

Invading parasites cause a structural shift in red fox dynamics

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The influence of parasites on host life histories and populations is pronounced. Among several diseases affecting animal populations throughout the world, sarcoptic mange has influenced many carnivore populations dramatically and during the latest epizootic in Fennoscandia reduced the abundance of red fox by over 70%. While the numerical responses of red fox populations, their prey and their competitors as well as clinical implications are well known, knowledge of how sarcoptic mange affects the structure of the dynamics of red fox populations is lacking. Integrating ecological theory and statistical modelling, we analysed the long-term dynamics (1955–1996) of 14 Danish red fox populations. As suggested by the model, invading sarcoptic mange significantly affected direct and delayed density dependence in red fox dynamics and concomitant shifts in fluctuation patterns were observed. Our statistical analyses also revealed that the spatial progressive spread of mange mites was mirrored in the autocovariate structures of red fox populations progressively exposed to sarcoptic mange.

Keywords: autocovariate structure; direct and delayed density dependence; intra- and intertrophic interactions; population dynamics; red fox; sarcoptic mange

1. INTRODUCTION

By being inferior in size, parasites exert a superior influence on the life histories of numerous organisms with severe cascading effects on their host's interactions with the environment (Begon *et al.* 1996a). For example, microphallid trematodes, which are parasites of bottom-dwelling marine amphipods and gastropods, not only reduce their host's survival and fecundity severely, thereby affecting growth rates, but can also increase their host's surface activity, rendering them more accessible to predators as well as reducing intraguild competition (Mouritsen & Jensen 1994, 1997; Jensen *et al.* 1998). This example is not unique. Parasite-induced changes in host survival, growth and fecundity with concomitant consequences for behavioural, intraspecific (e.g. epigamic selection), intraguild (e.g. competition) and intertrophic (e.g. predator–prey) interactions have been reported extensively in plants, insects, birds and mammals (Grenfell & Dobson 1995; Begon *et al.* 1996a).

Consequently, as first formulated in a series of theoretical papers by Anderson & May (1978, 1980, 1981; May & Anderson 1979; Anderson *et al.* 1981) parasites can, through their influence on individual hosts, play a significant role in their hosts long-term population dynamics. Indeed, negative numerical responses of host populations to parasites have been documented in numerous animals (Dobson & Hudson 1995; Hudson & Dobson 1995). However, although well-founded theoretically (Grenfell & Dobson 1995), studies specifically addressing how parasites may alter the structural dynamics of natural host populations are few and most evidence comes from

experimental laboratory populations (Hudson & Dobson 1995; Begon *et al.* 1996a).

Among several diseases affecting animal populations throughout the world, sarcoptic mange has influenced many carnivore populations dramatically (Samuel 1981; Lindström 1992; Vos 1995; Martin *et al.* 1998). During the 1970s and 1980s, sarcoptic mange spread throughout most of the Nordic red fox (*Vulpes vulpes*) populations (Lindström & Mörner 1985; Holt & Berg 1990; Bak *et al.* 1997). By considerably reducing its abundance (> 70%), this epizootic revealed the Nordic red fox as an important factor in limiting prey populations of hares and grouse (Danell & Hörnfeldt 1987; Lindström 1992; Lindström *et al.* 1994; Asferg 1996; Smedshaug *et al.* 1999) as well as showing its competitive dominance of other northern predators (Lindström *et al.* 1995; Asferg 1998; Selås 1998; Smedshaug *et al.* 1999). These studies focused primarily on the numerical responses of fox populations, their prey and competitors, while others focused on the clinical aspects of sarcoptic mange (Mörner & Christensson 1984; Bornstein *et al.* 1995; Little *et al.* 1998a,b; Martin *et al.* 1998), but studies on how sarcoptic mange affects the structural dynamics (i.e. how population growth relates to abundance) in red fox populations are lacking.

Here, we bridge this gap by statistically analysing the long-term (1955–1996) dynamics of 14 red fox populations in Denmark. As opposed to the outbreaks in Sweden and Norway, sarcoptic mange did not spread to all Danish fox populations, thereby creating a unique opportunity of comparing infected and non-infected red fox population dynamics. By combining ecological theory with statistical modelling, we explore how the spread of sarcoptic mange, directly (intertrophic) and indirectly (by altering intraspecific interactions), is portrayed in the spatio-temporal dynamics of red fox populations.

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2. MATERIAL AND METHODS

(a) *The species and the data*

The red fox is common throughout Denmark. It is highly territorial and territory size depends on habitat type, resource availability and the density of foxes. A large majority of females start to breed as yearlings and their annual fecundity is high with an average litter size of four to five cubs (range one to ten cubs) (Corbet & Harris 1991). Mortality and, in some populations, also fecundity have been documented to be density dependent (Harris 1979). In Denmark, the red fox is a generalist predator preying upon rodents, partridges (*Perdix perdix*), pheasants (*Phasianus colchicus*), brown hares (*Lepus europaeus*) and roe deer (*Capreolus capreolus*) fawns (Jensen & Sequeira 1978).

Since 1955, the annual numbers of red foxes shot per county have been recorded by the National Environmental Research Institute (Strandgaard & Asferg 1980; Madsen *et al.* 1996) and the data for between 1955 and 1996 form the basis for our study. Due to an administrative reform in 1970 primarily affecting the spatial distribution of the counties of København, Roskilde, Vejle and Ribe (Strandgaard & Asferg 1980), the time-series from these were restricted to the period 1970–1996. Until 1967, the red fox was hunted throughout the year, but between 1967 and 1993 the hunting period covered 8.5 months and from 1994 five months (Strandgaard & Asferg 1980; Madsen *et al.* 1996). To evaluate whether there was any significant effect of temporal changes in hunting efficiency on the annual number of bagged foxes we followed previous procedures (Cattadori *et al.* 1999) and calculated the annual number of foxes shot per hunting effort (the number of hunters multiplied by the length of the hunting period). This could be done on a national level for an earlier period (1941–1976) and showed no significant difference between the annual number of foxes bagged and the number of foxes shot per unit hunting effort (figure 1a). In corroboration, previous studies (Forchhammer *et al.* 1998; Stenseth *et al.* 1998, 1999; Cattadori *et al.* 1999) have found hunting statistics to be good proxies for actual population abundances. Hence, we used the time-series of the annual number of foxes harvested as an index for the annual population abundance between 1955 and 1996 (figure 1b) in subsequent analyses.

