

How do variations in seasonality affect population cycles?

Electronic Supplementary Material

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S1 Model details

We use the model of Turchin and Hanski (1997):

$$\frac{dN}{d\tau} = r \left(1 - \frac{N}{K}\right) N - \frac{GN^2}{N^2 + H^2} - \frac{CNP}{N + D} \quad (\text{S1.1a})$$

$$\frac{dP}{d\tau} = s \left(1 - Q\frac{P}{N}\right) P, \quad (\text{S1.1b})$$

where $N(\tau)$ and $P(\tau)$ are the densities of prey and specialist predator at time τ respectively. The prey undergo logistic growth with growth rate r and carrying capacity K . They are affected by two predation terms, representing generalist and specialist predation. Generalist predation is a Holling Type III functional form because generalists will switch to other prey items when prey numbers are low. The specialist predation is the Holling Type II functional form which incorporates handling time of prey. The predators have a logistic growth with growth rate s and a carrying capacity which is determined by the number of prey.

We non-dimensionalise the model using the following scalings: $x = \frac{N}{K}$, $y = \frac{PQ}{K}$, $t = \tau$ and new parameters: $g = \frac{r}{K}$, $h = \frac{H}{K}$, $d = \frac{D}{K}$ and $a = \frac{C}{Q}$. This is shown in dimensionless form in (S1.2), which includes seasonal forcing in the growth rates and implicitly also in the carrying capacities through the term $S(t)$:

$$\frac{dx}{dt} = rS(t)x - rx^2 - \frac{gx^2}{x^2 + h^2} - \frac{axy}{x + d} \quad (\text{S1.2a})$$

$$\frac{dy}{dt} = sS(t)y - s\frac{y^2}{x}. \quad (\text{S1.2b})$$

There is a long history of using a sinusoidal function for the seasonal term as follows:

$$S(t) = 1 + \epsilon \sin(2\pi t) \quad (\text{S1.3})$$

(Dietz, 1976; Rinaldi et al., 1993; Turchin and Hanski, 1997). However, as we wish to consider how changes in breeding season length affect population dynamics, we adapt the forcing term as follows:

$$S(t) = 2(\frac{1}{2}(1 + \epsilon \sin(2\pi t)))^l. \quad (\text{S1.4})$$

The new parameter l determines the length of the breeding season, which we define as when the forced growth term is above the unforced value of the parameter, i.e. when $S(t) > 1$. When $l = 1$, the breeding season length is half a year and the forcing term (S1.4) reduces to (S1.3). As l is increased the breeding season length decreases and vice versa. We wish the amplitude of the seasonal term to be large to represent strong seasonal forcing: nevertheless we require $\epsilon \leq 1$ so that the forcing term is not negative. We choose $\epsilon = 0.95$ to avoid the numerical problems that

occur for $\epsilon = 1$ when l is small. Although we vary l from 0 – 5, the range $0.5 < l < 3.9$ is most relevant for Fennoscandian voles, since this leads to a breeding season between 3 months and 8 months long, which corresponds to the variation observed in field data (Nelson et al., 1991; Hansen et al., 1999; Dalkvist et al., 2011).

