The response of the woodpigeon (*Columba palumbus*) to relaxation of intraspecific competition: A hybrid modelling approach

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ABSTRACT

The recent rapid growth of the woodpigeon population in the British Isles is a cause for concern for environmental managers. It is unclear what has driven their increase in abundance. Using a mathematical model, we explored two possible mechanisms, reduced intraspecific competition for food and increased reproductive success. We developed an age-structured hybrid model consisting of a system of ordinary differential equations that describes density-dependent mortality and a discrete component, which represents the birth-pulse. We investigated equilibrium population dynamics using our model. The two hypotheses predict contrasting population age profiles at equilibrium. We adapted the model to examine the impacts of control measures. We showed that an annual shooting season that follows the period of density-dependent mortality is the most effective control strategy because it simultaneously removes adult and juvenile woodpigeons. The model is a first step towards understanding the processes that influence the dynamics of woodpigeon populations.

1. Introduction

The woodpigeon, *Columba palumbus*, is a multi-brooded herbivore and therefore likely to benefit from global warming and climate change (Jiguet et al., 2007). It is a well-known agricultural pest, which has appeared to have benefitted from changing agricultural practices, particularly in Britain (Inglis et al., 1990). The pest status of woodpigeon led to a detailed research programme into its biology and management in the 1960s (Murton, 1958, 1961, 1965, 1971; Murton et al., 1964, 1966, 1974; Murton and Isaacson, 1964). During this period, the population was reasonably stable, although large fluctuations in numbers occurred within years, i.e., the population increased rapidly over the breeding season and then declined drastically during the winter months so that the total observed each year remained relatively constant. The amount of grain available determined numbers that survived after the breeding season until the period when woodpigeons switched to their clover food supply in December. Juveniles required grain to aid their development in the months after fledging whereas adults could more readily consume less nutritious clover leaves. The timing of the minimum in woodpigeon numbers occurred in February and March,

i.e., the period of least plentiful clover stocks. When food supplies became depleted, the effects of intraspecific competition intensified and were density-dependent (Murton et al., 1966, 1971), i.e., if the size of a flock was high relative to the quantity of food available, then mortality was higher. Mortality principally affected subordinate individuals and juveniles. It is important to note that during the period of Murton's studies, winters were noticeably longer and colder than in the period 1976–2000 (Houghton et al., 2001).

The recent increase in the woodpigeon population of the British Isles (Baillie et al., 2009; Crowe et al., 2010) has become a cause for concern for agriculture (Tayleur, 2008), but also for aviation safety, because the species is increasingly involved in birdstrikes (Kelly et al., unpublished data). The exact reasons for this increase are unknown (Saari, 1997). One hypothesis is that climate change has induced the earlier onset of the growing season (Carroll et al., 2009; Donnelly et al., 2009; Menzel et al., 2006; Møller et al., 2010). Since the food supply does not fluctuate to the same extent as it did in the 1960s, food is more readily available to woodpigeons throughout the year. Consequently, woodpigeon numbers are no longer regulated by natural fluctuations of the food supply, as they were before the onset of climate change. Therefore, decreased intraspecific competition for food during winter may be the mechanism behind the sustained increase. Alternatively, woodpigeons may be particularly adapted to benefit from climate change because they are multi-brooded; the ability to produce multiple broods per year,

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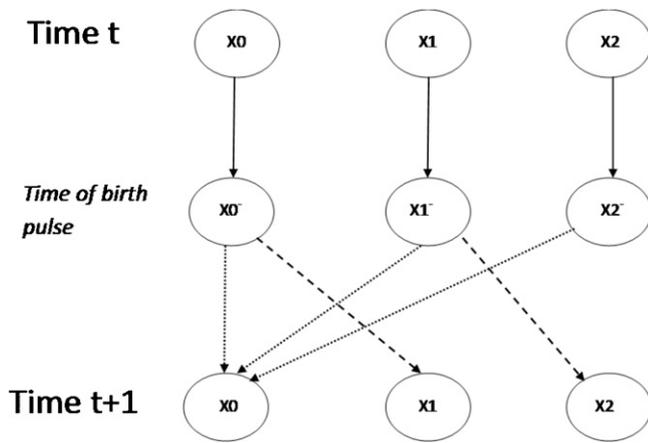
Fig. 1. At time t, the number of fledglings, 1-year olds and 2-year olds are censused. Some of these birds may die before they can reproduce. The number of birds from each age class that survive during the year to reproduce are indicated by x_i^-, $i = 0$, 1, 2. All age classes reproduce just before they turn $i+1$-year-old (indicated by the dotted arrows from x_i^- to x_i). After the birth pulse, the dashed arrows from x_0^- to x_1 and x_1^- to x_2 indicate that woodpigeons about to turn 1- and 2-year-old respectively survive to be counted at time $t+1$. Pigeons about to turn 3 years old, indicated by x_2^-, do not survive to be counted at the next population census. These assumptions are incorporated into the Leslie matrix model and the discrete component of the hybrid model.

coupled with earlier availability of food resources, is known to lead to increases in population size (Jiguet et al., 2007; Møller et al., 2010).

To explore these hypotheses, we developed a hybrid dynamical model of the baseline 1960s scenario of a stable population controlled by the density-dependent effects of intraspecific competition. Hybrid models, or semi-discrete models, have recently gained much attention in ecological modelling (Mailleret and Lemesle, 2009) and have been used to model consumer-resource dynamics (Geritz and Kisdi, 2004; Pachepsky et al., 2008), predator-prey and host-parasitoid interactions (Ives et al., 2000; Singh and Nisbet, 2007) and the effects of harvest (Kokko and Lindström, 1998). Here, we present a novel method for determining the unknown parameters of the hybrid model from the stable age distribution of a Leslie matrix model, which was parameterised using data from Murton's work. Using the hybrid model, we investigate the effects of increased fecundity and decreased intraspecific competition for food on the stable 1960s population. We show that, when considered in isolation, the number of successfully fledged daughters per female per year has a more dramatic impact on long-term population dynamics than the intensity of density-dependent mortality. We also compare different control strategies using our model. We show that an annual harvest season that follows the period of density-dependent mortality is an effective mitigation strategy.

2. Methods

2.1. Leslie matrix projection model

The woodpigeon life cycle is described in Fig. 1. Denoting by $\mathbf{x}_t$ the population vector at time t, the Leslie matrix model,

$$\mathbf{x_{t+1}} = \mathbf{L}\mathbf{x_t}, \tag{1}$$

consists of a standard post-birth-pulse matrix, which is given by

$$\mathbf{L} = \begin{bmatrix} \alpha\beta_0 & \alpha\beta_1 & \alpha\beta_1 \\ \beta_0 & 0 & 0 \\ 0 & \beta_1 & 0 \end{bmatrix}. \tag{2}$$

The definitions of the parameters are given in Table 1. Following the classical assumptions of Leslie matrix models (Leslie, 1945; Caswell, 2001), we consider a female woodpigeon population that consists of three distinct age classes: fledglings, 1-year olds and 2-year olds. Fledglings are juveniles that have hatched successfully and have just departed from the nest. We assume fledglings have not completed the post-juvenile moult, i.e., they have not attained the white neck "bars" that typify adult plumage. Through his analysis of ringing returns, Murton found that the average age of adult recoveries, after omitting juvenile recoveries, was 38 months (Murton, 1961). When juveniles were included, the average age was 24.8 months. In the 1960s, there was a single breeding season (Murton and Isaacson, 1964). Therefore, we assume that there is a single annual birth pulse and the annual population census takes place immediately after the birth pulse. All female fledglings enter the population on the 1st of October each year, i.e., after the breeding season, because the woodpigeon population is at its height at the end of September (Lack, 1966). Juveniles are not considered mature until they are a year old (Murton, 1965).

We assume that the average number of female fledglings produced per female woodpigeon per year (α) does not vary with age. We assume that the annual survival probability of adult woodpigeons (β_1) remains constant after the first year because death is usually accidental and woodpigeons rarely die as a consequence of old age (Murton, 1966). The probability that a 2-year-old will reach the age of three years is zero because we assume that 2-year olds die at the very instant before the population census as a result of old age. However, 2-year olds may contribute to the population through reproduction prior to their death. The juveniles that have survived to become 1-year-old may also contribute to the population.

