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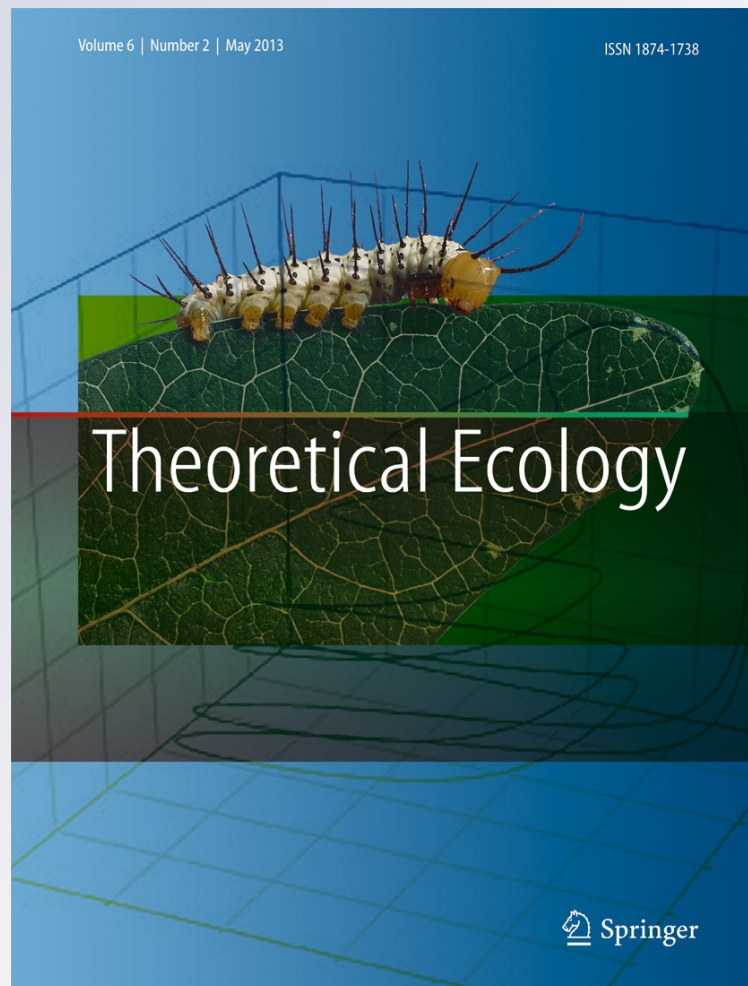
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A comparison of the dynamical impact of seasonal mechanisms in a herbivore–plant defence system

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Abstract Plant defences can reduce herbivore fitness and may promote cycles in some herbivore populations. In this study, we model the interaction between plant defences and herbivores and include seasonal forcing, a ubiquitous environmental influence in natural systems. We compare the impacts of two different seasonal mechanisms on the dynamics of the herbivore–plant defence system. The first mechanism involves a fixed breeding season length and a variable birth rate within the breeding season; the second involves a variable breeding season length and a fixed birth rate within the breeding season. When parameterised for a specific cyclic system, namely field voles and silica, our model predicts that a variable season length gives multi-year cycles for a larger region in parameter space than a variable birth rate. Our results highlight the complexity of the dynamical effects of seasonal forcing and that these effects are strongly dependent on the type of seasonal mechanism.

Keywords Seasonal forcing · Population cycles · Inducible plant defences · Herbivore dynamics

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Introduction

Cyclic patterns in animal populations have long been a focus of scientific interest (Elton 1924; Turchin 2003). Despite extensive research, the mechanisms underpinning multi-year population cycles are a subject of much debate (Krebs 1996; Turchin 2003). Elton (1924) described the widespread existence of periodic fluctuations in animal abundance and attributed this to climatic variations. Since then, many hypotheses concerning the factors determining population cycles have been developed. However, firm evidence for causality is rare and the elucidation of the processes driving population cycles is a key topic of interest in population ecology. Also, it is becoming increasingly recognised that different and/or multiple mechanisms may operate in different systems (Turchin 2003).

One hypothesis is that interactions with food resources can cause population cycles (Lack 1954). This includes classical studies that focus on predator–prey interactions (Lotka 1925; Volterra 1926; May 1972) but also includes plant–herbivore interactions. There are two main distinct ways in which herbivore populations can be affected by interactions with the food plants. Firstly, the consumption of plant tissue may limit the quantity of food available to later-feeding herbivores; secondly, herbivore damage may elicit inducible resistance in the plant, thereby reducing the nutritional quality of the plant tissue (Karban and Baldwin 1997). Both of these pathways could play important roles in the long-term population dynamics of herbivores (Abbott et al. 2008). Changes in the abundance of food is thought unlikely to cause cycling, because a sufficient depletion of plant biomass is rarely observed, with many plant species recovering rapidly after grazing

(e.g. Krebs et al. 1986; Desy and Batzli 1989; Boonstra et al. 1998). However, there is significant evidence that in some systems, population cycles are related to the deterioration in the quality of food due to induced defences of the plant in response to intense grazing at the population peak.

In many plants, damage by herbivory induces changes in the composition of the foliage (Fowler and Lawton 1985). Many plant characteristics, ranging from secondary chemistry to physical features such as thorn density, can change in response to herbivore damage (Karban and Baldwin 1997). These inducible defences have been shown to adversely affect herbivore growth and/or reproduction (e.g. Bryant 1981; Schultz and Baldwin 1982; Karban and Carey 1984; Massey et al. 2006; Massey and Hartley 2006). As a result, inducible defences are predicted to significantly influence the dynamics of herbivore populations. Indeed, it has been argued that inducible defences contribute to driving cyclic fluctuations in a number of herbivore populations (Benz 1974; Haukioja 1980; Fox and Bryant 1984; Haukioja 1991). For example, Fox and Bryant (1984) demonstrate that the responses of Alaskan woody plants could account for the oscillatory nature of the snowshoe hare population. Benz (1974) shows that the larch tree responds to high levels of feeding by the larch budmoth by growing short needles of reduced nutritional quality, which causes a decrease in budmoth population density. This interaction is claimed to contribute to the population cycles of the larch budmoth. It should be noted that there is also evidence contrary to the hypothesis that inducible defences cause cycles; for example, the findings of Sinclair et al. (1988) suggest that inducible changes in the levels of plant secondary compounds do not cause the cyclic population dynamics of the snowshoe hare.

There is also a growing body of theoretical evidence that grazing-induced plant defences contribute to cyclicity (Lundberg et al. 1994; Underwood 1999). Underwood (1999) developed a model framework that focuses on the impact of induced resistance due to herbivorous insect populations. Lundberg et al. (1994) model herbivore population density and the plant population, stratified into discrete classes to represent the different plant defence levels that result from the grazing intensity the plant has been subject to. The model is applied to understand the changes in abundance observed in lemmings. These studies provide theoretical support for the idea that inducible defences in plants can cause fluctuations. In contrast, Edelstein-Keshet and Rausher (1989) develop a general mathematical framework and find that inducible defences cause persistent fluctuations only under un-

usual conditions. Lundberg et al. (1994) conclude that inducible defence may be an important factor for explaining the cyclic dynamics of herbivore populations, but their model does not generate stable limit cycles. They believe that seasonal perturbations may maintain the cycles, although no evidence for this is given. The aim of this paper is to investigate in detail the way in which seasonal forcing affects the dynamics of a herbivore population regulated by inducible plant defences. We develop a simple model to represent the herbivore–plant interaction and examine the effects on the population dynamics of adding seasonality.