S2 Method Details

In order to study the predator-prey system (S1.2) we employed both bifurcation and simulation methods, following the procedure in Taylor et al. (2012). The bifurcation diagrams were created using essentially standard numerical continuation techniques via the software AUTO (Doedel, 1981). The simulation results were produced in Matlab (`ode15s`), solving equations (S1.2) for 2000 years. Once the solutions had settled to their dynamic attractor, a test to determine whether there existed a periodic solution of 1 - 9 years was performed; if not, the solution was labelled as quasi-periodic. The choice of 9 years as a maximum test period is arbitrary; there could in principle be solutions with any finite integer period, but an upper limit is required for numerical study. To test whether a solution had a period of, for example, four years, we recorded the prey density for 20 time points at intervals of 4 years, after an initial time interval of sufficient length that transients had decayed. If the difference between the maximum and minimum of these numbers was less than 2.5% of their mean value, then it was classified as a four year solution. Tests of some difficult cases near bifurcation curves or within multiple solution regions led to the choices of 2000 years run time, 20 test points and 2.5% variation; these enabled periodic and quasi-periodic solutions to be distinguished. We considered the parameter region $0 < l < 5$, $0 < g < 1$. For each set of parameter values, solutions were replicated 50 times using different (random) initial conditions between 0 and 1, independently chosen for both prey and predator. However, for parameter pairs lying in region B of Figure 3 (main text) we used 500 simulations to gain increased accuracy of the relative sizes of the basins of attractions because of the possibility of multiple solution behaviour in this region. Furthermore, fast Fourier transforms were used to determine the period most closely reflected in the solution (“dominant period”). In order to plot these results in a similar manner to the cycles method, all the dominant periods were rounded to the nearest integer. If a dominant period was higher than 9.5 then the solution was classified as quasi-periodic. The fast Fourier transform method is not as accurate for calculating stability of the solutions, for example, see Figure 3b and c (main text) at $(l, g) = (0.5, 0.6)$ where (b) shows that 2 year cycles are stable while the dominant period in (c) is given as 1 year. However, it is very useful for calculating approximate periods of the quasi-periodic solutions.

S3 Further Results

S3.1 Bifurcation Definitions

Definitions of period-doubling, saddle-node and Neimark-Sacker bifurcation curves are included here to aid understanding of the bifurcation diagrams shown in Figures 4, S3.1, S3.2, S4.1 and S4.3. General bifurcation theory can be found in Kuznetsov (1995) while detailed theory specifically applied to seasonally forced predator-prey systems can be found in Rinaldi et al. (1993); Taylor et al. (2012).

The standard procedure for locating bifurcations uses the Poincaré (or stroboscopic) map that transforms the continuous system into a discrete one by sampling the solution once in each forcing period; one year in our case. Note that the stable/unstable annual cycles become stable/unstable fixed points of the Poincaré map. Discrete bifurcation theory reveals that this fixed point is unstable if one of the eigenvalues of its linearisation has modulus larger than 1. Changes in stability are of three possible types. If the eigenvalue is equal to -1 , it is a *period-*

doubling (flip) bifurcation; if the eigenvalue is equal to $+1$ it is a *fold (saddle-node, tangent) bifurcation*; and if there is a pair of complex conjugate eigenvalues with modulus 1, it is a *Neimark-Sacker (torus) bifurcation*.

At a period-doubling bifurcation curve (shown in blue), which we denote by PDk , a stable cycle of period k loses stability and a stable cycle of period $2k$ arises.

On one side of a saddle-node bifurcation curve denoted by FDk there is no solution but on the other side there are both stable and unstable solution branches of a cycle of period k , which have a fold at the bifurcation point. These are shown in red.

A Neimark-Sacker bifurcation is often described as a discrete version of a Hopf bifurcation because for a standard supercritical bifurcation, the fixed point on the Poincaré section becomes unstable and a stable closed invariant curve arises around the point. Each iteration of the Poincaré map brings the solution back to a different point on the closed invariant curve. Therefore, in the continuous setting when crossing a Neimark-Sacker bifurcation curve, denoted by NSk , a cycle of period k loses stability and a quasi-periodic solution arises. That is, the solution may superficially appear periodic but in fact it has no finite period. Neimark-Sacker bifurcation curves are shown in green.

