varying one parameter at a time, focusing on each of r and h , to
135 isolate its effect. Although the deterministic model inevitably produces a constant cycle period
136 and we are of course interested in period variability, these results are useful for considering the
137 mechanisms through which noise in specific parameters may impact cycles.

138 Next, we study the stochastic model (equation (1) in which either r or h varies stochastically
139 according to equation (2)). Specifically, we compute the temporal CV in the simulated cycle
140 periods for different intensities of noise in each of the two parameters. We also partition the
141 cycle into a sequence of six segments (figure 1), **A**: passage by $(0,0)$; **B**: prey growth from near 0
142 to near K ; **C**: passage by $(K,0)$; **D**: predator growth and prey decline (that is, movement from
143 near $(K,0)$ toward the y -axis); **E**: the transition from predator growth to predator decline (i.e.
144 passage across the predator's nullcline); and **F**: finally, sharp predator decline to again approach
145 $(0,0)$. Our hypothesis that saddle crawlby's drive cycle period variability leads us to predict that
146 significant variance should be observed in the passage times near $(0,0)$ and $(K,0)$. We calculate

147 times spent transitioning through each of the six segments as the populations undergo a cycle,
148 based on times when trajectories cross partition entrance and exit boundaries at locations that
149 we specify in the (x, y) plane. The locations used for these boundaries for most of our
150 simulations are listed in Table B1 in Appendix B; for a few special cases with altered cycle paths
151 (cases 6-9 in Table 2), we used other boundaries. The boundary locations ensure that
152 fluctuations rarely cause spurious crossings, while even those orbits with relatively large
153 fluctuations do not miss any boundaries. Passage times through partition segments are
154 computed sequentially, with the exit boundary from one region also serving as the entrance
155 boundary for the next region (see figure 1). For example, once a trajectory exits a region
156 through its exit boundary, re-entry through the exit boundary due to stochasticity does not
157 count as another passage through the original region; rather, it is ignored, and the calculation of
158 the time of passage through the next region continues until that region's exit boundary is
159 crossed. This subdivision allows us to decompose the variance in the full cycle period based on
160 the variance in the time needed to complete each step.

161 All of our numerical results on stochastic dynamics represent averages derived from
162 simulations run for 20,000 time units. For each run, we discard an initial period extending from
163 time 0 up until the time of the first crossing of a boundary into any of our defined cycle
164 segments (figure 1). Each sample on which averaging is performed includes at least 400 cycles
165 during which population sizes stay above the extinction threshold.

166 Two additional analyses supplement our numerical results. First, we used small-noise
167 approximations to derive analytical relationships between certain model features and passage
168 times along the axes and near the saddle points. Due both to their extent and to the innovative
169 mathematics involved, we plan to publish these analytical results elsewhere, but we provide a
170 summary in Appendix A.

171 Second, in addition to simulations that subjected the deterministic skeleton (1) to
172 environmental noise (2), we investigated the influence of demographic noise. We used the
173 standard Gillespie algorithm (Gillespie 1976, 1977) to recast the system (1),(2) as a
174 continuous-time Markov jump process, whereby exponential holding times alternate with

175 Markov events (each term in the differential equations (1) is treated as an event rate for changes
176 in the numbers of predators and prey). The degree of demographic stochasticity in the Gillespie
177 simulations is determined by the prey carrying capacity K , which we set to 8000 in all our
178 simulations. To avoid extinctions, we included an additional, small, constant immigration rate
179 (ab); at each immigration event, one predator and $\lceil 1/b \rceil$ prey were added. The time to the next
180 event is drawn from an exponential distribution with mean equal to the inverse of the total rate
181 at which events of any type occur. The probability that the event is of a given type is the ratio of
182 its event rate to the total event rate. The Gillespie simulations are important for confirming that
183 none of our main findings are expected to disappear in the presence of demographic noise and
184 that they are not due simply to specific modeling or methodological choices. We show results
185 from the Gillespie simulations alongside our main numerical results for select, key findings.

186 Results

187 *Cycle period depends on model parameters and crawlby effects*

188 Depending on the parameter values, the deterministic Rosenzweig-MacArthur model can
189 exhibit a stable equilibrium or a stable limit cycle. Cycles arise when the system undergoes a
190 supercritical Andronov-Hopf (AH) bifurcation, which occurs at
191 $h = h_{AH} := K(ab - m)/(ab + m)$. As h decreases below this threshold, orbits grow quickly from
192 zero amplitude to large cycles that approach the axes in the (x, y) plane (figure 2A-B). Passage
193 along the y -axis corresponds to low levels of prey (x) and declining numbers of predators (y).
194 This is followed by passage near the saddle point at extinction $(0, 0)$, and then by passage along
195 the x -axis in which there are low levels of predators and recovering prey.

196 Decreasing the prey's growth rate, r , or the predator's half-saturation constant, h , results in
197 longer-period cycles (figure 2C-D, solid black lines). Because the AH bifurcation threshold, h_{AH} ,
198 does not involve the parameter r , changing r cannot induce cycles in system (1). Nevertheless,
199 when cycles exist, lowering r lengthens the oscillation period by slowing the recovery of the
200 prey population. This effect prolongs the crawlby past both the extinction point $(0, 0)$ and the
201 carrying capacity $(K, 0)$ (figure 2C, red dashed and blue dotted lines, respectively). However,

202 the crawlby is slowed somewhat less than passage through other parts of the cycle, so the
203 system spends proportionately less time in crawlby as r decreases (figure 2C, dotted black line
204 in lower panel).

205 In contrast, reducing h can induce an AH bifurcation and drive the system deeper into the
206 cyclic regime. Decreasing the value of h drives trajectories closer to both axes (figure 2B). This
207 prolongs the two saddle crawlby (figure 2D, red and blue lines) by placing the populations
208 closer to the saddles. The saddle crawlby is not only slower with lower h , but they also take
209 up proportionately more of the time needed to complete a cycle (figure 2C, dotted black line).

210 In sum, slowing the overall dynamics (by decreasing the prey's population growth rate, r)
211 and pushing trajectories closer to the two saddle points (by decreasing the predator's
212 half-saturation constant, h) will each extend the cycle period, but they do so through different
213 mechanisms. Decreasing the prey's growth rate extends the duration of saddle crawlby, but
214 only by slowing the dynamics as a whole and prolonging the entire cycle period. Decreasing the
215 half-saturation constant enhances the degree to which predators can overexploit their prey,
216 leading to more pronounced population crashes. These crashes exaggerate the crawlby effect by
217 placing the populations closer to the two saddle points at joint extinction and the prey carrying
218 capacity. The result is longer cycles that are made up of relatively more time spent for prey
219 recovery (passage near $(0,0)$) and then predator recovery (passage near $(K,0)$).

220 *Stochasticity can cause variance in cycle period, but not all stochasticity is equal*

221 Adding Cox-Ingersoll-Ross parameter noise (equation (2)) to the Rosenzweig-MacArthur model
222 results in noisy cycles such as the ones shown in figure 3. Figure 3A-B shows an example in
223 which noise in r causes cycles to vary in amplitude but maintain a close to constant period.
224 Figure 3C-D shows that for the same noise amplitude (σ value in equation (2)), the cycle period
225 is much more variable for noise in h .

226 Figure 3 shows just two examples, but they are representative of the systematic differences
227 we found when we explored different intensities of environmental noise acting on different
228 model parameters. For the same absolute noise magnitudes (σ values), the cycle period becomes

229 much more variable when noise affects handling time than when it affects prey growth rate
230 (figure 4). Specifically, for noise in r , the mean cycle duration changed little with increasing σ
231 from the deterministic value of 24.83 time units, while the standard deviation of these durations
232 depended only weakly on σ (figure 4A). Conversely, mean cycle durations and variability
233 increased substantially with σ when noise entered through h (figure 4B), with a distribution
234 featuring a tail of long cycle durations. For comparison with the biological data (see Methods),
235 note that the results plotted here yield CVs from 0.04 to 0.12 with noise in r and from 0.11 to
236 0.33 with noise in h . Results for $\sigma = 0.2$ (red bars in figure 4) are also summarized in table 2
237 (cases 2-3). Finally, if noise enters into both h and r simultaneously (table 2 case 4, implemented
238 via two copies of equation (2) that either share (correlated) or have independent (uncorrelated)
239 instantiations of the Wiener process W), the results are similar to the case with noise in h alone
240 (case 3).

241 There are several possible explanations for the stronger effect of noise in h than noise in r in
242 generating variable cycle periods. This is the pattern we expect if cycle period variability is
243 driven by variation in the time it takes to complete saddle crawlby, because changes in h
244 exaggerate the influence of crawlby while changes in r do not (figure 2C-D). We continue this
245 thread in the next subsection. Alternatively, or perhaps in addition, noise of a particular
246 magnitude may have a larger impact when it enters through h simply because our baseline
247 value of h is lower. In other words, a noise amplitude of, say, $\sigma = 0.2$ acting on an \bar{r} of 1.0 might
248 reasonably have less effect than the same $\sigma = 0.2$ acting on an \bar{h} of 0.15. We tested this idea in
249 two ways. First, we reduced \bar{r} to 0.15 to eliminate the difference in magnitudes between r and h .
250 This results in unrealistically long cycles, but allows a straightforward comparison of standard
251 deviation and CV. Again, the CV in cycle period is much higher when noise enters through h
252 (table 2, cases 6-7). Second, we returned to the baseline parameter set and increased the noise
253 amplitude on r (by rescaling by $\sqrt{\bar{h}}$) to allow the prey population to become quite small at
254 times, approaching the x -axis and now allowing the exaggerated crawlby effect to be seen via
255 noise in r . The result is a cycle period CV that is now quite comparable to the baseline case with
256 noise in h (table 2, case 5 compared to case 3).

257 We thus found evidence of true differences (table 2, cases 2-3 and 6-7) in how noise in the
258 prey growth rate and noise in the handling time affect variability in the cycle period. We
259 attribute these differences to the way changes in h affect the relative speed of the crawlby and
260 investigate this hypothesis in more detail below. We also found evidence that at some
261 sufficiently high level, noise in either parameter can lead to exaggerated crawlby that cause
262 cycle periods to become more variable (table 2, cases 3 and 5).

263 Finally, we note that the half-saturation constant, h , is not unique in its ability to drive the
264 system through the AH bifurcation and produce cycles of increasingly large magnitude, as
265 shown in figure 2B; in fact, all parameters except r have that property in this model. Therefore,
266 we consider one more scenario before moving on: we increase m from its baseline value of 0.6 to
267 0.65. In the absence of stochasticity, this change moves the periodic orbit of the deterministic
268 system (1) from the outer cycle in figure 2A to one of the interior paths. That is, while the
269 system is still cycling with $m = 0.65$, the expected (mean) trajectory does not pass as close to the
270 saddle points. Interestingly, changing m in this way *increases* the variability in cycle periods
271 (figure 5 and table 2, cases 8-9 compared to 2-3). Once again, this effect is particularly strong for
272 handling time noise (table 2). Although we might have expected more cycle period variability
273 deeper into the crawlby region (smaller m), it appears that being closer to the bifurcation – and
274 even on the stable side of it (figure 5D) – may increase the flexibility in the paths that orbits can
275 take. The long durations are still associated with close crawlby, but crawlby occur less
276 consistently, leading to a greater mix of longer and shorter cycles. These trends persist with
277 additional increases in m and are reversed by decreases in m (results not shown).