Understanding seasonality in ecological systems is of great importance since natural populations are embedded in periodically varying environments. Imposing periodic forcing on a biological system can lead to major changes in system behaviour: it has long been established that unforced systems with simple dynamic behaviour can become very complex when periodically forced (Guckenheimer and Holmes 1986). Identifying the role played by seasonal forcing in driving dynamical behaviours is therefore a key issue.

Despite the ubiquitous nature of seasonality, exploring its consequences for population dynamics poses a challenge. Seasonal mechanisms can be difficult to pinpoint empirically and can give rise to complex population fluctuations (Altizer et al. 2006). One area where the effects of seasonality on population dynamics has been relatively well explored is in infectious diseases. Seasonality has been incorporated into epidemiological models in the areas of childhood diseases (Dietz 1982; Schwartz and Smith 1983; Keeling et al. 2001) and wildlife diseases (Roberts and Kao 1998; Ireland et al. 2004; Smith et al. 2008). If the underlying non-seasonal model has periodic solutions, then the dynamics once seasonal forcing is imposed can become more complex; the seasonality can interact with underlying oscillations, resonate, and result in a range of complex behaviours including chaos (Ireland et al. 2007). If the non-seasonal model does not have periodic solutions, the application of seasonality can, in some cases, cause oscillations with period an integer multiple of the forcing period (Schwartz and Smith 1983; Greenman et al. 2004). In addition, there have been a number of studies on seasonality in predator–prey systems (Kuznetsov et al. 1992; Rinaldi et al. 1993; Gakkhar et al. 2009). These models show a rich variety of behaviour, including stable and unstable periodic solutions of various periods, quasiperiodicity and chaos. Moreover, the behaviours can be transitory. These examples illustrate the complexity of the role of seasonality in shaping population dynamics. Adding seasonality can lead to interesting

and biologically important dynamics and can help to explain complex empirical data.

In strategic theoretical studies, seasonal forcing is typically incorporated by setting a specific model life history parameter to periodically vary in time, for instance, by simple sinusoidal variation of the parameter (e.g. Rinaldi et al. 1993; Greenman et al. 2004; Greenman and Norman 2007; Ireland et al. 2007). Alternatively, seasonal variation is incorporated in a manner motivated by the biological reality of the specific system being studied: for example, models of childhood diseases incorporate seasonal variation in contact rates by imposing an increased rate during school terms compared to school holidays (Keeling et al. 2001). Many natural systems have defined breeding seasons and therefore seasonality can be applied to the birth rate by defining a distinct reproductive and non-reproductive season (Smith et al. 2008).

In this paper, we apply seasonal forcing to the herbivore birth rate in a simple plant defence–herbivore model. We examine the effects of two different seasonal mechanisms to explore the role of seasonality in driving population fluctuations. The first seasonal mechanism involves a birth rate dependent on the level of plant defence, with a fixed breeding season length. The second involves a breeding season length dependent on the plant defence, with a constant birth rate in the breeding season. We undertake a comparison of these two types of seasonal forcing and their effects on the herbivore population dynamics. In order for a full investigation to be carried out, we choose a specific system as a case study, namely the interaction between voles and the silica content of the grass they consume.

Model

We use a general model framework to represent the interaction between herbivores and an inducible plant defence:

$$\frac{dH}{dt} = a(S(t), t)H(t) - b\,H(t) \tag{1}$$

$$\frac{dS}{dt} = \frac{K(H(t-\tau))^n}{H_0^n + (H(t-\tau))^n} + cS_0 - cS(t) \tag{2}$$

where $H(t)$ is the herbivore density and $S(t)$ the level of plant defence at time t. Inducible plant defences have been shown to affect growth or reproduction in individual herbivores adversely (e.g. Bryant 1981; Schultz and Baldwin 1982; Karban and Carey 1984; Massey et al. 2006; Massey and Hartley 2006); in line with this evidence, we take the herbivore birth rate a to be a function of the level of the inducible factor.

Parameter b is the herbivore death rate. We denote by cS_0 the background level of plant defence production; here, S_0 is the background level of the inducible factor, i.e., its level in the absence of herbivory. The induction rate depends on the herbivore density. By definition, the induction level drops to zero in the absence of herbivores, and physiological constraints mean that its production must saturate at high levels of herbivory. H_0 is the herbivore density at which induction is half of the maximum possible, and $K + cS_0$ is the maximum possible rate of production of the inducible factor. The time delay τ represents the time taken for the inducible factor to be produced after herbivory occurs. Parameter c is the decay rate of the inducible factor. The plant defences decay when herbivory diminishes; Rhoades (1983) argues that this is because inducible defences are costly to a plant and are therefore not likely to be maintained unless a need for them exists.

We denote by a_{max} and a_{min} the maximum and minimum birth rates, respectively. We make the assumption that for $S < S_0$, there is no effect of the plant defence on the herbivore, so the birth rate is at its maximum. Above inducible factor levels of S_0, the birth rate decreases linearly with concentration.

In reality, many animal species have seasonal birth rates, so we impose a seasonally forced herbivore birth rate by introducing a breeding season and non-breeding season each year. This is typical of the life-history of many herbivore species in temperate climates. We let the length of the breeding season be denoted by l. In the non-breeding season, the herbivore birth rate a is taken to be zero.

We consider two different seasonal mechanisms, both affecting the herbivore birth rate. Firstly, the birth rate a in the breeding season is dependent on the concentration of inducible factor, and secondly, the breeding season length l is dependent on the concentration of inducible factor. We denote by l_{max} the maximum breeding season length and by l_{min} the minimum breeding season length. The addition of seasonal forcing typically complicates and potentially destabilises the population dynamics of a system. By examining two different mechanisms, we intend to test whether the way seasonality is manifested influences its effects on the population dynamics.

Case study

In order to analyse this model, we focus on a specific case study. Our aim is to compare two different seasonal mechanisms operating on the herbivore birth rate. We therefore focus on a particular ecological

system where both mechanisms can potentially operate, namely the interaction between voles and the silica content of the grass they consume. The choice of voles as the herbivore species is a natural one due to the abundance of literature on the potential causes of vole population cycles.

Silica (silicon dioxide, SiO_2) in the tissues of grasses acts as an antiherbivore defence strategy to reduce levels of grazing by both vertebrate (McNaughton and Tarrants 1983; Gali-Muhtasib et al. 1992; Massey and Hartley 2006) and invertebrate herbivores (O'Reagain and Mentis 1989; Vicari and Bazely 1993; Massey et al. 2006). Silica has been proposed as the primary defence in many grasses (Massey et al. 2007a), and there is evidence that it has a range of detrimental effects on herbivores that ingest it (Jones and Handreck 1967). Silica reduces foliage digestibility, leading to reductions in herbivore growth rates (Massey et al. 2006, 2008; Massey and Hartley 2006). In addition, silica increases the abrasiveness of grass, deterring feeding by herbivores (Massey et al. 2006, 2007a; Massey and Hartley 2006). Therefore, silica acts to reduce the quality of the plant as food for herbivores. Food quality is especially important for voles due to their relatively high metabolic rates and because they have a limited capacity to increase food consumption to compensate for poor-quality diets (Zynel and Wunder 2002). In addition, their growth rates early in development are highly dependent upon nutrient intake. Therefore, vole food quality has the potential to dictate the time taken to reach sexual maturity and the onset of breeding each year (Krebs and Myers 1974; Ergon et al. 2001).

