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Modelling populations of long-lived birds of prey for conservation: A study of imperial eagles (*Aquila heliaca*) in Kazakhstan

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ABSTRACT

Eagle populations worldwide are in decline and their demography is generally poorly understood. We use novel sensitivity analysis of stochastic simulation models to analyse the demography of the world's highest-density and longest-studied population of eastern imperial eagles (*Aquila heliaca*), at the Naurzum National Nature Reserve in Kazakhstan. Single variable perturbation (a simple elasticity-type analysis) showed that population growth was most sensitive to changes in adult survival but provided no information on how interactions between parameters may influence population growth. Multiple-variable perturbations (a more comprehensive elasticity-type analysis) suggested that population growth is relatively more sensitive to adult survival than is indicated by single-variable perturbation but also that when adult survival is within a biologically reasonable range, other parameters are still highly consequential to model outputs. For Naurzum's imperial eagles, and for other structured populations of vertebrates, effective conservation and management likely requires an approach that addresses the importance of simultaneous variation in multiple vital rates including both survivorship and reproductive output.

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1. Introduction

Populations of raptors worldwide are in decline and many species are threatened with extinction (IUCN, 2002). Eagles (*Aquila* spp., *Haliaeetus* spp., etc.) as a group are of particular concern, because they have great symbolic significance in many cultures and because of their potential value as indicator or umbrella species (Simberloff, 1998). Furthermore, of approximately 68 eagle species, at least 22 (~33%) are listed as threatened or endangered and in nearly each of those 22 cases population trends are negative (Ferguson-Lees et al., 2001; IUCN, 2002). The cross-species nature of these declines implies that there

may be group-level demographic characteristics of eagles that make them particularly vulnerable to novel stresses in human-altered environments. In cases where declines have been evaluated, their causes are generally similar to those that threaten all large predators (Whitfield et al., 2004a).

Strategies to conserve eagles have primarily involved reintroduction or management to control poisoning, electrocution and shooting (Negro and Ferrer, 1995; Green et al., 1996; Ferrer, 2001; Whitfield et al., 2004b). In nearly all cases, these actions have focussed on small or severely declining populations for which specific threats were readily identified. However, effective conservation calls for proactive, not

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exclusively reactive, management, and proactive management depends on a good understanding of species ecology and accurate identification of the factors that limit populations. In spite of this, eagle ecology is, with a few notable exceptions (golden eagles *Aquila chrysaetos* – Watson, 1997; Spanish imperial eagles *Aquila adalberti* – Ferrer, 2001; white-tailed sea eagles *Haliaeetus albicilla* – Watson et al., 1992; Green et al., 1996; Helander et al., 2003), poorly understood and identifying potentially limiting demographic characteristics for proactive management is difficult. Demographic models built to improve understanding of eagle populations may therefore be an important complement to field studies in the development of conservation strategies for these species. Previous modelling studies of eagle populations have included PVA-type models for white-tailed sea eagles (Green et al., 1996) and Bonelli's eagles (*Hieraetus fasciatus*; Real and Manosa, 1997), territory-based models for Bonelli's eagles (Carrete et al., 2002), and models focussed on specific demographic characteristics of golden eagles (Whitfield et al., 2004b).

The eastern imperial eagle (*Aquila heliaca*) is a rare but widely distributed Palearctic species listed as Vulnerable on the IUCN Red List (VU CI; IUCN, 2002). Historically, populations bred in forest-steppe from western Europe across Eurasia, through Lake Baikal in Russia and even into Pakistan (Galushin and Belik, 1999). This is no longer the case. Eastern imperial eagle populations have declined extensively range-wide and, in the western Palearctic and in eastern Russia, distributions are now highly fragmented (Snow and Perrins, 1998; Galushin and Belik, 1999). Populations in central Russia and Kazakhstan close to the centre of the species distribution seem relatively stable. The status of Imperial Eagle populations appears to be tied closely to anthropogenic impacts on the forest-steppe zone they occupy. Given the apparent variation in population-level trends in different parts of the species range and, in many cases, our inability to understand the reason for these differences, there is a clear need to develop a better understanding of imperial eagle ecology and to identify factors that may limit their demography range-wide.

We used novel sensitivity-type analyses of stochastic simulation models to explore the population dynamics of eastern imperial eagles and to address the broader need for improved understanding of eagle demography. Our model is parameterised with data from >25 years of field study at a nature reserve in Kazakhstan. To evaluate sensitivity of population growth to changes in parameter values, we repeatedly stochastically simulated the dynamics of our age-structured population and, for each group of simulations, randomly picked model parameters from a plausible range of values. This approach distinguishes our modelling exercise from nearly all other previous sensitivity analyses and it permits us to interpret a wider range of possible population trajectories than would be possible otherwise. As a consequence, our models are more robust than they would otherwise be to parameter uncertainty and they provide important and novel insight into the population dynamics of eagles.

The imperial eagle population we modelled has a number of characteristics that make this exercise especially valuable. First, this population is large and, by all external appearances, demographically stable. The vast majority of PVA-type models focus on declining populations whose dynamics are often

different than those of a stable population (Beissinger, 2002). Such models may not help us to understand or to proactively manage apparently stable but vulnerable communities. Second this population is, to our knowledge, the largest and highest-density population of imperial eagles in the world. Its importance for conservation is further enhanced because it occurs within a protected nature reserve. Third, this is the longest continuously monitored eastern imperial eagle population in the world, and some of the model parameters we use are built on over 25 years of field observation. Few demographic models, and none which focus on eagles, are built on such a long-term data-collection effort. Finally, this modelling exercise is valuable because imperial eagles and central Asia are among the least well-known north-temperate eagles and bio-geographic regions, respectively. Models of at-risk or indicator species can be especially valuable at poorly known sites where it is difficult to collect baseline data but where effective conservation still requires understanding of species-specific demographic characteristics.

2. Methods

2.1. Study area

The Naurzum National Nature Reserve in north-central Kazakhstan (51° N, 64° E, near the city of Kostanay) supports a denser population of Imperial Eagles than any other known area in the world. Habitat at the Reserve is ecotonal at both the landscape and political scales; it is here that southern fragments of Siberian forest meet both central Asian steppe and the failed agricultural policies of the former Soviet Union. About one-third of the reserve and much of the surrounding interstitial area is comprised of sandy and mixed soils with feather (*Stipa* spp.) and bunch grasses, or denser clay soils with low sagebrush (*Artemisia* spp.) and other nutrient-rich shrubs and grasses (Formozov, 1966). More than 50% of this steppe has been ploughed; although many of those fields now are fallow, their outlines still are visible in satellite images, even as they are being recolonised by their original floral and faunal communities (T. Katzner personal observations). Interspersed within the steppe matrix are three distinct woodland patches – named Tersec, Sip-sin, and Naurzum – that comprise much of the protected reserve land (Fig. 1). Because eagle ecology is different in the northern and southern sections of the Naurzum forest, we consider data from these regions separately (Katzner et al., 2003). Thus, although there are three forested areas in the reserve, our models use parameters from four ecological regions (Tersec, Sip-sin, north Naurzum, south Naurzum). All forested areas are dominated almost exclusively by pine (*Pinus sylvestris*), birch (*Betula* spp.) and aspen (*Populus* spp.), in single-species (Tersec and Sip-Sin) and mixed-species (Naurzum) stands of various sizes (Fig. 1). The remaining protected area includes dry steppe and numerous permanent and ephemeral lakes with saline or fresh water. These wetlands provide important breeding habitat for a wide variety of passerines and waterbirds, and the permanent ponds serve as critical stopover, molting, and staging areas for many thousands of waterfowl. Greater details on the habitat at the Naurzum Reserve are published elsewhere (Katzner et al., 2003, 2005).