278 *Demographic noise does not overwhelm environmental noise effects*

279 Until now, we have included noise in model (1) as Cox-Ingersoll-Ross parameter noise (equation
280 (2)), representing environmental variability. In reality, population dynamics necessarily include
281 demographic noise as well. In theory, this variability across individuals could induce dynamic
282 effects that dominate the overall cycle paths, reducing the impacts we have documented of
283 environmental fluctuations. We tested this possibility by performing Gillespie simulations (see

284 Methods) in which all aspects of the population dynamics are treated as events with certain
285 expected rates, and events are implemented sequentially at random, with likelihoods and
286 timings based on these expected rates. These simulations emulate demographic noise effects;
287 moreover, within each simulation, we also modulated either the prey growth rate (r) or the
288 predator's half-saturation constant (h) stochastically. We found that these simulations yielded
289 very similar distributions of cycle durations to our direct simulations of system (1)-(2), matching
290 the differences between noise in r and noise in h as well as those across noise amplitudes σ
291 (figure 4).

292 *Cycle variability is driven by variable passage times near extinction and prey carrying capacity*

293 We have seen that in the deterministic case, trajectories traverse each cycle at non-uniform rates,
294 spending more time near the saddles at $(0,0)$ and $(K,0)$ than in other regions of the phase plane
295 (figure 2A,C,D). This observation raises the question of whether this non-uniformity manifests
296 in the stochastic case and, if so, whether it is relevant for cycle variability. That is, from a naive
297 perspective, longer passage times may translate into more opportunity for fluctuations,
298 resulting in enhanced variability. On the other hand, we have seen (from the contrast in
299 simulations with noisy r versus noisy h) that longer passage times do not inevitably result in
300 variable cycle periods. Moreover, it is also possible that the strong contraction near the stable
301 manifold of each saddle could constrain trajectories, and hence passage times, to be more
302 similar rather than more variable, relative to what occurs in other regions of phase space.

303 As the noise amplitude σ increases, trajectories continue to spend significant portions of
304 each cycle near the $(0,0)$ and $(K,0)$ saddles, although the precise locations where this time is
305 spent become progressively more diverse (figure 6 shows this for noise in r ; the effect is similar
306 but not shown for noise in h). In fact, by comparing plots with no noise to those with $\sigma \geq 0.2$, it
307 appears that with increasing σ , trajectories spend relatively less time transitioning from the
308 neighborhood of $(K,0)$ back to the neighborhood of the y -axis, although it is not obvious by
309 inspection where that time is spent instead.

310 To quantify these effects, we used linear sections to partition the part of the phase plane

311 visited by the stochastic trajectories into six disjoint regions, proceeding counterclockwise as
312 follows (figure 1), **A**: neighborhood of the origin, **B**: passage along the x -axis, **C**: neighborhood
313 of the $(K, 0)$ saddle, **D**: passage along the unstable manifold of $(K, 0)$, which defines the
314 direction in which trajectories depart from the neighborhood of $(K, 0)$, **E**: crossing of the
315 y -nullcline, which is the curve where dy/dt switches from positive to negative, and **F**: passage
316 along the y -axis. The distributions of times spent in these regions differ significantly in their
317 variability (figure 7). By a clear margin, the most variability arises in the passage times through
318 regions **A** and **C**, corresponding to crawlby near the saddles. Moreover, substantially more
319 variability occurred in these regions with noise in h than with noise in r ; note the differences in
320 x -axis details between histograms in figure 4A,C and those in figure 4B,D. The Gillespie
321 simulations shown in figure 4C,D yielded qualitatively, and in many cases quantitatively,
322 similar results (tables 3, 4).

323 Although the variability in the durations of the crawlbys (that is, in passage times near $(0, 0)$
324 and $(K, 0)$) becomes substantial, these segments of each cycle still dominate the overall cycle
325 period. For example, the positive correlation between period and these passage times, but not
326 between period and passage time along the x -axis, is readily apparent in figure 8. Interestingly,
327 these relationships, especially for the passage time near $(0, 0)$, are even tighter with noise in r
328 than with noise in h , although the passage times themselves are less widely distributed when
329 the noise is in r .

330 *Loss of prey strongly influences each cycle period, with little history dependence between cycles*

331 So far, we have shown strong evidence that environmental noise has different impacts on the
332 distribution of cycle periods, depending on the origin of the noise, and that variability in cycle
333 periods is dominated by variability in the duration of the two saddle crawlby near $(0, 0)$ and
334 $(K, 0)$. To conclude our characterization of these effects, we ask what factors best predict these
335 crawlby durations. Longer crawlbys elevate the risk of stochastic extinction by prolonging the
336 time during which one or both populations are small. Longer crawlbys also delay the time until
337 the next population peak, with important consequences for some cyclic species like outbreaking

338 forest insects. We therefore ask, what should we look for in a population's history to help us
339 anticipate the durations of upcoming saddle crawlby?

340 In a deterministic system, passage time near a saddle is well understood. We can consider
341 the population trajectory to have started the crawlby past extinction (that is, to have entered the
342 neighborhood of the $(0,0)$ saddle) once predator density, y , drops below some threshold, $y_{0,in}$.
343 Suppose the prey density when the $y = y_{0,in}$ threshold is crossed is $x_{0,in}$. We will say the $(0,0)$
344 crawlby is complete once prey density grows beyond another threshold, $x_{0,out}$. Near $(0,0)$,
345 $x^2 \approx 0$ and $xy \approx 0$, so the dynamics of the deterministic Rosenzweig-MacArthur model
346 (equation (1)) is well approximated by $dx/dt = rx$, $dy/dt = -my$. In this approximation, the
347 time needed to complete the saddle crawlby is $t_{pass} = (1/r) \ln(x_{0,out}/x_{0,in})$; that is, the crawlby
348 duration depends linearly on $\ln(x_{0,in})$. A similar calculation implies that the log predator
349 density at entry into the neighborhood of the $(K,0)$ saddle, $y_{K,in}$, also depends linearly on
350 $\ln(x_{0,in})$.

351 If the relationships for the deterministic model still hold in the presence of environmental
352 stochasticity, then we expect $\ln(x_{0,in})$, the log prey density when the populations first enter the
353 vicinity of the extinction state $(0,0)$, to predict the duration of both saddle crawlbys. This is
354 indeed what we find. There is a strong correlation between $\ln(x_{0,in})$ and the passage time by the
355 $(0,0)$ saddle (figure 9A,B). There is also a strong correlation between log prey density, $\ln(x_{0,in})$,
356 and log predator density upon entry into the neighborhood of the $(K,0)$ saddle (figure 9C,D),
357 and between the time of passage near $(K,0)$ and this log predator density (figure 9E,F). Thus,
358 even in the presence of noise, the prey's population density at the end of the predator-decline
359 portion of the cycle strongly influences the durations of both saddle crawlbys, which in turn
360 strongly influence the time it will take to complete the current cycle.

361 The effects of noise during the passage around the rest of the cycle eliminates the effects of
362 these entry positions, so that the positions of entry into the neighborhoods of the saddles in the
363 next cycle are effectively independent of past history (Appendix B, figure B1). This means that
364 we expect no meaningful autocorrelation in the periods of consecutive cycles. It also validates
365 our decision (see Methods) to omit individual cycles with unrealistically low population sizes

366 from our analyses. The consistency of Gillespie simulation results with those from simulating
367 (1)-(2) provides additional evidence that successive cycles are effectively independent.

368 Finally, referring back to Figure 9 and comparing the two columns, we notice that the
369 predator and prey densities upon entry into the two saddle neighborhoods differ, depending on
370 the source of noise. When noise enters through the prey's population growth rate, r , the entry
371 values seem to be symmetrically distributed on the logarithmic scale, while when noise enters
372 through the handling time, they become skewed toward smaller values even on the logarithmic
373 scale, corresponding to the skew toward longer passage times (figures B2-B3). Interestingly,
374 both patterns of entry densities correspond well to a lognormal distribution function. This
375 suggests a characteristic distribution of densities upon approach to a saddle in this model, with
376 moments that depend on the source of the noise.

377 Discussion

378 Although real cyclic populations can display considerable variability in cycle period, previous
379 authors have observed that stochastic ecological models typically predict cycles with much
380 more regular periods (Dwyer et al. 2004, Greenman and Pasour 2011). Inspired by recent work
381 characterising saddle crawlby's in non-equilibrium ecological dynamics (Hastings et al. 2018),
382 we hypothesized that stochasticity that causes variation in how close populations come to
383 saddle points during their cycles might promote variability in cycle periods. Our numerical
384 study of stochastic Rosenzweig-MacArthur predator-prey cycles confirms this idea. For the
385 cycles that we observe in model simulations, variability in period is dominated by deviation in
386 the passage times past the saddle points (figures 7, 8); further evidence for the central impact of
387 saddle crawlby's arises in the scaling of these passage times with proximity to the stable
388 manifolds of the two saddles (i.e. the x - and y -axes; figure 9). Our results thus update our
389 understanding of the conditions under which environmental stochasticity can contribute
390 meaningfully to observed cycle period variation in nature.

391 Within this qualitatively general phenomenon of crawlby-induced variability, quantitative
392 differences arise depending on the source and amplitude of the stochasticity in the dynamics of

393 population interactions. Comparing deviations of similar amplitude, we find that handling time
394 noise, which causes variation in the efficiency with which predators exploit their prey and
395 hence in the extent of the population crashes experienced on each passage around the cycle,
396 induces more variability in cycle period than does noise in the prey's population growth rate
397 (figures 3, 4, 7; Table 2, cases 2-3). Rescaling our noise sources to equalize the CV of the
398 fluctuations from these sources, rather than their amplitude, seems to mitigate this difference
399 (Table 2, case 3 vs. case 5). Yet, when we vary parameters to induce closer passage near the axes
400 and saddles, corresponding to more extreme population losses during cycle troughs, and also to
401 equalize the noise source CVs, the difference between these noise sources re-emerges (Table 2,
402 case 6 vs. case 7). A heuristic idea of the cause of this distinction comes from the observation
403 that for fixed predator level y , noise in r enters the dynamic equation for x in equation (1) in a
404 linear manner, with small deviations in r multiplying the small term $x(1 - x/K) \sim x$ near $x = 0$.
405 On the other hand, noise in h enters the equations like $1/h$, such that even small deviations in h
406 can have an amplifying effect (Appendix A).

407 Another quantitative, and perhaps initially surprising, observation emerging from our study
408 is that crawlby-induced variability is strongest when the mean cycle trajectory is not too close to
409 the saddle points (figures 2A, 5), such that individual cycles represent a mix of crawlbys and
410 non-crawlbys. Indeed, even though crawlbys are responsible for the overall cycle duration
411 variability, the most heterogeneous mixture of long and short passage times past saddles results
412 when crawlbys are only influential on a subset of cycles. In these cases, the coefficient of
413 variation in cycle period approaches 0.3, the mean value estimated from GPDD data. We
414 therefore conclude that variance in the duration of saddle crawlbys provides a viable
415 explanation for some, although not all, observed instances of variability in cycle periods. This
416 result also highlights the point that even though cyclic populations do not come close to
417 extinction during several consecutive cycles, their population dynamics may hold the
418 ingredients to produce significant crashes under environmental fluctuations that are within the
419 range of expected occurrence.