Silica defences in grasses are induced by herbivore grazing (McNaughton and Tarrants 1983; Massey et al. 2007b). The induction of defences in response to herbivore damage is widely recognised as an effective plant defence strategy, particularly in cases where defences are costly or the threat of herbivore attack is intermittent (Karban and Baldwin 1997). It has been shown that silica can be induced by vole grazing to levels sufficient to deter further feeding and also affect herbivore performance (Massey and Hartley 2006).

To parameterise this model, we use the particular case of field voles (*Microtus agrestis*) in Kielder Forest, Northern UK. This vole population fluctuates cyclically over a range of about 20–700 voles/hectare in optimal habitats with a characteristic period of 3–5 years (see Lambin et al. 2000 for details). There are long-term data sets on vole populations, and intensive studies on the field vole, its predators and its food plants have been conducted. The roles of predation by the common weasel, a vole specialist, and intrinsic mechanisms (e.g. maternal effects) have been tested and rejected

as causal mechanisms for vole population cycles in this area (Ergon et al. 2001; Graham and Lambin 2002). In contrast, grazing-induced changes in plant quality, affecting vole nutrition and their ability to reach reproductive status in the spring, could offer a plausible explanation.

In Kielder Forest, the grass species *Deschampsia caespitosa* is the dominant food plant for voles, and in winter and early spring, when energetic demands for voles are at their highest, there is no significant alternative food source. There is growing evidence that, in this area, silica levels in the grass may be a determinant of cyclic population patterns. A correlation between vole population density, and therefore grazing intensity, and grass silica content has been noted in the field (Massey et al. 2008): in sites where vole population density was high, silica levels in grass leaves collected several months later were also high, and vole populations subsequently declined; in sites where vole population density was low, silica levels were low and population density subsequently increased. These findings highlight the potential importance of interactions between silica defences and vole abundance, and suggest that, for this specific population, silica-based defences in grasses may play an important role in driving vole population cycles.

We take the inducible factor S in Eqs. 1 and 2 to be silica (in percentage of dry mass), and the herbivore density H to be the density of field voles (per hectare). Using a least squares method, we have previously derived parameter estimates for K, H_0, n, S_0, c and τ using greenhouse data on silica induction and relaxation (Reynolds et al. 2012). Field data (Graham and Lambin 2002; Burthe 2005) give monthly survival probabilities, which lead to an estimate for the vole death rate of $b = 0.22$ per month (corresponding to a monthly survival of about 80 %) (Smith et al. 2006). These parameter values are shown in Table 1. (Note that the

Table 1 Parameter estimates for the case study

Parameter	Value	
K	5.42	per month
H_0	79.77	per hectare
S_0	2.54	% dry mass
c	0.25	per month
b	0.22	per month
τ	1.7	months
n	2	(unitless)

For details on the derivation of these estimates, see Reynolds et al. (2012). Note that $n = 2$ means that the induction term in Eq. 2 is a sigmoidal function. We explore the effects of changing the value of the delay τ from this estimate in the "Results" section
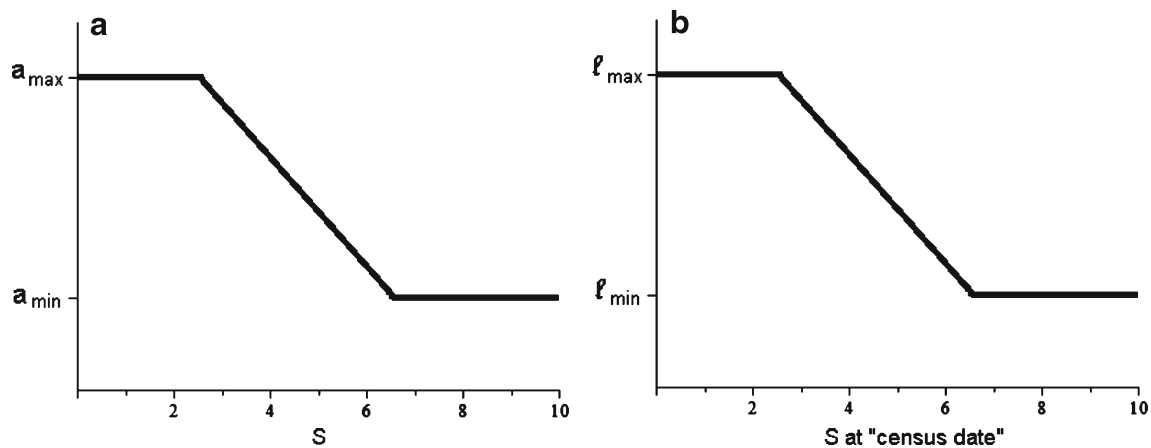
Fig. 1 **a** Vole birth rate *a* and **b** vole breeding season length *l* as functions of silica *S*. For **a**, the birth rate is dependent on silica at the present time, whereas for **b**, the breeding season length is dependent on silica at the "census date"

estimates of parameters K and H_0 are chosen in order to set an absolute scale for the population densities.)

We assume that the birth rate is at its minimum value (i.e. silica has its maximum effect) for silica levels of 6.6 and above. This value is taken from experimental data of Massey et al. (2008): a vole growth rate of 0 corresponds to a silica content of 6.6 % dry mass. Between silica levels of 2.54 (the background level of silica, S_0) and 6.6, we assume the birth rate decreases linearly with silica. Figure 1a illustrates the vole birth rate function used in our model.

There is a significant variation in the available estimates for the maximum birth rate of voles, a_{max}. Time series data from Kielder Forest imply a value of at least 0.3 per month (Smith et al. 2006), whereas trapping data imply a figure of 0.9 (Smith et al. 2008). Studies of similar rodent taxa have suggested values of 1.2 and 1.3 (Turchin and Ostfeld 1997). We therefore regard this parameter as variable and investigate the effects on the model solutions of changing a_{max}.

Seasonal models

We consider two different seasonal models.

Seasonal model 1 The breeding season length is fixed; we denote it by l_{max}. During this part of the year, the birth rate is given by the function $a(S(t))$ (illustrated in Fig. 1a), and in the remainder of the year the birth rate is set to zero.

An increase in the grass silica level reduces the quality of the grass as food for voles; this has the potential to increase the time taken to reach sexual maturity and thus delay the onset of breeding each year (Krebs and Myers 1974; Ergon et al. 2001). The timing of spring reproduction shows substantial variation in Kielder Forest (Ergon et al. 2011); the onset of the breeding season varies from mid-March to early June in different years. It has been shown that these changes in the timing of reproduction covary strongly with past vole density (Ergon et al. 2011). A correlation between vole population density and grass silica content has been noted in the field (Massey et al. 2008). On the basis of this evidence, it is hypothesised that the onset of reproduction is delayed as a result of a high silica diet; this affects the total births in a season by reducing the breeding season length (Smith et al. 2006). We therefore consider a second seasonal model. In this model, silica affects vole breeding through the regulation of the season length:

Seasonal model 2 The breeding season length l depends on silica as depicted in Fig. 1b. We assign a "census date" at the earliest possible time in the year at which the breeding season can start, and it is the silica level at this date that determines the breeding season length for that year. Specifically, the onset of the breeding season changes with the census date silica level, giving the change in breeding season length. The birth rate in the breeding season is always fixed at its maximum value a_{max}. The birth rate is zero in the non-breeding season.