The disease sarcoptic mange is caused by the skin-dwelling mite (*Sarcoptes scabiei* var. *vulpes*) and has been reported in red fox populations in Europe, North America and Russia (Danell & Hörnfeldt 1987). Approximately one month after exposure, infected foxes commonly develop skin lesions characteristic of hyperkeratosis (Bornstein *et al.* 1995). Severe loss of hair and progressive deterioration of body condition then follows and, in the majority of observed cases, infected foxes eventually die from starvation (Mörner & Christensson 1984).

In Denmark, red foxes infected by sarcoptic mange were first detected in the county of Sønderjylland in 1984. Then the mange mite apparently spread meridionally on the Jylland Peninsula with first observations of infected foxes in 1985 in Vejle county, in 1987 in Ribe and Ringkøbing counties, in 1989 in Aarhus county and in the southern regions of Viborg and Nordjylland counties and, finally, in 1991 in the northern regions of Viborg and Nordjylland counties (figure 1b). The spread of mange in Jylland proceeded faster in the western counties than in the eastern counties (Bak *et al.* 1997). Sarcoptic mange was first observed on the isolated island of Bornholm in 1986. However, in contrast to the most recent epizootic of sarcoptic mange in Sweden and Norway, where it spread throughout both countries (Lindström & Mörner 1985; Holt & Berg 1990), the

epizootic in Denmark never reached Fyn and Sjælland and associated islands (figure 1b) (Bak *et al.* 1997).

(b) *Scabies–fox dynamics: linking ecological theory and statistical modelling*

The biological environment with which individuals interact can basically be divided into intratrophic and intertrophic interactions (Krebs 1978). To understand how these interactions may affect the temporal population dynamics of the red fox ecologically, consider the scenario in figure 2. Here, the interactions are specified by following ecological interaction coefficients: α_{XX} and α_{YX} determine the intraspecific, density-dependent influence in the red fox and in the ‘other-than-fox’ trophic-level organism (Y), respectively, whereas α_{XY} and α_{YX} describe the strength of intertrophic interaction on the Y -level organism and on the red fox, respectively. Whether ecological density dependence (α_{XX} and α_{YY}) is negative or positive will, in general, depend on specific social behaviour (e.g. degree of territoriality), the distribution of resources and population size, but often has a negative effect on abundance (Begon *et al.* 1996a). The specific signs of α_{XY} and α_{YX} will depend on the nature of the Y -level organism, that is whether it represents a parasite (such as the mange mite depicted in figure 2) or a prey (May 1981).

The choice of the general ecological functions $f(\cdot)$ and $g(\cdot)$ (figure 2) is not trivial as many functional forms have been suggested (May 1981). Since we focus here on estimating the autocovariance of population growth (M_t/M_{t-1}) and previous abundance (M_{t-d}) in red fox populations and linearity was not rejected in any of the 14 fox time-series (likelihood ratio test: λ -values $< \lambda_{0.05} = 11.18$) (Tong 1990), a useful approximation is for $f(\cdot)$ and $g(\cdot)$ to be linear in \log_e -transformed abundances (X_t and Y_t) (Royama 1992; Dennis & Taper 1994; Bjørnstad *et al.* 1995; Stenseth *et al.* 1996a,b). Hence, under \log_e -linear approximation, we may write the population model for the trophic system displayed in figure 2 as

$$M_t = M_{t-1} \exp(\alpha_{X0} + \alpha_{XX}X_{t-1} + \alpha_{YX}Y_{t-1}), \quad (1)$$

and

$$N_t = N_{t-1} \exp(\alpha_{Y0} + \alpha_{YY}Y_{t-1} + \alpha_{XY}X_{t-1}), \quad (2)$$

where α_{X0} and α_{Y0} represent the intrinsic growth rates, without intratrophic or intertrophic influence, for the red fox ($f(0,0)$) and the Y -level organism ($g(0,0)$), respectively. Taking natural logarithms on both sides of equations (1) and (2) and rearranging we obtain

$$X_t - X_{t-1} = \alpha_{X0} + \alpha_{XX}X_{t-1} + \alpha_{YX}Y_{t-1}, \quad (3)$$

and

$$Y_t - Y_{t-1} = \alpha_{Y0} + \alpha_{YY}Y_{t-1} + \alpha_{XY}X_{t-1}. \quad (4)$$

Equation (3) states that the population growth of the red fox ($X_t - X_{t-1}$) is affected by both density-dependent ($\alpha_{XX}X_{t-1}$) and intertrophic ($\alpha_{YX}Y_{t-1}$) constraints, dynamics which are similar to those emerging from a previously formulated rabies–fox model by Anderson *et al.* (1981). From the trophic model in equations (3) and (4), we can derive the fox dynamics as a univariate delay function in X_t by isolating Y_{t-1} in equation (3), inserting this in equation (4) and rearranging:

$$X_t = (\alpha_{Y0}\alpha_{YX} - \alpha_{X0}\alpha_{YY}) + (2 + \alpha_{XX} + \alpha_{YY})X_{t-1} + (\alpha_{YX}\alpha_{XY} - \alpha_{YY}\alpha_{XX} - \alpha_{XX} - \alpha_{YY} - 1)X_{t-2}. \quad (5)$$