S3.2 Bifurcation Results

Figure 3a (main text) is based on a bifurcation diagram produced in AUTO which shows the full range of potential behaviour. In Figure S3.1 we show this bifurcation diagram for annual, quasi-periodic and 2 year cycles, as well as behaviour resulting from period-doubling of the 2 year cycle. The whole bifurcation diagram (Figure S3.2) is quite complicated, with a number of different curves overlapping, so it is helpful to consider first the partial bifurcation diagram in Figure S3.1. In region 0 there are stable annual cycles but then as g is decreased one crosses the Neimark-Sacker bifurcation curve, $NS1$, leading to loss of stability of the annual cycles and a gain of stability of quasi-periodic cycles in region 1. The rest of the region is bounded within the saddle-node curve $FD2$ and the period-doubling curve $PD1$. As one crosses the period-doubling curve one loses stability of the yearly cycles and gains two year cycles, which also exist outside the period-doubling region due to the saddle-node curve. In fact, we can see the existence and stability of these two year cycles in greater detail in Figure 4a (main text). The Neimark-Sacker bifurcation curve, $NS2$, within this region leads to instability of all the 2 year cycles below the green line. There is also a period-doubling curve within the 2 year cycles region denoting the existence of four year cycles, as can be seen in Figure 4c. This is the start of a period-doubling cascade.

We also note that the point where the continuation of the first Neimark-Sacker bifurcation ($NS1$), hits the $l = 0$ axis is where the unforced system undergoes a Hopf bifurcation. This bifurcation is subcritical, and this subcriticality extends to the Neimark-Sacker bifurcation so that quasi-periodic solutions exist alongside the yearly solutions above the curve. Combined with the quasi-periodic solution generated by curve $NS2$, this produces the shape of the two regions C and D in Figure 3.

In Figure S3.2 we include all the bifurcation curves for each of the different period cycles that were found. For 2-5 year cycles, these were studied individually in Figure 4 but we show them all together in Figure S3.2 in order to see the full picture and the overlapping behaviour. This new bifurcation diagram includes all the saddle-node bifurcation curves for all the cycles that were found between 3 and 9 years. There are further bifurcation curves within these bounded regions, as seen in Figure 4, denoting changes in stability to these solutions but we omit these in Figure S3.2 in order to gain a clearer representation of existence of the cycles. Furthermore, there are undoubtedly more fold bifurcation curves indicating additional regions of multi-year cycles for any integer period, but we either didn't find these or they are too small to be traced.