2.2. Hybrid model

The Leslie matrix model (1) does not keep track of woodpigeon population dynamics during winter. A hybrid system is more suitable to model population dynamics that are continuous most of the time but experience an abrupt change (Mailleret and Lemesle, 2009). The hybrid system we develop here consists of a continuous-time system with a discrete component representing the abrupt change, i.e., the birth pulse in this case. Unlike the Leslie matrix model, a hybrid system allows the explicit consideration of the density-dependent processes driving the rate of change of the woodpigeon population between these abrupt changes. The hybrid model that we develop has a positive equilibrium; if the parameters of the hybrid model are perturbed, we may locate the new equilibrium state corresponding to the change in parameters. In contrast, if the parameters of the Leslie matrix model are perturbed, e.g., by increasing fecundity or survival probabilities, the model will predict asymptotic growth at a fixed rate (Caswell, 2001).

The hybrid model keeps track of fledglings, pigeons aged between one and two years and pigeons aged between two and three years. We denote by $x_0(t)$ the juvenile population aged between zero and one years, $x_1(t)$ the population aged between one and two years and $x_2(t)$ the population aged between two and three years at time t. Time is assumed to be a continuous variable and thus, we follow each member of each age class continuously throughout their lives. Fledglings leave the nest at the same time each year at time $t = 1, 2, 3, \ldots$ and are kept track of throughout the year. Just before turning one years old, they may reproduce, provided they are still alive. In addition, those that are about to turn 2- and 3-year-old may contribute to the number of fledglings counted at the next time step. As in the Leslie matrix model, we denote by α the expected number of female fledglings that each female in age class i at time t will produce aged $i+1$ at time $t+1$, $i = 0, 1, 2$. We denote the time that the members of each age class i reproduce by

Table 1
Typical parameter values.

Parameter	Values	Period of study	Source
Mean number of fledged females per female[a]	1.05	1955 and 1957	Murton (1958)
	1.445	1959–1962	Murton and Isaacson (1964)[b]
	0.905	1971–1983	Inglis et al. (1994) [b]
Annual adult survival probability	63%	Prior to 1950	Murton (1961)
	65%	1950–1958	Murton (1961)
	70%	1959–1962	Murton et al. (1964)[b]
	64.4%	1911–1952	Murton (1966)
	59.5%	1952–1964	Murton (1966)
	64.38% (Mean)		
Annual juvenile survival probability	21%	1959–1962	Murton et al. (1964)[b]
	34%	1909–1958	Murton (1965)
	22–36%	1911–1965	Murton (1966)

[a] These figures must be multiplied by two to obtain the mean number of fledged young per pair.
[b] These studies were conducted in Carlton wood, Suffolk, England. All other studies were conducted throughout England.

$t+1^-$, i.e., just prior to the population census. We thus denote by $x_i(t+1^-)$ the number of birds from each age class that survive during the year to reproduce at the end of the year, $i = 0, 1, 2$. Then the reproduction contribution of each age class at time $t+1$ is given by

$$x_0(t+1) = \alpha x_0(t+1^-) + \alpha x_1(t+1^-) + \alpha x_2(t+1^-), \tag{3}$$

where $x_0(t+1)$ denotes the fledgling population at time $t+1$.

The Leslie matrix model (1) assumes that the numbers of females at time $t+1$ that are aged i at time t are determined by the annual survival probabilities β_0 and β_1. A hybrid model allows one to investigate the effect of processes that cause mortality. The flexibility of the hybrid framework allows us to incorporate a density-dependent mortality process, i.e., as numbers increase, the respective survival rates are assumed to decline (Lebreton, 2009). Our hybrid model will assume that competition for resources is the main process that affects the number of females that survive to the next census and is, therefore, the main cause of decline of the numbers in each age class. We develop a nonlinear system of ordinary differential equations, incorporating Eq. (3) representing the population census, to model the effect of intra- and inter-age competition among the three age classes.

In the 1960s, the starvation of juvenile woodpigeon was the main cause of the population decline in winter. The elimination of juveniles was exacerbated by their subtle interactions with dominant adult individuals (Murton et al., 1964, 1966, 1971; Newton, 1998). Superior members of the flock populated its centre and inhibited submissive individuals through "subtle supplanting attacks" (Murton et al., 1966). In contrast, inexperienced birds occupied the front of the flock, were uneasy in their feeding behaviour and endeavoured to avoid conflict with dominants. Juveniles were also less efficient at feeding than adults and were less effective at obtaining adequate food supplies, especially when resources were low. Therefore, it is natural to assume that the rate of decline of juveniles, x_0, will increase as the total flock-size increases. We assume that the greater the number of birds in age class j, the greater the number of direct or indirect competitive interactions that a bird of type i will have, and therefore, the greater the degree of inhibition a pigeon aged i will suffer.

Let $z(t)$ be the total woodpigeon population at time t, i.e., $z(t) = x_0(t) + x_1(t) + x_2(t)$. Assuming that woodpigeon mortality is density-dependent, the rate of change of the entire woodpigeon population during the winter months may be given by the following differential equation,

$$\frac{dz}{dt} = f(z)z, \tag{4}$$

where $f(z)$ is the per-capita mortality rate. If mortality is density-dependent, then $f(z)$ cannot be a constant function. Typically,

$f(z) = -\tilde{k}z$, where $\tilde{k}$ is a positive constant of proportionality that represents the per-capita decline of the population per unit time. Our age-structured model assumes that the rate of change of the total woodpigeon population obeys Eq. (4). We assume that pigeons aged between zero and one years, one and two years and two and three years may all compete with each other during the year, leading to nonlinear declines in the numbers that comprise each age class. Therefore, we require a specific equation for each age class to describe its rate of change. We assume that the rate of change of each age class x_i is a function of all age classes, i.e., we have

$$\frac{dx_i}{dt} = f_i(x_0, x_1, x_2)x_i,$$

where $f_i(x_0, x_1, x_2)$ is the per-capita mortality rate of x_i, $i = 0, 1, 2$. We assume that each f_i is a linear combination of x_0, x_1 and x_2, i.e., the per-capita mortality rate of each age class is proportional to some combination of the total woodpigeon population. However, different age classes die at different rates because we assume that individuals in different age classes are not competitively equal. We assume numbers of the juvenile age class x_0 will decline more rapidly than the adult age classes, x_1 and x_2, because juveniles are frequently out-competed by adults for food. Furthermore, we assume that both inter-age competition between birds aged i and j and intra-age competition between pigeons in the same age class occur simultaneously.

The following system of ordinary differential equations describes the rate of change of each age class during the year, i.e., between the time of the introduction of fledglings (at time t) described by Eq. (3) and the next birth pulse that occurs prior to the population census at time $t+1$,

$$\frac{dx_0}{dt} = -k(c_{00}x_0 + c_{01}x_1 + c_{02}x_2)x_0,$$

$$\frac{dx_1}{dt} = -k(c_{10}x_0 + c_{11}x_1 + c_{12}x_2)x_1, \tag{5}$$

$$\frac{dx_2}{dt} = -k(c_{20}x_0 + c_{21}x_1 + c_{22}x_2)x_2.$$

The k parameter is the positive constant of proportionality that represents the per-capita mortality rate of the entire pigeon population, as a result of competition and the c_{ij} parameters are positive constants. The competitive ability of an avian species manifests in a variety of ways, e.g., brood-size, rate of success in aggressive encounters, feeding efficiency or social status (Newton, 1998). For example, the feeding efficiency of a woodpigeon aged i in the presence of a woodpigeon aged j may be one such metric that could be employed to measure competitive ability of woodpigeons in different age classes (Murton et al., 1966). Denoting the competitive

ability of a bird in age class i by c_i, $i = 0, 1, 2$, we define the following nondimensional parameters, which we call the competition coefficients,

$$c_{ij} = \frac{\text{Competitive ability of bird } j}{\text{Combined competitive abilities of birds } i \text{ and } j} = \frac{c_j}{c_i + c_j}. \tag{6}$$

The competition coefficients may be interpreted as the probability of an interaction between a pigeon aged i and a pigeon aged j not leading to a 'successful' outcome for the pigeon aged i, i.e., the probability of interactions with the x_j population contributing to the decline of the x_i population. A negative interaction for an i-year-old might include starvation as a result of the presence of a j-year-old. We assume that the probability of a negative encounter with a pigeon in age class j for a bird in age class i depends only on age and not on size, social status, genetics, etc. By definition of the competition coefficients (6), $c_{ij} + c_{ji} = 1$, i.e., the probability that either pigeon will succeed in a competitive encounter is one. Therefore, we assume $c_{ji} = 1 - c_{ij}$. Note that we assume when food is scarce, there may be only one 'winner' of a competitive interaction. However, if there is plenty of food available, it is easy to imagine that this condition may be relaxed, i.e., there is a probability that the interaction of two birds in different age classes will not impact negatively on their respective population sizes.

