



Forms of density regulation and (quasi-) stationary distributions of population sizes in birds

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The theta-logistic model of density regulation is an especially flexible class of density regulation models where different forms of non-linear density regulation can be expressed by only one parameter, θ . Estimating the parameters of the theta-logistic model is, however, challenging. This is mainly due to the need for information concerning population growth at low densities as well as data on fluctuations around the carrying capacity K in order to estimate the strength of density regulation. Here we estimate parameters of the theta-logistic model for 28 populations of three species of birds that have grown from very small population sizes followed by a period of fluctuations around K . We then use these parameters to estimate the quasi-stationary distribution of population size. There were often large uncertainties in these parameters specifying the form of density regulation that were generally independent of the duration of the study period. In contrast, precision in the estimates of environmental variance increased with the length of the time series. In most of the populations, a large proportion of the probability density of the (quasi-) stationary distribution of population sizes was located at intermediate population sizes relative to K . Thus, we suggest that the (quasi-) stationary distribution of population sizes represents a useful summary statistic that in many cases provides a more robust characterisation of basic population dynamics (e.g. range of variation in population fluctuations or proportion of time spent close to K) than can be obtained from analyses of single model parameters.

The presence of density dependence, i.e. the relationship of the per capita growth rate on present and/or past population sizes (Murdoch and Walde 1989), has undoubtedly been among the most debated topics in ecology. Whereas some ecologists like Nicholson (1933) and Lack (1954) were strong advocates of density dependence controlling the size of populations, other ecologists forcefully argued that 'extrinsic factors could not be considered density-independent' (Andrewartha and Birch 1954). Turchin (1995) provided an important contribution that encompassed both of these alternative viewpoints. Following May (1973), he defined population regulation with the presence of a stationary distribution of population sizes. Such a distribution is characterized by bounded variance and a return tendency to an equilibrium population size, determined by the strength of density dependence.

In addition to providing some important qualitative characteristics of the patterns in population fluctuations, the stationary distribution may also reveal some quantitative information about the population dynamics. If we assume no age-structure effects, the stationary distribution of population size will be influenced by environmental stochasticity as well as the form of density regulation (Lande et al. 2003). By analysing simple deterministic models, May (1976) was able to demonstrate that changing critical parameters such as the specific population growth rate or the strength of density regulation, can result in large dynamical changes. Thus, the shape of the stationary distribution and hence the pattern of population fluctuations will be strongly influenced by the form of density regulation.

Many types of models of density regulation have been suggested for natural populations. One of the most familiar

and most commonly used models in population ecology is the loglinear model or the Gompertz model that assumes that density regulation is linear on a logarithmic scale (Royama 1992). Another familiar model is the logistic model in which the deterministic specific growth rate decreases linearly with population size (Lande et al. 2003). The model of density regulation used in turn strongly influences the form of the stationary distribution of population sizes. For instance, a loglinear model of density regulation is characterized by a lognormal stationary distribution (Lewontin and Cohen 1969), whereas the distribution is approximately gamma for the logistic model (Diserud and Engen 2000, Näsell 2001).

The theta-logistic model (Gilpin and Ayala 1973, Gilpin et al. 1976) defines a general class of models of density regulation as function of only a single parameter θ . For small values of θ , density regulation starts to act at small population sizes. In contrast, if θ is large there is almost no density regulation at smaller population sizes, whereas strong density regulation occurs around the carrying capacity K . Thus, the theta-logistic model allows us to specify the form of density regulation, which can also be used to calculate the stationary distribution of population sizes (Diserud and Engen 2000), assuming large enough population sizes to ignore the effects of demographic stochasticity.

The description of non-linear forms of density regulation using only one parameter has opened up the possibilities for analyses of general patterns. Based upon analyses of a huge number of time series, Sibly et al. (2005) suggested that density regulation operating at small densities was a general feature of the population dynamics of a large number of taxa. One implication of this result is that for most of the time populations fluctuate at sizes far below the carrying capacity K . In solitary birds, Sæther et al. (2002c) found that the value of θ increased with adult survival rate, because recruitment in long-lived species was dependent on the number of territories made vacant by the death of adult birds.

Although the theta-logistic model contains only a few parameters, obtaining reliable estimates from time series describing population fluctuations have proven difficult. One major reason for this is that suitable time series must include observations at very low population sizes as well as longer periods of fluctuations around K in order to facilitate estimation of the growth rate at small populations as well as of K and rates of return to the equilibrium. In general, the probability of identifying the presence of density dependence increases with the length of the time series (Woiwood and Hanski 1992, Brook and Bradshaw 2006). However, if the only available population estimates are those around K , then extrapolations over a wide range of population sizes is necessary, and this can easily result in biased estimates of population growth rates at small densities (Aanes et al. 2002, Getz and Lloyd-Smith 2006).

The purpose of this paper is to estimate the parameters of the theta-logistic model in several populations of three bird species. These time series of population sizes were chosen because they include small populations that increase up to and fluctuate around K . We include only time series that we believe are quite accurate in order to reduce biases in parameter estimates due to observation error in the

population counts (Dennis et al. 2006, Freckleton et al. 2006). We will use these estimates to calculate important characteristics of population fluctuations such as the (quasi-) stationary distribution of population sizes (Lande et al. 2003) and characteristic return times to equilibrium. This enables us to extend previous analyses of single populations (Sæther et al. 2000, 2002a, 2002b) to quantitatively assess the relative contribution of deterministic components as well as any stochastic influences on patterns in population fluctuations. Finally, we also use this comparative approach to examine how uncertainties in different population parameters are affected by characteristics of the time series (e.g. the length of the study period). Our overall aim is to evaluate under which conditions the theta-logistic model of density regulation is useful for characterizing the dynamics of bird populations.

The model

If N is the population size, the specific growth rate $r(N)$ in the theta-logistic model is

$$r(N) = r_0 [1 - (N/K)^\theta], \quad (1a)$$

where K is the carrying capacity, r_0 is specific growth rate at $N=0$ and θ denotes the form of density regulation. To make the model valid for any values of θ , we choose r_0 as a function of θ (Sæther et al. 2000, 2002b) so that

$$r(N) = r_1 \left[1 - \frac{N^\theta - 1}{K^\theta - 1} \right] \quad \text{for } \theta \neq 0, \quad (1b)$$

and the limiting form

$$r(N) = r_1 \left[1 - \frac{\ln N}{\ln K} \right] \quad \text{for } \theta = 0 \quad (1c)$$

where $r_1 = r_0(1 - K^{-\theta})$.