420 Like any model, ours is not a complete representation of reality. Real predators may

421 disperse, change behaviors, or evolve to avoid driving their prey, and thus themselves, too close
422 to extinction (van Baalen and Sabelis 1995). Alternatively, in biological systems, local
423 populations with high-amplitude cycles may routinely go extinct and then undergo
424 recolonization. Our results were conditioned on the populations not going extinct, and we do
425 not model dispersal in or out of the local community nor do we model complex behaviors,
426 alternative prey, and other such factors that are likely to influence the dynamics of real
427 populations. Nevertheless, the elements of our model, like population cycles and saddle
428 crawlbyes, and their connections to real dynamics are well studied (Murdoch et al. 2003). Our
429 contribution, therefore, is not to replicate or explain the dynamics of any specific single
430 population, but to extend our understanding of cycles and crawlbyes as mechanisms through
431 which environmental stochasticity can emerge within predator-prey dynamics in general. In
432 doing so, we reconcile a long-recognized mismatch between models and data in their view of
433 how variable the periods of cycle populations may be.

434 Because populations necessarily become small during the trough of each cycle, one might
435 reasonably expect demographic stochasticity to be important in this setting. However, our
436 Gillespie simulations reveal that the effects of environmental stochasticity on cycle period
437 variation are robust to the inclusion of demographic noise. It is nevertheless possible that other
438 dynamic mechanisms not considered in this study may also contribute to temporal variability in
439 cycle durations. Our intent is not to argue that saddle crawlbyes are the only or even the
440 predominant source of cycle period variability, but rather to highlight their putative role.

441 The observations in this paper represent interesting topics for future mathematical analysis,
442 particularly for models such as (1)-(2) to which the stochastic averaging methods of Skorokhod
443 et al. (2002) cannot be applied. Previous analytical and numerical work, some done in other
444 biological contexts, has discussed some of the differences in dynamics that arise from the details
445 of how stochasticity appears in a dynamical system (Lande 1993, Goldwyn and Shea-Brown
446 2011, Allen 2016, Vaddillo 2019). In contrast to the individual-level impact of demographic noise,
447 environmental noise is shared across entire populations, which is conducive to larger variability
448 and can increase the likelihood of extreme events such as extinction (Lande 1993). The specific

449 representation of stochasticity that we have implemented in equation (2) features biologically
450 desirable properties: it causes the stochastic parameter to remain positive, to be mean-reverting,
451 and to have some history-dependence, with a temporal autocorrelation that is nonzero and
452 decays exponentially (c.f. Allen 2016). To our knowledge, analytical work to date has not
453 addressed how such stochasticity impacts cycle durations and other properties in systems with
454 saddle crawlbys. A related direction that has been pursued analytically (Ashwin and
455 Postlethwaite 2016) is how stochasticity affects the passage of trajectories along a heteroclinic
456 cycle (i.e., a union of orbits that each form a connection from one saddle point to another, which
457 together form a closed loop). These systems may require noise to oscillate, unlike model (1), but
458 nonetheless the resulting oscillations do feature passage near saddle points. Ashwin and
459 Postlethwaite (2016) analyzed residence times near equilibria and switches between
460 neighborhoods of attractors (including heteroclinic cycles), while Giner-Baldó et al. (2017)
461 derived analytical approaches to compute the power spectra of observables in a planar system
462 with a heteroclinic cycle. Both of these analyses were done on systems with stochasticity in the
463 form of additive Gaussian white noise, however, whereas the CIR noise that we consider poses a
464 new challenge for future work.

465 Our results update our understanding of how environmental stochasticity can contribute
466 meaningfully to observed cycle period variation in nature. While our results for stochastic prey
467 growth rate, r , largely confirm past results that stochasticity has little effect on cycle period, we
468 have shown that some noise sources – specifically those that vary the distance from saddle
469 points as part of the normal cycle – can lead to substantial cycle period variation. Interestingly,
470 this effect is strongest when the mean cycle trajectory is not too close to the saddle points, such
471 that individual cycles represent a mix of crawlbys and non-crawlbys. In these cases, the
472 coefficient of variation in cycle period approached 0.3, the mean value estimated from time
473 series data. We therefore conclude that variance in the duration of saddle crawlbys provides a
474 viable explanation for some, though not all, observed instances of variability in cycle periods.

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Tables

Table 1. Baseline parameters of the model defined by equations (1) and (2).

parameter	meaning	value	unit
r	prey intrinsic growth rate	1	time ⁻¹ <i>per capita</i>
K	prey carrying capacity	1	prey biomass
a	maximum prey consumption rate	2	time ⁻¹ per predator
h	prey density at half maximum consumption rate	0.15	prey
b	prey to predator conversion efficiency	0.5	—
m	predator death rate	0.6	time ⁻¹ <i>per capita</i>
p	parameter subject to CIR process (r or h)		
γ	speed of adjustment to mean \bar{p}	1	time ⁻¹
σ	$\sigma\sqrt{\bar{p}}$ is standard deviation of CIR process	0–0.3	$\sqrt{\text{units of } p}$

For stochastic r or h , the values listed refer to \bar{r} or \bar{h} , respectively.

Table 2. Mean, standard deviation, and coefficient of variation of cycle periods under different scenarios.

case	noise site	parameter set	noise amplitude, σ	mean period	standard deviation	CV
1	none	baseline	0 (deterministic)	24.83	0	0
2	r	baseline	0.2	24.74	2.07	0.084
3	h	baseline	0.2	28.88	5.59	0.19
4 (uncorr)	r and h	baseline	$\sigma_r = \sigma_h = 0.2$	28.70	5.47	0.19
4 (corr)	r and h	baseline	$\sigma_r = \sigma_h = 0.2$	29.76	6.01	0.20
5	r	baseline	$0.2/\sqrt{h} = 0.516$	25.26	5.06	0.20
6	r	$\bar{r} = \bar{h} = 0.15$	0.2	68.04	4.30	0.063
7	h	$\bar{r} = \bar{h} = 0.15$	0.2	61.81	7.58	0.123
8	r	$m = 0.65$	0.2	23.79	2.30	0.097
9	h	$m = 0.65$	0.2	28.95	7.80	0.27

Our baseline parameter set given in Table 1 is used except where noted. With the exception of the deterministic case, either r or h (or both in case 4 where uncorr refers to uncorrelated, corr to correlated; see text) is made stochastic by applying equation (2).

Table 3. Mean (μ) and standard deviation (sd) of passage times through regions A-F (see figure 1) from model (1)-(2) (SDE) simulations.

noise site	noise amp., σ	μ_A	sd_A	μ_B	sd_B	μ_C	sd_C	μ_D	sd_D	μ_E	sd_E	μ_F	sd_F
<i>r</i>	0.1	4.34	0.32	2.59	0.14	9.32	0.69	3.31	0.07	2.95	0.11	2.19	0.05
<i>r</i>	0.2	4.34	0.68	2.61	0.29	9.32	1.49	3.31	0.15	2.95	0.25	2.21	0.13
<i>r</i>	0.3	4.43	0.98	2.64	0.48	9.52	2.12	3.30	0.22	2.92	0.41	2.24	0.29
<i>h</i>	0.1	6.34	0.98	1.49	0.09	11.07	2.53	2.77	0.25	2.75	0.15	1.32	0.15
<i>h</i>	0.2	7.36	2.10	1.51	0.24	13.19	5.21	2.76	0.48	2.70	0.34	1.36	0.47
<i>h</i>	0.3	8.13	2.63	1.64	1.54	14.52	6.21	2.80	0.84	2.57	0.43	1.45	0.76

Table 4. Mean (μ) and standard deviation (sd) of passage times through regions A-F (see figure 1) from Gillespie simulations.

noise site	noise amp., σ	μ_A	sd_A	μ_B	sd_B	μ_C	sd_C	μ_D	sd_D	μ_E	sd_E	μ_F	sd_F
<i>r</i>	0.1	4.34	0.57	2.61	0.18	9.22	1.91	3.31	0.24	2.96	0.16	2.21	0.12
<i>r</i>	0.2	4.35	0.78	2.62	0.31	9.25	2.18	3.30	0.28	2.95	0.26	2.23	0.16
<i>r</i>	0.3	4.34	1.11	2.67	0.48	9.15	2.58	3.33	0.98	2.93	0.37	2.27	0.60
<i>h</i>	0.1	6.31	1.15	1.50	0.11	10.80	3.06	2.78	0.32	2.76	0.18	1.33	0.19
<i>h</i>	0.2	6.95	1.80	1.55	0.77	11.77	4.23	2.75	0.52	2.72	0.32	1.36	0.42
<i>h</i>	0.3	7.69	2.01	1.65	1.79	13.22	4.96	2.76	1.39	2.62	0.44	1.51	1.37

Figure legends

545

546 **Figure 1.** Components of a typical cycle, **A:** passage by the origin when both species are rare, **B:**
547 recovery of the prey population, **C:** passage by the prey's carrying capacity, K , **D:** predator
548 recovery and prey decline, **E:** initiation of predator decline, and finally **F:** sharp predator decline
549 back toward the origin. Segments **A** and **C** involve saddle crawlby.

550 **Figure 2.** Oscillations in system (1) without noise. **A.** The predator-prey coexistence equilibrium
551 is unstable for $h \lesssim 0.25$ and baseline values of the other parameters. Periodic orbits for
552 successively smaller values of h , namely $h = 0.24$ (diamonds), $h = 0.195$ (circles), and $h = 0.15$
553 (squares; our baseline value) pass progressively closer to the coordinate axes. Shapes denote
554 points 1 time unit apart on each orbit and thus show the rates of passage through different parts
555 of the cycle. **B.** As h is reduced from 0.4 toward its baseline value (0.15), system (1) undergoes
556 an Andronov-Hopf bifurcation at which the coexistence equilibrium switches from stable (solid
557 black) to unstable (dashed black) and a family of stable periodic orbits emerges (blue and red
558 show maximal and minimal values of x and y , respectively, along these orbits). **C.** As r (baseline
559 value 1.0) decreases, the oscillation period grows (solid black line). This is partially explained by
560 prolonged crawlby past the saddles at $(0, 0)$ (blue dotted line) and $(K, 0)$ (red dashed line). The
561 purple dashed line shows the total amount of time during each cycle that is spent in a saddle
562 crawlby (red plus blue), and the dotted black line in the lower panel shows the remaining time
563 spent passing through other parts of the cycle (solid black minus purple). **D.** As h decreases, the
564 oscillation period grows, but less extremely than in **C**. The longer cycle duration is even more
565 strongly influenced by saddle crawlby; for low h , most of the time needed to complete a cycle
566 is spent crawling by the saddle points.

567 **Figure 3.** Typical behavior of system (1)-(2) with noise amplitude $\sigma = 0.3$ and noise in r (**A-B**) or
568 h (**C-D**). **A, C** show the dynamics over 2000 time units in the (x, y) phase plane. **B, D** show time
569 series of x (black) and y (red) for the first 500 of the 2000 time units shown in **A, C**.