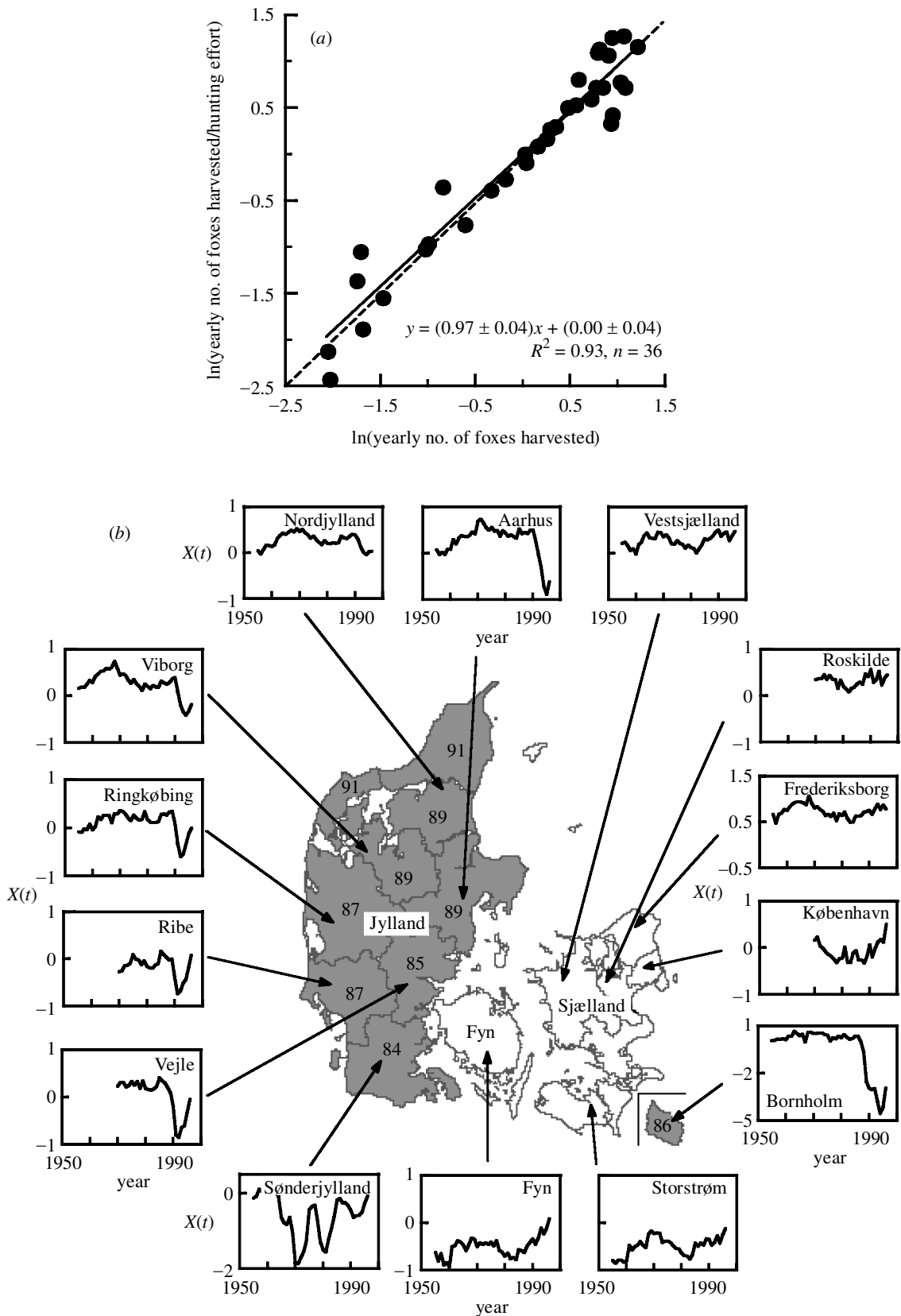


Figure 1. (a) Relationship between the yearly number of red foxes harvested per unit hunting effort (the number of hunters \times the length of the hunting period) and the yearly number of red foxes harvested. Both variables were standardized $((x - \mu)/\sigma)$. The dashed line denotes $x = y$. (b) Geographical locations and temporal dynamics of the \log_e -transformed abundances ($X(t)$) of the 14 Danish red fox populations (1955–1996). The time-series consist of the annual number of red foxes harvested per square kilometre (Strandgaard & Asferg 1980; T. Asferg, unpublished data). Shading indicates populations exposed to sarcoptic mange. The numbers refer to the year mange was first observed.

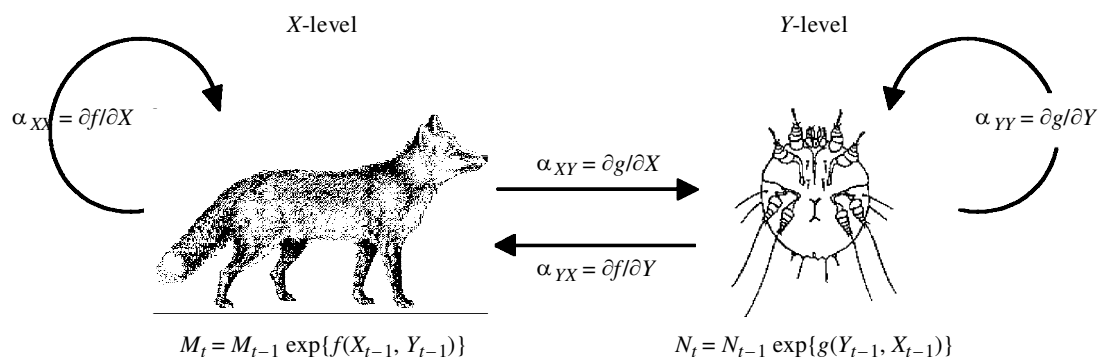


Figure 2. Graphical illustration of the intra- and intertrophic interactions in relation to red fox population dynamics. The trophic level of the red fox is called the 'X-level' and the level of the 'other-than-fox' trophic-level organism (depicted by the mange mite) is denoted the 'Y-level'. M_t and N_t denote the population abundances of the red fox and Y-level organism, respectively. The ecological functions $f(\cdot)$ and $g(\cdot)$ in X_t ($\ln M_t$) and Y_t ($\ln N_t$) (a general Gompertz population model) (Dennis & Taper 1994) describe the changes in M_t and N_t following the intra- and intertrophic interactions visualized with arrows and associated interaction coefficients (α_{ij} is the influence of species i on species j). The general relationship between the interaction coefficients and ecological functions is defined by the partial differentials of $f(\cdot)$ and $g(\cdot)$. For a detailed description of such models see, for example, May (1973) and Stenseth *et al.* (1996a).