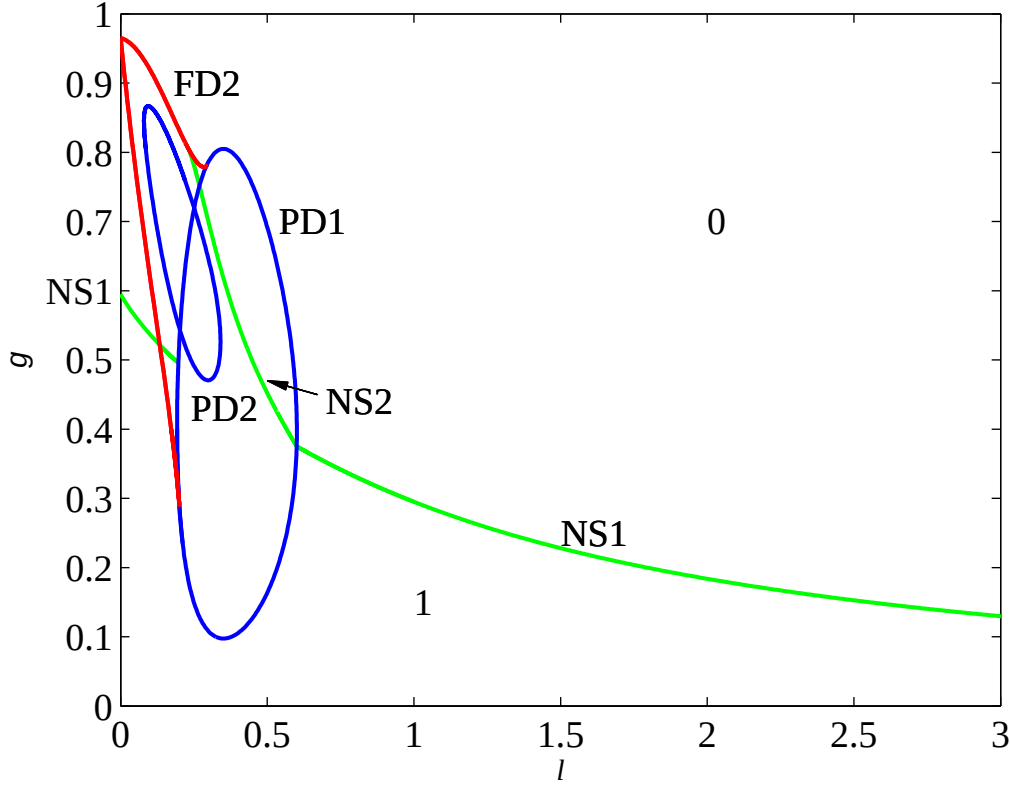


Figure S3.1: Partial bifurcation diagram in season length parameter (l) and extent of generalist predation (g). Only the bifurcations resulting from the annual cycle are shown. The different bifurcation curves shown by colour: blue: period-doubling, red: saddle-node, green: Neimark-Sacker bifurcation. In region 0 (bounded below by the NS1, PD1 and FD2 curves) there are annual cycles; in region 1 (bounded above by the same curves) there are quasi-periodic cycles

S4 Prey-only Forcing

In the model (S1.2) we forced both the prey and predator growth rates with the same forcing term. Although weasels are able to breed throughout the whole year, this only happens in peak years of vole populations (King, 1989). Therefore, including a weasel breeding season is valid but it is unclear whether this should follow the same pattern as the vole breeding season, on which the forcing term was based. In order to understand the effects of different forcing in the predator growth rate, we consider the scenario where the prey growth rate is forced (S1.2a) but there is no forcing in the predator equation (S1.2b). We analyse the model using the same methods as in the main text, namely through bifurcation and simulation analysis. The bifurcation diagram, Figure S4.1, shows the Neimark-Sacker bifurcation curve, NS1, the period-doubling curve PD1 and the two fold curves, FD3 and FD4, for the model without predator forcing (which can be compared to Figure S3.2 when both predator and prey are forced). We did not determine the higher period fold curves for this scenario. Whereas in Figure S3.1 the period-doubling curve PD1 intersected the Neimark-Sacker bifurcation curve, NS1, for the case with no predator forcing this period-doubling curve does not exist and the Neimark-Sacker bifurcation curve is now continuous. Both the three year and four year cyclic regions have changed in shape, with the three year region shrinking and the four year region increasing in size. This indicates the potential for a large area of stable four year cycles. The Neimark-Sacker bifurcation has also moved up in the $l - g$ plane so that it now hits the $l = 0$ axis at $g = 1$. The upward shift in the Neimark-Sacker curve and the expansion of the period four fold curve indicates that when