The underlying silica-dependent functional form is the same for both models (Fig. 1); the season length in model 2 depends on silica in the same way as the birth rate depends on silica in the first seasonal model. For low silica levels (i.e. less than or equal to 2.54 % dry mass), the two models become equivalent: there is a birth rate of a_{max} for l_{max} months. We impose these conditions to allow us to compare the two models in an effective way.

Results

Our aim is to compare the effects of the two different seasonal mechanisms on the population dynamics. There are two steady states: the trivial $(H, S) = (0, S_0)$

and another with non-zero H. We can determine for which parameter values the trivial steady state is stable using Floquet theory (see Appendix A). When the trivial steady state is unstable, the non-trivial steady state is relevant. The seasonal forcing means that any
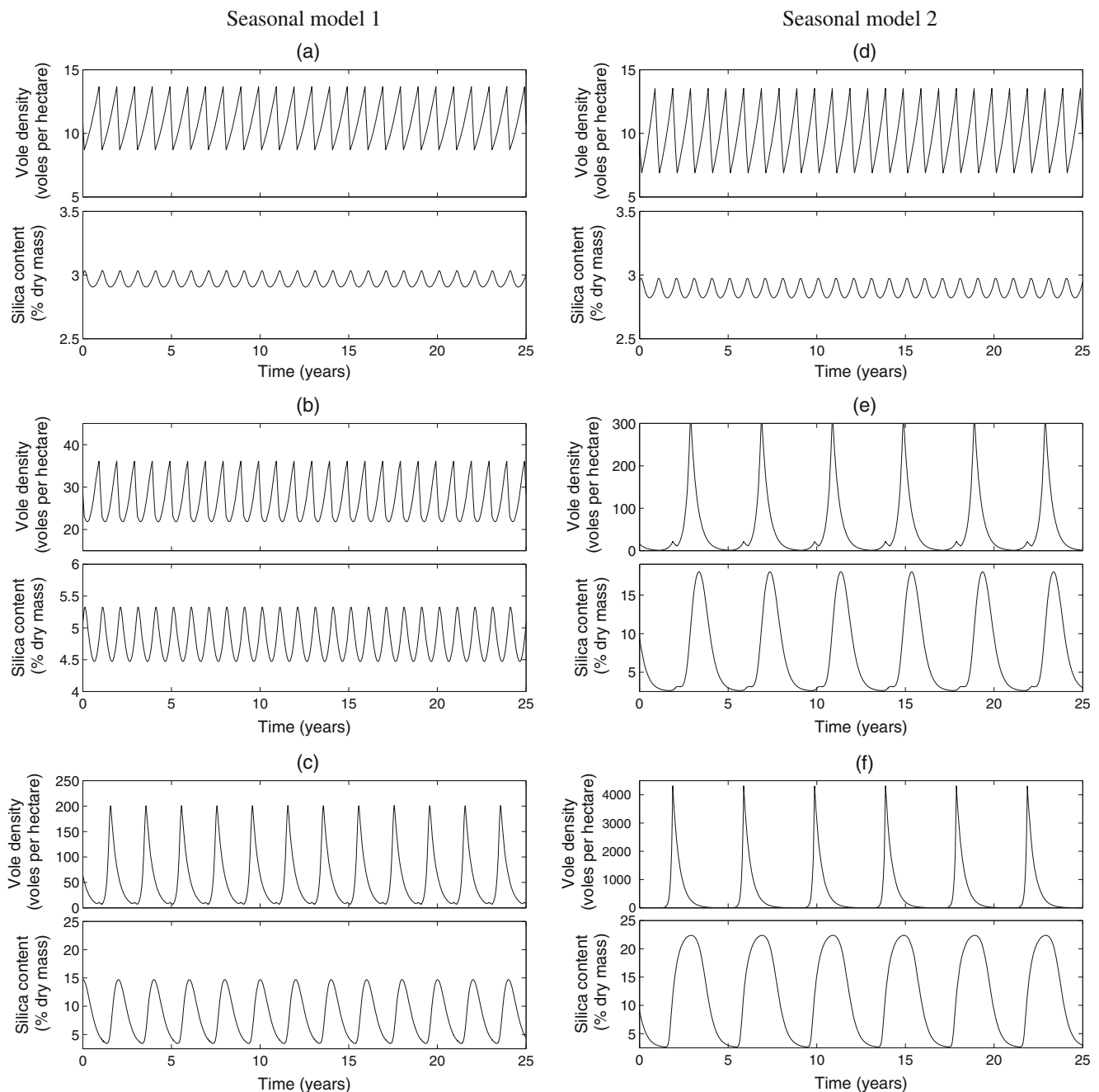

Fig. 2 Cycles generated for seasonal model 1 and seasonal model 2 for three different values of a_{max}, the maximum birth rate. $a_{max} = 0.3$ (per month) for **a** and **d**; $a_{max} = 0.6$ for **b** and **e**; $a_{max} = 1.2$ for **c** and **f**. Here, $a_{min} = l_{min} = 0$, and $l_{max} = 10$ as explained in the main text. These simulations are produced by MATLAB using the delay differential equation solver dde23.

Initial conditions are $S = 5$ % dry mass and $H = 25$ per hectare for $t \leq 0$. Solutions are shown after 450 years. Note that in order for the cycles to be seen clearly, the scales on the y-axes are not all the same. Seasonal model 2 has a greater tendency to produce multi-year cycles

solution will be cyclic, displaying either annual or multi-year cycles. The annual cyclic behaviour is due simply to the dynamics being entrained to the annual seasonal forcing. Our focus is an investigation of the causes of multi-year cycles, which here refer to repeated oscillations in abundance with a cycle period longer than 1 year.

To compare the two seasonal models, we initially set $a_{\min} = l_{\min} = 0$. The maximum reproductive season length for field voles in Kielder Forest is 10 months (Ergon et al. 2001), so we set $l_{\max} = 10$ here. Figure 2 shows the cycles generated for both models for three different values of the maximum herbivore birth rate, $a_{\max}$. This figure shows that as $a_{\max}$ increases, cycles change from annual to multi-year. We find that seasonal model 2 gives multi-year cycles for lower values of the maximum herbivore birth rate than seasonal model 1. Specifically, model 1 generates multi-year cycles for $a_{\max}$ values of 0.73 per month and above; model 2 generates multi-year cycles for values of 0.44 per month and above. So model 2 has the largest region in parameter space where there are multi-year cycles.

We can compare the results of these seasonal models with the results of the model *without* seasonality. By definition, the non-seasonal model does not have distinct non-breeding and breeding seasons; rather, breeding occurs throughout the year, with the birth rate depending on silica as shown in Fig. 1a. Due to the absence of seasonality, there is no underlying annual cycling for this non-seasonal framework. The non-seasonal model predicts cycles for $a_{\max}$ values of 0.70 per month and above. Below this value, the solutions are non-cyclic. Therefore, the seasonality mechanism in model 1 actually slightly reduces the region in parameter space where there are multi-year cycles. In contrast, this parameter region is significantly larger for seasonal model 2. Note that in order to make a comparison between the seasonal and non-seasonal models, we scale the birth rate for the non-seasonal model, so that over one year the birth rate is equivalent to that of the seasonal models.