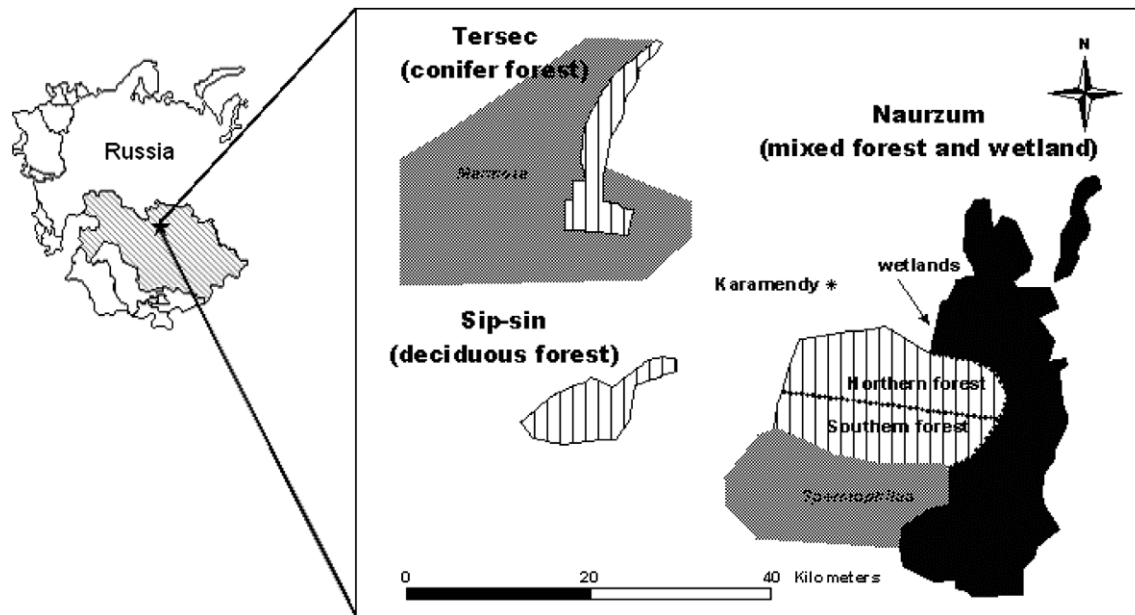


Fig. 1 – Map of the Naurzum Reserve, Kazakhstan, showing its location in the former Soviet Union, the three forested and four ecological regions of the reserve, and the approximate locations of marmot and ground squirrel colonies.

2.2. Imperial eagle ecology at the Naurzum Reserve

Demography of imperial eagles at the Naurzum Reserve has been studied for more than 25 years (Bragin, 2000; Bragin and Katzner, 2004). Imperial eagles in northern Kazakhstan are migratory and initiate the on-territory component of their breeding cycle in March (E. Bragin, personal observations). There are approximately 40 breeding territories distributed throughout each of the three forests of the Reserve and breeding is attempted at 20–35 of these in each year. The number of territories has remained either stable or has slightly increased over the 25 years of study at the reserve. Nests are built in pine, birch, and occasionally aspen trees; conspecific nearest neighbour distances among active nests average 2.9–3.9 km but vary among regions (Katzner et al., 2003). Eagles at Naurzum forage on a wide variety of primarily steppe-living prey and nesting density is correlated with eagle diet (Katzner et al., 2005). Among the most important prey are mammals, primarily bobak (steppe) marmots (*Marmota bobac*), susliks (ground squirrels: *Spermophilus fulvus*, *S. major*, *S. pygmeus*), hares (*Lepus* spp.), and small mammals (Muridae), and birds including corvids (*Corvus corone*, *C. frugilegus*, *Pica pica*), bustard (*Tetrax tetrax*), and several species of waterfowl and raptors. There is a large suslik colony (diameter >15 km; primarily *S. fulvus*) south of Naurzum forest and there is a large marmot colony (diameter >20 km) west and south of Tersec.

Rates of breeding failure of eagles are correlated with regional patterns in dietary diversity (Katzner et al., 2005). When breeding is successful, imperial eagles at Naurzum produce 1–3 chicks that fledge in early to mid-August. Fledglings stay in the general area of the nest for 30–60 days, gradually moving further and further away. Eventually they migrate south; one bird marked as a nestling at the Reserve was observed on the Arabian peninsula during winter (T. Katzner

and E. Bragin, unpublished data). Once fledged, imperial eagles go through a prolonged “pre-adult” phase, during which their plumage is different than adults and they only rarely hold breeding territories. Every year many pre-adult imperial eagles summer at Naurzum, foraging primarily on susliks and roosting communally in areas between those defended by territorial breeders (T. Katzner and E. Bragin, unpublished data). Preliminary genetic analyses suggests that a few (<5%) of these birds were originally born at the Reserve (J. Rudnick, unpublished data). In addition to these pre-adults, an unknown number of adult floaters are present – birds that are capable of reproducing but that do not hold a territory (Hunt, 1998).

2.3. Field methods

The specific parameters that we measured for this study were: the number of occupied eagle territories, the number of territories where breeding occurs (“breeding territories”), the number of territories where chicks fledge (“successful territories”) and the number of chicks produced at each successful nest. From 1978 to the present the entire reserve has been searched each year for nesting eagles (see Bragin and Katzner, 2004, for methodologies); the vast majority of nesting territories were identified by 1980. Any area where a single adult eagle was repeatedly observed in one or more years was considered an eagle territory. A territory was considered occupied if we regularly observed a pair of adult or pre-adult birds and found an old nest, or if we observed signs of territory defence, nest building, or other reproductive activity. Occupied territories were mapped and, since 1998, nest locations were determined with a GPS. Nests at which breeding occurred were monitored at least twice a year, once in the second half of April and again in late July or early August. The first survey was designed to determine if territories were occupied, the

second was to determine breeding success and usually involved climbing to the nest. Many nests were also monitored on a more regular basis in the context of other research into eagle ecology. We have not observed any sign that our nest monitoring negatively influences breeding by these eagles.

In addition to our field monitoring, a recently initiated genetic study of the imperial eagles of the Reserve provided preliminary information on sex ratios of chicks and survivorship of adults (Rudnick et al., 2005). An ongoing study involving conventional telemetry of nestlings also provides us with some information on pre-adult survivorship.

2.4. Modelling

2.4.1. The demographic model

We built an age-structured demographic model of the female component of the imperial eagle population at the Naurzum Reserve. The model reflects age-related behaviour patterns that we have observed and that are shown by other *Aquila* eagles (Watson, 1997; Ferrer, 2001; Whitfield et al., 2004b). The model is not spatially explicit in a strict sense, although it does reflect spatial structure in the environment because we use separate demographic parameters for each of the four regions within the Reserve.

Our model is constructed to follow the life cycle of the eagles (Fig. 2). We outline the model here and subsequently provide a more detailed description of the component calculations. Each year begins by calculating age-specific survival during the preceding non-breeding season. The number of territories occupied in that year is computed based on the number of breeding-capable individuals present in the population, region-specific probabilities that a territory remains occupied, and a Reserve-wide probability that an empty territory is filled. The number of nests where breeding is success-

ful is calculated based on the number of occupied territories, the proportion of territories where breeding is attempted and the proportion where breeding is successful. The number of female chicks produced is estimated based on multiple random draws from binomial distributions. The effects of age-related behaviour, environmental and demographic stochasticity, and density dependence are included in the model as described below.