570 **Figure 4.** Distributions of relative cycle durations for various noise amplitudes σ . **A-B.** Results

571 from simulations with model (1),(2). **A**. With noise in r , the mean duration stays nearly constant
572 while the distribution widens and remains symmetric as σ increases. **B**. With noise in h , the
573 mean duration increases and the distribution widens and becomes skewed, with a tail of long
574 duration cycles, as σ increases. Note that the two panels show different ranges of cycle
575 durations. **C-D**. Results from Gillespie simulations of model (1) with carrying capacity $K = 8000$
576 and environmental noise in r (**C**) or in h (**D**) are similar to those from the simulations with *only*
577 environmental noise shown in **A, B**. These plots were derived from equal time simulations
578 across noise conditions, which led to the following numbers of cycles. For the Gillespie case:
579 $\sigma_h = 0.1$, 978 cycles; $\sigma_h = 0.2$, 915 cycles; $\sigma_h = 0.3$, 839 cycles; $\sigma_r = 0.1$, 1018 cycles; $\sigma_r = 0.2$, 1018
580 cycles; $\sigma_r = 0.3$, 1003 cycles. For simulations of (1), (2): $\sigma_h = 0.1$, 775 cycles; $\sigma_h = 0.2$, 668 cycles;
581 $\sigma_h = 0.3$, 410 cycles; $\sigma_r = 0.1$, 809 cycles; $\sigma_r = 0.2$, 808 cycles; $\sigma_r = 0.3$, 798 cycles.

582 **Figure 5.** Time series for **A**: $m = 0.6$, **B**: $m = 0.65$, **C**: $m = 0.7$, and **D**: $m = 0.75$ with noise of
583 amplitude $\sigma = 0.2$ in h . The system undergoes an Andronov-Hopf bifurcation at $m \in (0.7, 0.75)$.
584 Thus, the deterministic model would show limit cycles for the parameter values in **A-C** and
585 stable predator-prey coexistence for the values in **D**.

586 **Figure 6.** Histograms of relative times spent in bins in the (x, y) plane during simulations with
587 durations of 2000 time units, with **A** no noise and with **B-D** increasing levels of noise amplitude
588 σ . These results are for noise in the prey carrying capacity r , and are similar to what we see
589 with noise in the predator's half-saturation constant h .

590 **Figure 7.** Histograms of time spent by trajectories with noise of amplitude σ in r (top plot per
591 pair) or in h (bottom) in successive regions of phase space, **A**: near the origin, **B**: along the
592 x -axis, **C**: near the $(K, 0)$ saddle point, **D**: along the unstable manifold of $(K, 0)$, **E**: traversing the
593 y -nullcline, **F**: along the y -axis. For noise in h , note that the distributions in regions **B** and **F** have
594 sharp minima corresponding to the passage times generated by $dx/dt = rx(1 - x/K)$ and
595 $dy/dt = -my$, respectively, which are approached on cycles for which the stochastic xy term
596 (the functional response) becomes so small that it has very limited influence over the passage
597 times along the axes. The numbers of cycles incorporated in these histograms are as in Figure 4.

598 **Figure 8.** Correlations between the different durations for **A-B**: noise in the prey growth rate (r)
599 or **C-D**: noise in the handling time (implemented as noise in the predator’s half-saturation
600 constant, h) for baseline parameter values and noise amplitude $\sigma = 0.2$. **A,C.** The full cycle
601 period (per) is tightly correlated with passage times near the $(0,0)$ and $(K,0)$ saddle points
602 (blue triangles and red circles, respectively). In contrast, it is effectively independent of the time
603 it takes to transition between the saddles (“ x -axis passage”, cyan markers). Here, noise is
604 applied with $\sigma = 0.2$ in all cases. **B,D.** Cycle period is highly correlated with the total time
605 needed to complete both saddle crawlby (“sum”, black dots). It is uncorrelated with the time
606 needed to complete all other parts of the cycle (“difference”, i.e. the total cycle period minus the
607 sum of the two saddle crawlby durations; green dots).

608 **Figure 9.** Strong dependence of passage times through saddle neighborhoods on entry positions
609 into those neighborhoods. In **A,C,E** the prey growth rate, r , is the stochastic parameter and in
610 **B,D,F** the predator’s prey handling time, h , is stochastic. **A-B** show the dependence of the $(0,0)$
611 saddle crawlby duration on the log of the prey’s density upon entry into that neighborhood,
612 $(\ln(x_{0,\text{in}}))$. **C-D** show dependence of log predator density upon entry into the neighborhood of
613 $(K,0)$, $(\ln(y_{K,\text{in}}))$, on $\ln(x_{0,\text{in}})$. Finally, **E-F** show how $\ln(y_{K,\text{in}})$ determines the duration of the
614 $(K,0)$ saddle crawlby. Results for noise amplitude $\sigma = 0.1, 0.2$ and 0.3 are shown in **A,B,E,F**,
615 while **C,D** show $\sigma = 0.2$.

Figures

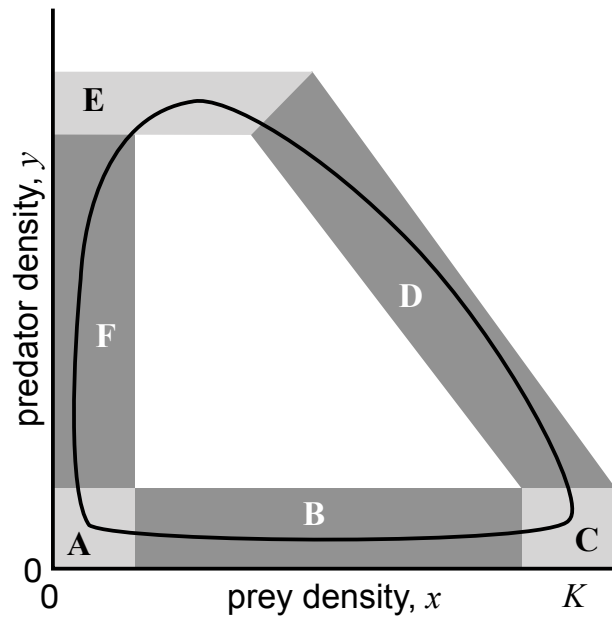


Figure 1

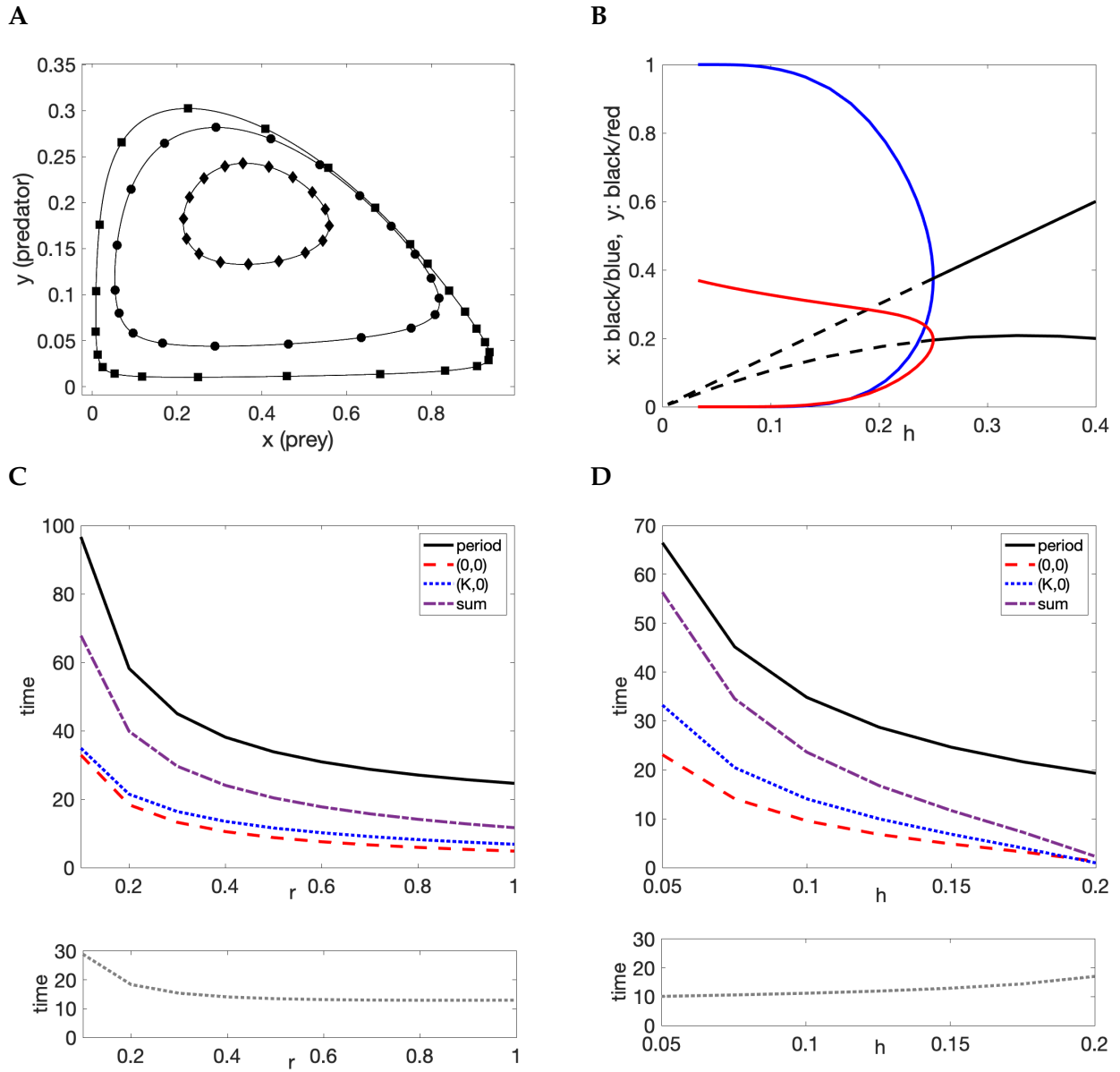
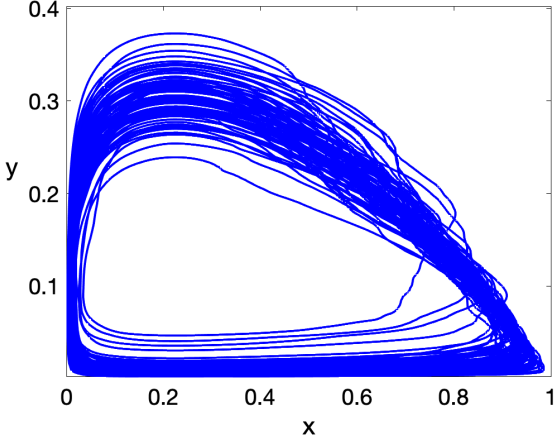
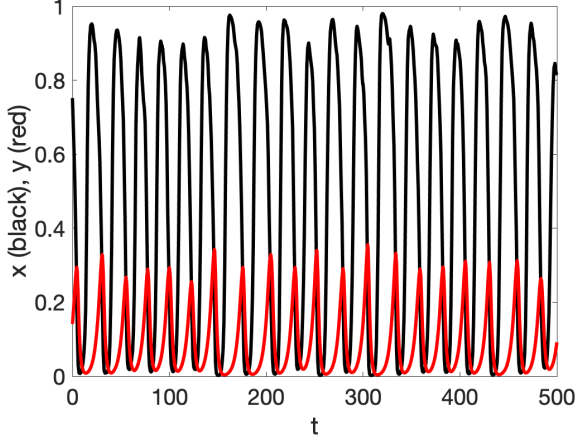