From equation (5) it follows that direct density dependence (X_{t-1}) in fox populations is influenced by the intraspecific dynamics of the Y-level organism (α_{YY}), whereas delayed density dependence (X_{t-2}) depends on intertrophic interactions ($\alpha_{YX}\alpha_{XY}$) and a complex function of intratrophic interactions ($-\alpha_{YY}\alpha_{XX} - \alpha_{XX} - \alpha_{YY} - 1$). In addition, equation (5) is equivalent to a statistical two-dimensional autoregressive (AR(2)) process, $X_t = \beta_0 + (1 + \beta_1)X_{t-1} + \beta_2 X_{t-2} + \varepsilon_t$, where ε_t is some stochastic term affecting the growth of red fox populations. Hence, any detected statistical, direct density dependence ($1 + \beta_1$) in the fox time-series will depend on ecological density dependence (α_{XX} and α_{YY}) and any statistical, delayed density dependence (β_2) will also be a function of trophic interactions between the red fox and the Y-level organism ($\alpha_{YX}\alpha_{XY}$).

For each of the 14 red fox time-series, we used the Akaike information criterion (Sakamoto *et al.* 1986) to determine the most parsimonious dimension (d) of the AR(d) processes. We considered values of d between 0 and 3 to cover the delay function specified in equation (5). The AR coefficients were estimated using the AUTOREG procedure with maximum-likelihood estimation in SAS v.6.12 for Windows (SAS Institute, Inc. 1996). Since most time-series were non-stationary (figure 1b), they were detrended by simultaneously incorporating time (i.e. year) in the AUTOREG procedure (SAS Institute, Inc. 1990). The autocorrelation functions were calculated using S-plus 4.0 for Windows (Mathsoft, Inc. 1997).

3. RESULTS

Equivalent to equation (5), 11 out of 14 Danish red fox populations had temporal dynamics best characterized by an AR(2) process (table 1). However, the autoregressive analyses did document a spatial segregation of exposed and non-exposed fox populations with respect to population-specific autocovariate structures. First, three out of six populations not affected by sarcoptic mange were best described by an AR(2) process and the remaining populations described by an AR(1) process, whereas all populations exposed to mange were best described by AR(2) models. Second, significant, negative, direct density dependence ($1 + \beta_1 < 1$) was recorded in all non-mange

populations, while all the exposed populations had no significant direct density dependence ($1 + \beta_1 = 1$). Finally, all eight fox populations exposed to sarcoptic mange displayed a negative, delayed density dependence ($\beta_2 < 0$; statistically significant in seven populations), whereas two of the non-exposed populations displayed significant, positive, delayed density dependence ($\beta_2 > 0$) (table 1). As revealed by the Durbin-Watson statistic (Durbin & Watson 1951), the residuals from the estimated AR models did not contain additional deterministic patterns (table 1).

Plotting the AR coefficients from table 1 in a two-dimensional $(1 + \beta_1) - \beta_2$ plane (figure 3a) and calculating autocorrelation functions (figure 3b) for the 14 fox populations revealed additional aspects of their dynamics. First, most populations exhibited a tendency towards damped fluctuations albeit with different lengths (figure 3a,b). Second, the presence of sarcoptic mange increased the length of fluctuations significantly as shown by the location of mange-exposed populations in the lower right part of the triangle in figure 3a and by their skewed autocorrelation function distributions in figure 3b. Third and most strikingly, the spread of sarcoptic mange northwards through Jylland was mirrored exactly in the spatial gradient of the structural dynamics of the exposed populations: from the point of origin in Sønderjylland county to the northern county of Nordjylland, the delayed density-dependent effect decreased progressively from -0.56 to 0 (inset in figure 3a). Finally, the time-series analyses of the exposed red fox populations in Jylland and on Bornholm Island prior to the epizootic (i.e. between 1955 and 1980), showed that the structural dynamics of the populations here were similar to the non-exposed populations (figure 3a).

4. DISCUSSION

Our results document a pronounced influence of the parasitic mange mite on the temporal dynamics of Danish red fox populations (table 1 and figure 3a). Specifically, the direct negative effect of sarcoptic mange on red fox populations (α_{YX}) (figure 2) was predicted to

Table 1. Summary of the AR analyses of the red fox population dynamics (1955–1996) in the 14 Danish counties

(The sample size (n) is the number of consecutive years and the order (d) of the most parsimonious model is determined by the lowest Akaike information criterion (AIC), δ AIC specifies, if $d = 1$, the difference between the criterion-profile minimum and the AIC for $d = 2$. δ AIC ≤ 1 is considered being insignificant with respect to model choice (Sakamoto *et al.* 1986). For each population, the AR(1) and AR(2) coefficients are given with standard error of means (s.e.m.). For the most-parsimonious model, the total R^2 -value, the estimated standard deviation of the Gaussian noise (σ) and the Durbin–Watson statistic of model residuals (DW; Durbin & Watson 1951) are given for each population. A DW-value significantly different from 2 indicates a remaining non-random pattern in the residuals. Bold values indicate significance ($p < 0.05$, two-tailed).)