Let $\Delta X_t = \ln N_{t+1} - \ln N_t$ be the change in the logarithm of population size from year t to $t+1$. If $r_1(t)$ fluctuates in time, annual changes in (log) population size can be modelled as

$$\Delta X = r_1(t) - \frac{1}{2} \sigma_e^2 - \frac{1}{2N} \sigma_d^2 - \bar{r}_1 \frac{N^\theta - 1}{K^\theta - 1} \quad (2a)$$

with variance

$$\text{var}(\Delta X|X) = \sigma_e^2 + \sigma_d^2/N \quad (2b)$$

Here \bar{r}_1 is the mean of $r_1(t)$, and σ_e^2 and σ_d^2 the environmental and demographic variance, respectively, so that $\text{var}(r(t)) = \sigma_e^2 + \sigma_d^2/N$ (Lande et al. 2003).

The characteristic return time to equilibrium T_R , i.e. the time required for a deviation from K to reach a small fraction of its initial value (May 1974), defines the strength of density regulation

$$\gamma = 1/T_R = r_0\theta = r_1\theta/(1 - K^{-\theta}) \quad \text{for } \theta \neq 0 \quad (3a)$$

and

$$\gamma = 1/T_R = r_1/\ln K \quad \text{for } \theta = 0. \quad (3b)$$

We see that the characteristic return time to equilibrium for the theta-logistic model equals the product of r_0 and θ .

Assuming $\sigma_d^2 = 0$, Diserud and Engen (2000) showed using a diffusion approximation that the stationary distribution of population size of the theta-logistic model is a generalized gamma distribution for $\theta \neq 0$

$$f(N; K, \alpha, \theta) = \frac{|\theta| \left(\frac{\alpha + 1}{\theta}\right)^{\alpha/\theta}}{\Gamma(\alpha/\theta)} (N/K)^{\alpha-1} e^{-\frac{(\alpha+1)}{\theta} (N/K)^\theta} \quad (4)$$

where $\alpha = (2r_0/\sigma_e^2)(1 - K^{-\theta})^{-1} - 1$ and Γ denotes the gamma function.

In Fig. 1 we have computed the stationary distribution for different values of θ . It is apparent that a wide range of distributions can be obtained by varying just a single parameter. For $\theta = 1$ this becomes the gamma distribution with shape parameter α and scale parameter $(\alpha + 1)/K$. For $\theta = -1$ we get the inverse gamma distribution. Two special limiting distributions also exist. When θ approaches 0, the limiting distribution is the lognormal distribution, and when θ approaches infinity $f(N; K, \alpha, \infty) = \frac{\alpha}{K^\alpha} (N)^{\alpha-1}$ for $0 \leq N \leq K$, and otherwise zero.

The moments γ of the stationary distribution are

$$E(X)^m = \frac{K^m \Gamma[(\alpha + m)/\theta]}{[(\alpha + 1)/\theta]^{m/\theta} \Gamma(\alpha/\theta)} \quad (5)$$

$m = 1, 2, \dots$, from which we compute the variance as $\sigma_N^2 = EX^2 - (EX)^2$.

In populations with a small K (i.e. $K < 50$) demographic stochasticity cannot be ignored. In these cases we use the Green function (Appendix 1) that expresses how long time the population is expected to spend in each state. By integrating the Green function (Karlin and Taylor 1981) numerically from the extinction barrier at $N = 1$ up to infinity, and scaling it by its integral, we obtain the quasi-stationary distribution of population size (Sæther et al. 2002b, Lande et al. 2003). This distribution summarizes the properties of the population fluctuations from the initial population size until the chosen extinction barrier is reached. Thus, in contrast to the stationary distribution, this distribution depends upon initial population size although in practice this relationship is quite weak (Lande

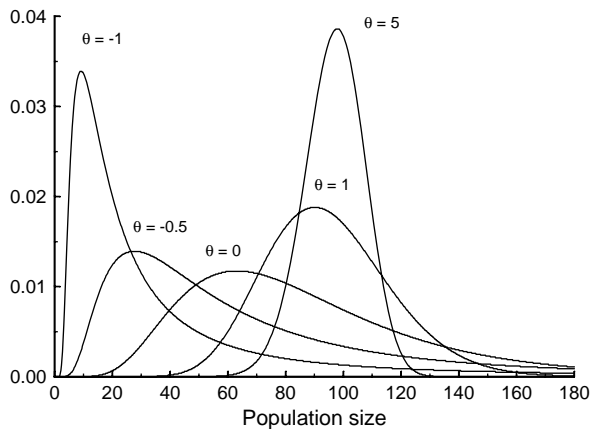


Figure 1. The stationary distribution of population sizes for different values of θ in the theta-logistic model. The other parameters are $K = 100$, $\sigma_e^2 = 0.01$ and $r_1 = 0.1$.

et al. 2003) and expresses the expected relative time spent at each population size before extinction.

Methods

We use data from three European bird species: the great cormorant *Phalacrocorax carbo sinensis*; the pied flycatcher *Ficedula hypoleuca*; and the white stork *Ciconia ciconia*. These species were chosen because population sizes can be estimated more accurately than for most other bird species. The great cormorant and white stork build large conspicuous nests that are relatively easy to detect and to count. The pied flycatcher almost exclusively nests in nest-boxes whenever they are provided. Thus, we expect that errors in population estimates have only a minor influence on our parameter estimates for these species.

Another advantage by choosing these species is that population estimates are available over a wide range of population sizes. The great cormorant was heavily persecuted by humans over larger parts of central Europe until the 1960s and 1970s. When the persecution decreased, a rapid increase in the size of populations of continental great cormorant occurred over large areas (Van Eerden and Gregersen 1995). For instance, the population in Denmark grew from 250 pairs in 1970 to approximately 33 500 pairs in 1992 (Bregnballe and Gregersen 1995). In our studies we have included only those colonies for which data are available for 15 or more years for the range of population size from $0.1 K$ to K . The pied flycatcher is a commonly studied European cavity-nesting passerine that readily establish when nest boxes are provided. Here we analysed time series of 15 or more years of populations that have increased from less than 10 pairs and include a period of fluctuations around some mean population size $K > 19$ pairs. In addition, we include data for two populations of white storks from eastern Europe, which have increased in size and now fluctuate around some equilibrium.

The demographic variance σ_d^2 was estimated from individual based data (Sæther et al. 2004) and was assumed to be equal to the mean of the estimates that were available for each species, i.e. $\hat{\sigma}_d^2 = 0.566$, $\hat{\sigma}_d^2 = 0.267$ and $\hat{\sigma}_d^2 = 0.098$ for the pied flycatcher, the great cormorant and the white stork, respectively. The remaining parameters in the population model (Eq. 2) were estimated using maximum likelihood (Lande et al. 2003), considering σ_d^2 to be known. To obtain unbiased estimates of r_1 we employed bootstrap correction of the bias (Efron and Tibshirani 1993) as described in more detail by Sæther et al. (2000).