Figure 2

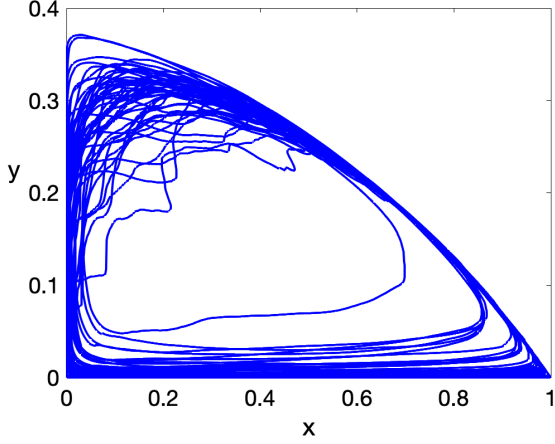
A. Noise in r



B. Noise in r



C. Noise in h



D. Noise in h

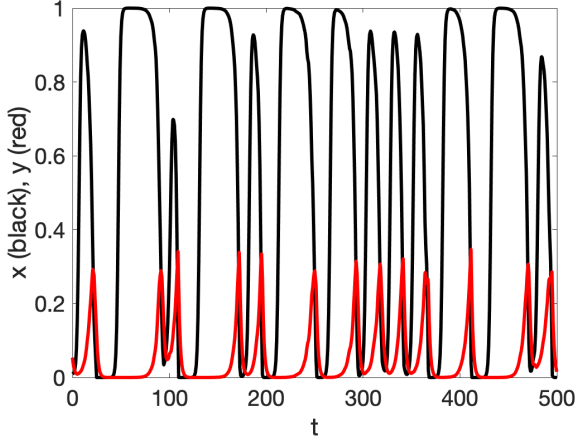
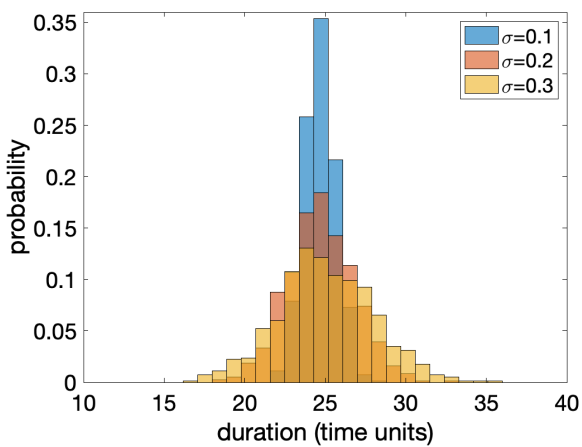
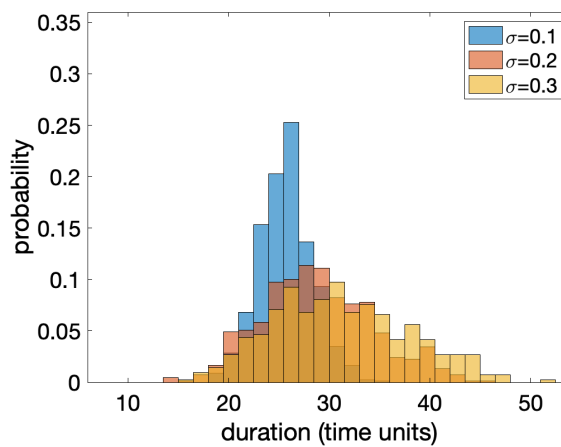


Figure 3

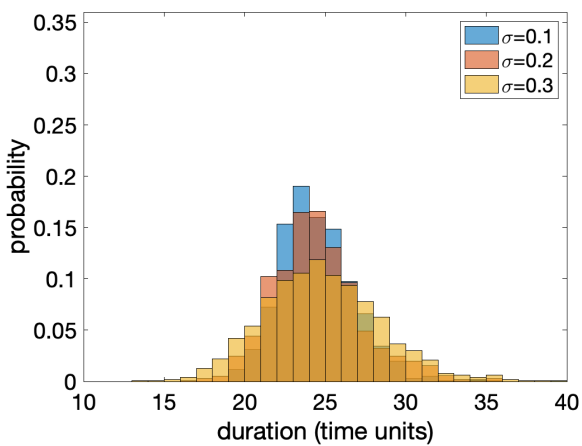
A. Noise in r , Eqns (1)-(2)



B. Noise in h , Eqns (1)-(2)



C. Noise in r , Gillespie algorithm



D. Noise in h , Gillespie algorithm

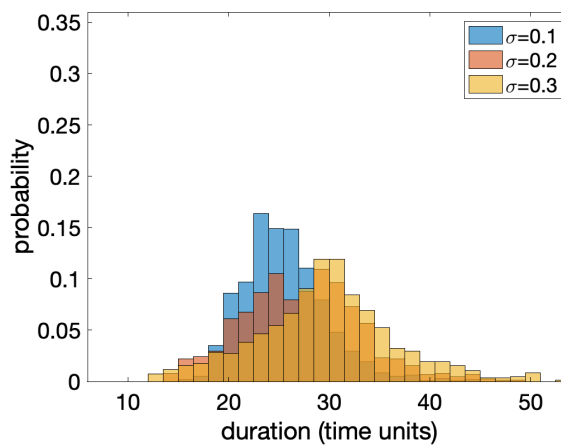
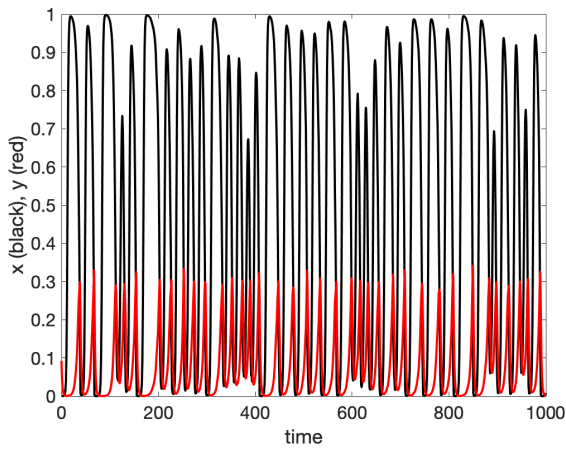
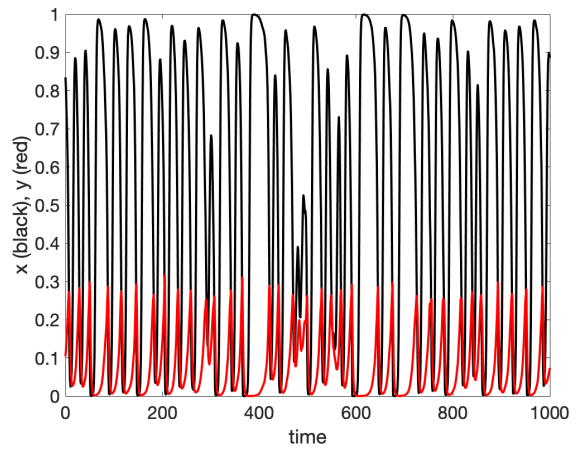