2.4.2. Age effects

Age can have significant effects on survivorship, the likelihood of breeding, and reproductive output in raptors (Newton, 1979; Penteriani et al., 2003). Specifically, immature (first-year) and sub-adult birds (2–4 years old) are expected to experience higher annual mortality rates than do adults, pre-adults (immatures and sub-adults together) are expected to breed rarely and less productively than adults, and reproductive capacity of adults may decline at advanced ages. The five age classes in our model (Fig. 2) allow us to incorporate mortality-related age effects into calculations of demographic parameters. In addition, we assume that adult birds, if present, will always occupy territories ahead of pre-adults and that birds younger than four years old never breed (Baltontin et al., 2003; Ferrer et al., 2003). Although age-related reproductive senescence has been demonstrated to exist in some species (Newton and Rothery, 1997; Nielsen and Drachmann, 2003), we did not specifically model this process. However, the impact of senescence should be reflected, to some degree, in our data-based parameter estimates.

2.4.3. Environmental effects and demographic stochasticity

Environmental fluctuations and demographic variability among individuals can have strong influences on many stages of population growth. However, the effects of changes

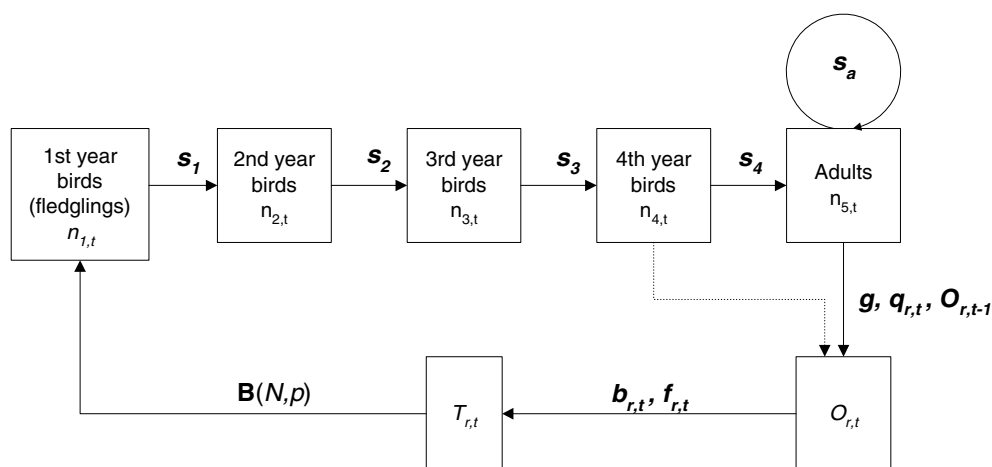


Fig. 2 – Representation of the model of imperial eagle demography at the Naurzum Reserve, Kazakhstan. Symbols are as follows: s : age-specific survivorship; g : the probability that a previously unoccupied territory will become occupied; q : the probability that a previously occupied territory will remain occupied; O : the number of occupied territories; b : the probability that birds at an occupied territory will attempt to breed; f : the probability that a breeding territory will fledge chicks; T : the number of territories fledging chicks; and $B(N,p)$: the number of chicks produced at successful territories, picked from binomial distributions with sample size T and region-specific probabilities p . Reproductive and territory-related parameters are subscripted by region (r), year (t), or both.

in environmental variables may be autocorrelated and difficult to disentangle from individual variation. We modelled the effects of stochastic fluctuations of all types on eagle demography by drawing, from normal random distributions, variables describing territory occupancy and re-occupancy, probability of breeding, and probability of breeding success. Mean and standard deviations for these distributions were region-specific (thus reflecting region-specific environmental effects) and based on field data (thus reflecting observed variation among individuals; Table 1). We incorporated stochasticity into our models of annual survival and annual chick production at successful nests by randomly picking these parameters from binomial or normal distributions. Annual chick production at successful nests was a region-specific data-based parameter. Survival estimates, which we assumed were similar across regions of the Reserve, were the only variables that we estimated from a combination of field data and the literature review.

2.4.4. Density dependence and immigration and emigration
Density dependence has the potential to influence a wide range of demographic parameters. Density dependence is included in our model in an absolute way because (a) population growth is limited by the cap on the maximum number of territories at the Reserve, and (b) the potential for pre-adult breeding depends on the number of adults in the population. Although eagle reproductive output and survivorship could theoretically both be linked to population density (by impacting age at first breeding [Whitfield et al., 2004a; Ferrer et al., 2004] and productivity [Ferrer and Donazar, 1996]) we did not explicitly model the impact of density on these parameters. We chose this modelling approach because previous research and observation at Naurzum have provided no quantifiable evidence that eagle productivity is density-dependent and we have no knowledge about potential density effects on survival (Katzner et al., 2005; E. Bragin and T. Katzner, personal observations). Although our knowledge of po-

Table 1 – Model input parameters, their scale, input value, source and the symbol used in Fig. 2^a

Parameter	Scale	Input Value ($\bar{X} \pm SD$)	Source	Symbol
# occupied territories	Reserve	45	1987–2003	
Proportion territories by region	Regional – NN	0.29	1997–2003	$O_{r,t}$
	Regional – S	0.17	1997–2003	$O_{r,t}$
	Regional – SN	0.25	1997–2003	$O_{r,t}$
	Regional – T	0.29	1997–2003	$O_{r,t}$
Prob. territory stays occupied	Regional – NN	0.89 ± 0.12	1987–2003	$q_{r,t}$
	Regional – S	0.86 ± 0.22	1988–2003	$q_{r,t}$
	Regional – SN	0.93 ± 0.08	1987–2003	$q_{r,t}$
	Regional – T	0.95 ± 0.07	1987–2003	$q_{r,t}$
Prob. territory gets occupied	Reserve	0.57 ± 0.31	1978–1992	g_t
Proportion breeding	Regional – NN	0.63 ± 0.13	1990–2003	$b_{r,t}$
	Regional – S	0.91 ± 0.12	1990–2003	$b_{r,t}$
	Regional – SN	0.75 ± 0.16	1990–2003	$b_{r,t}$
	Regional – T	0.87 ± 0.09	1990–2003	$b_{r,t}$
Proportion successful	Regional – NN	0.81 ± 0.15	1990–2003	$f_{r,t}$
	Regional – S	0.78 ± 0.22	1990–2003	$f_{r,t}$
	Regional – SN	0.93 ± 0.14	1990–2003	$f_{r,t}$
	Regional – T	0.85 ± 0.12	1990–2003	$f_{r,t}$
Prob. that one chick fledges ^b	Regional – NN	0.84	1990–2003	p
	Regional – S	0.73	1990–2003	p
	Regional – SN	0.72	1990–2003	p
	Regional – T	0.9	1990–2003	p
Prob. that two chicks fledge ^c	Regional – NN	0.6	1990–2003	p
	Regional – S	0.67	1990–2003	p
	Regional – SN	0.5	1990–2003	p
	Regional – T	0.53	1990–2003	p
1st year survival	Reserve	0.50 ± 0.02	Ferrer and Calderon (1990) ^d	$s_{i,j}$
2nd year survival	Reserve	0.70 ± 0.02	Ferrer and Calderon (1990) ^d	$s_{i,j}$
3rd year survival	Reserve	0.70 ± 0.02	Ferrer and Calderon (1990) ^d	$s_{i,j}$
4th year survival	Reserve	0.70 ± 0.02	Ferrer and Calderon (1990) ^d	$s_{i,j}$
Adult survival	Reserve	0.90 ± 0.02	Whitfield et al. (2004b) ^e	$s_{i,j}$

a Regions within the Reserve are North Naurzum (NN), Sip-sin (S), South Naurzum (SN) and Tersec (T). Years of data collected or literature sources are given for parameters based on field data and literature review. Prob. = probability.

b Picked from a binomial distribution $B(N, p)$, where p is the probability in the table and N = (the number of breeding territories) – (the number of territories producing two chicks).

c Picked from a binomial distribution $B(N, p)$, where p is the probability in the table and N = the number of breeding territories.

d Unpublished conventional telemetry studies of pre-adults at Naurzum provided data generally similar to these estimates.

e Many sources are reviewed in their Appendix A. Pre-publication data from Rudnick et al. (2005) were also considered in selecting this value.

tential density effects may be limited by the relatively low range of densities we have observed at Naurzum, lack of strict density dependence is consistent with the theoretical rationale for holding a territory and with most other models of eagle populations (Green et al., 1996; Real and Manosa, 1997; Whitfield et al., 2004b). To the extent that density dependence in productivity is regulated by habitat heterogeneity, our region-specific and empirically-based model parameters should incorporate many of these effects (as is the case for senescence, see above).