Moreover, since $c_{ij} + c_{ji} = 1$ and choosing $\tilde{k} = k/2$, we may write system (5) as,

$$\frac{dz}{dt} = -\frac{k}{2}z^2, \tag{7}$$

i.e., the rate of change of the woodpigeon population $z = x_0 + x_1 + x_2$ may be described in terms of one differential equation. The solution of Eq. (7) may be found explicitly, see Appendix A.

To ensure that the hybrid model and the Leslie matrix model correspond exactly, we cannot assume that pigeons aged between 2 and 3 can survive to be counted at the population census. In addition, juvenile and 1-year-old pigeons must move into the next age class at time $t + 1$. Therefore, denoting the pigeons that survive the effects of competition exactly prior to the next population census by $x_i(t + 1^-)$, $i = 0, 1$, the discrete survival component of the hybrid system is

$$x_1(t + 1) = x_0(t + 1^-),$$
$$x_2(t + 1) = x_1(t + 1^-). \tag{8}$$

By solving the hybrid system numerically, we may explore the dynamics of the age-structured woodpigeon population, using system (5) to track continuous-time dynamics during the year and then updating the populations each year according to Eqs. (3) and (8). Note that the hybrid model processes are also described by Fig. 1.

2.3. The hybrid system in terms of two parameters

Using the definition of the competition coefficients (6), we may reduce the number of unknown parameters of the system (5) from nine to two. It is convenient that $c_{ij} + c_{ji} = 1$ because we wish to keep the number of unknown parameters of the hybrid system small in order to identify them from the stationary age distribution vector of the Leslie matrix model (1). We will describe this procedure in detail in Section 4.2. Note that

$$c_{ii} = \frac{c_i}{c_i + c_i} = \frac{1}{2},$$

i.e., we assume that there is an equal probability of a successful outcome in a competitive encounter for pigeons that are in the same age class i.

Table 2
The inter-age competition coefficients c_{ij}, $i \neq j$, are expressed in terms of the relative competitive ability of 1-year olds to fledglings, $A = c_1/c_0$ and 2-year olds to fledglings, $B = c_2/c_0$. The numerical values for the relative competitive ability and competition coefficients were found using the optimization routine in *Mathematica*. These values were used to compute the stable one-periodic solution corresponding to the post-birth-pulse population at equilibrium.

Parameter	Symbol	Value
Fecundity	α	1.435
Relative competitive ability of 1-year-old to juvenile	c_1/c_0 (A)	8.37378
Relative competitive ability of 2-year-old to juvenile	c_2/c_0 (B)	8.37182
Inter-age competition coefficients	$c_{01} = A/(A + 1)$	0.893319
	$c_{02} = B/(B + 1)$	0.893297
	$c_{10} = 1/(A + 1)$	0.106681
	$c_{12} = B/(A + B)$	0.499941
	$c_{20} = 1/(B + 1)$	0.106703
	$c_{21} = A/(A + B)$	0.500059
Intra-age competition coefficients	c_{ii}, $i = 0, 1, 2$	0.5

Secondly, we may define the hybrid system in terms of c_1/c_0 and c_2/c_0, i.e., the ratios of the competitive ability of pigeons aged between one- and 2-year olds and the competitive ability of pigeons aged between 2- and 3-year olds to juveniles' competitive ability, respectively. We will refer to these parameters as the *relative competitive ability* of 1-year olds and 2-year olds to juveniles, respectively. All the inter-age competition coefficients c_{ij} may be described in terms of the relative competitive ability parameters, see Table 2. Therefore, the relative competitive ability parameters are the only unknown quantities to be determined from the stationary age distribution of the Leslie matrix model. In addition, we assume that adults have inherently more competitive ability compared to juveniles, i.e., c_1/c_0, $c_2/c_0 > 1$. It is reasonable for juveniles to have less ability to compete effectively than adults because inexperienced birds have been observed to be notably uneasy while feeding compared to adults and tended to avoid potential conflict situations (Murton et al., 1966). Furthermore, adults have been observed to have a greater feeding rate than juveniles during periods of low food supply (Murton et al., 1966; Newton, 1998). These factors may have led to the elimination of juveniles through starvation or emigration (Murton et al., 1964).

3. Theory

3.1. Relationship arising from the stationary age distribution

The population determined by the Leslie matrix model (1) will grow or decay at a rate λ (the dominant eigenvalue of the matrix $\mathbf{L}$). Furthermore, the population vector asymptotically becomes proportional to the associated eigenvector $\mathbf{v}$, which is known as the stable age distribution. If $\lambda = 1$, the population will stabilize to an equilibrium, depending on the initial condition. There are multiple equilibria, which form a straight line in the phase space. We refer to the line of equilibria corresponding to $\lambda = 1$ as the stationary age distribution.

If $\mathbf{L}$ is a Leslie matrix, then $\mathbf{L}\mathbf{v} = \lambda\mathbf{v}$. If $\mathbf{v} = (v_0, v_1, v_2)$ and $\lambda = 1$, the following relationships must hold for the Leslie matrix (2),

$$\alpha(\beta_0 v_0 + \beta_1(v_1 + v_2)) = v_0,$$
$$\beta_0 v_0 = v_1, \tag{9}$$
$$\beta_1 v_1 = v_2.$$
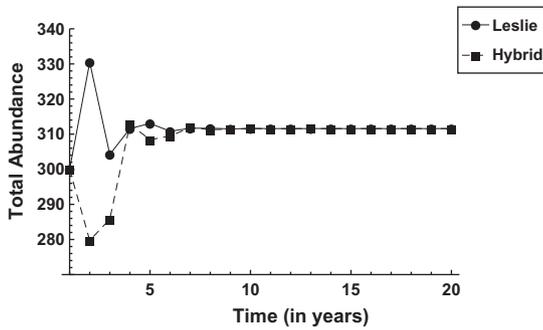
Fig. 2. A typical solution of the hybrid system computed from the parameter values described in Table 2 and a solution of the Leslie matrix model, $\alpha = 1.435$, $\beta_0 = 0.34$, $\beta_1 = 0.64$, starting from the initial condition (100, 100, 100). The short-term dynamics are somewhat different but the solutions tend to the same equilibrium in the long-term, provided k is chosen according to Eq. (A.5). Here, $k = 0.00793$ per pigeon per year ensures coalescence of the two solutions.

The stationary age distribution may thus be described by the following relations (Caswell, 2001),

$$v_0 \beta_0 = v_1,$$
$$v_0 \beta_0 \beta_1 = v_2. \tag{10}$$

Furthermore, from Eq. (9), we obtain an expression for the expected number of fledglings per female α,

$$\alpha = \frac{1}{\beta_0(1 + \beta_1 + \beta_1^2)}. \tag{11}$$

Note that if $\alpha > 1/\beta_0(1 + \beta_1 + \beta_1^2)$ then the population will grow but if $\alpha < 1/\beta_0(1 + \beta_1 + \beta_1^2)$, the population will decay. Under this formulation, α is bounded below by 1/3 since β_0 and β_1 are survival probabilities and cannot be greater than one.