This approach assumes that there is no autocorrelation in the noise (Lande et al. 2003). The validity of this assumption was examined by the Ljung-Box version of the Portemanteau test for whiteness of the residuals (Tong 1990), using the procedure portman.Q in R (R Development Core Team).

Uncertainties in parameters were determined by parametric bootstrapping (Efron and Tibshirani 1993). The uncertainty in the variance of the quasi-stationary distribution σ_N^2 was obtained by calculating the quasi-stationary distribution for each set of bootstrap replicates. By denoting the 5%, 50% and 95% quantile of the bootstrap distribution of parameter p as $q_{p,5}$, $q_{p,50}$ and $q_{p,95}$, respectively, the

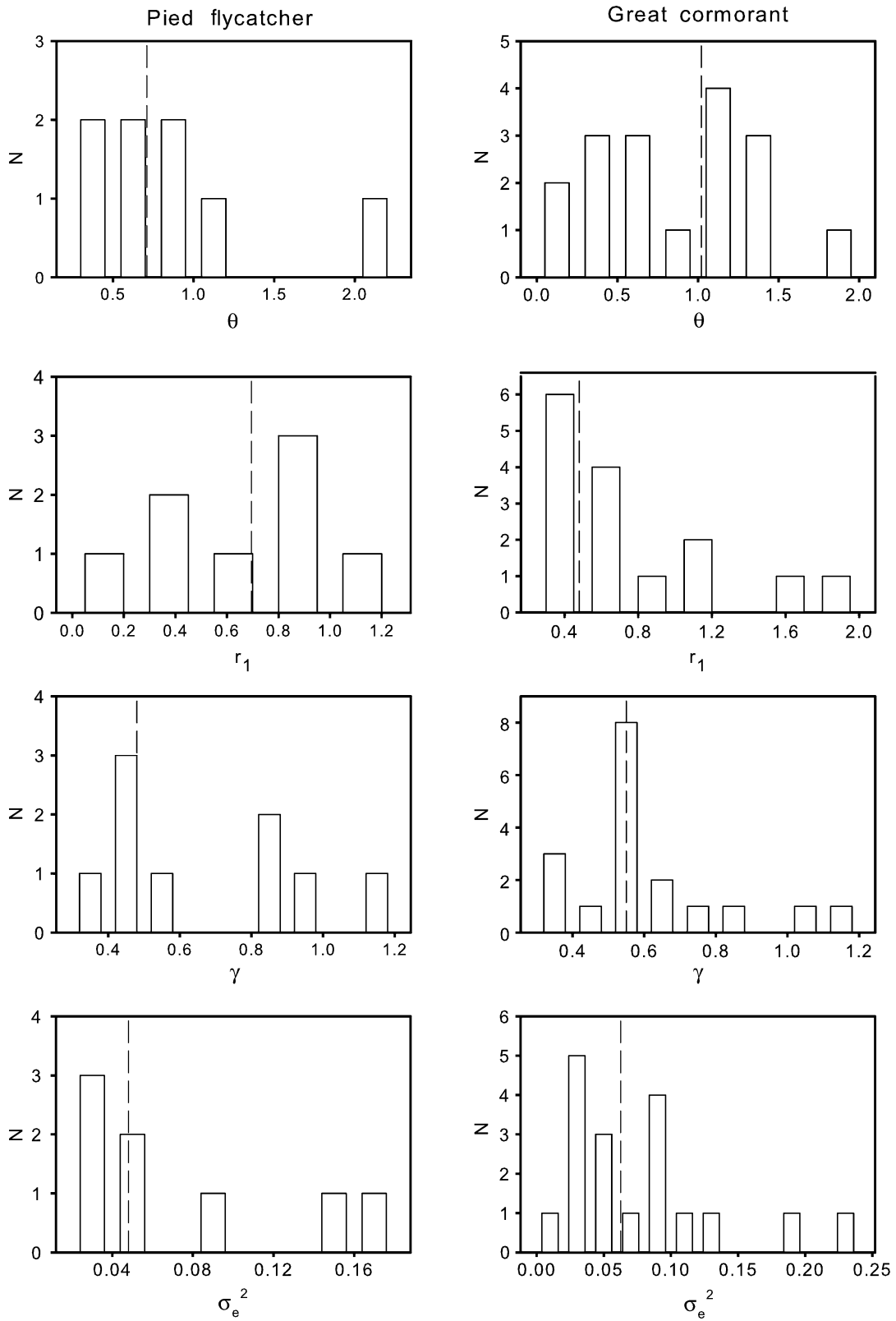


Figure 2. Distribution of the estimates of different parameters of the theta-logistic model across different populations of great cormorants ($n=18$) and pied flycatcher ($n=8$). The dashed lines indicate median values.

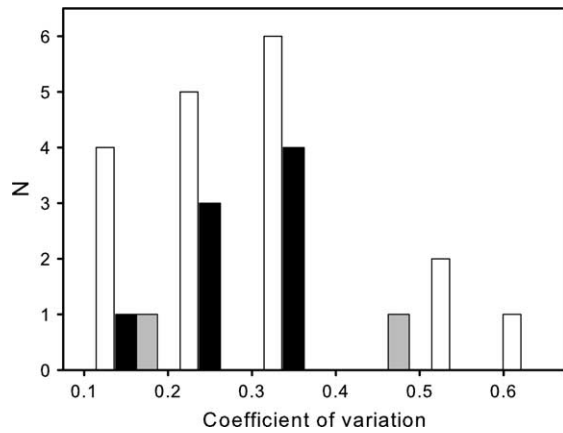


Figure 3. The distribution of the coefficient of variation of the (quasi-) stationary distribution of population size of great cormorant ($n=18$) (white columns), pied flycatcher ($n=8$) (black columns) and white stork ($n=2$) (grey columns).

relative uncertainty in the estimate γ of parameter p was expressed as $u_p = (q_{p,97.5} - q_{p,2.5})/q_{p,50}$.

Results

The distribution of parameter estimates across populations revealed large intraspecific variation (Fig. 2, Appendix 3). In great cormorant the estimates of θ ranged from 0.21 to 6.06, with a median value (1.02) suggesting that the logistic model ($\theta=1$) describes the pattern of density regulation quite well in this species. Similarly, estimates of θ around 1

were also found in several populations of pied flycatcher. Strong density regulation close to K was found for white storks ($\hat{\theta}=1.76$ and $\hat{\theta}=15.78$), which seems to be a general feature of the population dynamics of this species (Sæther et al. 2006). In some populations of both great cormorants and pied flycatchers, high growth rates were found at small population sizes. For instance, the largest estimate of $\lambda = e^{r_1}$ was 3.22 and 7.39 for pied flycatcher and great cormorant, respectively.