A delay term is known to be a potentially destabilising factor (Haberman 1977). The data used to parameterise the model for the vole–silica system clearly indicate a short delay (of 1.7 months) between herbivore damage and plant response (Reynolds et al. 2012). Moreover, other theoretical studies modelling herbivore–plant defence interactions also include a delay term (Underwood 1999). However, from the viewpoint of generality to other systems, it is important to explore the effects of changing the delay length τ, including the particular case of no delay. Figure 3 shows the lowest maximum birth rates for which multi-year

cycles are generated (as opposed to annual cycles) for both seasonal models, for a range of τ values, including $\tau = 0$. Seasonal model 2 consistently predicts multi-year cycling for a larger region in parameter space. Therefore our main conclusion remains the same regardless of the value of the delay term: seasonal model 2 generates multi-year cycles for lower values of $a_{\max}$ than seasonal model 1. For $\tau = 0$, values above 0.47 per month give multi-year cycles for model 2; the corresponding threshold value is 3.76 per month for model 1. It can be seen from these results that the delay plays an important role in the generation of multi-year cycles for seasonal model 1; the value of the maximum birth rate has to be increased significantly to give multi-year cycles in the case with no delay. However, for seasonal model 2, the delay has relatively little effect on the population dynamics.

Figure 3 also shows the lowest maximum birth rate values for which the corresponding non-seasonal model generates cycles. For this model, the solutions are non-cyclic below the line. This line is above that for seasonal model 2 for all values of the delay considered, but its relation to the line for seasonal model 1 is dependent on the delay value. The non-seasonal model does not produce cycles without the delay.
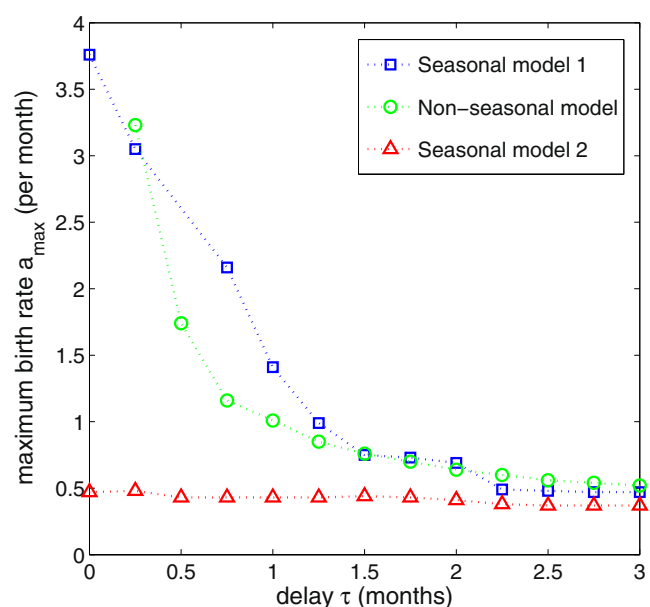

Fig. 3 The lowest maximum birth rates for which there are multi-year cycles, for varying values of the delay τ. Results are shown for both seasonal models and also for the non-seasonal framework as explained in the main text. For the seasonal models, there are annual cycles below the lines. For the non-seasonal model, the solutions are non-cyclic below the line

We can conclude that the seasonal mechanism of model 2 drives multi-year cycles more strongly than that of model 1. That is, a variable season length produces multi-year cycles for a larger range of parameters than a variable birth rate. This result holds irrespective of the value of the delay. Therefore, within the context of our model framework, a variable season length is more powerfully destabilising than a variable birth rate. One mechanism causes a significantly greater tendency to cycle than the other, indicating that the way seasonality is incorporated into a model is highly important. This emphasises that the way seasonality operates can have important implications for the population dynamics.

Combining seasonal mechanisms

Above, we study the two seasonal mechanisms in isolation. We now consider a model where a combination of both seasonal mechanisms is possible. We introduce two new parameters in order to characterise the combination of the seasonal mechanisms: p_{birth} and p_{length}, defined such that

$$a_{min} = a_{max}(1 - p_{birth}) \text{ and}$$

$$l_{min} = l_{max}(1 - p_{length}).$$

Parameter p_{birth} denotes the strength of the silica effect on birth rate. Similarly, p_{length} denotes the strength of the silica effect on the season length. Both parameters take values in the range of [0, 1]. For low silica levels, the breeding season length and birth rate are both at their maximum values, independent of p_{birth} and p_{length}. (Seasonal model 1 of the above analysis is recovered when $p_{birth} = 1$ and $p_{length} = 0$. Similarly, seasonal model 2 is recovered when $p_{birth} = 0$ and $p_{length} = 1$.)

In our model framework, we assume that any regulation of the birth rate and breeding season is due entirely to silica. This is because we want to examine the silica effect alone. We assume that any regulation is by silica on the birth rate (controlled by parameter p_{birth}) or by silica on the breeding season length (controlled by p_{length}); this allows an assessment of the relative impact of these factors. A consequence of this is that for low values of p_{length} and p_{birth} (i.e. weak silica effects), there is insufficient control on the population, leading to an unbounded increase in vole density. (This is an obviously unrealistic outcome; see Appendix B for more details.) In practice, population pressure is manifested in many different ways, and other forms of regulation will limit growth at high densities. The vole carrying capacity is notoriously difficult to estimate empirically (O'Mahony et al. 1999).

Our aim is to assess the role of different types of seasonal forcing in driving multi-year cycles. We therefore look at the division in parameter space between annual and non-annual cycles and also the behaviour of the non-annual cycles. Figure 4 shows the dominant periods of the cycles generated for a range of a_{max} and l_{max} values. It can be concluded that an increase in the maximum birth rate or the maximum breeding season length induces multi-year cycles in general: as a_{max} or l_{max} is increased, there are fewer annual cycles (dark blue/dark grey dots) and more multi-year cycles, and greater cycle periods are attained. In addition, the cycles with the longest periods are for high p_{length} and low p_{birth}, i.e. when the silica has a strong effect on the season length and a weak effect on the birth rate. Parameter p_{length} is more likely to promote multi-year cycles than p_{birth}. Combining the two seasonal mechanisms has confirmed that variability in the season length is a more powerful driver of cycles than variability in the birth rate.

In order to establish the dominant period of the multi-year time series predicted by the model, we use fast Fourier transform (this procedure is described in the legend to Fig. 4). Some examples of the cycles generated by the model are shown in Fig. 5. Each corresponds to a specific point from the grids of Fig. 4. Figure 5a shows typical annual cycles (period = 1), and the other plots show multi-year cycles of various periods. The fast Fourier transform procedure gives non-integer periods for certain points, because it assigns an "average" period. An example of this is shown in Fig. 5d. In this case, there is a repeating pattern of a cycle of period 2 followed by a cycle of period 3. The repeating pattern is not exact, and so the cycles are not of period 5. The average period of 2.5 represents/quantifies the cyclic behaviour generated in this instance.