3.2. Scaling of the hybrid system

We multiplied the competition coefficients of the system (5) by a positive constant k to scale the hybrid system appropriately. The constant k is an additional parameter that we may use to adjust the total population of pigeons to a given number, for example, a population with an age structure that is proportional to the stationary age distribution of the Leslie matrix model (1), given a particular set of parameters and an initial condition. For a given set of parameters α, β_0 and β_1, the Leslie matrix model converges to a line of equilibria corresponding to different initial conditions and the line of equilibria is spanned by the positive eigenvector **v** of the Leslie matrix. In contrast, the hybrid model converges to an isolated positive equilibrium for a given set of parameters α, c_1/c_0 and c_2/c_0. Therefore, the parameter k enables us to adjust the equilibrium of the hybrid model such that it will coincide with a specific equilibrium of the Leslie matrix model that corresponds to a particular initial condition. This may be done very simply as the equilibrium of the hybrid system, which we denote by z_0, scales linearly with k, i.e., $z_0 = (x_0^*, x_1^*, x_2^*) = (\tilde{x_0}^*/k, \tilde{x_1}^*/k, \tilde{x_2}^*/k)$.

Using the parameters in Table 2 and an appropriate k determined using the procedure described in Appendix A, it is possible to obtain complete agreement between a given equilibrium of the Leslie matrix model and the equilibrium of the hybrid model (Fig. 2). Section 4 describes how the parameters in Table 2 were obtained.

Finally, it is useful to obtain the characteristic time for the density-dependent mortality process, e.g., one may ask, how long does it take for the population to half in size in the time between birth pulses? If we replace $z(t)$ with $z(0)/2$ in Eq. (A.1), we obtain

$t = 2/kz_0$. The characteristic time for system (5) is given in terms of k and a characteristic population size $z(0)$,

$$T_c = \frac{1}{kz(0)}, \tag{12}$$

and we would expect it to be of the order of one year. At equilibrium, T_c may be calculated using expression (A.4) for k. Assuming that the population was at equilibrium in the 1960s and setting $\beta_0 = 0.34$ and $\beta_1 = 0.64$, which are reasonable values for the annual survival probabilities in the 1960s (see Table 1), we obtain a characteristic time of approximately 0.405 years. Indeed, the 1960s population would half in size in 0.81 years, which is reasonable because the population experienced dramatic crashes from September to March, i.e., within the first six months following the birth pulse (Murton et al., 1964).

3.3. Asymptotic behaviour of the hybrid system for large α

We establish the asymptotic behaviour of the equilibrium of the hybrid model (i.e., the post-birth-pulse equilibrium population z_0) for large values of the fecundity parameter α, e.g., $\alpha > 3$. Eq. (A.2) gives the total population before the birth pulse, i.e., Eq. (7) brings the equilibrium z_0 population to the equilibrium pre-birth-pulse population z_1 at the end of one year. Eq. (A.2) implies

$$\lim_{z_0 \to \infty} z_1 = \frac{2}{k}, \tag{13}$$

hence, $z_1 = x_0(t+1^-) + x_1(t+1^-) + x_2(t+1^-) < 2/k$ and thus, after the birth pulse,

$$x_0(t+1^-) + x_1(t+1^-) = x_1^* + x_2^* < \frac{2}{k}. \tag{14}$$

Therefore, the sum of the equilibrium populations of 1- and 2-year olds are uniformly bounded for all α. Furthermore,

$$\alpha z_1 < \alpha z_1 + x_1^* + x_2^* = z_0 < \alpha z_1 + z_1, \tag{15}$$

since $x_1^* + x_2^* < z_1$. Substituting Eq. (A.2) for z_1 in expression (15), we obtain

$$\frac{2(\alpha - 1)}{k} < z_0 < \frac{2\alpha}{k}, \tag{16}$$

for all $\alpha > 0$. Therefore, the total population at equilibrium after the birth pulse grows linearly with α between the lines $2(\alpha - 1)/k$ and $2\alpha/k$. The equilibrium fledgling population $x_0^* = z_0 - (x_1^* + x_2^*)$ eventually grows linearly as the fecundity parameter α increases because for large values of α, the vast majority of the population consists of fledglings (see inequality (14)). Following the birth pulse, density-dependence causes the large fledgling population to decrease sharply to a very small number given by $x_0(t+1^-)$. At the next birth pulse, the small number of fledglings that have survived the effects of intraspecific competition turn 1 year olds. Therefore, as $\alpha \to \infty$, the 1- and 2-year-old populations will always be very small after the birth pulse whereas the fledgling population will always be very large.

4. Calculation

4.1. Numerical values for the Leslie matrix model

In the 1960s, the woodpigeon population was stable. If woodpigeon population dynamics can be described by a Leslie matrix, then this scenario corresponds to the matrix (2) having a dominant eigenvalue of one. Therefore, we need to choose biologically reasonable parameters such that the dominant eigenvalue of the matrix (2), is approximately equal to one.

Using Haldane's technique, Murton (1966) calculated an annual adult survival probability of 64% and inferred from this that an

annual juvenile survival probability ranging from 22 to 36% would maintain the population at a stable level. Using a similar argument, he reasoned that the juvenile mortality rate must be approximately 66% in order to balance an adult mortality rate of 36%, assuming that the population remains constant each year (Murton, 1965). Setting $\beta_0 = 0.34$ and $\beta_1 = 0.64$ in Eq. (11), we obtain $\alpha = 1.435$. It is clear from Table 1 that values in the range of 1–1.5 are reasonable values for the expected number of fledged daughters per female per year in the 1960s.

4.2. Correspondence between the Leslie matrix model and the hybrid model

The Leslie matrix model (1), parameterized using the values described above, will project a given woodpigeon population to an equilibrium such that recruitment compensates for mortality. This equilibrium will have a particular stable age structure. In order to obtain numerical values for the competition coefficients of system (5) of the hybrid model, we require that the hybrid model represents a woodpigeon population that undergoes equal mortality and recruitment, similar to the Leslie matrix model. This assumption will ensure that the population described by the hybrid model will remain constant and that its stable age structure will be identical to that of the Leslie matrix model.

We know from Eq. (11) that the expected number of fledged daughters per female per year is 1.435 and thus, we may replace α in the reproduction contribution Eq. (3) of the hybrid model with this value. In order to ensure that the mortality rates of both systems correspond, we must determine the competition coefficients c_{ij} such that the age structure of the equilibrium of the hybrid model is equal to the stationary age distribution of the discrete Leslie matrix model. This is equivalent to saying that the equilibrium of the hybrid system must satisfy the relationship (10) arising from the stationary age distribution, i.e.,

$$\left(\frac{x_1^*}{x_0^*}, \frac{x_2^*}{x_0^*} \right) = \left(\beta_0, \beta_0 \beta_1 \right). \tag{17}$$

Note that relationship (17) is independent of the choice of k. The relative competitive ability parameters c_1/c_0 and c_2/c_0 were found through optimization of relationship (17) using the optimization function in *Mathematica 7.0*, which uses the Nelder-Mead algorithm. Table 2 shows the resulting values of the competition coefficients.