population	n	d	AIC	δ AIC	AR(2)	AR(1) coefficients		AR(2) coefficients		total R^2	σ	DW ^c
						$(1 + \beta_1) \pm$ s.e.m. ^a	$(1 + \beta_1) \pm$ s.e.m. ^a	$(1 + \beta_1) \pm$ s.e.m. ^a	$\beta_2 \pm$ s.e.m. ^b			
København (KBH)	27	1	-18.7	1.2	no	0.64 ± 0.17	0.60 ± 0.20	0.20 ± 0.20	0.40	0.02	1.8	
Frederiksborg (FRB)	42	2	-79.8	—	yes	0.73 ± 0.15	0.51 ± 0.15	0.31 ± 0.15	0.60	0.01	1.8	
Roskilde (ROS)	27	2	-39.8	—	yes	0.38 ± 0.18	0.25 ± 0.15	0.34 ± 0.15	0.26	0.01	2.0	
Vestsjælland (VSJ)	42	1	-81.9	2.0	no	0.77 ± 0.10	0.77 ± 0.16	0.01 ± 0.16	0.59	0.01	1.9	
Storstrøm (STS)	42	1	-59.8	1.9	no	0.85 ± 0.07	0.80 ± 0.16	0.07 ± 0.16	0.67	0.01	1.8	
Fyn (FYN)	42	2	-46.5	—	yes	0.83 ± 0.07	0.66 ± 0.16	0.22 ± 0.16	0.62	0.02	1.8	
Bornholm (BOR)	42	2	55.2	—	yes	0.96 ± 0.05	1.33 ± 0.18	-0.42 ± 0.18	0.91	0.18	1.9	
Sonderjylland (SJY)	42	2	16.9	—	yes	0.87 ± 0.08	1.36 ± 0.18	-0.56 ± 0.18	0.84	0.06	1.9	
Ribe (RIB)	27	2	-27.9	—	yes	0.85 ± 0.13	1.14 ± 0.18	-0.48 ± 0.18	0.68	0.02	2.1	
Vejle (VEJ)	27	2	-16.3	—	yes	0.95 ± 0.13	1.24 ± 0.19	-0.43 ± 0.19	0.81	0.03	2.0	
Ringkøbing (RIN)	42	2	-56.7	—	yes	0.83 ± 0.10	1.17 ± 0.14	-0.42 ± 0.14	0.76	0.01	2.0	
Viborg (VIB)	42	2	-68.9	—	yes	0.92 ± 0.06	1.24 ± 0.15	-0.36 ± 0.15	0.86	0.01	1.9	
Aarhus (ARH)	42	2	-40.3	—	yes	0.95 ± 0.06	1.22 ± 0.15	-0.31 ± 0.15	0.85	0.02	2.0	
Nordjylland (NJY)	42	1	-98.1	0.3	yes	0.91 ± 0.06	1.08 ± 0.15	-0.21 ± 0.15	0.80	0.01	1.8	

^a $H_0: (1 + \beta_1) = 1$.

^b $H_0: \beta_2 = 0$.

^c $H_0: DW = 2$.