Figure 4

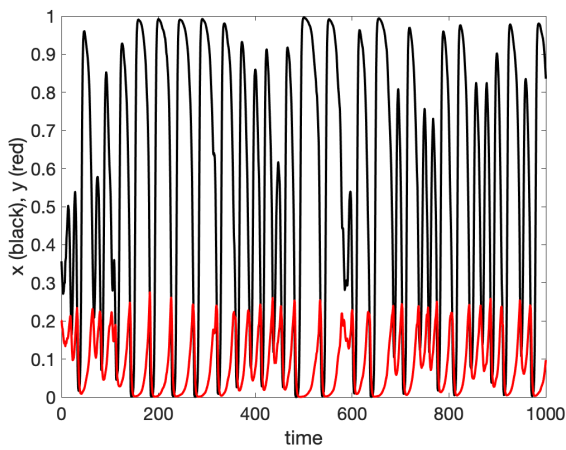
A. $m = 0.6$



B. $m = 0.65$



C. $m = 0.7$



D. $m = 0.75$

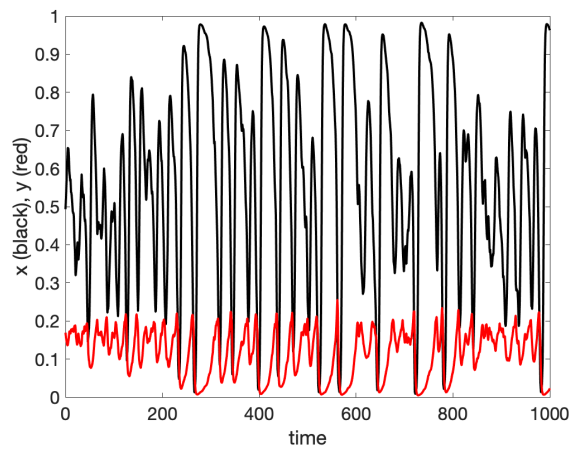


Figure 5

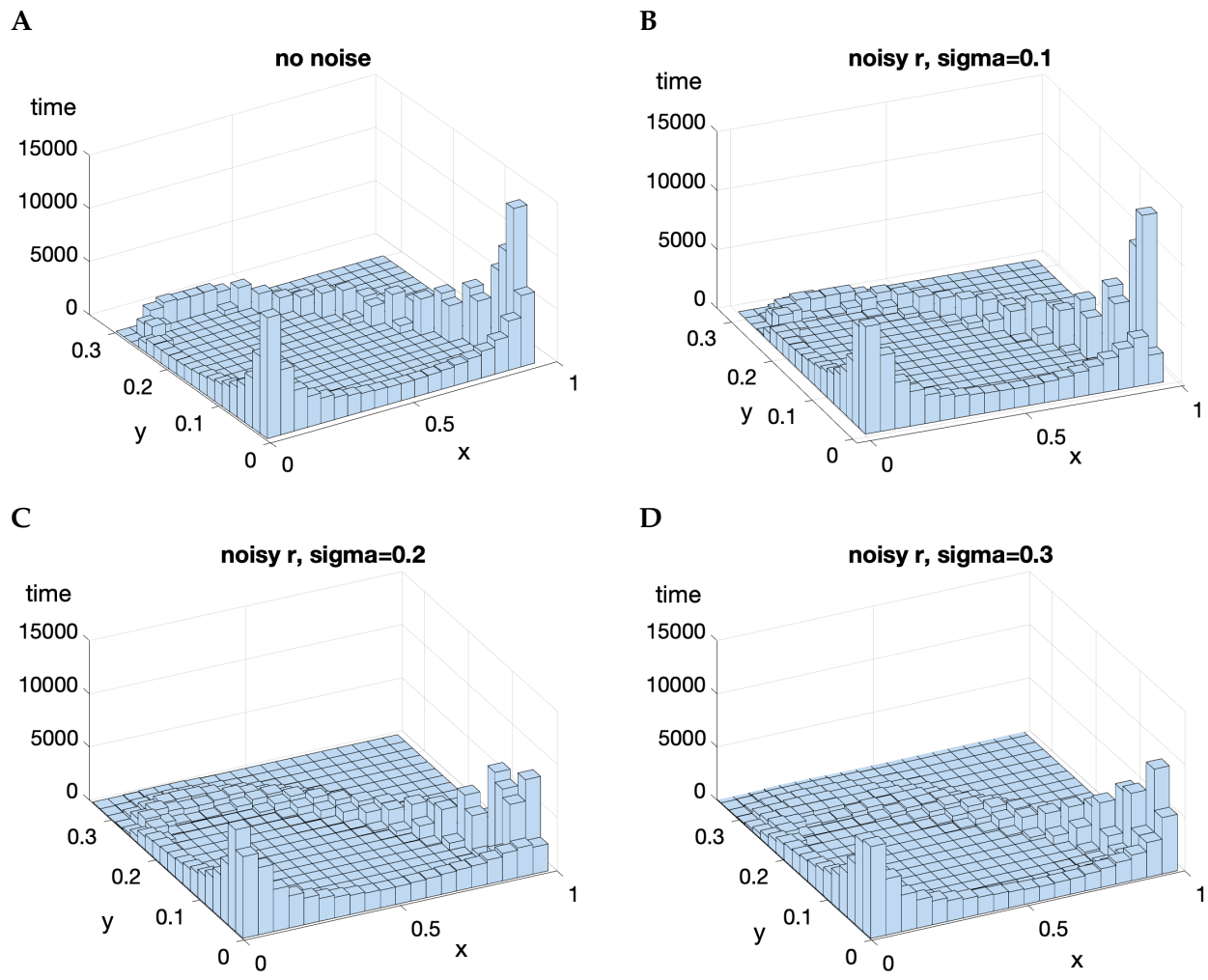


Figure 6

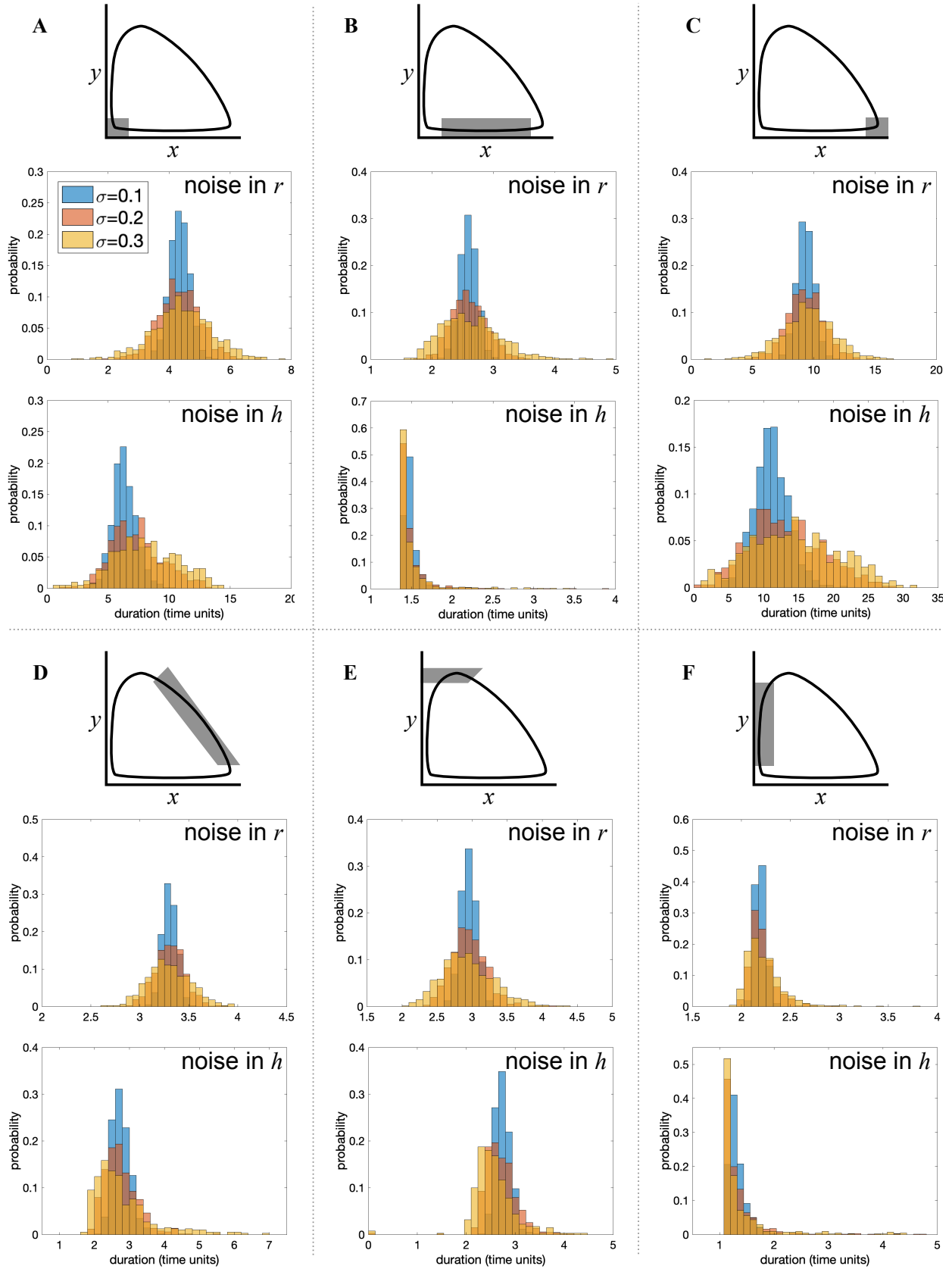
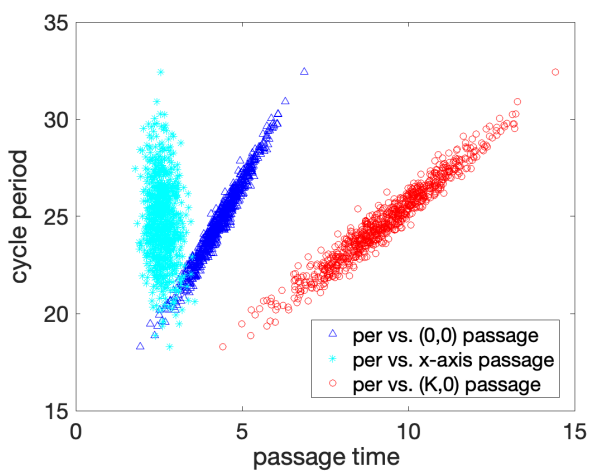
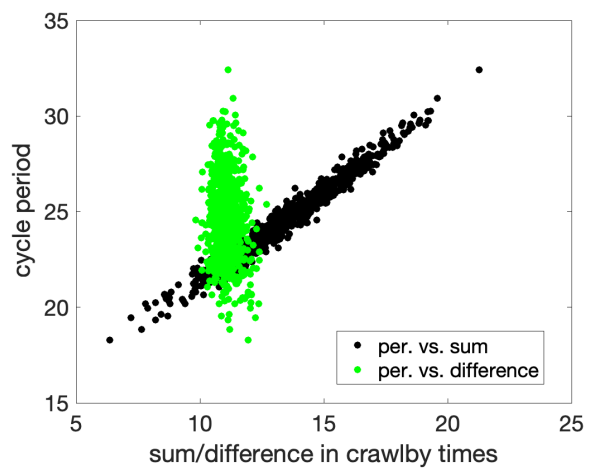


Figure 7

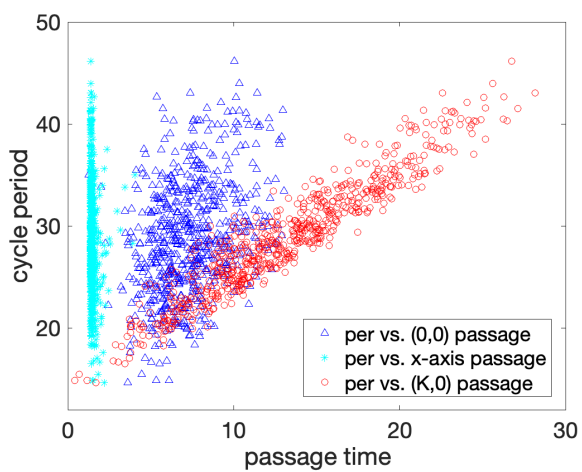
A. Noise in r



B. Noise in r



C. Noise in h



D. Noise in h

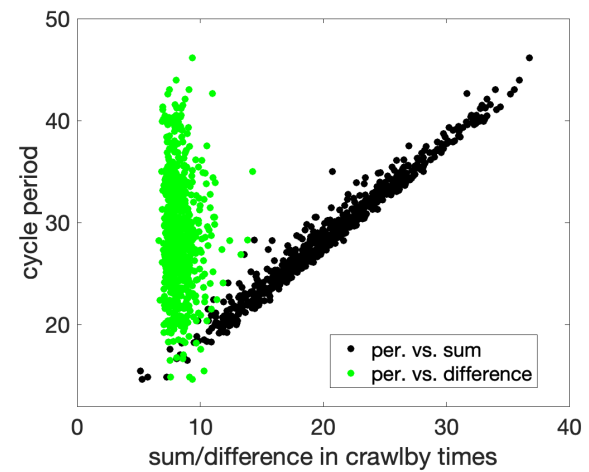
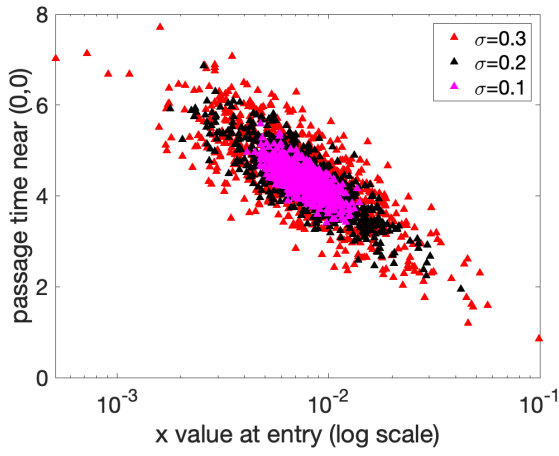
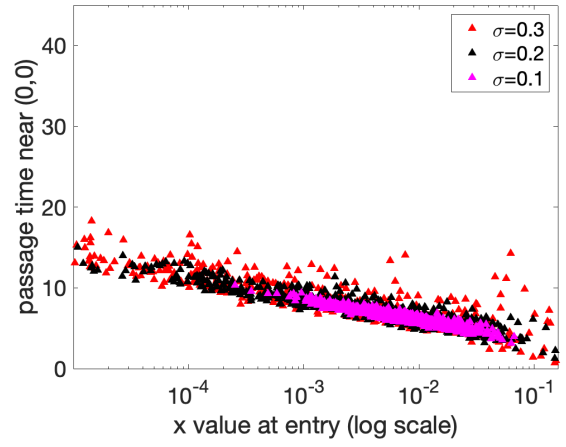