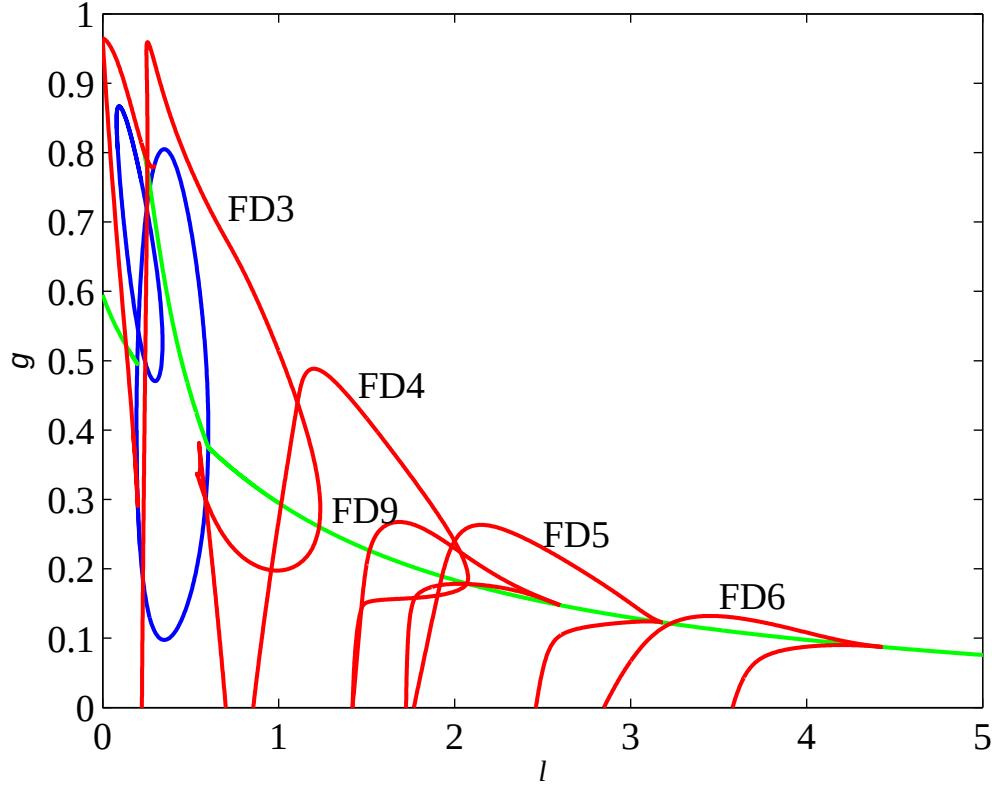


Figure S3.2: Full bifurcation diagram in season length parameter (l) and extent of generalist predation (g). The curves which are labelled are those which are not in Figure S3.1. All other details as in Figure S3.1. For the 3 year and higher cycles, only the bifurcation curves indicating existence are shown and not any that only indicate changes in stability; these can be found in Figure 4 (main text)

l is small, multi-year cycles are possible for more values of generalist predators, i.e. for a wider range of g values, compared to the predator forcing case in the main text.

We also produced simulation results for this prey-only forcing case, showing both the cycle periods and the dominant period (Figure S4.2). The influence of the large four year fold curve as seen in Figure S4.1 is clear, dominating the region containing multi-year cycles. However, 3, 7 and 8 year cycles are also found. This is interesting considering that the 7 and 8 year cycles were rare in the predator forcing case (see Figure 3b).

From these figures, it is clear that a number of results stated in the main text for the model with prey and predator forcing hold true when the forcing on the predator is removed. As before there is a diagonal split from top left to bottom right delineating multi-year cycles and annual cycles. As the extent of the generalist predators increases, such as when one moves south in Fennoscandia, there is a switch to annual cycles as expected. However, it is not a clear split and there is still the potential for 3 year cycles in a similar manner to the main text results in Figure 2. Also holding true is the fact that multi-year cycles exist for a wide range of values of l when g is small. The main difference between the results in the main text and these results for prey-only forcing is the fact that only annual cycles are indicated for the higher values of l , i.e. for breeding seasons around $3\frac{1}{2}$ months, although confirmation by simulation is needed to see if this continues for $l > 3$. This also ties in with the fact that the pattern of increasing period length for small g as l increases is less clearly defined. The dominance of the 4 year cycles makes it hard to determine this behaviour; identifying the bifurcation curves for the higher period cycles could clarify whether this pattern still holds.