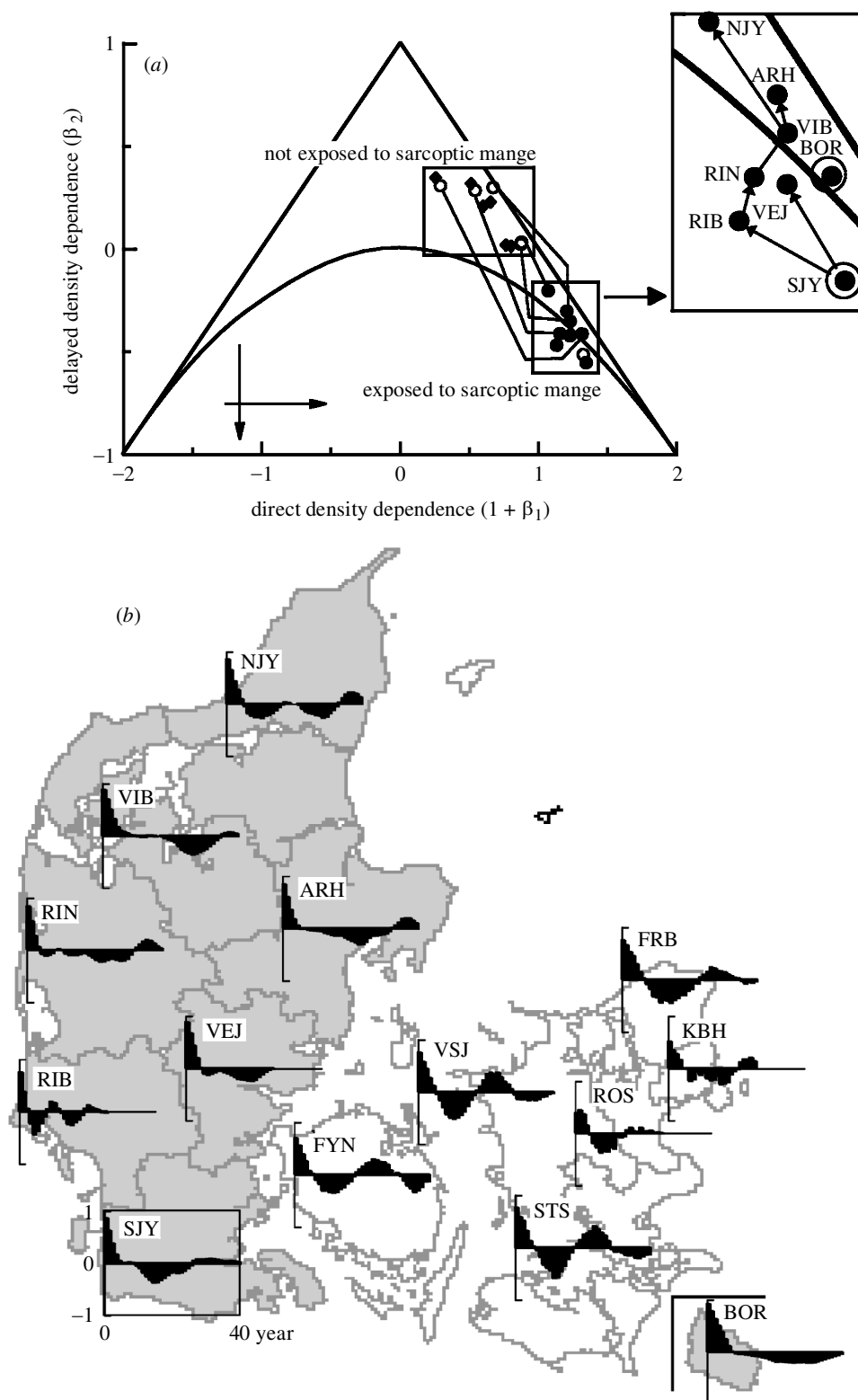


Figure 3. (a) The $(1 + \beta_1) - \beta_2$ plane displaying the AR(2) coefficients for the 14 red fox populations given in table 1. Red fox populations not exposed to sarcoptic mange are indicated by solid diamonds and populations exposed to sarcoptic mange are shown by solid circles which are connected to open circles indicating the exposed red fox populations but prior to the invasion of sarcoptic mange (before 1981). The counties of Ribe and Vejle were omitted from this comparison due to low sample sizes (see table 1). Parameter combinations outside the triangle lead to extinction of the population, whereas at locations inside the triangle, the dynamics are characterized by damped fluctuations (persistent if pronounced stochasticity is present). Superimposed arrows indicate increasing gradients of fluctuation length in population dynamics. For a full exposition of the model see Royama (1992) and Bjørnstad *et al.* (1995). Inset: enlargement of the $(1 + \beta_1) - \beta_2$ plane of the exposed red fox populations with arrows showing the spatial invasion of sarcoptic mange in Jylland. Ringed circles (SJY and BOR) indicate where the epizootic entered Denmark. (b) Superimposed on the map of Denmark are the autocorrelation functions for the 14 different red fox populations. Shading indicates populations exposed to sarcoptic mange and population acronyms refer to those given in table 1.

be expressed in a delayed density-dependent manner in the autoregressive analyses of the fox time-series (equation (5)). Indeed, in contrast to the non-exposed populations, all the mange-exposed populations did display a strong, negative, delayed density dependence (table 1). This delayed effect on red fox populations may reflect a parasite-induced reduction in the fecundity of cohorts exposed to sarcoptic mange as indicated by previous studies (Pence & Windberg 1994; Bak *et al.* 1997). In corroboration, May & Anderson (1978) demonstrated that a parasite-induced reduction in host fecundity in general destabilizes host dynamics.

In addition, as predicted by equation (5), our analyses demonstrated an interaction between sarcoptic mange and direct density dependence in red fox dynamics. Whereas significant, direct density dependence was found in all the non-exposed populations, none of the mange-exposed populations displayed direct density dependence (table 1), probably reflecting reduced competition for territories following the increased mange-induced mortality.

The spatial pattern of the invasion of sarcoptic mange (figure 1b) was found to mirror spatial variations in the autocovariate structure, that is the temporal covariance between population growth and density, across red fox populations on the Jylland Peninsula (inset in figure 3a). Although habitat type, resource availability and density vary across the Danish red fox populations (Strandgaard & Asferg 1980) and, hence, the interactions between red fox and prey (Asferg & Forchhammer 2000), three observations support this notion. First, before the epizootic, mange-exposed populations displayed dynamics similar to the non-exposed populations on the islands of Fyn and Sjælland (figure 3a). Second, as the time elapsing from exposure of sarcoptic mange decreased (moving across populations from south to north in Jylland) so did the delayed negative density dependence (inset in figure 3a). As shown in the $(1 + \beta_1) - (\beta_2)$ parameter plan, the northernmost and latest exposed population (NJY) displayed dynamics closest to those of the non-exposed populations (figure 3a). Finally, the exception supporting our proposition is the fox population in Sønderjylland (SJY), which was the only Danish fox population affected by the European rabies epidemic (T. Asferg, unpublished data) in the 1970s (Anderson *et al.* 1981). The dynamic structure of this population prior to the epizootic (between 1955 and 1980) still displayed a strong, negative, delayed density dependence (figure 3a) which would be expected being exposed to rabies (or a parasite in general) (see equation (5)).

The classic theory of predator–prey population dynamics predicts multigenerational fluctuations in both predator and prey abundance (May 1981; Begon *et al.* 1996a). Accordingly, red fox populations which had not been exposed to sarcoptic mange displayed damped fluctuations of 20–25 years length (figure 3b) and preliminary results show that, although variable across populations, both brown hares and partridges, two important prey species, display fluctuations in abundance of about ten and 20 years, respectively (T. Asferg and M. C. Forchhammer, unpublished data). However, following the addition of a third ecological interactor (i.e. sarcoptic mange) to fox–prey interactions, the 20–25 year fluctuating behaviour disappeared (figure 3b). Although

very different from the intertrophic action of sarcoptic mange described here, recent experimental work on the influence of pathogens on parasitoid–host systems (Asferg & Forchhammer 2000) have also documented pronounced shifts in temporal predator–prey fluctuations: cyclic one-generational dynamics increased to multigenerational cycles or disappeared altogether (Begon *et al.* 1996b). Why the red fox population in Ribe county (RIB) did not display the skewed autocorrelation function pattern similarly to the other mange-exposed populations (figure 3b) is unclear. Fox–prey–weather interactions, which are currently being analysed, may reveal interactions unaccounted for in the present univariate time-series modelling.