2.4.5. Parameter estimation

Model parameters were estimated either from data collected in the course of long-term field monitoring or inferred from a combination of published data on similar species and preliminary field data (Table 1). Because the long-term monitoring scheme at the Naurzum Reserve has evolved over time, different approaches to monitoring have been used in different periods. As a consequence, not all parameter estimates are derived from the same monitoring period.

Earlier work has shown the existence of ecologically important variability in dietary, habitat and demographic parameters of eagles in the different regions of the Reserve (Katzner et al., 2003; Katzner et al., 2005). Because of the rarity with which it occurred, territory abandonment and subsequent re-occupation could only be calculated at the Reserve-wide scale, and we have little insight into how this parameter may vary across the landscape of the Reserve. It is especially difficult to quantify because an abandoned territory may become incorporated into the space that neighbours defend; under these conditions, re-occupancy of the original territory is not possible.

We estimated that survival of immature and sub-adult imperial eagles over the first four years of their life was 0.17 – approximately equal to the highest survivorship reported in telemetry studies of Spanish imperial eagles (Table 1; Ferrer and Calderon, 1990). Although there is a great deal of variability in published estimates of pre-adult survival of raptors, our estimates are well within the ranges reported for other large migratory eagles (see Appendix A in Whitfield et al., 2004b). These rates are approximately equal to those that we have observed in limited telemetry studies conducted at the Naurzum Reserve (E. Bragin, unpublished data). The adult survival rates we used are also within the range of those reported for other eagles and they are consistent with preliminary data collected through non-invasive genetics-based monitoring of this eagle population (Rudnick et al., 2005).

2.4.6. Simulation of population dynamics

Population dynamics were simulated according to the following equation:

$$N_{t+1} = \sum_{i=1}^4 n_{i,t} s_{i,t} + \phi_t \quad (1)$$

where N_t is the number of female imperial eagles of all age-classes within the population at time t (in years), $n_{i,t}$ represents the number of individuals in each age group i at time t , $s_{i,t}$ represents the corresponding annual survivorship rates for each of those age groups, and ϕ_t represents the number of female chicks successfully fledged within the Reserve at

time t . Survival rates were Reserve-wide. When population size was <40 individuals, survivorship was randomly drawn from a binomial distribution $B(N, p)$ each year, where N was the number of birds in that age class and p was their survival probability (Hilborn and Mangel, 1997). At population size >40 survivorship was drawn from a normal random distribution, since at these sample sizes the binomial and normal distributions are essentially identical (Hilborn and Mangel, 1997).

We calculated the number of occupied territories in each region of the reserve ($O_{r,t}$) as follows:

$$O_{r,t} = O_{r,t-1} q_{r,t} + (\max_r - O_{r,t-1}) g_t \quad (2)$$

where $q_{r,t}$ is the rate at which territories occupied in the previous year are re-occupied in the current year, $\max_r$ is the maximum number of territories possible in region r , and g_t is an annual reserve-wide probability that an unoccupied territory will become occupied in the following year. Eq. (2) is calculated such that (a) the number of occupied territories can never be greater than the total number of adult and 4th-year sub-adult females in the eagle population; and (b) 4th-year sub-adults only occupy territories if there are no adult floaters. We also assume that new occupants fill territories by region according to the region's average productivity (occupying first south Naurzum, then Tersec, then north Naurzum, and then Sip-sin). All probabilities were drawn from truncated normal distributions with data-based mean and variance estimates.

The number of chicks produced and successfully fledged depended in part on the number of territories in each region where breeding was successful ($T_{r,t}$), which we calculated as follows:

$$T_{r,t} = O_{r,t} b_{r,t} f_{r,t} \quad (3)$$

where $b_{r,t}$ is the proportion of occupied territories where breeding is attempted in region r at time t , and $f_{r,t}$ is the proportion of breeding territories that successfully produce fledglings in region r at time t . Proportions were drawn from truncated normal distributions based on observed means and variances. This model does not explicitly include the possibility that eagles can re-nest if a first nest fails, but if this occurs, it is incorporated into our data-based productivity parameters.

The number of successfully breeding territories that produced two chicks (x_2) was drawn from a binomial distribution $B(N, p)$, where p was the region-specific probability of a nest having two chicks and $N = T_{r,t}$ (Hilborn and Mangel, 1997). Subsequently the number of successfully breeding territories producing one chick (x_1) was drawn from a binomial distribution $B(N, p)$, where p was the region-specific probability of a nest having one chick and $N = T_{r,t} - x_2$. The number of nests producing three chicks was then calculated as $T_{r,t} - x_2 - x_1$. The total number of chicks produced and successfully fledged in a given year t was then:

$$\text{Fledged} = \sum_{r=1}^R \left(\sum_{j=1}^{T_{r,t}} c_{j,r} \right) \quad (4)$$

where R is the number of regions, $T_{r,t}$ is the number of territories in region r at time t when breeding was successful, and $c_{j,r}$ is the number of chicks at nest j in region r . We calculated the number of female chicks at the reserve by assuming a bal-

anced offspring sex ratio, as is usually assumed in models of raptor populations.

To evaluate the behaviour of our model we simulated population dynamics over 100 years. When investigating model behaviour, we focussed on the relationships between input parameter values and the time-specific population growth rate, λ (calculated as $N(t+1)/N(t)$) averaged over the last five years of simulations (hereafter called “five-year mean” parameter values or outputs).

2.4.7. Sensitivity analyses

The sensitivity analyses we conducted included single variable and multiple variable perturbations. Single variable perturbations involved evaluating model outputs across a range of proportional changes in input parameters. Our approach to multiple variable perturbations was derived from Life Stage Simulation Analysis (LSA; Wisdom and Mills, 1997; Gerber et al., 2004) and permitted us to consider model behaviour under a wide range of stochastic conditions. LSA is based on a “regression approach” to sensitivity and involves plotting values of λ against key demographic parameters. Data for plots are developed from a series of replicate models whose key components are randomly picked from a bounded uniform probability distribution. In some cases composite values of multiple parameters were manipulated together (Wisdom and Mills, 1997).

We modified the LSA approach to suit our goal of evaluating sensitivity over a range of possible model outcomes. First, as in classical LSA, we randomly picked 1000 sets of initial parameter values. Then, for each set, we ran our model to completion (for 100 years) ten separate times. Initial parameter values were picked from a uniform random distribution based on a range of “reasonable” parameter values approximated from the literature and from our field observations. Initial values for the number of territories ranged from 25 to 45, for proportion of territories breeding and successful from 0.5 to 1.0, for juvenile survivorship from 0.20 to 0.80, and for adult survival from 0.75 to 1.0. We evaluated the impact of variability in those starting conditions by plotting initial parameter values against the five-year mean λ values output from the 10,000 runs. This approach differs from classical LSA because our parameter values change as the model runs through a single simulation (parameter values are constant in each LSA simulation) and λ is calculated from the mean of five years of simulated data (rather than estimated from eigenvalues, as occurs in LSA). The consequence of this parameter fluctuation means that the number of territories changes as population size changes (i.e., with population dynamics), and survivorship varies according to a random distribution around the randomly drawn initial means. Because we consider a wide range of possible parameter values, the inputs to this perturbation analysis do not depend on our initial parameter estimates (Table 1) and thus this analysis is highly robust to uncertainty in parameter estimates.