The median of the estimates of the strength of density dependence was 0.48 and 0.55 for great cormorants and pied flycatchers, respectively, resulting in characteristic return times to equilibrium $T_R = 1/\gamma$ of approximately two years for these two species. For white storks, the median value of γ was larger (0.72). The largest values for $\hat{\gamma}$ were 1.19, 1.14 and 1.15 for white stork, pied flycatcher and great cormorant, respectively.

For pied flycatcher and great cormorant the largest relative intraspecific variation was found in the estimates of environmental variance σ_e^2 (Fig. 2). For this parameter the largest $\hat{\sigma}_e^2$ was 12.7 and 6.2 times larger than the smallest $\hat{\sigma}_e^2$ for great cormorant and pied flycatcher, respectively. The median value of $\hat{\sigma}_e^2$ (0.023) for the two populations of white stork was smaller than for the two other species. Accordingly, large variation was also found in the coefficient of variation of the (quasi-) stationary distribution of population size $CV_N = \sigma_N/K$ (Fig. 3), ranging from 0.13 to 0.60, resulting in large differences in the shape of the (quasi-) stationary distribution of population size even within the same species (Fig. 4). However, the median of the estimates of CV_N was quite similar for all three species

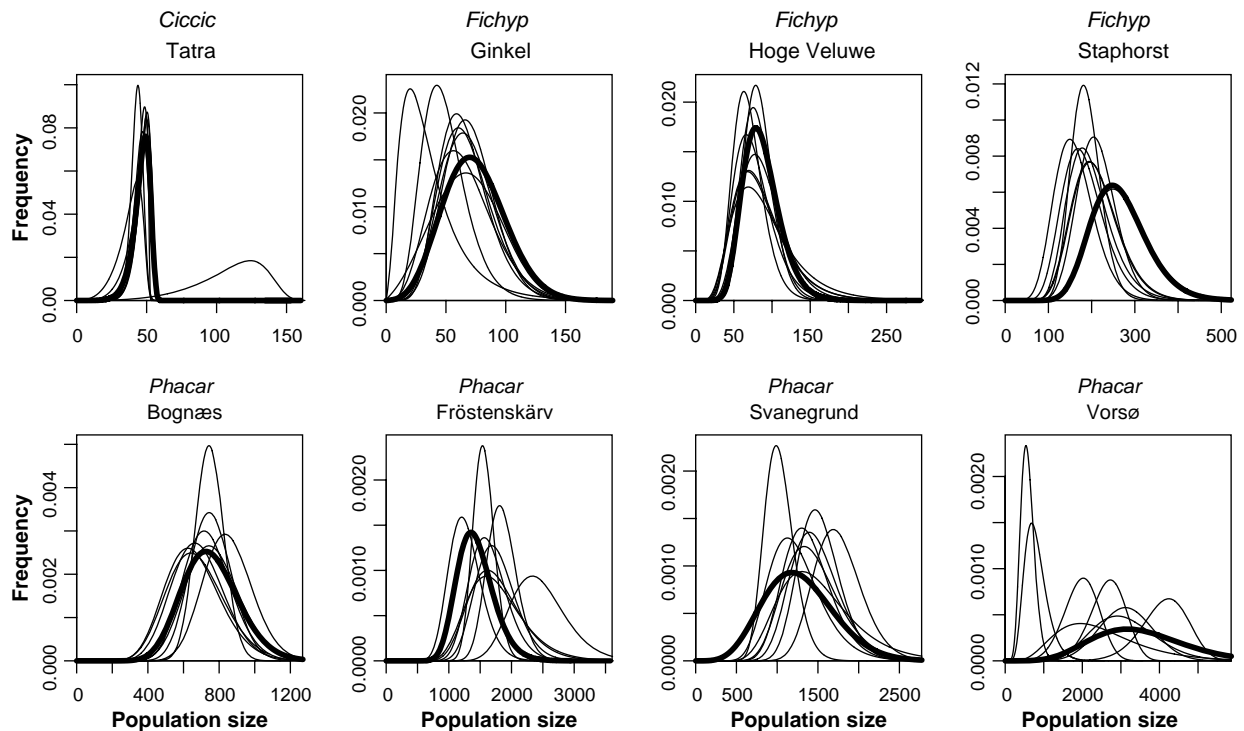


Figure 4. The estimated (quasi-) stationary distribution of population size (black line) and the distribution calculated for eight randomly chosen set of boot strap replicates of the parameters (thin lines) in the theta-logistic model for one population of white stork (*Ciccic*), three populations of the pied flycatcher (*Fichyp*) and four populations of great cormorant (*Phacar*).

(0.28, 0.31 and 0.32 for the white stork, pied flycatcher and great cormorant, respectively).

An examination of the residuals showed that few series deviated significantly ($p > 0.05$) from a model of white noise. The only exceptions were a significant negative 1-year lag in the pied flycatcher population in Wittenberg ($p < 0.001$) and a positive two-years lag for the great cormorant population at Svanegrund ($p = 0.0369$).

The estimates of the population parameters were generally uncertain (Fig. 5). In all species, the largest uncertainties were apparent in the estimates of θ , followed by r_1 . The highest precision was found in the estimates of K . The large uncertainties especially in parameters describing the form of density regulation gave rise to estimates of the variance of the (quasi-) stationary distribution of population size that in some of the populations were very uncertain (Fig. 4,5).

In addition, there was also a sampling correlation between the estimates of several of the parameters (Fig. 6). In particular, a strong negative sampling correlation was found between estimates of θ and r_1 , i.e. large estimates of r_1 was in all populations related to small values of θ . This negative sampling covariance may also explain that the estimate of the strength of the density dependence γ was more certain than the estimates of θ . Furthermore, in great cormorant there was a negative sampling correlation between θ and σ_c^2 in 16 populations ($p = 0.0044$) as well as a positive sampling correlation between K and σ_c^2 in 15 populations ($p = 0.019$).

Uncertainty in the estimate of $\log \sigma_c^2$ decreased with the logarithm of the length of the study period (correlation coefficient = -0.95 , $p < 0.001$, $n = 18$ and correlation coefficient = -0.42 , $p = 0.08$, $n = 8$ for great cormorant and pied flycatcher, respectively). In contrast, uncertainty in the estimates of K of populations of great cormorant

increased with the duration of the study period (correlation coefficient = 0.23 , $p = 0.04$, $n = 18$).