5. Results

5.1. Linear stability analysis

Determining the unknown parameters of the hybrid model from the stable age distribution of the Leslie matrix model enables the numerical exploration of the effect of perturbations to the positive equilibrium. The system has two biologically relevant equilibria, which are the zero equilibrium and the positive equilibrium $z_0 = (x_0^*, x_1^*, x_2^*)$. As the fecundity parameter α is varied, the zero equilibrium and the positive equilibrium meet and exchange stability at $\alpha = 1/3$, i.e., the system undergoes a transcritical bifurcation (Fig. 3(a)). The positive equilibrium changes from stable to unstable at $\alpha = 1/3$. It is noteworthy that the spectral radius of the linearization of the hybrid system at its zero equilibrium (i.e., the supremum among the absolute values of the eigenvalues of the system at the zero equilibrium) becomes greater than one as α increases beyond $1/3$ (Fig. 3(b)). Under our formulation, a value of α less than, or equal to, $1/3$ is not biologically relevant because Eq. (11) assumes that α is a function of the survival probabilities β_0 and β_1. Therefore, the positive equilibrium is locally stable and isolated for biologically
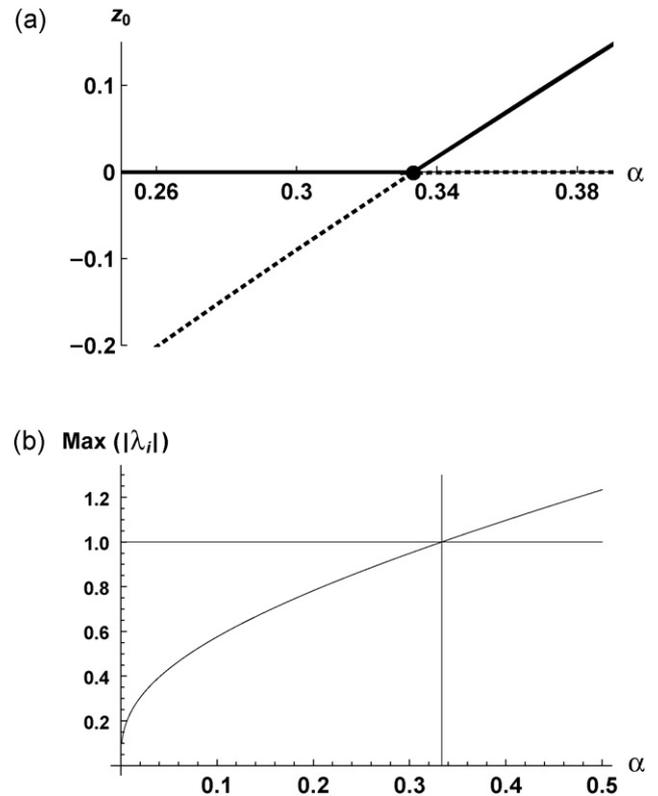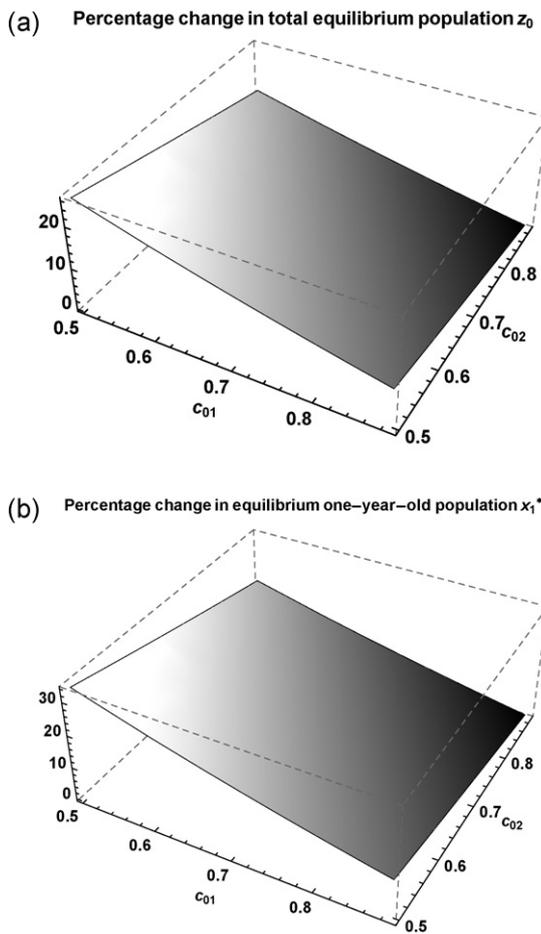

Fig. 3. (a) shows the bifurcation diagram. The thick line represents the stable branch of fixed points (i.e., the total equilibrium population z_0 corresponding to each α value) and the dotted line shows the unstable branch of fixed points. The stable and unstable fixed points coalesce at the bifurcation point $\alpha = 1/3$. As this point, the stable positive equilibrium and the unstable zero equilibrium exchange stability. (b) shows the spectral radius of the linearization of the hybrid system at the zero equilibrium, as a function of α. At $\alpha = 1/3$, the spectral radius equals one. The zero equilibrium is stable to the left of the vertical line at $\alpha = 1/3$ (i.e., in the region where the spectral radius is less than one) and unstable to the right of it.

realistic parameters and the zero equilibrium is unstable. Extensive numerical simulations and a plot of the spectral radius of the linearization of the hybrid system at its positive equilibrium for various values of α showed that no further bifurcations occur for biologically relevant values of α (figures not shown). Furthermore, varying the relative competitive ability parameters do not have a dramatic effect on system dynamics (details not shown). Therefore, the positive equilibrium is locally stable to any perturbation to the parameters, i.e., solutions of the system (3)–(8) are eventually one-periodic. Biologically, this means that the post-birth-pulse population will be the same each year in the long-term, provided the fecundity and relative competitive ability parameters do not change.

### 5.2. Effect of increasing the competitive ability of juveniles on system long-term behaviour

Processes such as reduced intraspecific competition, arising from a greater availability of food supplies, are hypothesised to cause the increase in woodpigeon numbers observed in the past forty years. We investigated the effect of reducing the inhibitive effect of adults on juveniles on long-term population numbers and on the long-term age structure of the population. This involved incrementally reducing the relative competitive ability pairs (c_1/c_0, c_2/c_0) relating to the per-capita mortality rate of the juvenile population only, i.e., only the coefficients c_{01} and c_{02} were decreased. We relaxed the assumptions $c_{01} = 1 - c_{10}$ and $c_{02} = 1 - c_{20}$, i.e., the probabilities of interactions with 1- and 2-year-old adults

(a) **Percentage change in total equilibrium population z_0**

(b) **Percentage change in equilibrium one−year−old population x_1^***

Fig. 4. (a) shows the percentage difference in the total equilibrium population as a function of the inter-age competition coefficients c_{01} and c_{02}. As these parameters decrease, the total population observed in the long-term increases. (b) shows the percentage change in the 1-year-old population at equilibrium for each (c_{01}, c_{02}) pair. In both figures, darker intensities indicate little change relative to the equilibrium of the hybrid model attained using the parameters in Table 2 while the regions of lightest intensity indicate larger increases relative to this equilibrium. For each (c_{01}, c_{02}) pair, the equilibria of the hybrid model were computed using $\alpha = 1.435$, $k = 1$ and initial condition $(1, 1, 1)$. The percentage difference between these equilibria and the equilibrium of the hybrid model computed from the parameters in Table 3 is shown in both figures.

contributing negatively to the juvenile population were no longer strictly related to the probability of adults having negative interactions with juveniles. Juveniles were not assumed to inhibit adults more than before; hence, the values of c_{10} and c_{20} were kept fixed in the equations for the rates of change of one- and 2-year olds in system (5). All other competition coefficients were kept fixed, as in Table 2, for the numerical experiments. Furthermore, the experiments calculate percentage differences between the total equilibrium of the hybrid model z_0 (computed using the parameters in Table 2) and the new equilibrium calculated from each (c_{01}, c_{02}) pair, i.e., $100 \times (z_{new} - z_0)/z_0$. Expressing population changes in proportion to z_0 has the advantage of making the choice of k arbitrary for all experiments.