We also used a second approach to more fully understand the sensitivity of λ to changes in demographic parameters in our model. In this case we picked four key parameters (adult and pre-adult survivorship, maximum number of territories, and a composite of reproductive output) and varied each in a systematic manner. To cover a wide range of possible initial

conditions, we modified our original input parameter values by a proportional multiplier. We had six multipliers ranging from 0.7 to 1.30 at intervals of 0.12. We stepped through all possible combinations of these multipliers and the four parameters we considered, creating 1296 different initial conditions. Proportional input values were capped at 1.0. For each of these initial conditions, we ran the model to completion (for 100 years) 100 separate times. Once again, unlike in classical LSA, our parameter values varied from initial values over the 100 simulated years. We averaged the five-year mean parameter values for the 100 model runs and plotted the 1296 output means against input parameters.

Finally, to evaluate from another perspective the relative variability in response of λ to changes in parameter values, we bootstrapped output parameter values from the preceding analysis. We then regressed these bootstrapped means as dependent variables against input multipliers. The regression coefficients these analyses produce do not have the direct relationship to analytical sensitivities and elasticities that are described in Wisdom and Mills (1997). However, they do have meaning in the context of sensitivity analysis and are particularly useful because they, like elasticities, are directly comparable among parameters.

This model was programmed in MicroSoft VisualBasic.NET (Microsoft Development Environment, Version 7.1, 2003) code by the authors. All analyses were performed within VisualBasic, or with SAS software (SAS, Cary, NC, version 8.01, 1999) or a spreadsheet (Excel 2000, Microsoft, Redmond WA, 1999).

3. Results

3.1. Model validation

We validated our model in several ways. First, we evaluated model behaviour under standard conditions – the input parameters of Table 1 – and compared simulated model outputs with those observed during field data collection (Table 2). Simulated average reproductive output (number of chicks fledged) and number of occupied territories were both close to mean data-based values for these parameters. Distributions of chicks produced were similar to those observed over 10 years of monitoring. Population growth (λ) was close to 1, which is consistent with field observations on territory occupancy, although these field observations do not include estimates of dispersal or adult turnover. Finally, qualitative comparison suggested close relationships between simulated and observed trends in inter-regional demographic patterns.

To confirm that the relationships between parameters that we observed in the field also existed within our model, we investigated correlations among output model parameter values in 100 runs of the model under standard conditions (Fig. 3; Bro et al., 2000). Variability in these outcomes is due to stochasticity, not to differences in input parameter values. Because productivity of eagles is often driven by factors such as environmental conditions (Steenhof et al., 1997), we can expect a good, but not perfect, relationship between the number of occupied eagle territories and the number of chicks produced. This was the case in model outputs (Fig. 3a; $r = 0.83$). Likewise, we expected that at small population sizes the number of occupied territories should be tightly corre-

Table 2 – Model outputs under standard model conditions (those parameters described in Table 1), with stochasticity^a

Parameter	Simulated data ($\pm$ SE)	Observed data ($\pm$ SD)	Time period observed
# of chicks fledged	33.26 $\pm$ 0.92 ^b	34.53 $\pm$ 9.27	1987–2003
# of 2nd year eagles	8.18 $\pm$ 0.21	–	–
# of 3rd year eagles	5.87 $\pm$ 0.17	–	–
# of 4th year eagles	4.09 $\pm$ 0.14	–	–
# of adult eagles	29.18 $\pm$ 0.86	–	–
# occupied territories	30.31 $\pm$ 0.69	31.12 $\pm$ 3.64	1987–2003
# of floaters	1.96 $\pm$ 0.41	–	–
Total pop. size	63.95 $\pm$ 1.70	–	–
Population growth	1.0003 $\pm$ 0.0036	–	–

a In cases where field data were collected, those parameters are also shown, for comparison. Simulated values are the mean of 100 averages from the last five years of 100-year simulation. All parameters are Reserve-wide.

b Simulated productivity of female chicks was doubled for inclusion in this table to facilitate comparison with observed field data, which includes both sexes.

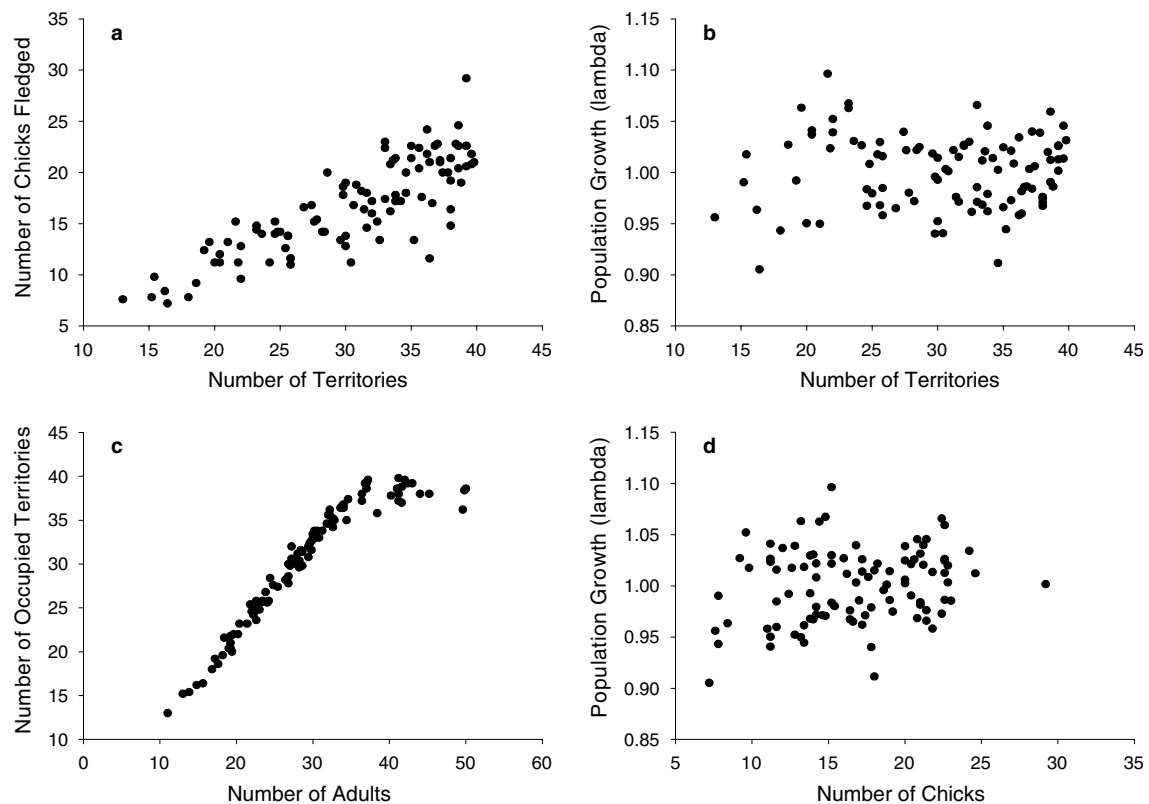


Fig. 3 – Relationships between pairs of simulated model output parameters. Plots represent model behaviour under standard conditions (Table 1), based on 100 averages from the last 5 years of 100 years of simulations. Variability in model outcomes is due strictly to stochasticity, not to changes in parameter inputs.

lated with the number of adults within the population but that at larger population sizes this relationship should disappear. This pattern also existed within our model (Fig. 3c; $r = 0.94$). We expected that weak or non-existent relationships should exist between population growth and the number of occupied territories and the number of chicks produced. These patterns also were consistent with model outputs (Fig. 3b and d; $r = 0.01$ and $r = 0.21$, respectively). Finally, field research suggests that the presence of floaters is important as a buffer against population decline. We therefore expected that floaters should only be present in populations when

most territories are occupied and population size is high. Model behaviour conforms with these predictions.