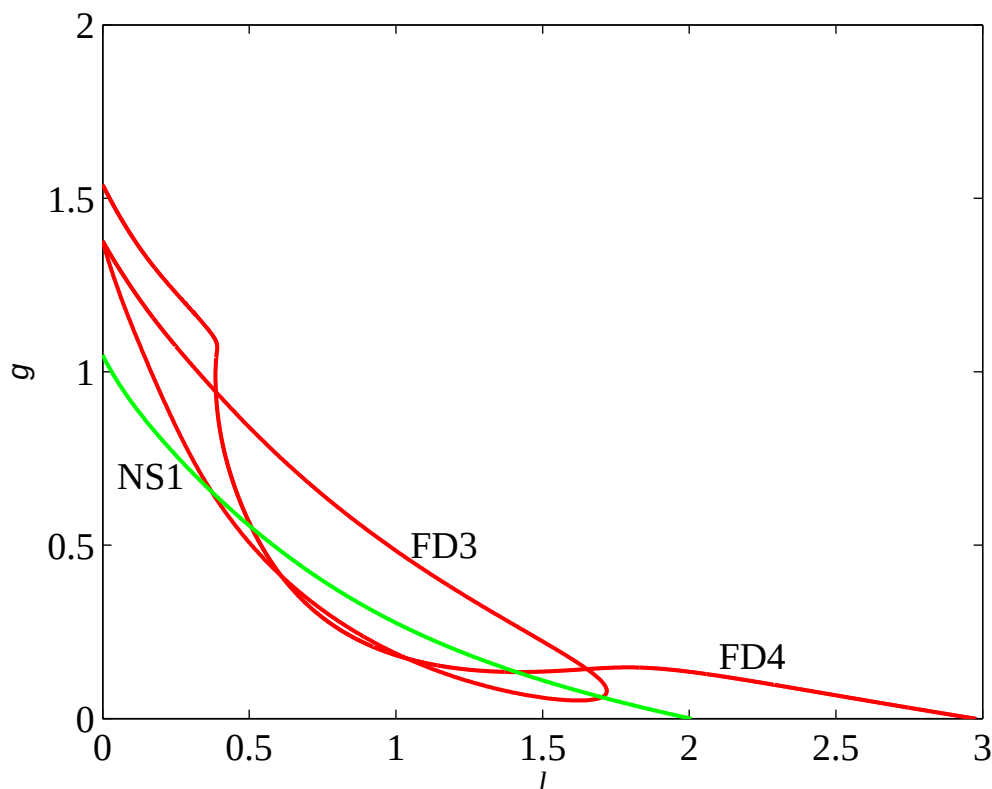


Figure S4.1: Bifurcation diagram in season length parameter (l) and extent of generalist predation (g) when the predators are not forced. Only the four curves NS1, PD1, FD3 and FD4 were found, although the period-doubling curve, PD1, has in fact disappeared for this scenario. The different bifurcation curves shown by colour: red: saddle-node, green: Neimark-Sacker bifurcation

S4.1 Reducing forcing in the predator growth rate

The case of no predator forcing above shows that the period-doubling curve has disappeared. It is possible that the curve does exist but we were unable to find it while doing the bifurcation analysis. However, confirmation of how the period-doubling curve, and the other curves, change can be found by analysing the system as it moves from the original scenario of both prey and predator being forced towards the case with prey-only forcing. We do this by tracing along a gradient of reduced forcing for the predator determined by a new parameter ξ , using the adapted forcing term $S^*(t)$ for the predator:

$$S^*(t) = 1 - \xi + \xi S(t). \quad (\text{S4.1})$$

Therefore, $\xi = 1$ is the case in the main text while $\xi = 0$ is the case of no forcing for the predator. By reducing ξ from 1 to 0 we can determine how the four curves (NS1, PD1, FD3 and FD4) change as we move towards prey-only forcing. We consider the bifurcation diagram for different values of ξ , as shown in Figure S4.3.

Through consideration of the full range of ξ values (Figures S3.2, S4.1, S4.3) it is clear how the different curves change shape. The Neimark-Sacker bifurcation curve is increasing in g as ξ is reduced. The break between the two sections of the Neimark-Sacker bifurcation reduces in size as ξ decreases until $\xi = 0$ where it is now continuous (Figure S4.1). This is due to the reduction in size of the period-doubling region as seen in Figure S4.3. In fact, as ξ is reduced from 1 to 0, the period-doubling curve, PD1, gets smaller until it disappears just below $\xi = 0.155$. The three

year fold curve, FD3, reduces in size and is no longer connected to the $g = 0$ axis. Figure S4.3 also indicates that the Hopf bifurcation on the $l = 0$ axis is still subcritical (as in Figure S3.2)