Extensions to the model

From the results described above, we can conclude that variability in the breeding season length (controlled by parameter p_{length}) is a more significant driver of cycles than variability in the herbivore birth rate (controlled by parameter p_{birth}). The season length is dependent on S at a given census date, and the birth rate is dependent on S at the present time. In an attempt to elucidate the reasons behind our results, we consider an alternative seasonal model, where we set the birth rate to depend on the inducible defence level S at the census date. Note that this modification is not motivated by biological realism but is done to further our understanding of
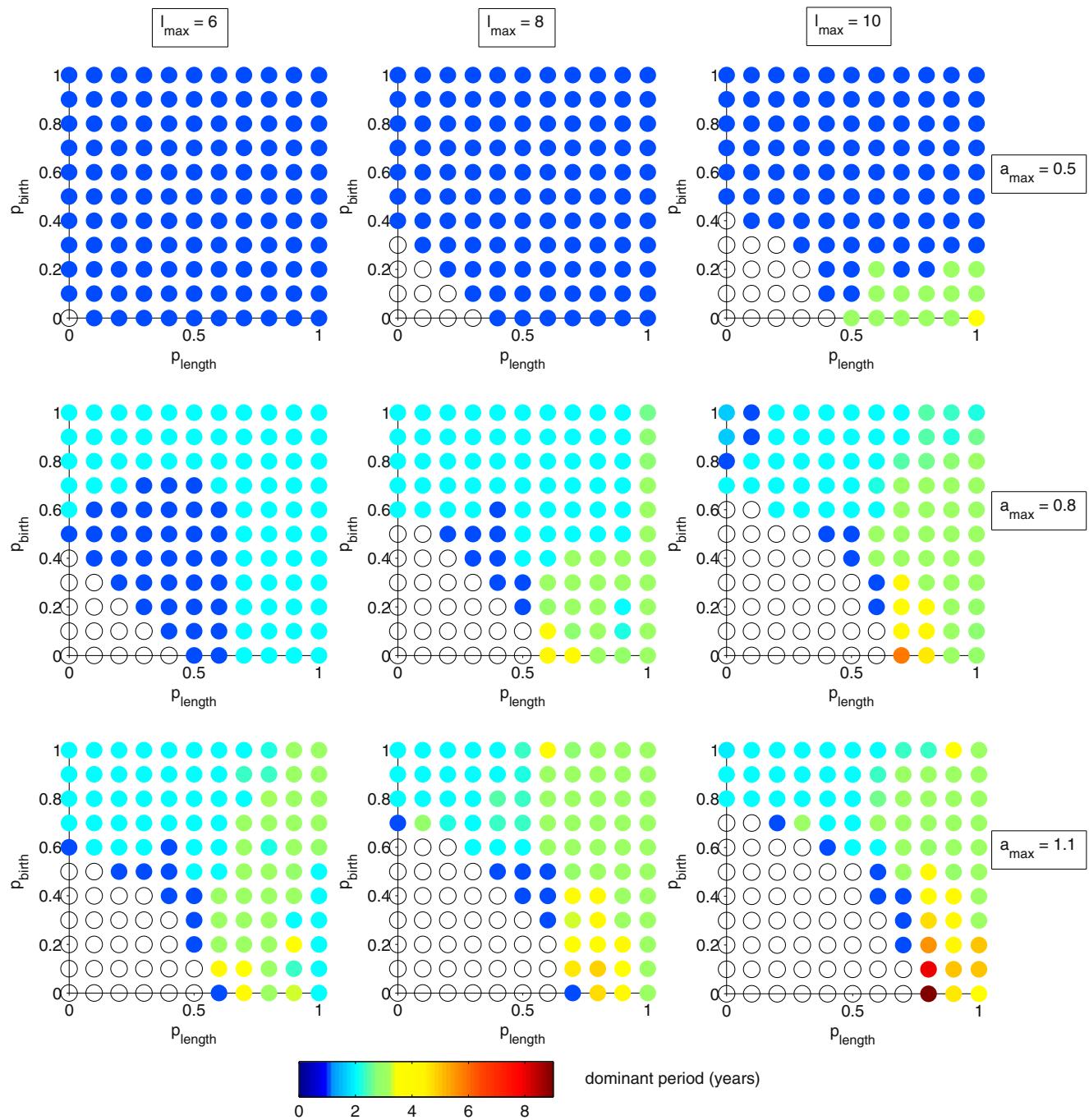
Fig. 4 Dominant periods of the population cycles, for different parameter combinations. The *uncoloured dots* denote when the vole density increases without bound (due to lack of regulation by silica; see Appendix B). After 490 years, the densities are assessed at yearly intervals over 10 years. The difference between the maximum and minimum densities is compared to 5 % (chosen arbitrarily) of the mean density. If the difference is smaller, then the cycles are deemed annual (*dark blue/dark grey dots*); if larger, they are non-annual. For the non-annual cycles, fast Fourier transform is used to generate power spectra, from which the dominant period is established. The periods considered are restricted to those that are factors of the length of the time series data set processed. Therefore, in order to accurately capture the cyclic nature of the time series, we consider a range of different lengths of data. We record the period with the largest associated power value for each data length. These power values are scaled so that they can be compared, and the period corresponding to the largest power value (after scaling) across all the range is said to be the dominant period. Initial conditions are as for Fig. 2
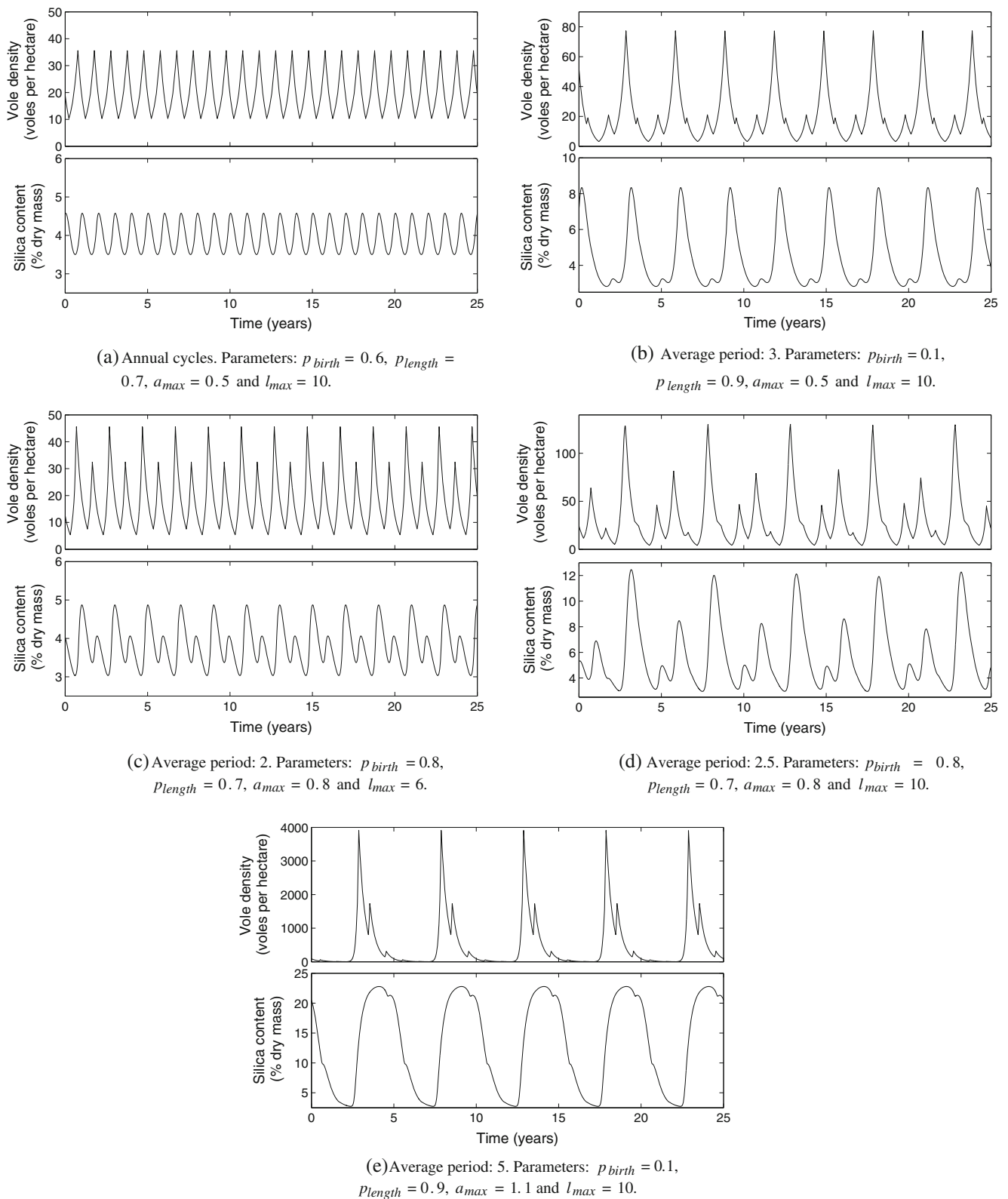
(a) Annual cycles. Parameters: $p_{birth} = 0.6$, $p_{length} = 0.7$, $a_{max} = 0.5$ and $l_{max} = 10$.