3.2. Sensitivity analyses

3.2.1. Single variable perturbations

Proportional changes in single variables sometimes had significant impacts on population growth rate (λ ; Fig. 4). Changes in the number of territories that were occupied had little influence on λ . However, changes in reproductive output, pre-adult survival and adult survival all impacted λ . Because

our data were sigmoidal in form we used least-squares regression to fit output data from plots a, c and d to the following 3-parameter sigmoidal function:

$$y = \frac{a}{1 + e^{-\left(\frac{x-x_0}{b}\right)}} \quad (5)$$

in which the parameter a describes the asymptotic value of the curve, x_0 describes the inflection point, and b describes the steepness of the ascent of the curve, such that lower values of b result in steeper inclines. All three regressions fit the data extremely well (Fig. 4; $r^2 = 0.99$). Because the value of a is essentially constant, changes in b are indicative of the response of λ to proportional changes in inputs and are directly comparable among regressions (in this regard these analyses are similar to elasticities). Lambda was most responsive to changes in adult survival. The slope parameter for the equation describing output response was about two times less for changes in adult survivorship ($b = 0.017$) than for changes in pre-adult survival ($b = 0.030$), and more than three times less than that for changes in reproduction ($b = 0.055$).

3.2.2. Random multiple variable perturbation

Classical life-stage simulation analysis regressions of λ versus changes in parameter values produce clear correlations with the coefficient of determination (r^2) being a measure of the proportion of variation in λ explained by change in the parameter value (Wisdom and Mills, 1997). However, when

output parameter values are the product of stochastic simulation, such figures are of little use (Fig. 5a–c) and r^2 values have little meaning. Plotting mean λ for groups of input values (Fig. 5d–f) shows a more interpretable relationship between change in input parameter values and λ . From this perspective, changes in adult survival appear to have the most significant effect on λ , but there is extensive variation around the means. Furthermore, because these changes are considered in the context of absolute, not relative, changes in parameter values, it is difficult to compare the relative impact of changes in different parameters λ .

3.2.3. Systematic multiple variable perturbations

To allow us to quantitatively compare the impact of changes in different input parameters on λ , we structured our simulations in a systematic and proportional manner, creating 1296 different starting conditions. We then bootstrapped these λ s to generate means and distributions under each set of conditions. The output from these simulations was both interpretable and comparable (Fig. 6a–d). When interpreting these plots, it is important to understand that each represents exactly the same 1296 λ values plotted on different x-axes. This accounts for the seemingly wide range of possible outputs at each of the different input conditions.

These results again show that survivorship, especially adult survivorship, is a key variable in determining model outputs. However, under all conditions except extraordinarily

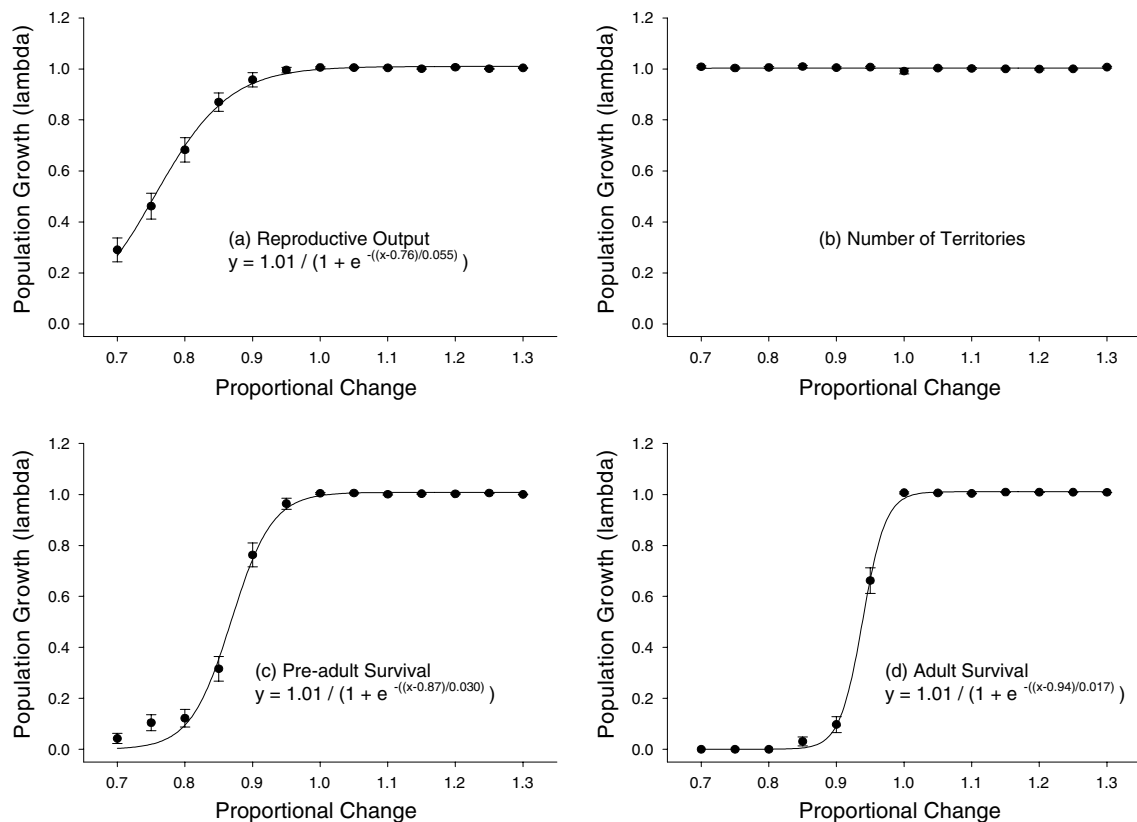


Fig. 4 – The effect of single variable perturbations on mean λ values ($\pm$ SE). Lambda was calculated as the mean of 100 averages from the last 5 years of a 100-year simulation. Parameters input into the model are the product of standard values (Table 1) and the multiplier shown; proportional parameters were assigned a maximum value of 1. Reproduction and pre-adult survival are composite variables, all others are single parameters.