Discussion

This study shows large intraspecific variation in the population dynamics of three species caused by differences in the form of the density regulation as well as in the effects of environmental stochasticity (Fig. 2). Such large differences in dynamical characteristics of populations of the same species seem to be a general feature (Bjørnstad et al. 1995, Mysterud et al. 2000, Peltonen et al. 2002, Aanes et al. 2003, Sæther et al. 2003, Williams et al. 2003). However, uncertainties in the parameter estimates are often large (Fig. 5) and strong sampling correlations may be present (Fig. 6).

The theta-logistic model should be useful for analysing density regulation in natural populations because a wide variety of non-linear forms of density regulation can be obtained by varying only a single parameter, θ (Fig. 1). Nevertheless, obtaining reliable parameter estimates even in this simple model requires data concerning growth at small population sizes in order to estimate r_1 , as well as long-term data on population fluctuations around K to obtain information about the form of density regulation such as the characteristic return times to equilibrium. Estimating these parameters from time series of stationary fluctuations around K requires extrapolation over a wide range of population sizes that may easily result in biased estimates of r_1 and hence θ (Aanes et al. 2002, Getz and Lloyd-Smith 2006) due to the negative sampling covariance between these two parameters (Fig. 6). Although the strength of density dependence $\gamma = r_0\theta$ often can be estimated with good precision, each factor r_0 and θ can be very uncertain.

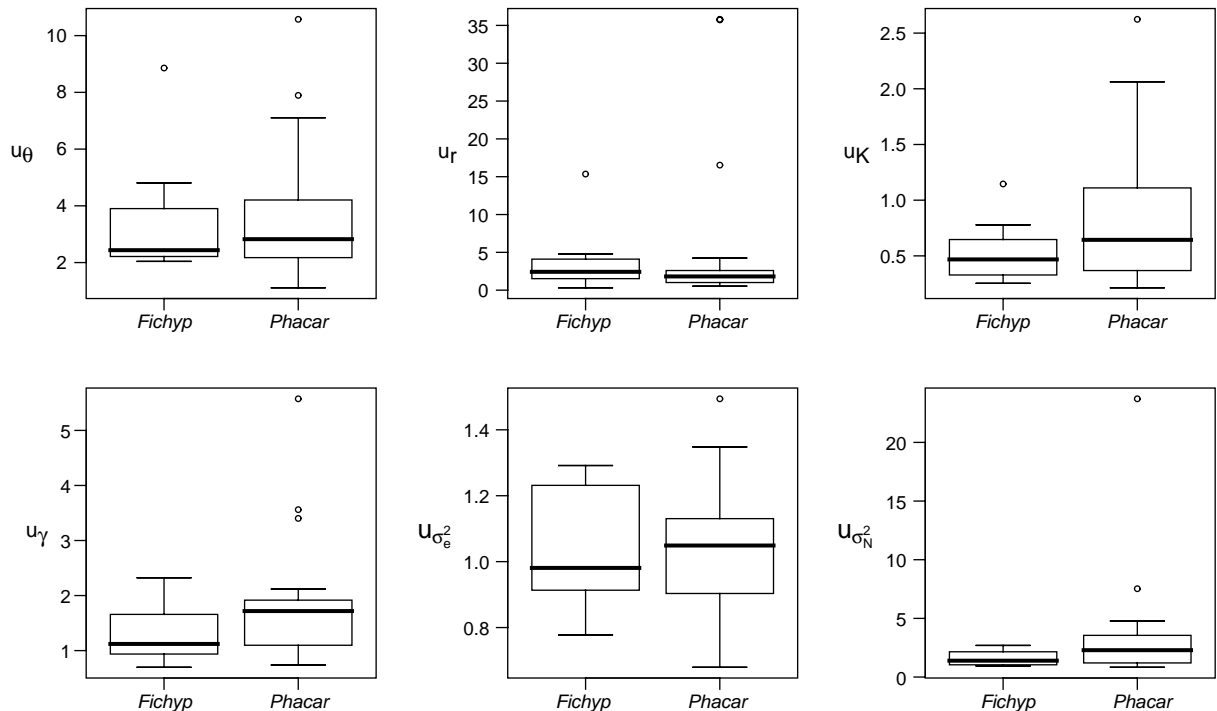


Figure 5. Box-plots of the relative uncertainty u in the estimates of the parameters of the theta-logistic model (Eq. 1) across populations of the pied flycatcher (*Fichyp*) ($n = 8$) and the great cormorant (*Phacar*) ($n = 18$).