Recent statistical analyses of time-series have shown the strength of statistical modelling of time-series in disentangling complex interactions across trophic levels under different abiotic regimes (Royama 1992; Bjørnstad *et al.* 1995; Stenseth *et al.* 1996a,b, 1998, 1999; Forchhammer *et al.* 1998). Here, we have extended this approach to parasite–host interactions demonstrating that, although the population dynamics of the parasite are numerically unknown, it is possible to describe the direct and indirect effects of parasites on natural host populations by autoregressive modelling of host time-series.

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REFERENCES

- Anderson, R. M. & May, R. M. 1978 Regulation and stability of host–parasite population interactions. I. Regulatory processes. *J. Anim. Ecol.* **47**, 219–248.
- Anderson, R. M. & May, R. M. 1980 Infectious diseases and population cycles of forest insects. *Science* **210**, 658–661.
- Anderson, R. M. & May, R. M. 1981 The population dynamics of microparasites and their invertebrate hosts. *Phil. Trans. R. Soc. Lond.* **B 291**, 451–524.
- Anderson, R. M., Jackson, H. C., May, R. M. & Smith, A. M. 1981 Population dynamics of fox rabies in Europe. *Nature* **289**, 765–771.
- Asferg, T. 1996 Ræven kommer igen. *Jæger* **5**, 16–19. (In Danish.)
- Asferg, T. 1998 Are Danish feral mink populations regulated by the red fox? In *Proceedings of the 16th Mustelid Colloquium* (ed. A. B. Madsen, T. Asferg, M. Elmeros & K. Zaluski), pp. 28–29. Copenhagen: Ministry of Environment and Energy, National Environmental Research Institute.
- Asferg, T. & Forchhammer, M. C. 2000 Variations in climate and habitat affect fox–prey interactions. (In preparation.)
- Bak, U., Hesselund, K. & Lykkegaard, J. 1997 (In Danish.) Ræveskab. MSc thesis, University of Aarhus, Denmark.
- Begon, M., Harper, J. L. & Townsend, C. R. 1996a *Ecology: individuals, populations and ecology*. Oxford, UK: Blackwell Scientific.
- Begon, M., Sait, S. M. & Thompson, D. J. 1996b Predator–prey cycles with period shifts between two- and three-species systems. *Nature* **381**, 311–315.
- Bjørnstad, O. N., Falck, W. & Stenseth, N. C. 1995 A geographic gradient in small rodent density fluctuations: a statistical modelling approach. *Proc. R. Soc. Lond.* **B 262**, 127–133.
- Bornstein, S., Zakrisson, G. & Thebo, P. 1995 Clinical picture and antibody response to experimental *Sarcoptes scabiei* var. *vulpes* infection in red foxes (*Vulpes vulpes*). *Acta Vet. Scand.* **36**, 509–519.