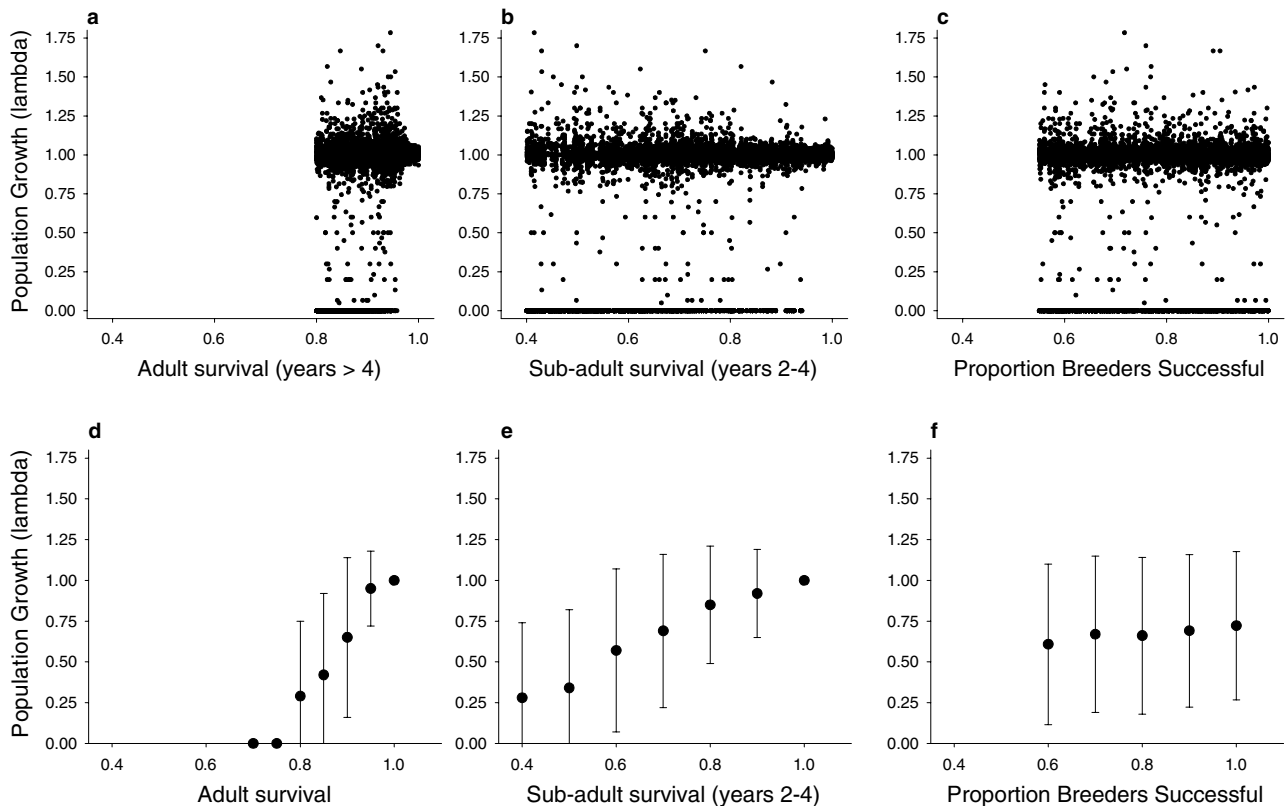


Fig. 5 – LSA-style regression plots of model output population growth (λ) against input adult survival, sub-adult survival, and the proportion of successful breeders in the population, for outputs from models of an imperial eagle population in north-central Kazakhstan. The x-axis shows the change in parameter input value (Table 1) used in model runs. Upper plots (a, b, c) are standard LSA-style regressions; lower plots (d, e, f) show data grouped into intervals (mean $\pm$ 95% CI).

high adult survivorship, it was possible for the population to go extinct ($\lambda = 0$). We used least-squares regression to fit bootstrap mean data to the same sigmoidal function used in Fig. 4. The fit of this function to the data was good (r^2 always >0.9), but in this multiple-variable perturbation there were greater differences among parameters in the shape of the fitted curve than occurred in single-variable perturbation. In the multiple-variable perturbation, changes in λ showed a sigmoidal response only to changes in adult survival (Fig. 5d), and changes in other parameters had considerably less impact on λ . The implication of these results is that when other parameters are fluctuating in a stochastically-variable environment, changes in adult survival are of greater importance proportional to other parameters than is suggested by single-variable perturbation analysis. However, comparison of the value of the b parameter in this equation ($b = 0.089$) with those in the single-variable perturbation (Fig. 4) suggests that the response of λ to changes in adult survival is less than that implied by single-variable changes in any parameter, even reproductive output. Thus, even though changes in adult survival have a greater relative impact on λ than single-variable perturbation predicts, in absolute terms adult survival is less consequential to λ than single-variable perturbations predict.

Another way to measure the relative impact of change in different model parameters on model output is to compare the magnitudes of the range of λ s under those different conditions (Fig. 7). To facilitate this comparison, we eliminated

the effects of outliers by not considering the smallest and largest 5% λ s and scaled our ranges to the output means. In this analysis, variation in the number of territories did not change the magnitude of the range of λ s. However, this magnitude did change dramatically when adult survival varied. When adult survivorship was high the range of outputs was small, indicating that variation in other parameters has little influence on model outputs. When adult survivorship was low, the range of outputs is large, indicating that other variables determine model outcome. Changes in sub-adult survivorship and reproductive parameters produce similar but less distinct patterns.

4. Discussion

Classical demographic theory and empirical data suggest that adult survival should be the most important demographic parameter for the population dynamics of long-lived vertebrates (Gaillard et al., 1998; Saether and Bakke, 2000). Although our analyses of Naurzum's eagles generally support this perspective, they also suggest that exclusive focus on adult survival over-simplifies the complexity of this system.

Our single variable perturbations tell a similar story to that told by standard sensitivity analyses and demographic models of other long-lived species (Fig. 3). The effects on population growth of simulated changes in adult survival were best characterised by threshold-type impacts such that above

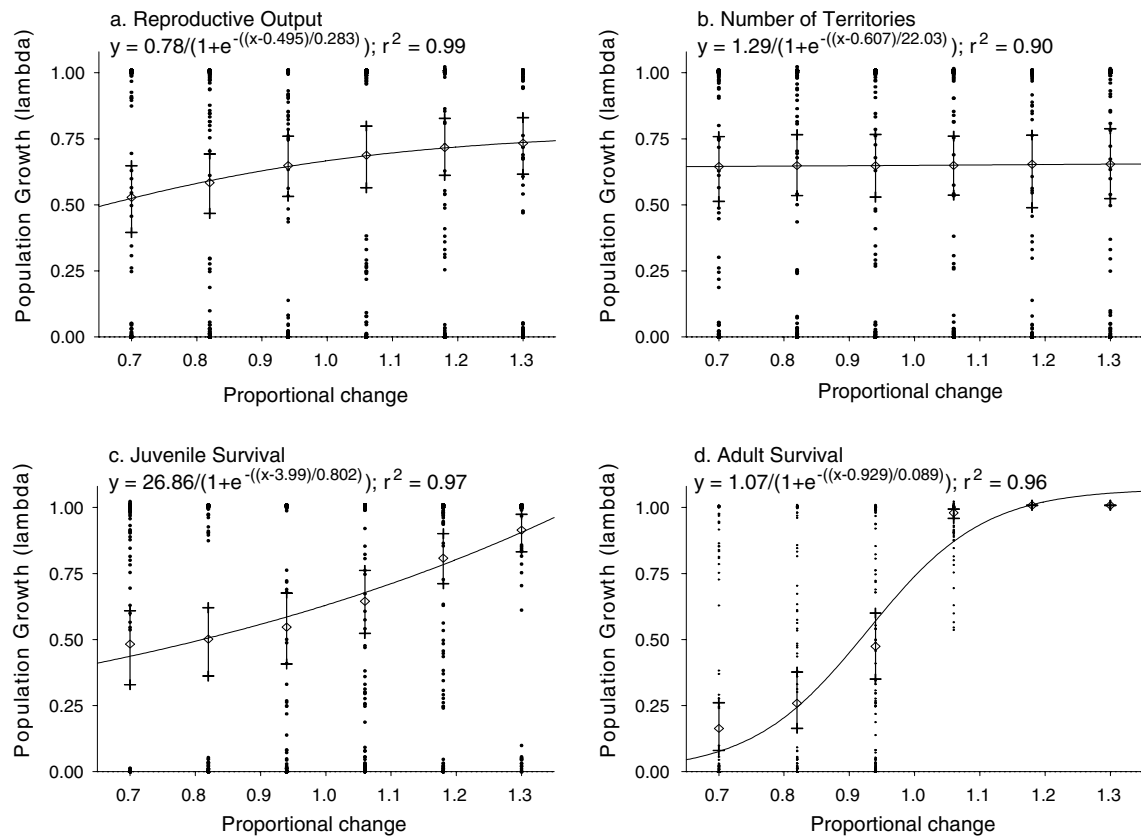


Fig. 6 – Plots showing the effects of systematic perturbation on output λ values. Each plot contains the same data points organized against different x-axes. x-Axis shows the proportion of the original parameter value (Table 1) input for the model run. Means ($\pm$ SE) of a bootstrap analysis of the same data are shown, as are regressions for those bootstrap means.