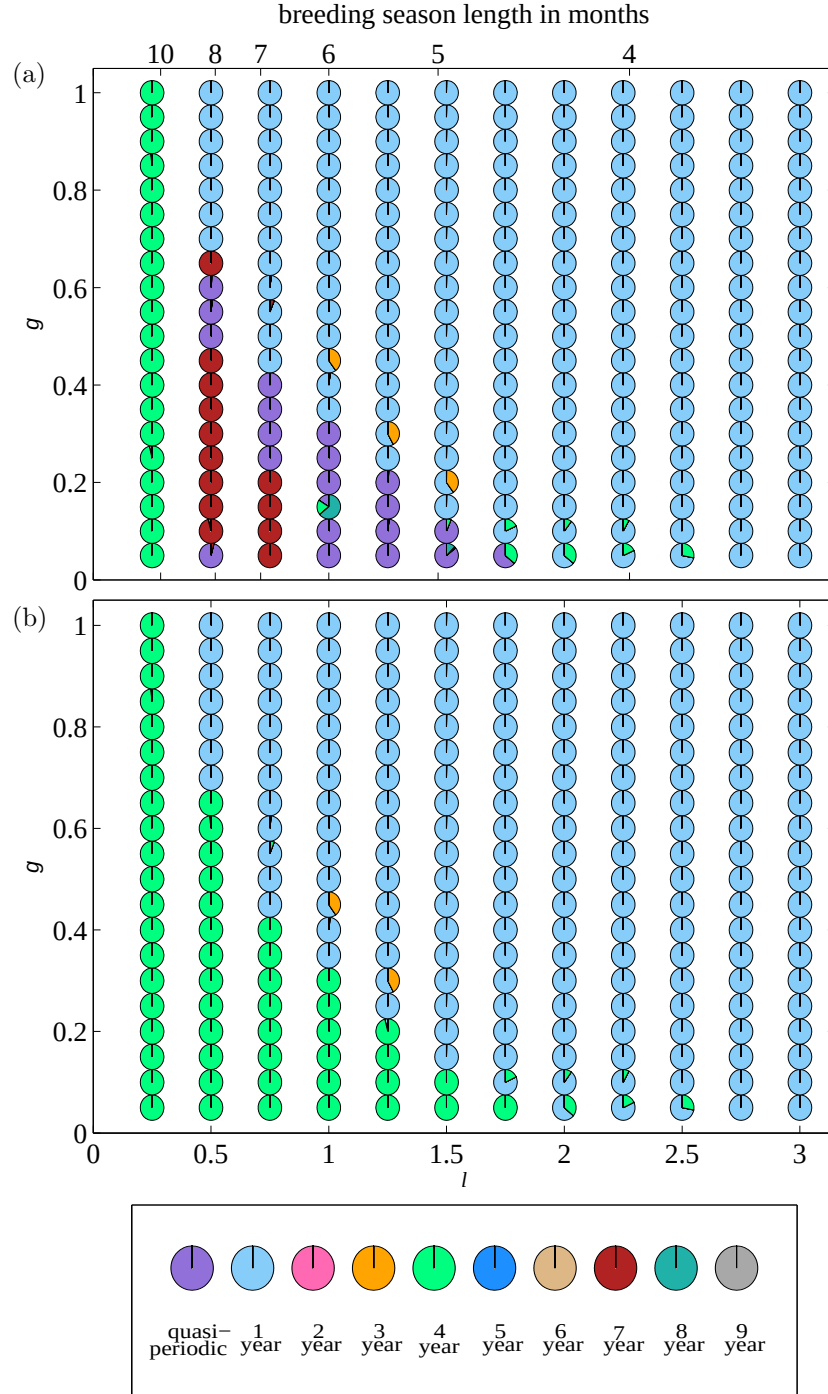


Figure S4.2: Simulation results when the predators are not forced. The diagrams show season length parameter (l) against extent of generalist predation (g). The breeding season length is indicated on the top axis. In (a) a simulation diagram with a grid of pie charts showing what proportion of the 50 simulations had a particular period, indicated by the legend. Each simulation was run with random initial conditions (between 0 and 1 for both prey and predator) and the period was tested after 2000 years. In (b) these same simulations were tested using fast Fourier transforms to determine the dominant period of the solutions. Other parameter values are $r = 6$, $s = 1.25$, $d = 0.04$, $a = 15$, $h = 0.1$, $\epsilon = 0.95$

because the three year fold curve hits the axis above the Neimark-Sacker bifurcation curve. The four year fold curve, FD4, lowers in g as ξ is reduced at first, although by $\xi = 0$ the fold curve has increased again so that for $\xi = 0$, it exists up to $g = 1.5$ for low values of l . It also exists for more values of l as ξ decreases.