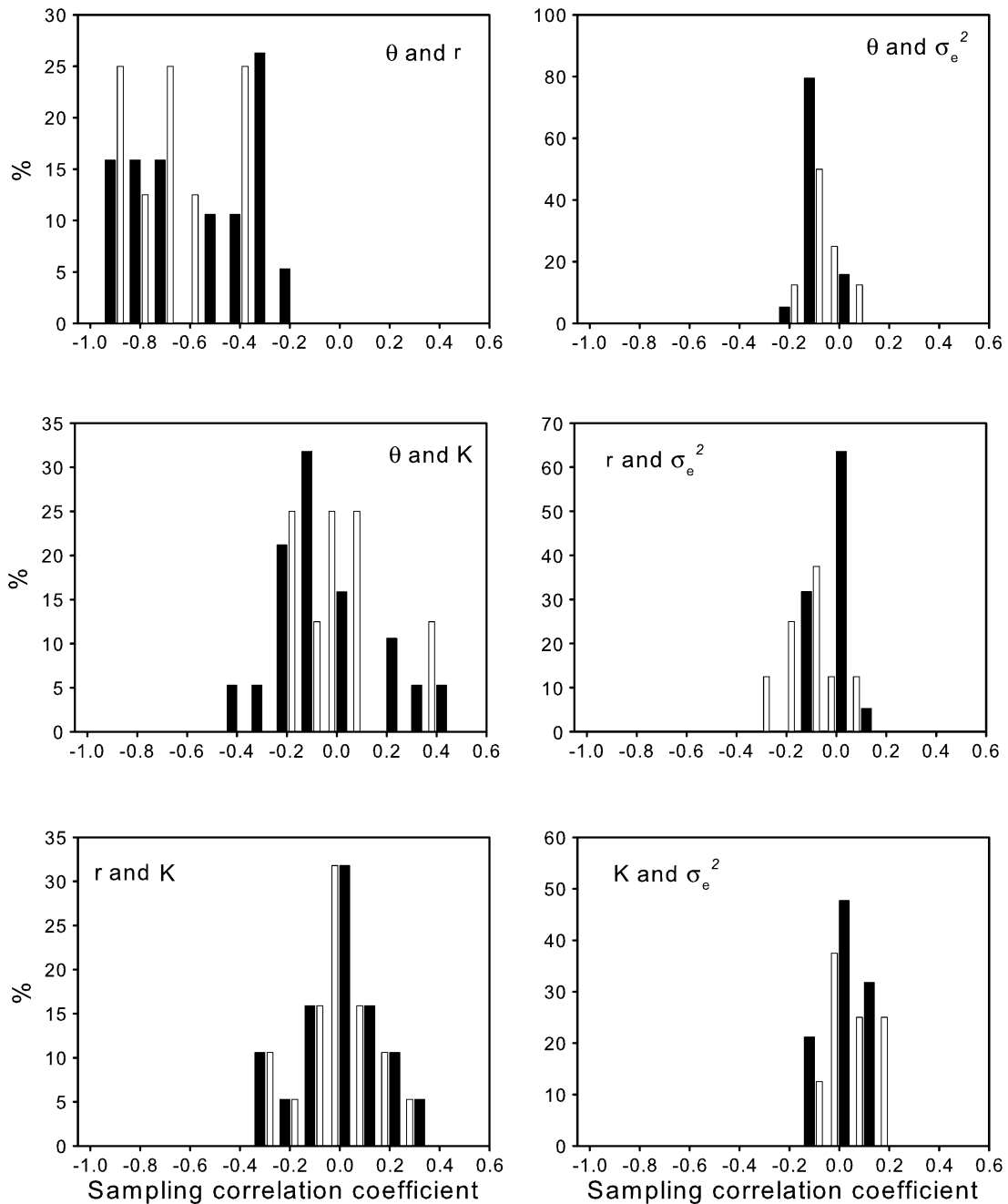


Figure 6. The distribution of the sampling correlation between different parameters of the theta-logistic equation (Eq. 1) in populations of the pied flycatcher (white columns) ($n = 8$) and the great cormorant (black columns) ($n = 18$). The sampling correlation was estimated using 1000 bootstrap replicates in each population of the estimated set of parameters.

In many cases this will give estimates of r_1 that are biologically unrealistic. Thus, such an overestimation of r_1 will inevitably result in an underestimation of θ because of the strong negative sampling correlation (Fig. 6) between these two parameters. This problem may explain why Sibly et al. (2005) obtained such a high proportion of negative values of θ in their comparative analyses of population dynamics in a wide variety of taxa. Accordingly, in the present study estimates of θ were significantly larger than 0 in 43% of the populations, whereas in no instance was θ less than 0. This shows that population fluctuations occurring predominantly at population sizes far below K (Fig. 1,4)

are not a general characteristics of the population dynamics of any of these species.

In this study we restricted the allowable range of variation in θ by setting $\theta = -1$ as lower limit. This constraint mostly provides estimates of r_1 that can be considered biologically reasonable, especially when considering that estimates of r_1 will also be affected by dispersal, which is not uncommon in these systems. For instance, in the great cormorant dispersal between colonies occurs frequently (Hénaux et al. 2007). In spite of the restriction on the range of variation, the estimates of θ were uncertain (Fig. 5). However, in all but one case (the Tatra population

of white stork) the logistic model ($\theta = 1$) was located within the 95% confidence interval around $\hat{\theta}$, which supports previous choices of density regulation model for these species (Sæther et al. 2003, Engen et al. 2005). Accordingly, a large proportion of the probability density of the (quasi-) stationary distribution of population sizes was located at intermediate population sizes relative to K in most of the populations (Fig. 4). Thus, the populations spent the larger proportion of the time at population sizes around $K/2$. Similarly, a consistent pattern in many long-term time series of population fluctuations is that the skewness of the distribution of population sizes is less than expected from a lognormal distribution (Halley and Inchausti 2002).

Although the estimates of r_1 and θ were uncertain, there was higher precision in the estimates of the strength of density dependence γ (Fig. 5). This was because of a negative sampling covariance between these two parameters that makes their product γ (Eq. 3) can be more accurately estimated from periods of fluctuations around K (Lande et al. 2003). Stationarity of any discrete time series requires that $\sigma_e^2/(2\gamma - \gamma^2) > 0$, which means that $0 < \gamma < 2$. In all populations, $\hat{\gamma}$ was significantly less than 2 (Fig. 2). This therefore indicates that the strength of density regulation of these populations was far from inducing any chaos-like fluctuations. Indeed, such absence of chaos seems to be a general pattern in natural populations (Hassel et al. 1976, Ellner and Turchin 1995, but see Turchin and Ellner 2000).

An examination of the (quasi-) stationary distribution of population sizes, calculated from bootstraps of parameter estimates, showed in most cases relatively small variation around the distribution calculated from the maximum likelihood estimates of the parameters (Fig. 5). However, large uncertainties in the form of the (quasi-) stationary distribution were found, especially in two populations of great cormorants. These populations (Vorsø and Lepelaar-plassen) were characterized by recent declines in population size (Appendix 2) that made the estimates of K uncertain. This effect is the result of a particular feature often observed in the colony dynamics of this species (Bregnballe and Gregersen 1997, van Eerden and van Rijn 2003), i.e. a period of growth or stable fluctuations is followed by a period in which the numbers drop due to changes in the food supply, destruction of nesting habitats as trees die after accumulation of great cormorant guano, and sudden shifts in nesting colonies by adults.

In general, these analyses show that obtaining precise estimates of the form of density regulation is often difficult, even when using relatively long-term time series with small sampling errors such as those analysed here. Care should therefore be taken when interpreting results from fitting complex time-series models that involve estimating a large number of parameters (Stenseth et al. 2004). In addition, if population estimates are uncertain, even larger uncertainties and biases will occur (Staples et al. 2004, Dennis et al. 2006, Freckleton et al. 2006). As an alternative to the simultaneous estimation of all parameters from a time series, we suggest that fixation of one parameter (e.g. r_1) should be considered. This may be done using estimates from demographic data (Sæther et al. 2002a) or from time

series of growth of populations that establish themselves in a new area (Sæther et al. 2006). Another approach could be to make a priori assumptions concerning the form of density dependence, e.g. from the social organisation of the species (Sæther et al. 2005). If none of these approaches are possible, we suggest that calculation of the (quasi-) stationary distribution of population size (Fig. 4) can prove useful in revealing many useful characteristics of the population dynamics such as the range of population sizes at which the population will spend most of the time.

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Appendix 1.