- Cattadori, I. M., Hudson, P. J., Merler, S. & Rizzoli, A. 1999 Synchrony, scale and temporal dynamics of rock partridge (*Alec graeca saxatilis*) populations in the dolomites. *J. Anim. Ecol.* **68**, 540–549.
- Corbet, G. B. & Harris, S. 1991 *The handbook of British mammals*. Oxford, UK: Blackwell Scientific.
- Danell, K. & Hörnfeldt, B. 1987 Numerical responses by populations of red fox and mountain hare during an outbreak of sarcoptic mange. *Oecologia* **73**, 533–536.
- Dennis, B. & Taper, M. L. 1994 Density dependence in time series observations of natural populations: estimation and testing. *Ecol. Monogr.* **64**, 205–224.
- Dobson, A. P. & Hudson, P. J. 1995 Microparasites: observed patterns. In *Ecology of infectious diseases in natural populations* (ed. B. T. Grenfell & A. P. Dobson), pp. 52–91. Cambridge University Press.
- Durbin, J. & Watson, G. S. 1951 Testing for serial correlation in least square regression II. *Biometrika* **38**, 159–178.
- Forchhammer, M. C., Stenseth, N. C., Post, E. & Langvatn, R. 1998 Population dynamics of Norwegian red deer: density-dependence and climatic variation. *Proc. R. Soc. Lond. B* **265**, 341–350.
- Grenfell, B. T. & Dobson, A. P. 1995 *Ecology of infectious diseases in natural populations*. Cambridge University Press.
- Harris, S. 1979 Age-related fertility and productivity in red foxes, *Vulpes vulpes*, in suburban London. *J. Zool.* **187**, 195–199.
- Holt, G. & Berg, C. 1990 Sarcoptic mange in red fox and other wild carnivores in Norway (in Norwegian with an English summary). *Norsk Vet. Tidsskrift* **102**, 427–432.
- Hudson, P. J. & Dobson, A. P. 1995 Macroparasites: observed patterns. In *Ecology of infectious diseases in natural populations* (ed. B. T. Grenfell & A. P. Dobson), pp. 144–176. Cambridge University Press.
- Jensen, B. & Sequeira, D. M. 1978 The diet of the red fox in Denmark. *Danish Rev. Game Biol.* **10**, 1–16.
- Jensen, T., Jensen, K. T. & Mouritsen, K. N. 1998 The influence of the trematode *Microphallus claviformis* on two congeneric intermediate host species (*Corophium*): infection characteristics and host survival. *J. Exp. Mar. Biol. Ecol.* **227**, 35–48.
- Krebs, C. J. 1978 *Ecology: the experimental analysis of distribution and abundance*, 2nd edn. New York: Harper & Row Publishers.
- Lindström, E. 1992 Diet and demographics of the red fox (*Vulpes vulpes*) in relation to population density—the sarcoptic mange event in Scandinavia. In *Wildlife 2001: populations* (ed. D. R. McCullough & R. H. Barret), pp. 922–931. London: Elsevier.
- Lindström, E. & Mörner, T. 1985 The spreading of sarcoptic mange among Swedish red foxes (*Vulpes vulpes*) in relation to fox population dynamics. *Rev. d'Écol. (La Terra et la Vie)* **40**, 211–216.
- Lindström, E. R., Andrén, H., Angelstam, P., Cederlund, G., Hörnfeldt, B., Jäderberg, L., Lemnell, P.-A., Martinsson, B., Sköld, K. & Swenson, J. E. 1994 Disease reveals the predator: sarcoptic mange, red fox predation, and prey populations. *Ecology* **75**, 1042–1049.
- Lindström, E. R., Brainerd, S. M., Helldin, J. O. & Overskaug, K. 1995 Pine martin red fox interactions—a case of intra-guild predation. *A. Zool. Fenn.* **32**, 123–130.
- Little, S. E., Davidson, W. R., Rakich, P. M., Nixon, T. L., Bounous, D. I. & Nettles, V. F. 1998a Response of red foxes to first and second infection with *Sarcoptes scabiei*. *J. Wildl. Dis.* **34**, 600–611.
- Little, S. E., Davidson, W. R., Howerth, E. W., Rakich, P. M. & Nettles, V. F. 1998b Diseases diagnosed in red foxes from the southeastern United States. *J. Wildl. Dis.* **34**, 620–624.
- Madsen, J., Asferg, T., Clausager, I. & Noer, H. 1996 Status og jagttider for danske vildtarter. *Tema-rapport* **6**, 1–112. (In Danish.)
- Martin, R. W., Handasyde, K. A. & Skerratt, L. F. 1998 Current distribution of sarcoptic mange in wombats. *Aust. Vet. J.* **76**, 411–414.
- Mathsoft, Inc. 1997 *S-plus 4.0 release 2 for Windows*. Seattle, WA: Mathsoft, Inc.
- May, R. M. 1973 *Stability and complexity in model ecosystems*. Princeton University Press.
- May, R. M. 1981 *Theoretical ecology: principles and applications*. Oxford, UK: Blackwell Scientific.
- May, R. M. & Anderson, R. M. 1978 Regulation and stability of host–parasite population interactions. I. Regulatory processes. *J. Anim. Ecol.* **47**, 249–267.
- May, R. M. & Anderson, R. M. 1979 Population biology of infectious diseases. *Nature* **280**, 455–461.
- Mörner, T. & Christensson, D. 1984 Experimental infection of red foxes (*Vulpes vulpes*) with *Sarcoptes scabiei* var. *vulpes*. *Vet. Parasitol.* **15**, 159–164.
- Mouritsen, K. M. & Jensen, K. T. 1994 The enigma of gigantism—effects of larval trematodes on growth, fecundity, egestion and locomotion in *Hydrobia ulvae* (Pennant) (Gastropoda, Prosobranchia). *J. Exp. Mar. Biol. Ecol.* **181**, 53–66.
- Mouritsen, K. M. & Jensen, K. T. 1997 Parasite transmission between soft-bottom invertebrates: temperature mediated infection rates and mortality in *Corophium volutator*. *Mar. Ecol. Prog. Ser.* **151**, 123–134.
- Pence, D. B. & Windberg, L. A. 1994 Impact of a sarcoptic mange epizootic on a coyote population. *J. Wildl. Manage.* **58**, 624–633.
- Royama, T. 1992 *Analytic population dynamics*. London: Chapman & Hall.
- Sakamoto, Y., Ishiguro, M. & Kitagawa, G. 1986 *Akaike information criterion statistics*. Tokyo: KTK Scientific Publishers.
- Samuel, W. M. 1981 Attempted experimental transfer of sarcoptic mange (*Sarcoptes scabiei*, Acarina, Sarcoptidae) among red fox, coyote, wolf and dog. *J. Wildl. Dis.* **17**, 343–347.
- SAS Institute, Inc. 1990 *SAS/ETS user's guide*, v. 6, 4th edn. Cary, NC: SAS Institute, Inc.
- SAS Institute, Inc. 1996 *The SAS system for Windows*, v. 6.12. Cary, NC: SAS Institute, Inc.
- Selås, V. 1998 Does food competition from red fox (*Vulpes vulpes*) influence the breeding density of goshawk (*Accipiter gentilis*)? Evidence from a natural experiment. *J. Zool.* **246**, 325–335.
- Smedshaug, C. A., Selås, V., Lund, S. E. & Sonerud, G. A. 1999 The effect of a natural reduction of red fox *Vulpes vulpes* on small game hunting bags in Norway. *Wildl. Biol.* **5**, 157–166.
- Stenseth, N. C., Bjørnstad, O. N. & Falck, W. 1996a Is spacing behaviour coupled with predation causing the microtine density cycle? A synthesis of current process-oriented and pattern-oriented studies. *Proc. R. Soc. Lond. B* **263**, 1423–1435.
- Stenseth, N. C., Bjørnstad, O. N. & Saitoh, T. 1996b A gradient from stable to cyclic populations of the *Clethrionomys rufocanus* in Hokkaido, Japan. *Proc. R. Soc. Lond. B* **263**, 1117–1126.
- Stenseth, N. C., Falck, W., Chan, K.-S., Bjørnstad, O. N., O'Donoghue, M., Tong, H., Boonstra, R., Boutin, S., Krebs, C. J. & Yoccoz, N. G. 1998 From patterns to processes: phase and density dependencies in the Canadian lynx cycle. *Proc. Natl Acad. Sci. USA* **95**, 15 430–15 435.
- Stenseth, N. C. (and 10 others) 1999 Common dynamic structure of Canada lynx populations within three climatic regions. *Science* **285**, 1071–1073.
- Strandgaard, H. & Asferg, T. 1980 The Danish bag record II. *Danish Rev. Game Biol.* **11**, 1–112.
- Tong, H. 1990 *Non-linear time series*. Oxford, UK: Clarendon Press.
- Vos, A. 1995 Population dynamics of the red fox (*Vulpes vulpes*) after the disappearance of rabies in county Garmisch-Partenkirchen, Germany, 1987–1992. *A. Zool. Fenn.* **32**, 93–97.

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