Fig. 4(a) shows the percentage difference between the total equilibrium of the hybrid model (computed using the parameters in Table 2) and the new equilibrium calculated from each (c_{01}, c_{02}) pair. The grey intensities relate to different percentage increases, e.g., the black region describes the region of parameter space where there is little change in the long-term total population. As the inter-age competition parameters are relaxed, the total population increases by up to 25% relative to the 1960s population, if juveniles

(a) x_1^*/x_0^*

(b) x_2^*/x_1^*
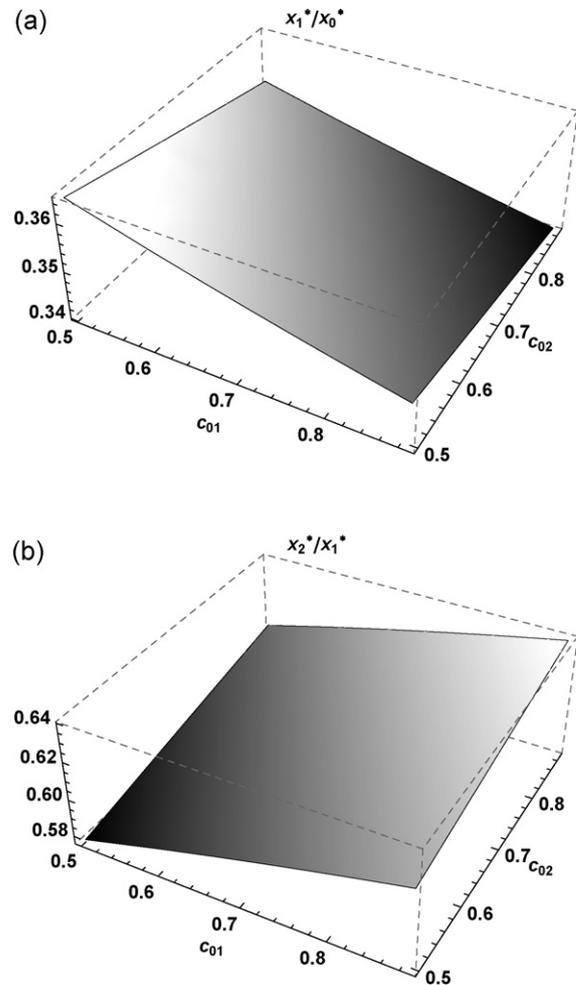
Fig. 5. The number of 1-year olds relative to juveniles at equilibrium increases as c_{01} and c_{02} decrease in (a) and the number of 2-year olds relative to 1-year olds at equilibrium declines as c_{01} and c_{02} decrease in (b). Darker intensities indicate little change relative to the hybrid equilibrium age structure attained using the parameters in Table 2 while the regions of lightest intensity indicate larger increases relative to this structure.

can compete equally with adults. By examining the grey intensities of the three-dimensional figure, it is clear that the total equilibrium population is more sensitive to decreases in c_{01} than c_{02}, i.e., reducing the probability of juveniles having negative interactions with 1-year olds has a greater effect on the long-term population. The same trends are observed in the fledgling, 1-year-old and 2-year-old populations at equilibrium except that the 1-year-old population increases by up to 30%. Only the 1-year-old population is shown (Fig. 4(b)) because the three-dimensional surfaces for the fledgling and 2-year-old populations look very similar to Fig. 4(b).

Fig. 5(a) and (b) shows the corresponding change in the age profile of the population. The number of 1-year olds relative to fledglings increases by 3% and the number of 2-year olds relative to 1-year olds declines by 6%. By relaxing the competitive effects of adults on juveniles, more juveniles survive to become 1-year olds and hence, the number of 1-year olds in the population increases more than any other age group. We therefore expect the number of 1-year olds relative to juveniles at equilibrium to increase as the probability of juveniles having interactions with adults that impact negatively on juvenile numbers is decreased.

5.3. Effect of increasing fecundity on system long-term behaviour

The number of offspring produced by woodpigeons annually may increase as a result of better environmental conditions.
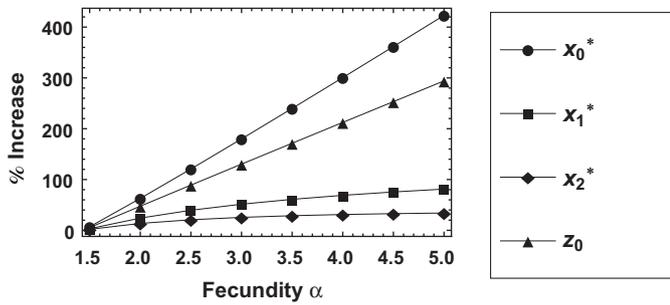
Fig. 6. The equilibrium woodpigeon population becomes overwhelmed with juveniles (x_0^*) as recruitment increases. For each α value, where α is the average number of daughters fledged per female, the equilibrium of the hybrid model (x_0^*, x_1^*, x_2^*) was computed using the competition coefficients in Table 2, $k = 1$ and initial condition $(1, 1, 1)$. The percentage difference between these equilibria and the equilibrium of the hybrid model computed from the parameters in Table 2 is shown here.

To investigate the effect of increased fecundity on long-term population dynamics, we incrementally increased the fecundity parameter α from 1.5 up to 5, i.e., up to five fully fledged daughters per female could be produced during the birth pulse. All of the competition coefficients were kept fixed, as in Table 2, for the numerical experiments. Comparisons between equilibria were standardised by expressing population changes in proportion to the equilibrium of the hybrid model (computed using the parameters in Table 2). We examined the effect of increased fecundity on long-term population numbers and on the long-term age structure of the population.

Fig. 6 shows the percentage difference between the equilibrium of the hybrid model and the new equilibrium calculated from each successive α value. It is clear that the total woodpigeon population dramatically increases, by up to 300% relative to the 1960s population for $\alpha = 5$. The linear relationship between fecundity, the equilibrium total populations and the fledgling equilibrium populations is clear, which confirms the result of the theoretical analysis in Section 3.3. The population becomes overwhelmed with fledglings, in contrast to the scenario when the effects of inter-age competition on 0–1-year olds are relaxed, whereby the fledgling population only increases marginally.

Increased fecundity induces a very different age profile of the population to that predicted by reduced inter-age competition. The age structure ratios x_1^*/x_0^* and x_2^*/x_1^* decline as fecundity increases (Fig. 7(a) and (b)). This is because we consider long-term equilibrium dynamics, and if the population is to remain stable in the long-term, then the rate of recruitment will eventually equal the death rate. Naturally, if recruitment is very high, then mortality will also be high to maintain a stable population. The density-dependent death rate will particularly affect fledglings since their numbers increase most dramatically. The ratio x_1^*/x_0^* increases because $x_1^*/x_0^* = x_0(t+1^-)/x_0^*$; density-dependent mortality intensifies with increasing α, and therefore, the smaller $x_0(t+1^-)$ will be relative to x_0^*.

5.4. Effect of control measures on the 1960s population

The woodpigeon is a pest species and therefore, knowledge of the conditions that would induce an optimum population decline is of interest to environmental managers. Harvest is an obvious strategy for controlling woodpigeon numbers, either on a continuous basis throughout the year or through an annual hunting season. The evidence for the effectiveness of harvest for managing the woodpigeon population is inconclusive, mainly because it is extremely difficult to obtain precise population estimates (Hobson et al., 2009). There is evidence that harvest is effective in managing the influx of migrant woodpigeons from Northern Continental
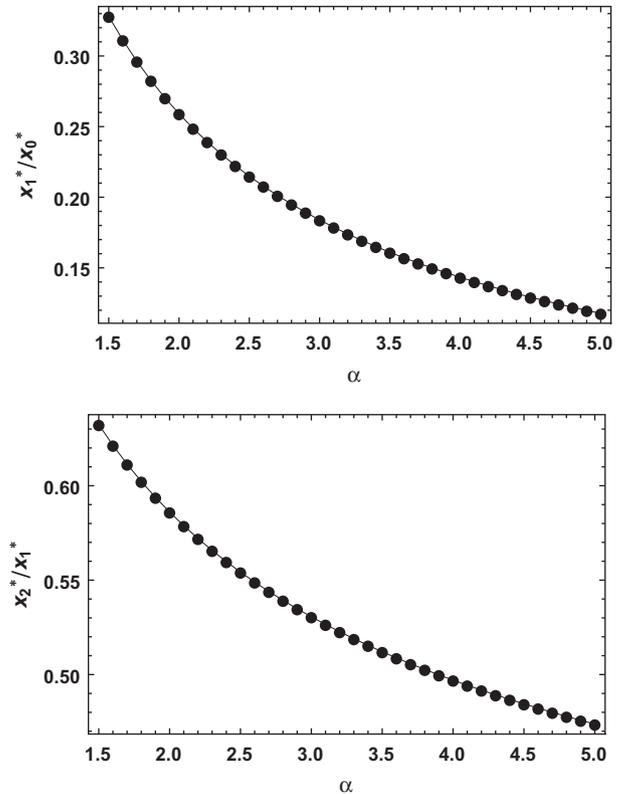
Fig. 7. The number of 1-year olds x_1^* relative to juveniles x_0^* and the number of 2-year olds x_2^* relative to 1-year olds x_1^* at equilibrium both decrease as the fecundity parameter α increases. The vectors (x_0^*, x_1^*, x_2^*) were computed using the competition coefficients in Table 2, $k = 1$ and initial condition $(1, 1, 1)$ for each α value.