Here we will define the Green function (Karlin and Taylor 1981, Lande et al. 2003) and show how it can be used to compute the quasi-stationary distributions of population sizes. Writing $E(\Delta X|X = x) = \mu(x)$ and $\text{var}(\Delta X|X = x) = v(x)$, the diffusion approximation for the process $x = \ln N$ has infinitesimal mean $\mu(x)$ and variance $v(x)$, respectively. If the population is density regulated so that $\mu(x)$ is negative for large values of x , the Green function for the process can be written (Lande et al. 2003) as

$$G(x, x_0) = \begin{cases} 2m(x)S(x) & \text{for } a < x < x_0 \\ 2m(x)S(x_0) & \text{for } a < x_0 < x \end{cases}$$

where a is the extinction barrier and x_0 is the initial state. Writing

$$s(x) = e^{-2 \int_a^x \frac{\mu(z)}{v(z)} dz}$$

the functions $S(x)$ and $m(x)$ are

$$S(x) = \int_a^x s(z) dz$$

and

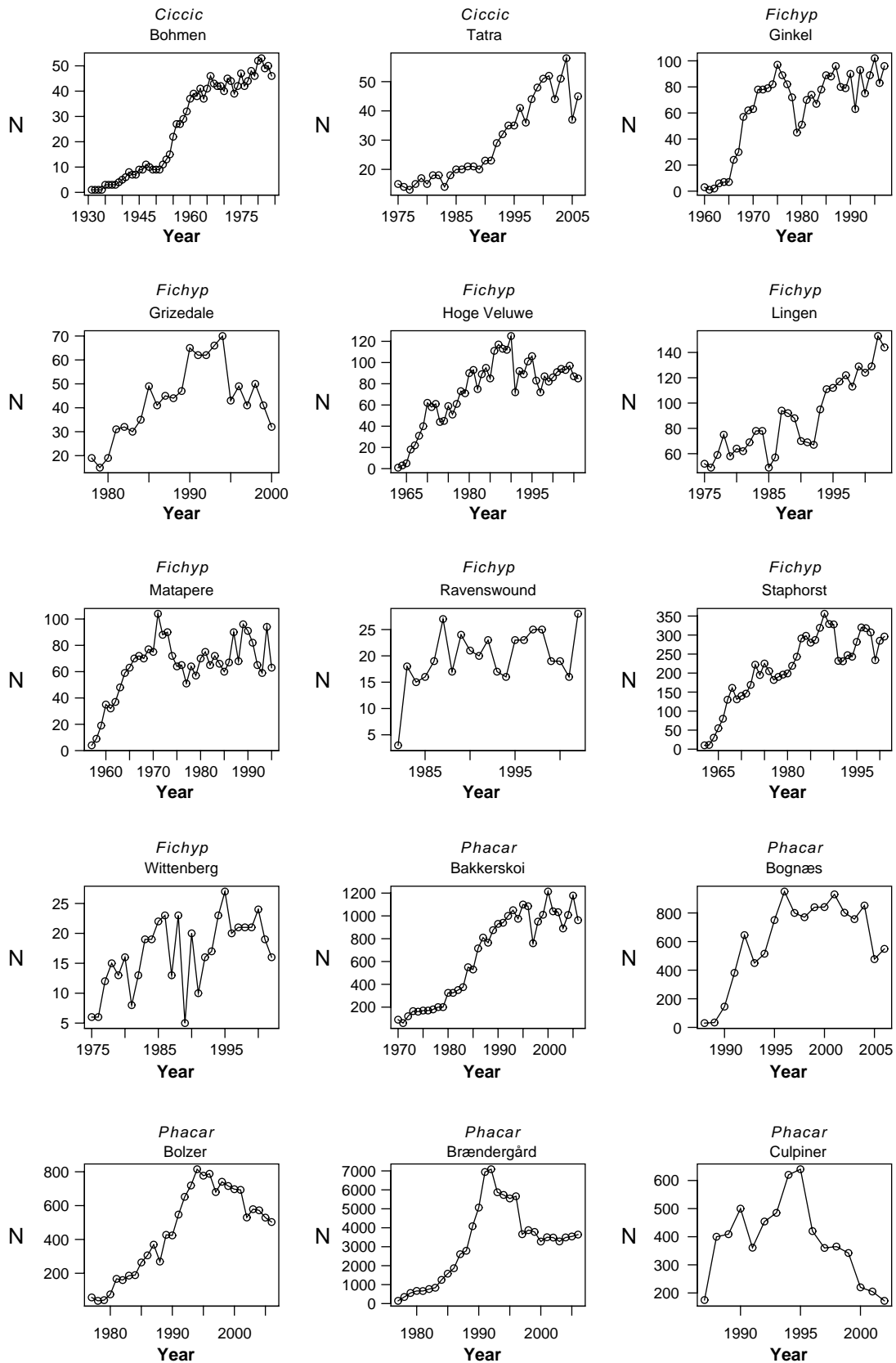
$$m(x) = \frac{1}{v(x)s(x)}.$$

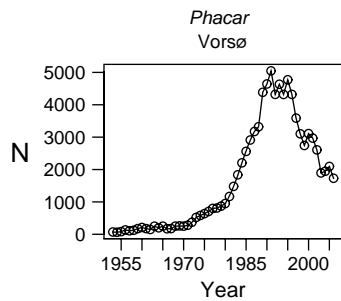
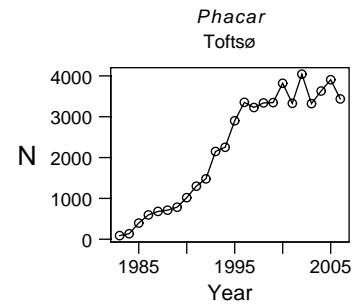
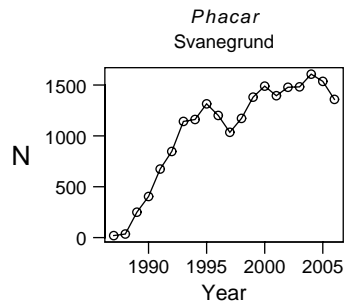
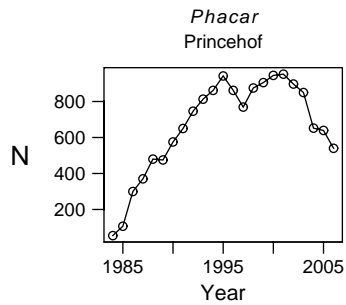
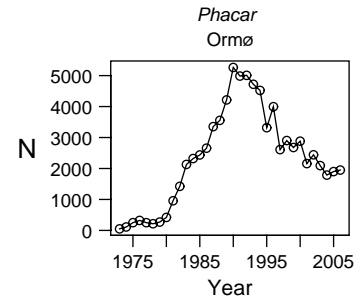
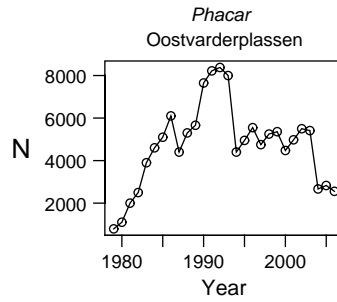
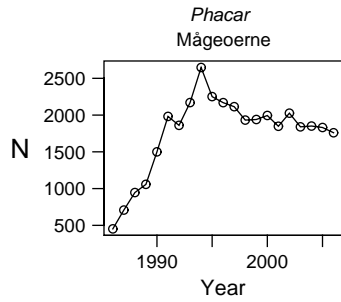
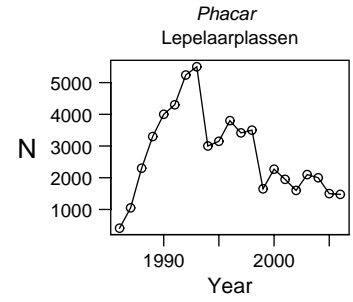
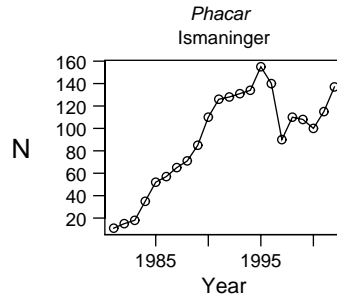
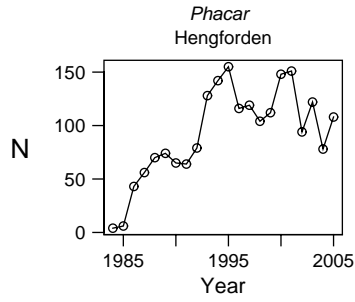
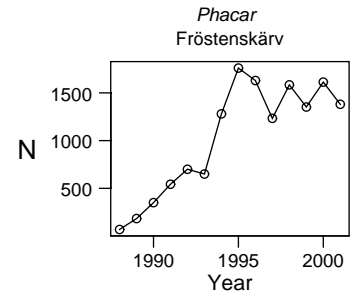
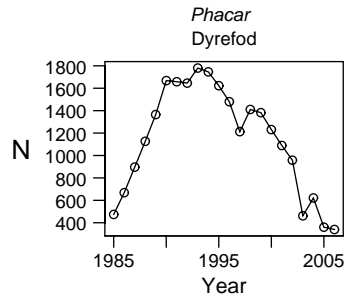
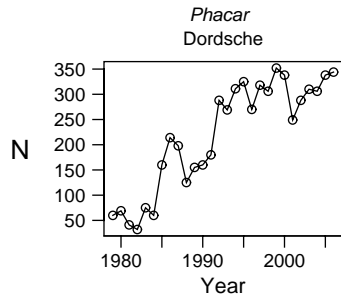
The practical interpretation of the Green function is that $G(x, x + \Delta x)$ represents the expected time the diffusion process is in $(x, x + \Delta x)$ before it finally reaches extinction at $x = a$. This implies that the expected time to extinction is

$$T = \int_a^\infty G(x, x_0) dx.$$

The quasi-stationary distribution represents the relative expected time in intervals $(x, x + \Delta x)$, that is $f(x, x_0) = \frac{G(x, x_0)}{T}$

Appendix 2. Time series included in the analyses.