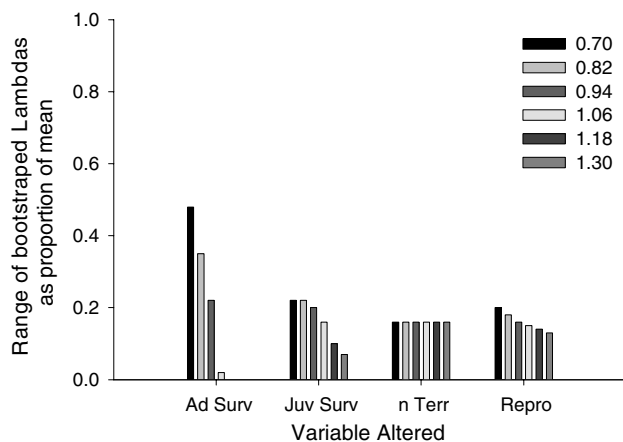


Fig. 7 – Range of bootstrap means as a proportion of average bootstrap means. Bootstraps are of simulated data where parameter values are the product of standard values and the indicated multiplier. Small ranges imply that other parameters have little influence on model outputs; large ranges imply that other parameters have strong influences on model outputs.

a certain level of adult survival the population grows and below that level the population declines to extinction. No other demographic parameter had as controlling an influence on

population growth. If these sensitivity analyses were the only ones conducted, we would conclude by finding that, of the four variables we perturbed, population growth (and conservation of eagles) is most sensitive to changes in adult survival.

PVA studies traditionally have used single variable perturbation analyses such as these to justify a research or management focus on a single key life-stage. Models in these studies usually are time-invariant and populations are considered independent of their density, context or spatial structure. However, real populations propagate through space and time and parameter permutations have cascading, synergistic consequences that are more easily understood through stochastic simulation than through parameter estimation based on eigenvalues (Kremer, 1983; Benton and Grant, 1999; Caswell, 2001; Strand et al., 2002; Norris and McCulloch, 2003). Therefore, multiple variable perturbations of stochastically simulated models should be more informative than single variable perturbations about population dynamics in real-world scenarios involving interactions among demographic parameters (Mills and Lindberg, 2002).

A further strength of our multiple variable perturbations is that they depend on a ranges of input values, rather than on any single estimate, and therefore they are robust to uncertainty in parameter estimates. This has important conservation consequences for the particular population we model because of the high year-to-year variability in recently published estimates of annual adult survivorship (Rudnick

et al., 2005). Our model validation uses data from the year in that study with the most robust survivorship estimate. However, the two other years vary considerably and our multiple variable perturbation analysis covers a broader range of possible inputs than exist in the three years of field data from that paper. If adult survivorship is lower than we have estimated in our model validation, then the perturbation analysis shows that if the population is to remain stable, immigration or pre-adult survivorship must be greater than we assume.

Our multiple variable perturbation analyses suggest two key biological insights that are not readily apparent from the single variable perturbations or even from classical life-stage simulation analysis (LSA). First, in a structured stochastic system, adult survivorship can be more consequential to population growth, relative to other parameters, than is apparent from single-variable perturbations. Second, in absolute terms adult survival is less consequential to population growth than is apparent from single-variable perturbations and this eagle population can go extinct at nearly any biologically reasonable level of adult survivorship (≤ 0.95 ; Whitfield et al., 2004b). Thus, even when adult survivorship is high, other life-history characteristics (and their covariance; Coulson et al., 2005) are still highly relevant to the population dynamics of Naurzum's imperial eagles.

The importance to population growth of parameters other than survivorship may be a product of our modelling approach, but it also likely reflects the biological characteristics of this population. In particular it is worth considering that this is the first demographic model constructed of a highly migratory eagle population. Other eagle populations that have been modelled – white-tailed sea eagles (Green et al., 1996), golden eagles (Whitfield et al., 2004b), Spanish imperial eagles (Ferrer and Calderon, 1990) and Bonelli's eagles (Real and Manosa, 1997; Carrete et al., 2005) – are either sedentary year-round or make relatively short-distance migratory movements. Because migration may impact mortality risk, accepting this risk is often seen in the context of an evolutionary trade-off that provides migrants with the opportunity to increase reproductive output (Alerstam et al., 2003). If this trade-off is relevant to eagles, it follows that reproductive output should be more significant to the dynamics of Naurzum's highly migrant populations than it is to non-migrants. An unexplored but interesting alternative possibility with important conservation consequences is that the presence of migration decreases the difference in survivorship between adults and pre-adults. In this scenario, pre-adult survivorship would be relatively more important for population persistence in a migratory population than it would be in a non-migratory population.

The utility of elasticity and sensitivity analyses for interpreting dynamics of natural populations is influenced by the interplay between parameter elasticity and variance. For large herbivores, temporal variation may actually overrule elasticity in determining population dynamics (Gaillard et al., 2000). Likewise, estimates of the proportional variance in reproductive output of Naurzum's eagles appear higher than those estimated for survivorship. Correspondingly, multiple variable perturbation of our models suggests the important role that this higher variability can have in determining population growth. However, migratory raptors are fundamen-

tally different than ungulates and recent history shows the importance to population trends of drastic fluctuations, not only in reproduction (e.g., the effects of DDT; Cade et al., 1988; Newton and Wyllie, 1992), but also in survivorship (e.g., the effects of monocrotophos and diclofenac; Goldstein et al., 1999; Green et al., 2004). Since eagles clearly are at risk of drastic population fluctuations, explicitly considering a wide range of scenarios, as we have done, is especially important to modelling and managing for their conservation (Benton and Grant, 1999).

Our stochastically simulated sensitivity analysis was distinct from previous demographic modelling of raptors and it provided insight into population dynamics that we would not have achieved with analytical models. The results of sensitivity analysis can also be used to prioritize conservation action (Whitfield et al., 2004b). In this case, we interpret our analyses to mean that the least well understood aspects of raptor demography – adult and pre-adult survivorship – should be research and conservation priorities. However, the previously noted catastrophic changes in bird populations and the broad range of stochastically simulated model outcomes even when survivorship is high should serve as a caveat with important implications for management. Specifically they suggest that although it is important to manage for key parameters, ignoring other parameters and life stages can have potentially severe consequences. In this regard our findings agree closely with those of Hiraldo et al. (1996), who concluded that management for lesser kestrels (*Falco naumanni*) should focus on maintaining or increasing both reproductive output and adult survival. Likewise, a strategy to protect adults at all costs is unlikely to be well suited to managing Naurzum's imperial eagle population. Instead, in this and other structured populations of vertebrates, an approach that addresses the importance of variation in multiple vital rates is key to effective conservation and management.

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