European countries into France and the Iberian peninsula (Hobson et al., 2009). It is worth noting that in Continental Europe (excluding the U.K. and Ireland), approximately 9.5 million woodpigeons are taken by hunters (Saari, 1997). However, other empirical studies conducted in Britain have shown that woodpigeon numbers are difficult to control through harvest (Murton et al., 1964, 1974). Managing the woodpigeon population in the British Isles would require achieving additive mortality, a difficult and expensive task (Murton et al., 1974).

Here, we compare the effects of (a) elimination of nestlings by the removal of eggs from the nest and (b) an annual shooting season before the birth pulse. Both control strategies reduce the number of fledglings that enter the population.

To reduce the post-breeding-season population through the removal of eggs, we modify the hybrid model by removing a fraction h of the eggs immediately prior to the population census. Continuous-time dynamics remain the same as in system (5) and the parameter k is fixed at one for all harvest numerical experiments. Each female successfully rears $\alpha(1 - h)$ fledglings and the discrete component of the hybrid system becomes

$$x_0(t + 1) = \tilde{\alpha}[x_0(t + 1^-) + x_1(t + 1^-) + x_2(t + 1^-)],$$
$$x_1(t + 1) = x_0(t + 1^-), \tag{18}$$
$$x_2(t + 1) = x_1(t + 1^-),$$

where $\tilde{\alpha} = \alpha(1 - h)$. This model is exactly the same as the hybrid system without control except the control changes the parameter α to $\tilde{\alpha}$. We denote the positive equilibrium of the egg removal model by $z_0^{h_1}$.

To model the effect of a shooting season, we modify the hybrid model by the removal of a fraction h of the total population immediately prior to the birth-pulse and thus, $1 - h$ of the total population
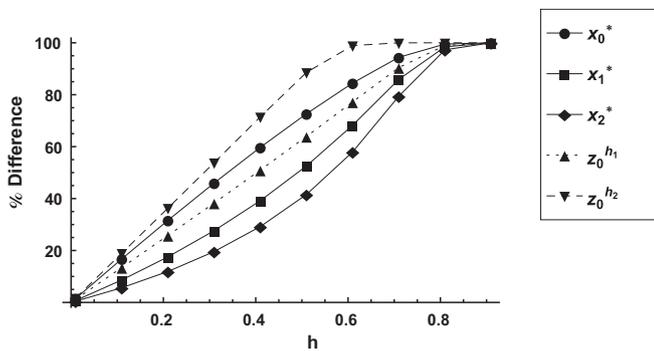
Fig. 8. The dotted and dashed lines in this figure show the percentage declines in the total equilibrium population sizes with controls, $z_0^{h_1}$ and $z_0^{h_2}$, respectively, relative to the hybrid model equilibrium without harvest (z_0), as functions of the fraction of eggs removed and the harvest pressure h, respectively. The percentage declines in the fledgling, 1-year-old and 2-year-old equilibrium populations controlled by egg removal relative to their counterparts without control are also shown. The parameters in Table 2 were used to compute each equilibrium population for each value of h, where h was increased from 0 to 1 in increments of 0.1. The initial condition for each experiment is the equilibrium of the hybrid model without harvest computed from the parameters in Table 2.

remain to breed. Consequently, the discrete component is modified as follows,

$$x_0(t+1) = \tilde{\alpha}[x_0(t+1^-) + x_1(t+1^-) + x_2(t+1^-)],$$
$$x_1(t+1) = (1-h)x_0(t+1^-), \qquad (19)$$
$$x_2(t+1) = (1-h)x_1(t+1^-).$$

The positive equilibrium of the shooting season model is denoted by $z_0^{h_2}$.

Recall that the total equilibrium population of the hybrid model without control, z_0, has the same age structure as the 1960s wood-pigeon population and is computed from the parameters in Table 2. Fig. 8 shows that around 60% of the 1960s population would have to be annually harvested through a shooting season prior to the birth pulse to drive the population to extinction. From this figure, we may read off the harvest pressure h required to induce a particular percentage decline in the post-breeding season population relative to the hybrid equilibrium without control. For example, to induce an eventual 40% decline in the total post-breeding population through shooting, 25% of each age class would have to be removed following the period when the effects of intraspecific competition are at their most severe. For clarity, the percentage declines in the equilibrium fledgling, 1-year-old and 2-year-old populations are not included in the figure because their declines deviate little from the dotted line in Fig. 8. However, we show the percentage declines in the equilibrium fledgling, 1-year-old and 2-year-old populations, in the case where woodpigeons are subjected to control through egg removal. Fig. 8 shows that an eventual 40% decline is induced in the total post-breeding population if 35% of eggs are removed during the birth pulse but a removal of 50% is required to cause the same percentage decline in the 2-year-old population at equilibrium.

From our asymptotic analysis in Section 3.3, we know that if the fecundity parameter α is sufficiently large, then the population size at equilibrium of system (18) will experience a linear decline as the harvest pressure h increases. We may establish this formally for the harvest models (18) and (19). Using the argument outlined in Section 3.3, we obtain the following bounds, for sufficiently large α, for the elimination of eggs equilibrium $z_0^{h_1}$,

$$\frac{2(\tilde{\alpha}-1)}{k} < z_0^{h_1} < \frac{2\tilde{\alpha}}{k}, \qquad (20)$$
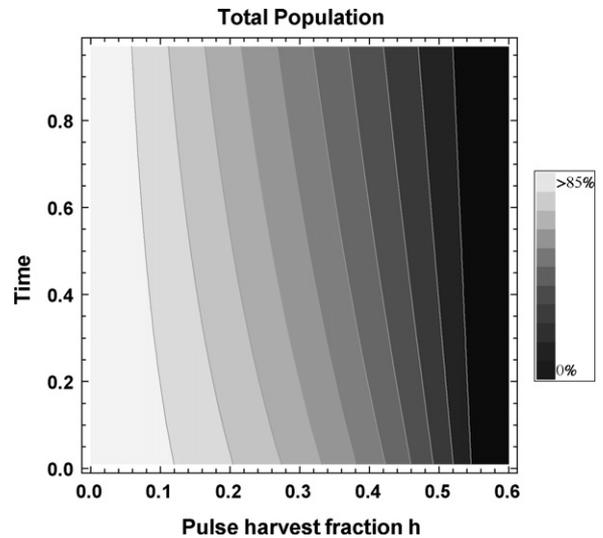
Fig. 9. The percentage differences in the total equilibrium population, compared to the equilibrium of the hybrid model without harvest, as a function of the fraction of the population harvested h and the timing of harvest pulse, e.g., $t = 0.5$ means that the shooting season occurs halfway through the year. Darker intensities indicate large percentage decreases relative to the hybrid equilibrium attained using the parameters in Table 2 while the regions of lightest intensity indicate percentage decreases between 0 and 15% relative to this equilibrium. The parameters in Table 2 were used to compute each harvested equilibrium population and the initial condition for each experiment is the equilibrium of the hybrid model without harvest.

and

$$\frac{2(\tilde{\alpha}-1)}{k} < z_0^{h_2} < \frac{2(\tilde{\alpha}-h)}{k}, \qquad (21)$$

for the shooting season model equilibrium $z_0^{h_2}$. Consequently, as $\alpha \to \infty$, then the ratios $z_0^{h_1}/z_0 \to 1 - h$ and $z_0^{h_2}/z_0 \to 1 - h$. Therefore, the asymptotic behaviour of both harvest models is the same, i.e., if fecundity is sufficiently high, the eradication of eggs is as effective as harvest as a means of population control.