Figure 8

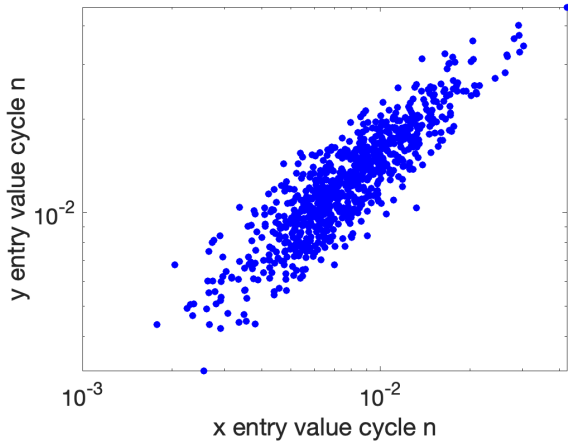
A. Noise in r



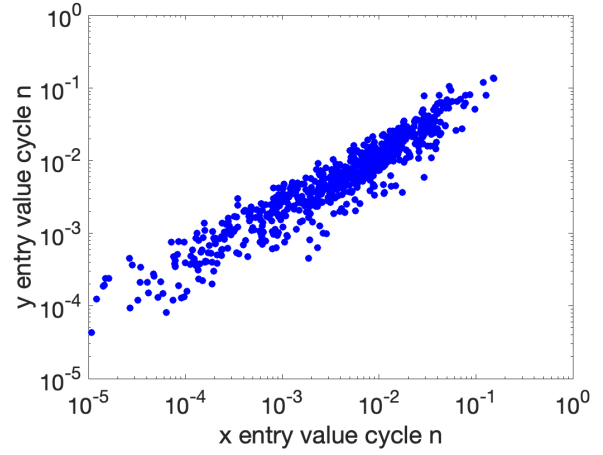
B. Noise in h



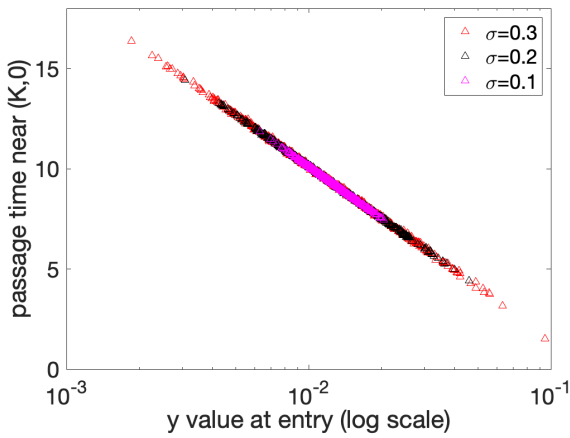
C. Noise in r



D. Noise in h



E. Noise in r



F. Noise in h

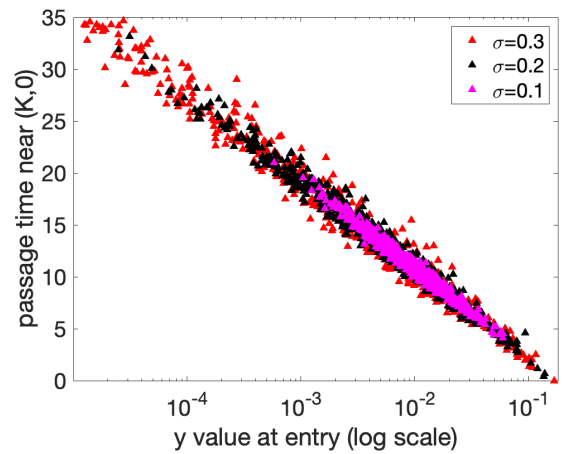


Figure 9

Appendix A: Boundary Layer Analysis

617

618 The equations (1) are unfortunately analytically intractable, but the stable limit cycle has
 619 segments that are approximately parallel to the x and y axes, which approach closer and closer
 620 to the axes as r or h decreases. This allows us to approximate the trajectory via the method of
 621 boundary layers, linearizing along the axes.

622 To do so, we introduce a small, dimensionless parameter ϵ , and substitute $x(t) = \epsilon\zeta(t)$ or
 623 $y(t) = \epsilon\psi(t)$, as appropriate, into (1). We then take the limit as $\epsilon \rightarrow 0$. This is equivalent to
 624 focusing on the part of the orbit where the transformed variable(s) are small, and allows us to
 625 obtain approximate solutions along the x -axis and y -axis and at the origin. Similarly, letting
 626 $x(t) = K + \epsilon\zeta(t)$ and $y(t) = \epsilon\psi(t)$, we can approximate the trajectory near the $(K, 0)$ saddle.

We illustrate the method by computing the solution along the y -axis: substituting
 $x(t) = \epsilon\zeta(t)$ into (1) gives

$$\begin{aligned} \epsilon\dot{\zeta} &= \epsilon r\zeta \left(1 - \frac{\epsilon\zeta}{K}\right) - \epsilon \frac{a\zeta y}{\epsilon\zeta + h} \\ \dot{y} &= \epsilon \frac{ab\zeta y}{\epsilon\zeta + h} - my. \end{aligned} \tag{A1}$$

In the limit as $\epsilon \rightarrow 0$, these equations simplify to

$$\begin{aligned} \dot{\zeta} &= \left(r - \frac{ay}{h}\right) \zeta \\ \dot{y} &= -my, \end{aligned} \tag{A2}$$

627 which may be solved to yield $y(t) = y(0)e^{-mt}$ and $\zeta(t) = \zeta(0)e^{rt - \frac{ay(0)}{mh}(1-e^{-mt})}$, where $y(0)$ and
 628 $x(0) = \epsilon\zeta(0)$ are the (unspecified) point of entry into a neighborhood of the y -axis. We may also
 629 return to the original variables, taking $x(t) = \epsilon\zeta(t) = x(0)e^{rt - \frac{ay(0)}{mh}(1-e^{-mt})}$.

When h is allowed to vary stochastically according to equation (2), we need to modify our
 solution to (A2) to account for the fact that h is a (random) function of time, giving us

$$x(t) = x(0)e^{rt - ay(0) \int_0^t \frac{e^{-mu}}{h(u)} du}. \tag{A3}$$

630 Proceeding similarly, we can obtain approximate local solutions for stochastically varying r

631 or h , which we summarize in Table A1.

632 Comparing the solutions along the y -axis for varying r vs. varying h gives some intuition for
633 the greater impact of noise in the latter: in this region, the noise enters as $\frac{1}{h}$, whereas h itself
634 fluctuates about a mean of $\bar{h} = 0.15$, and thus will regularly approach values very close to 0. If
635 this happens near the y -axis, $x(t)$, which is proportional to $e^{-\int_0^t \frac{e^{-mu}}{h(u)} du}$, can become quite small.
636 This can cause the perturbed trajectory to make a very close approach to the unstable node at
637 the origin and the consequent slow-down of the passage. By contrast, in the same region, noise
638 in r enters linearly, and only a rare, large fluctuation in r will cause the trajectory to have a
639 similar excursion towards the crawlby region near the origin.

Table A1. Linearized solutions for the model defined by equations (1) and (2) in different regions of the phase space.

noise site	region	$x(t)$	$y(t)$
r	origin	$x(0)e^{\int_0^t r(u) du}$	$y(0)e^{-mt}$
r	$(K, 0)$	$K + (x(0) - K)e^{-\int_0^t r(u) du}$ $+ \frac{ay(0)}{1+h} \int_0^t e^{-\int_s^t r(u) du} + (\frac{ab}{1+h} - m)s ds$	$y(0)e^{(\frac{ab}{1+h} - m)t}$
r	x -axis	$\frac{x(0)}{x(0) + (1-x(0))e^{-\int_0^t r(u) du}}$	$y(0)e^{abx(0) \int_0^t \frac{1}{x(0)(1+h) + h(1-x(0))e^{-\int_0^u r(v) dv}} du - mt}$
r	y -axis	$x(0)e^{\int_0^t r(u) du - \frac{ay(0)}{mh}(1-e^{-mt})}$	$y(0)e^{-mt}$
h	origin	$x(0)e^{rt}$	$y(0)e^{-mt}$
h	$(K, 0)$	$K + (x(0) - K)e^{-rt} + \frac{y(0)}{b} e^{ab \int_0^t \frac{1}{1+h(u)} du - mt}$ $+ \frac{y(0)(r-m)}{b} e^{-rt} \int_0^t e^{ab \int_0^s \frac{1}{1+h(u)} du} + (r-m)s ds$	$y(0)e^{ab \int_0^t \frac{1}{1+h(u)} du - mt}$
h	x -axis	$\frac{x(0)}{x(0) + (1-x(0))e^{-rt}}$	$y(0)e^{abx(0) \int_0^t \frac{1}{x(0)(1+h(u)) + h(u)(1-x(0))e^{-ru}} du - mt}$
h	y -axis	$x(0)e^{rt - ay(0) \int_0^t \frac{e^{-mu}}{h(u)} du}$	$y(0)e^{-mt}$

Appendix B: Supplemental numerical information and figures

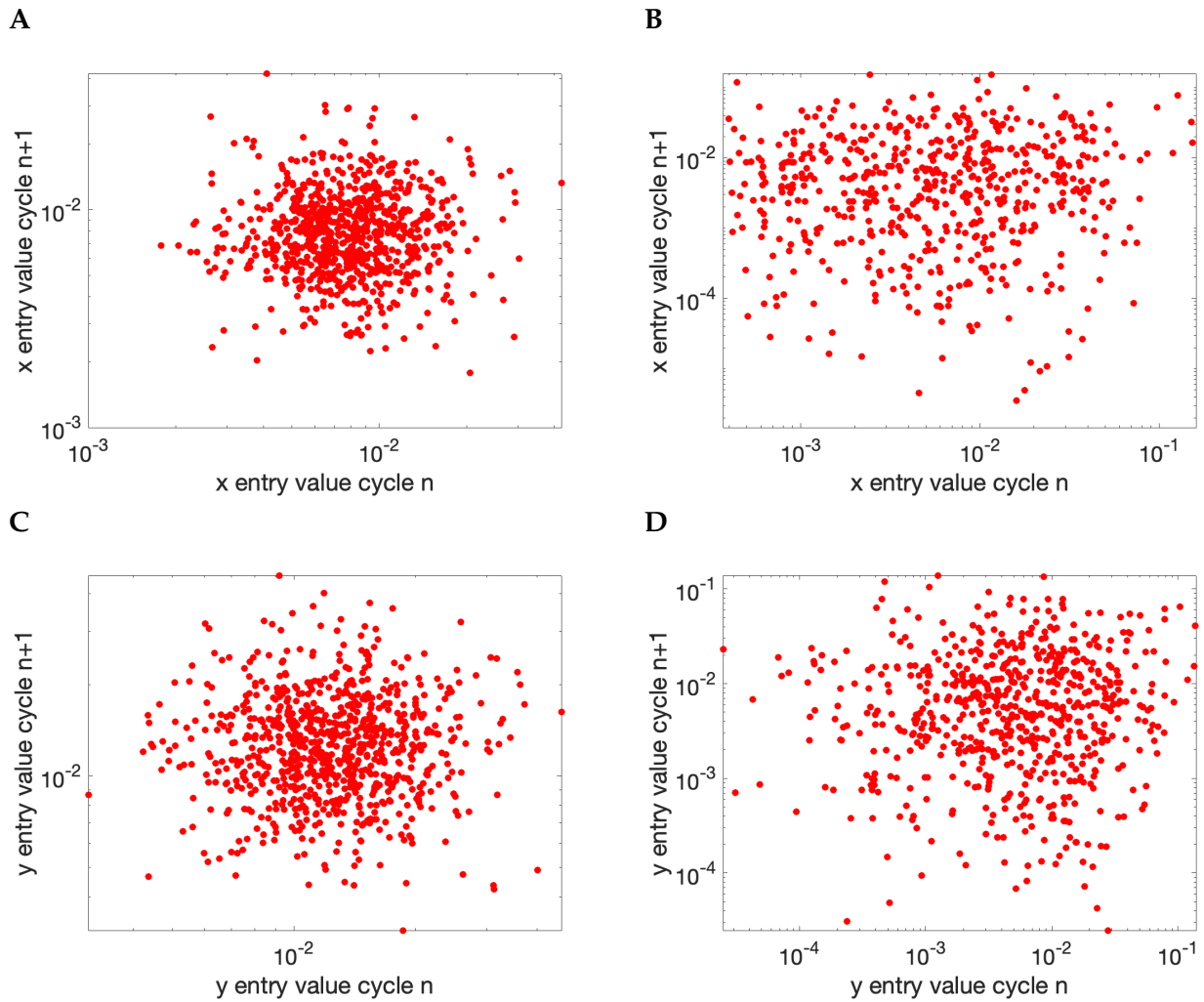


Figure B1. Independence from one cycle to the next of the population densities upon entry into the neighborhoods of the saddles. The stochastic parameter is prey growth rate, r , in **A,C** and predator's prey handling time, h , in **B,D**. **A-B** show the lack of a correlation between prey density upon entry into the $(0,0)$ neighborhood, $\ln(x_{0,\text{in}})$, from the n^{th} to the $n+1^{\text{st}}$ cycle. **C-D** show the same for predator density upon entry into the $(K,0)$ neighborhood, $\ln(y_{K,\text{in}})$. In all cases, $\sigma = 0.2$ and axes are on logarithmic scales. Note that results in **C** include some values of x_{n+1} below the extinction cutoff of 10^{-5} ; these were not used in any of the duration calculations discussed in the main text.