Appendix 3. The estimates of the parameters of the theta-logistic model for the different populations. θ is the parameter describing the form of the density dependence, r_1 is the specific growth rate at $N = 1$, σ_e^2 is the environmental variance, K is the carrying capacity and σ_N is the standard deviation of the quasi-stationary distribution of population sizes.

Species	Locality	Period	θ	r_1	σ_e^2	K	σ_N
White stork	Böhmen	1930–1984	1.61	0.07	0.030	48	16.72
White stork	Tatra	1974–2006	15.78	0.08	0.015	51	6.11
Pied flycatcher	Ginkel	1959–1997	2.11	0.41	0.147	88	25.79
Pied flycatcher	Grizedale	1977–2000	0.77	0.27	0.038	54	17.41
Pied flycatcher	Hoge Veluwe	1962–2006	0.27	0.94	0.047	92	24.41
Pied flycatcher	Lingen	1974–2003	1.16	0.23	0.049	118	35.88
Pied flycatcher	Matapere	1956–1995	0.44	0.88	0.027	73	14.09
Pied flycatcher	Ravenswound	1981–2002	0.84	1.17	0.081	22	4.86
Pied flycatcher	Staphorst	1961–2001	0.52	0.51	0.030	279	65.16
Pied flycatcher	Wittenberg	1974–2002	0.65	0.94	0.167	19	6.68
Great cormorant	Bakkerskoi	1969–2006	6.06	0.14	0.033	1043	163.06
Great cormorant	Bolzer	1976–2006	1.2	0.32	0.060	704	189.54
Great cormorant	Bognæs	1987–2006	1.36	0.80	0.091	794	159.36
Great cormorant	Brændergård	1976–2006	0.62	0.48	0.034	4824	1120.32
Great cormorant	Culpiner	1986–2002	0.98	0.51	0.107	456	141.23
Great cormorant	Dordsche	1978–2006	0.42	0.44	0.096	371	163.26
Great cormorant	Dyrefod	1984–2006	1.06	0.36	0.093	1483	485.26
Great cormorant	Fröstenskärv	1987–2001	0.21	1.74	0.038	1470	293.28
Great cormorant	Hengforden	1983–2005	0.56	0.67	0.184	136	58.61
Great cormorant	Ismaninger	1980–2006	1.07	0.42	0.018	122	18.07
Great cormorant	Lepelaarpl	1985–2006	0.31	1.09	0.228	4136	2009.02
Great cormorant	Mågeørne	1985–2006	0.21	2.00	0.022	2010	289.25
Great cormorant	Oostvardepl	1978–2006	1.06	0.63	0.081	5843	1394.52
Great cormorant	Ormø	1972–2006	0.55	0.44	0.056	3688	1184.08
Great cormorant	Princehof	1983–2006	1.45	0.70	0.059	836	140.97
Great cormorant	Svanegrund	1986–2006	1.77	0.20	0.065	1474	430.16
Great cormorant	Toftsø	1982–2006	0.46	1.07	0.133	3527	1209.45
Great cormorant	Vorsø	1952–2006	1.46	0.12	0.034	3977	1181.23