The time that the harvest season occurs within the year is crucial for optimum population control (Kokko and Lindström, 1998; Jonzén and Lundberg, 1999). To investigate the interplay between harvest pressure h and the timing of the shooting season on the equilibrium total population, we plotted the percentage change in the equilibrium total population with shooting as a control compared to the default total population without any control (i.e., the equilibrium of the hybrid model calculated from the parameters in Table 2). It is clear from Fig. 9 that the change in the total population is more sensitive to harvest pressure than the timing of the shooting season but the timing of the harvest becomes more important for heavy harvest pressure. For low harvest pressure, e.g., $h \le 0.1$, the percentage change in the total population is linear as the timing of the harvest pulse becomes later but the percentage change is faster than linear for high harvest pressure, e.g., $h = 0.5$.

6. Discussion

We considered in isolation decreased effects of intraspecific competition and increased fecundity as possible drivers of the observed increase in woodpigeon. Firstly, we reduced the inter-age competition coefficients relating to the per-capita mortality rate of the juvenile population such that adults and juvenile woodpigeons were competitively equal and thereby assuming that more juveniles survived to contribute to the population in subsequent years. We found that decreasing the extent of density-dependent mortality induces a maximal 25% increase in the total population relative to the total equilibrium population of the 1960s. However, it is clear that increasing the average number of female fledglings produced

per female per birth-pulse has a much more dramatic effect on the equilibrium population size than increasing the numbers that survive the density-dependent process of intraspecific competition (cf. Figs. 4(a) and 6). When we increase the reproductive output of females, the post-birth-pulse equilibrium fledgling population increases by 400%. The increase in fledglings is much more dramatic compared to those of the 1- and 2-year-old age classes. In contrast, when we relax the inhibitive effects of adults on juveniles, the 1-year-old population at equilibrium undergoes a larger percentage increase (up to 30%) than the juvenile and 2-year-old age classes. It is useful to note that x_1^*/x_0^* declines as recruitment increases but the ratio increases if competition is relaxed. Such contrasting age distributions offer predictions that may be tested in the field.

If increased fecundity is driving the population increase, our model predicts that density-dependent mortality should also increase to retain equilibrium population dynamics. However, since woodpigeon numbers have been increasing consistently since the mid 1970s (Baillie et al., 2009), it appears that the current population has not yet reached its carrying capacity determined by the environment. Future empirical investigations should focus on exploring the hypothesis that as a result of the lengthening of the growing season, the maximum number of woodpigeons that the environment can hold is increasing slowly year on year, i.e., the woodpigeon population is no longer regulated by seasonal fluctuations in its food supply.

The competition coefficients of system (5) are defined in terms of the relative competitive ability parameters, which are dimensionless. It is difficult to establish empirically how different mechanisms determine the values of the coefficients (Tilman, 1982), or the strengths of interactions in food webs in general (Laska and Wootton, 1998); a variety of approaches may be used (MacArthur, 1970; Case and Gilpin, 1974; Berlow et al., 2004). To estimate the strengths of interaction empirically, explicit modeling assumptions for the competition coefficients, which we have made in this paper, can clarify the most important data for collection (Laska and Wootton, 1998).

However, there are some limitations to our modeling approach. We assume that all fledglings are produced in a single pulse, resulting in a sudden increase in fledglings each year. In the 1960s, there was strong evidence that there was a single breeding season each year (Murton and Isaacson, 1964). Although this may not currently be the case, a single breeding season is reasonable if we assume that a pair may successfully fledge more than one brood during this period (i.e., the fecundity parameter α increases in our model). Furthermore, the survival probability and fecundity estimates that we used to parameterize the Leslie matrix model were annual estimates. If reproductive output has indeed increased, it may be appropriate to model the creation of new fledglings as a series of equally-spaced birth pulses throughout the year. However, an intensive data collection campaign using capture-mark-recapture methods would be required to obtain survival and fecundity estimates over a shorter time frame, e.g., three months or six months, to parameterize a hybrid model with multiple birth pulses.

6.1. The effect of control

We examined the effect of two harvest strategies, a hunting season and removal of eggs, on long-term population dynamics. Both strategies were implemented after density-dependent mortality had taken place. We found that an annual shooting season, which targets all age groups, is more effective than annually removing a proportion of eggs laid during the birth-pulse. Harvest induces a linear decline in all age groups but egg removal causes a slower decline in the 1- and 2-year-old populations at equilibrium, particularly for low values of fecundity (Fig. 8). If fecundity is sufficiently large, the asymptotic analysis in Section 5.4 shows that the effects of both control measures on the total equilibrium population sizes $z_0^{h_1}$ and $z_0^{h_2}$ are similar. However, the corresponding age structures of the equilibrium populations are different. The population controlled by the eradication of eggs will contain more 1- and 2-year olds at equilibrium than the population controlled by shooting. Clearly adult woodpigeons have higher reproductive value than woodpigeons in their first calendar year, which suggests that an annual harvest season would be a more effective control strategy than the removal of eggs from nests.

We found that intense harvest pressure, coupled with a shooting season that follows the period of density-dependent mortality, leads to the most dramatic decline in the woodpigeon population. Fig. 9 confirms that there is a synergistic effect between late timing of the harvest pulse and heavy harvest pressure. This synergistic effect is not observed for low harvest pressure values, as the timing of the harvest pulse occurs at later intervals. The correct timing of the hunting season is very important to avoid compensation for harvest mortality through other means (Kokko and Lindström, 1998; Choisy and Rohani, 2006). If a sequence of density-dependent processes occur after the harvest season, then compensation may occur but it depends on the order of occurrence of these processes (Åström et al., 1996; Boyce et al., 1999; Jonzén and Lundberg, 1999; Ratikainen et al., 2008). The harvest models (18) and (19) do not exhibit compensation; the equilibrium population size always declines as a result of control because the harvest and reproduction processes are linear mappings.

6.2. Conclusions

Although the growth of the woodpigeon population is a serious problem, to our knowledge, no mathematical models have been constructed to clarify the drivers of woodpigeon population dynamics. Using a hybrid model, we showed that increased reproductive output of all age groups during the breeding season is a more likely mechanism behind the sustained increase in the woodpigeon population than a decline in density-dependent mortality. This conclusion is consistent with the empirical findings of Inglis et al. (1994), who conducted a long-term study of the breeding biology of the woodpigeon in Carlton, England. Moreover, our results offer two different predictions for the age structure of the woodpigeon population (cf. Figs. 5(a), (b) and 7(a) and (b)), which could be tested experimentally. Finally, the hybrid model may be readily adapted to describe the population dynamics of other Columbidae species such as the collared dove (*Streptopelia decaocto*), which has rapidly increased in abundance in North America since the 1970s (Hengeveld, 1993).

Appendix A.

The explicit solution of Eq. (7) at time t is

$$z(t) = \frac{2z(0)}{2 + kz(0)t}. \tag{A.1}$$

Hence, at equilibrium, the total population at the end of one year just before the birth pulse, which we denote by z_1, is given by

$$z_1 = \frac{2z_0}{2 + kz_0}. \tag{A.2}$$

Using relationship (10), which describes the stationary age distribution, we may determine the total population at equilibrium prior to the birth pulse,

$$z_1 = \frac{\beta_0(1 + \beta_1 + \beta_1^2)z_0}{1 + \beta_0 + \beta_0\beta_1}. \tag{A.3}$$

Equating expressions (A.2) and (A.3), we obtain the following expression for k in terms of the total population z_0:

$$k = \frac{2(1 - \beta_0\beta_1^2)}{\beta_0(1 + \beta_1 + \beta_1^2)z_0}. \tag{A.4}$$

Eq. (A.4) is used to compute the characteristic time of system (5). Finally, recall that at equilibrium, the age structure of the population is given by the stationary age distribution (10) and therefore, $z_0 = x_0^* + \beta_0 x_0^* + \beta_0\beta_1 x_0^*$. Hence, we obtain the following expression for k in terms of a given fledgling population x_0^*,

$$k = \frac{2(1 - \beta_0\beta_1^2)}{x_0^*\beta_0(1 + \beta_0 + \beta_0\beta_1)(1 + \beta_1 + \beta_1^2)}. \tag{A.5}$$

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