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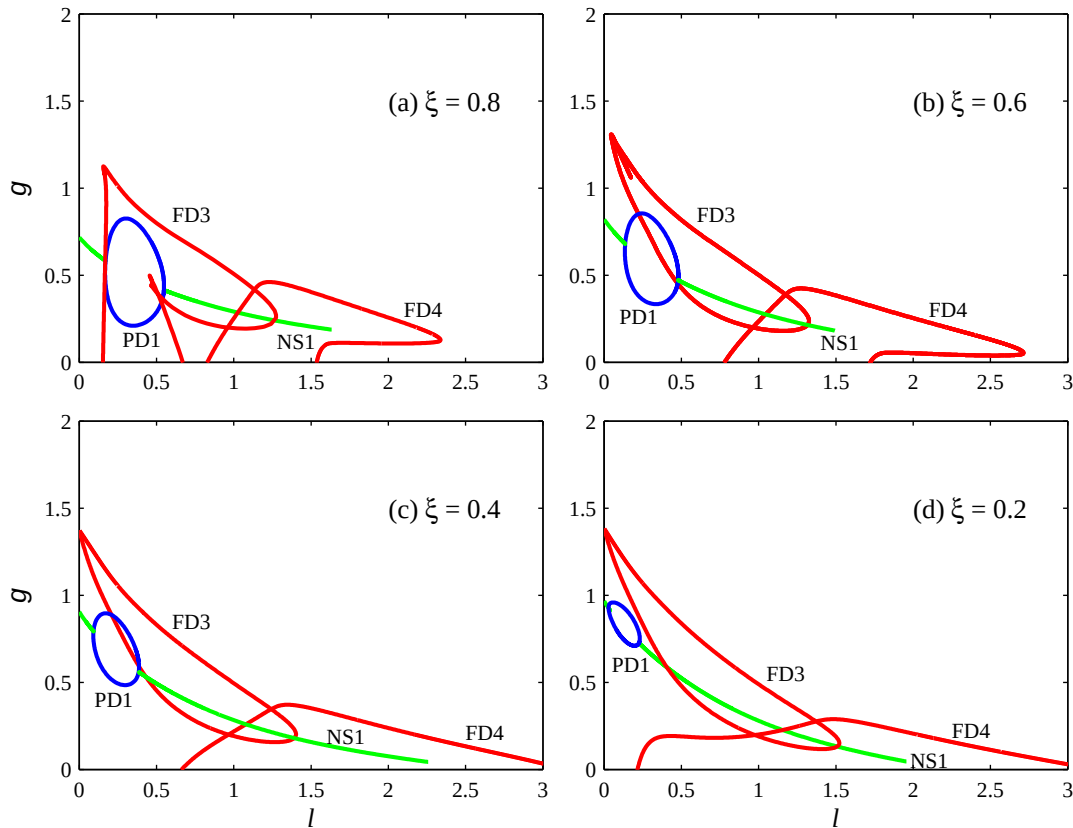


Figure S4.3: Four bifurcation diagrams in season length parameter (l) and extent of generalist predation (g) as the level of forcing in the predator equation is reduced. Four different values of ξ are shown, namely (a) $\xi = 0.8$, (b) $\xi = 0.6$, (c) $\xi = 0.4$, (d) $\xi = 0.2$. For $\xi = 0$ see Figure S4.1. The different bifurcation curves shown by colour: blue: period-doubling, red: saddle-node, green: Neimark-Sacker bifurcation

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