Table B1. Entry and exit sections used to define our phase space regions.

noise site	region	entry boundary	exit boundary
h	origin	$y = 0.12$	$x = 0.2$
h	x -axis	$x = 0.2$	$x = 0.5$
h	$(K, 0)$	$x = 0.5$	$y = 0.15$
h	unstable manifold	$y = 0.15$	$y = x - 0.2$
h	y -nullcline	$y = x - 0.2$	$y = 0.23$
h	y -axis	$y = 0.23$	$y = 0.12$
r	origin	$y = 0.07$	$x = 0.12$
r	x -axis	$x = 0.12$	$x = 0.6$
r	$(K, 0)$	$x = 0.6$	$y = 0.13$
r	unstable manifold	$y = 0.13$	$y = 0.55x$
r	y -nullcline	$y = 0.55x$	$y = 0.22$
r	y -axis	$y = 0.22$	$y = 0.07$

These values were used for all results except cases 6-9 in Table 2, for which sections were slightly adjusted to reflect altered orbit paths.

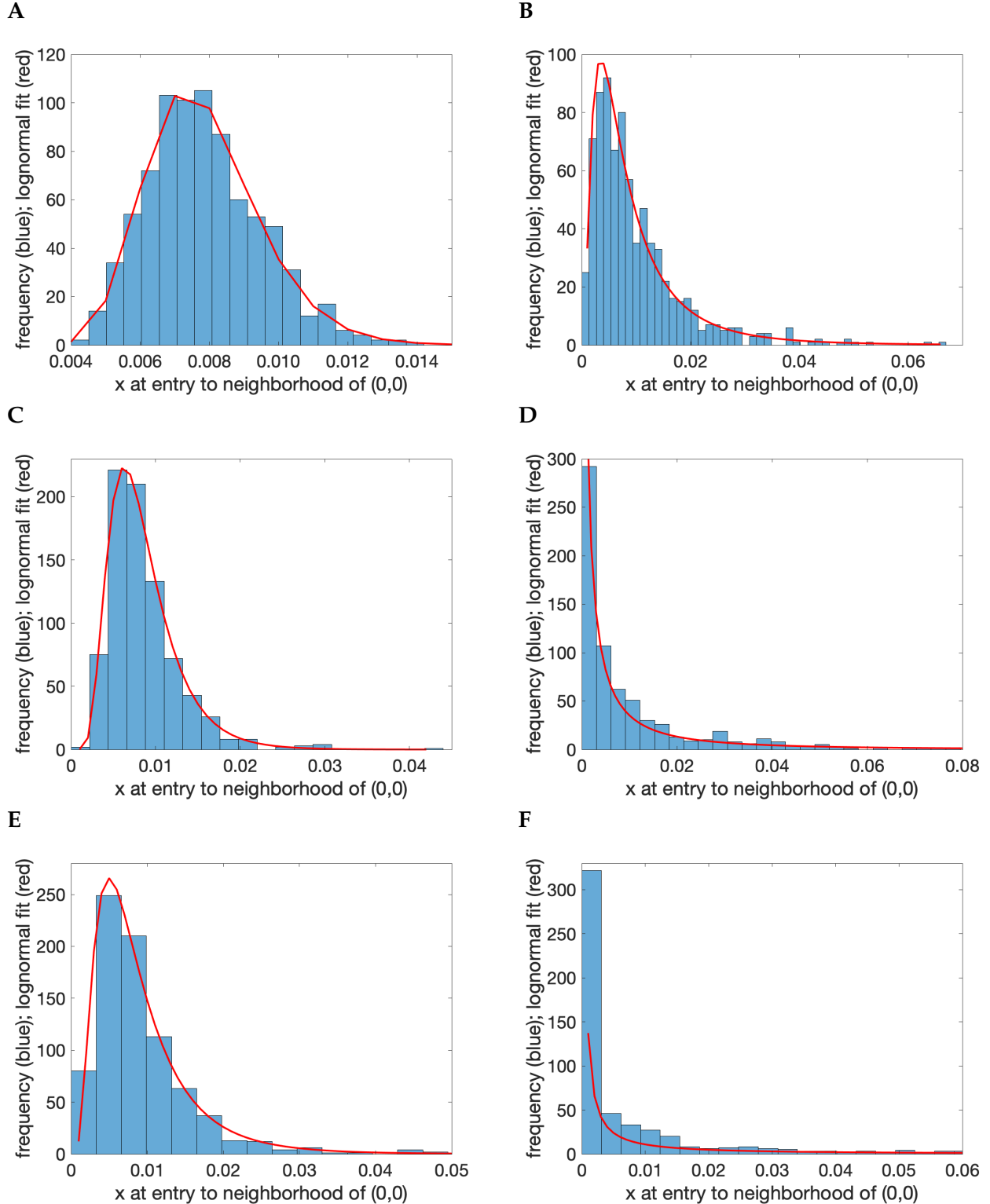


Figure B2. Distributions of prey densities, $\ln(x_{0,\text{in}})$, at crossing of a Poincaré section of constant $y = y_{0,\text{in}}$, which marks entry into the neighborhood of $(0,0)$. **A,B:** $\sigma = 0.1$, **C,D:** $\sigma = 0.2$, **E,F:** $\sigma = 0.3$. The noisy parameter is r in the left panels (with $y_{0,\text{in}} = 0.07$) and h in the right panels (with $y_{0,\text{in}} = 0.12$). In each panel, the red curve shows the best lognormal fit to each distribution.

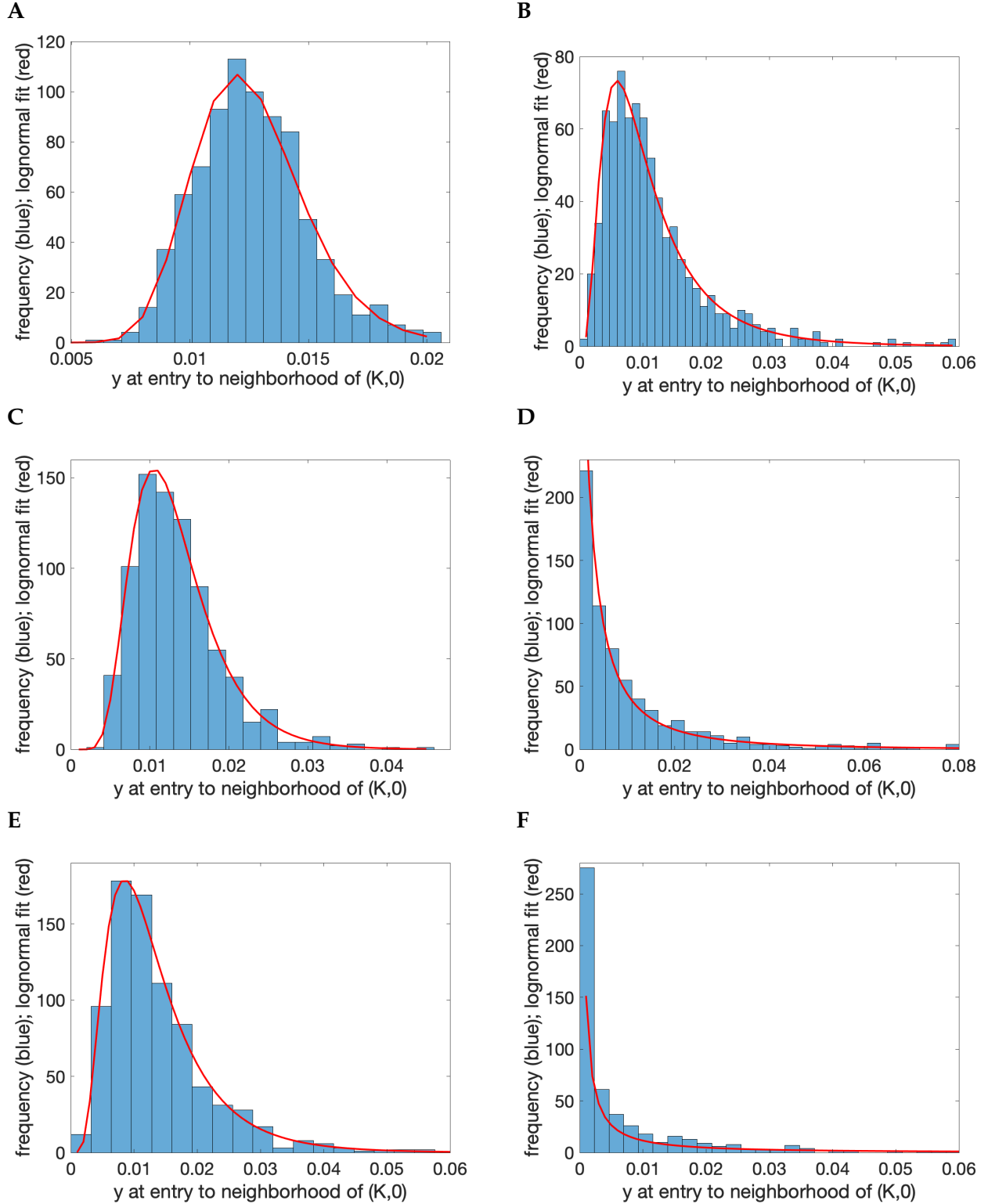


Figure B3. Distributions of predator densities, $y_{K,in}$, at crossing of a Poincaré section of constant $x = x_{K,in}$, marking entry into the neighborhood of $(K,0)$. **A,B:** $\sigma = 0.1$, **C,D:** $\sigma = 0.2$, **E,F:** $\sigma = 0.3$. The noisy parameter is r in the left panels (with $x_{K,in} = 0.6$) and h in the right panels (with $x_{K,in} = 0.5$). In each panel, the red curve shows the best lognormal fit to each distribution.