(b) Average period: 3. Parameters: $p_{birth} = 0.1$, $p_{length} = 0.9$, $a_{max} = 0.5$ and $l_{max} = 10$.

(c) Average period: 2. Parameters: $p_{birth} = 0.8$, $p_{length} = 0.7$, $a_{max} = 0.8$ and $l_{max} = 6$.

(d) Average period: 2.5. Parameters: $p_{birth} = 0.8$, $p_{length} = 0.7$, $a_{max} = 0.8$ and $l_{max} = 10$.

(e) Average period: 5. Parameters: $p_{birth} = 0.1$, $p_{length} = 0.9$, $a_{max} = 1.1$ and $l_{max} = 10$.

Fig. 5 Examples of cyclic behaviour predicted by the model for different values of the parameters p_{birth} and p_{length} (characterising the strength of the silica effect), a_{max} (the maximum herbivore birth rate) and l_{max} (the maximum breeding season length). Each example corresponds to a particular point on the grids of Fig. 4. Initial conditions are as for Fig. 2 and solutions are shown after 450 years

the model. Parameters p_{birth} and p_{length} are defined in the same manner as for the original seasonal model.

With this new framework, parameter p_{birth} has a similar effect to that of parameter p_{length}. Figure 6 displays the dynamical predictions of this amended model in $p_{length} - p_{birth}$ parameter space. Comparing this figure to the corresponding (bottom middle) panel of Fig. 4, one can see that the pattern is more symmetric for the new model: there is a similar variation in both directions. To compare the effects of the seasonal mechanisms in isolation, we compare the results of the model with $p_{birth} = 0$ and $p_{length} = 1$ to those with $p_{length} = 0$ and $p_{birth} = 1$. Both cases give multi-year cycles for similar values of the maximum birth rate, a_{max}. This confirms that in this new model set-up, a variable season length and a variable birth rate have a similar impact on the cyclic behaviour of the system; parameter p_{length} is no longer the dominant driver of multi-year cycles.
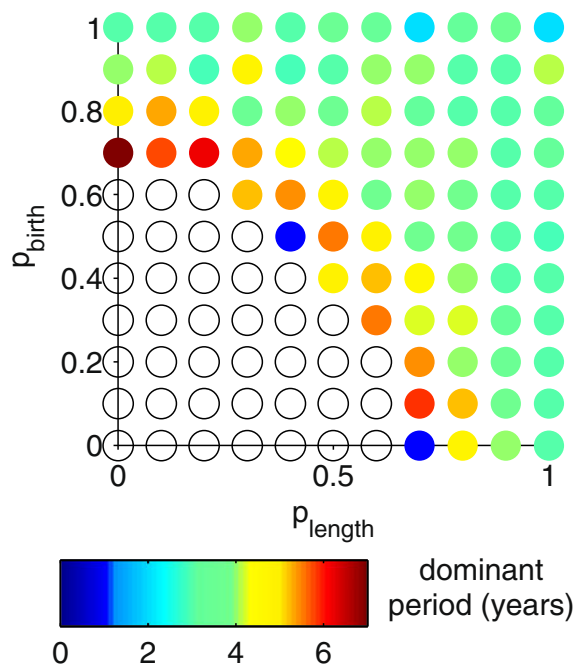

Fig. 6 Dominant periods of the cycles produced in $p_{length} - p_{birth}$ parameter space, with the vole birth rate dependent on the level of silica S at the census date (as well as the breeding season length). In this figure, the maximum birth rate $a_{max} = 1.1$, and the maximum season length $l_{max} = 8$. The *uncoloured dots* denote when the vole density increases unbounded (due to lack of regulation by silica; see Appendix B). The numerical method used to determine the periods is the same as is used in Fig. 4, and the same initial conditions are used. This figure should be compared to the bottom middle plot of Fig. 4, which shows the corresponding results for the original model set-up. In this figure, there is a more symmetrical pattern; parameters p_{length} and p_{birth} have more similar effects

These findings suggest that the mechanism by which the season length is determined is the important destabilising factor. The season length is dependent on the inducible factor at a specific date and is fixed for that year. When the birth rate is defined in the same way, then it becomes a similarly powerful driver of multi-year cycles.

The significance of the underlying mechanism has motivated a further extension to our model. In order to make the model more realistic, we additionally experiment with setting the vole birth rate and breeding season length to depend on the silica S averaged over the previous month, as opposed to the silica level at one time point only. The resulting patterns are similar to those in Fig. 4, but periods are generally lower. The overall conclusions are unaffected by this modification.

Discussion

In this study, we explore and compare the effects of plant defence strategies in combination with seasonality on the population dynamics of a herbivore. We examine two different mechanisms: firstly, with the herbivore birth rate dependent on the level of plant defence; secondly, with the length of the breeding season dependent on the level of plant defence. Our results indicate that the means by which seasonality is implemented is crucial. When the plant defence affects the breeding season length, there is a significantly higher likelihood of multi-year cycles compared to when it affects the birth rate.

We have parameterised our model for a specific system, namely field voles (*M. agrestis*) in Kielder Forest, Northern UK, and the silica content in the grass (*D. caespitosa*) they feed on. The implication of our findings is that a regulatory factor, silica in this instance, is important for the occurrence of multi-year cycles if it affects the season length but less significant if it affects the birth rate.

Our model includes a delay term representing the time taken for the inducible plant defence to be produced after herbivory has occurred, in concurrence with both experimental (Reynolds et al. 2012) and theoretical (Underwood 1999) studies. A delay is known to be a potentially destabilising factor (Haberman 1977; Underwood 1999), and as a result, we additionally considered the effects of changing the delay length and also the effect of removing this delay. We demonstrated that our main conclusion, that a variable breeding season length is a more powerful driver of multi-year cycles than a variable birth rate, holds irrespective

of the delay in the production of the inducible plant defence.

Seasonal variations are ubiquitous in natural systems and can exert strong pressures on population dynamics. Our findings highlight the complexity of the interaction between seasonal forcing and the unforced dynamics. This has also been shown in models of disease systems (Schwartz and Smith 1983) and in predator–prey models (e.g. Kuznetsov et al. 1992; Rinaldi et al. 1993). Here, we demonstrate that the way in which seasonality is incorporated makes a significant difference to its effect on the dynamics and that it is therefore crucial in seasonal models to incorporate patterns of forcing that most closely correspond to biologically realistic assumptions.

Changes in the length and intensity of the breeding season have been claimed by some authors to be an epiphenomenon of rodent cycles, with little demographic importance (Norrdahl and Korpimäki 2002). In contrast, Smith et al. (2006) found that variation in the breeding season length, with the length a function of past population densities, can give rise to realistic population cycles, demonstrating that a variable breeding season length may have important implications for the population dynamics of a system. Our model, with the additional effect of a plant defence mechanism, also predicts such population cycles and suggests that the breeding season length can have a significant effect on population behaviour. In addition, seasonality is shown to be important in shaping the population dynamics of the grey-sided vole (*Clethrionomys rufocanus*) in Hokkaido, Japan (Stenseth et al. 2003). In that study, using both data and models, it is demonstrated that the length of winter plays a key role in driving population cycles. Our findings, concerning a different vole species in a different location, are in agreement with this.

We have parameterised our model using empirical data on a specific herbivore–plant defence system and found that multi-year cycles can be generated for realistic parameters. In particular, we have shown that seasonality can give rise to cycles of similar periodicity to those seen in the field (Lambin et al. 2000). This result lends support to the hypothesis that inducible plant defences may contribute to cyclic fluctuations and is consistent with previous theoretical studies on other systems (Lundberg et al. 1994; Underwood 1999). The model of Lundberg et al. (1994) typically generates damped oscillations, and they speculate that seasonal perturbations may play a significant role in the maintenance of population cycles. Our work confirms the importance of seasonality in achieving population cycles resembling those seen in nature.

It should be noted that we have used data from greenhouse experiments to parameterise some components of this model. An important next step is to use field data to obtain parameter values, once this becomes available. In addition, a possible extension is to take the same model framework and reparameterize for a different herbivore–plant defence system.

Our work highlights the complexity of the role seasonal forcing plays in shaping population dynamics. We have found that seasonality can have dramatic dynamical effects and that this is strongly dependent on the type of seasonal mechanism. For a given ecological system, the elucidation of the seasonal mechanism involved is critical in order for the seasonal effects to be determined. The prospect that global climate change will rapidly modify current seasonal patterns provides further motivation for research into seasonality and its effects.

Appendix A

In this appendix, we determine the parameter values for which the trivial steady state $(H, S) = (0, S_0)$ is stable, using Floquet theory. At the trivial steady state, the herbivore birth rate will be at its maximum a_{max} in the breeding season. Let $a(t)$ represent the seasonal birth rate in this case. Then

$$a(t) = \begin{cases} a_{max} & \text{in the breeding season} \\ 0 & \text{in the non-breeding season.} \end{cases} \tag{3}$$

Thus, $a(t)$ is periodic with period 12 months.

Firstly, linearising the system Eqs. 1 and 2 with Eq. 3 about the trivial steady state gives

$$\frac{dH}{dt} = (a(t) - b)H(t) \tag{4}$$

$$\frac{dS^*}{dt} = -cS^*(t) \tag{5}$$

where $S^*(t) = S(t) - S_0$. Note that these equations are independent of the delay τ. The solution of Eq. 4 depends on the season:

$$H(t) = \begin{cases} m_1 e^{(a_{max}-b)t} & \text{in the breeding season} \\ m_2 e^{-bt} & \text{in the non-breeding season} \end{cases}$$

where m_1 and m_2 are constants. The solution of Eq. 5 is

$$S^*(t) = m_3 e^{-ct}$$

in both seasons, where m_3 is a constant.

We now seek a fundamental matrix for this system. To be specific, consider the solution over 12 months starting at the beginning of the non-breeding season. Initial conditions $(H(0), S^*(0)) = (0, 1)$ give $m_3 = 1$ and $S^*(12) = e^{-12c}$. Also, $m_2 = 0$ so $H = 0$ at the end of the non-breeding season, which is the start of the breeding season also. Therefore, $m_1 = 0$ and $H(12) = 0$.

Starting at $(1, 0)$ gives $m_3 = 0$ and $S^*(12) = 0$. Also, $m_2 = 1$ so $H(t) = e^{-bt}$ in the non-breeding season. At the end of the non-breeding season, and at the start of the breeding season, $t = 12 - l$. At the trivial equilibrium, the season length l will be at its maximum, $l_{\max}$. So

$$H(12-l) = e^{-b(12-l_{\max})} = m_1 e^{(a_{\max}-b)(12-l_{\max})}$$

$$\Rightarrow m_1 = \frac{e^{-b(12-l_{\max})}}{e^{(a_{\max}-b)(12-l_{\max})}} = e^{-a_{\max}(12-l_{\max})}$$

and

$$H(12) = e^{-a_{\max}(12-l_{\max})} e^{12(a_{\max}-b)} = e^{a_{\max}l_{\max}-12b}.$$

A fundamental matrix, denoted here by M, is therefore

$$M = \begin{bmatrix} 0 & 1 \\ 1 & 0 \end{bmatrix}^{-1} \begin{bmatrix} 0 & e^{a_{\max}l_{\max}-12b} \\ e^{-12c} & 0 \end{bmatrix} = \begin{bmatrix} e^{-12c} & 0 \\ 0 & e^{a_{\max}l_{\max}-12b} \end{bmatrix}$$

with eigenvalues

$$\mu_1 = e^{-12c} \quad \text{and} \quad \mu_2 = e^{a_{\max}l_{\max}-12b}.$$

Floquet theory implies that the condition for the trivial steady state to be stable is that both $|\mu_1| < 1$ and $|\mu_2| < 1$. Since $\mu_1 < 1$ always holds, the condition for stability is

$$\mu_2 < 1, \quad \text{i.e. } a_{\max}l_{\max} - 12b < 0, \quad \text{i.e. } a_{\max}l_{\max} < 12b.$$

This is the required condition.

Appendix B

In this appendix, we determine the parameter values for which the vole density $H \to \infty$. For large H, the equations become, to leading order,

$$\frac{dH}{dt} = (a(t) - b)H(t) \tag{6}$$

$$\frac{dS}{dt} = K + cS_0 - cS(t). \tag{7}$$

The silica level will be at its maximum to leading order for large H, so the breeding season length and birth rate will be at their minimum values. Therefore,

$$a(t) = \begin{cases} a_{\max}(1 - p_{\text{birth}}) & \text{in the breeding season} \\ 0 & \text{in the non-breeding season} \end{cases}$$

and the breeding season length is $l_{\max}(1 - p_{length})$. The solution of Eq. 6 is then

$$H(t) = \begin{cases} m_4 e^{(a_{\max}(1-p_{\text{birth}})-b)t} & \text{in the breeding season} \\ m_5 e^{-bt} & \text{in the non-breeding season} \end{cases}$$

where m_4 and m_5 are constants. Therefore, the solutions of Eq. 6 will tend to infinity if and only if

$$(a_{\max}(1 - p_{\text{birth}}) - b)\frac{l_{\max}(1 - p_{\text{length}})}{12}$$

$$- b\frac{(12 - l_{\max}(1 - p_{\text{length}}))}{12} \geq 0$$

$$\Leftrightarrow l_{\max}(1 - p_{\text{length}})a_{\max}(1 - p_{\text{birth}}) \geq 12b.$$

When this inequality holds, the silica effects are too weak to self-regulate; there is not enough control on the herbivore population by silica. In real systems, other factors will regulate the herbivore population, for example, the spread of disease may increase and resources may become limited at very high population densities.

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