
Using Modeling to Improve Monitoring of Structured Populations: Are We Collecting the Right Data?

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Abstract: *Population monitoring is central to most demographic studies and conservation efforts, but it may not always be directed at the most appropriate life stage. We used stochastic simulation modeling to evaluate the effectiveness of a monitoring program for a well-studied population of Eastern Imperial Eagles (*Aquila heliaca*) in Kazakhstan. Specifically, we asked whether the most appropriate data were being collected to understand system state and population dynamics. Our models were parameterized with data collected over the course of 25 years of study of this population. We used the models to conduct simulation experiments to evaluate relationships between monitored or potentially monitored parameters and the demographic variables of interest—population size (N) and population growth (λ). Static analyses showed that traditional territory-based monitoring was a poor indicator of eagle population size and growth and that monitoring survivorship would provide more information about these parameters. Nevertheless, these same traditionally monitored territory-based parameters had greater power to detect long-term changes in population size than did survivorship or population structure. Regardless of the taxa considered, threats can have immediate impacts on population size and growth or longer-term impacts on population dynamics. Prudently designed monitoring programs for any species will detect the demographic effects of both types of threats.*

Keywords: *Aquila heliaca*, demography, Eastern Imperial Eagle, life-stage simulation analysis, population monitoring, sensitivity analysis, stochastic simulation modeling

Utilización de Modelos para Mejorar el Monitoreo de Poblaciones Estructuradas: ¿Estamos Recolectando los Datos Correctos?

Resumen: *El monitoreo de poblaciones es central para la mayoría de los estudios demográficos y esfuerzos de conservación, pero puede no estar siempre dirigido a la etapa de vida más apropiada. Utilizamos modelos de simulación estocásticos para evaluar la efectividad de un programa de monitoreo para una población de Águila Imperial Oriental (*Aquila heliaca*) bien conocida en Kazajistán. Específicamente, nos preguntamos si se estaban recolectando los datos más apropiados para entender el estado del sistema y la dinámica de la población. Nuestros modelos fueron alimentados con datos recolectados a lo largo de 25 años de estudio de esta población. Utilizamos los modelos para desarrollar experimentos de simulación para evaluar relaciones entre parámetros monitoreados o potencialmente monitoreados y las variables demográficas de interés—tamaño de la población (N) y crecimiento poblacional (λ). Los análisis estáticos mostraron que el monitoreo tradicional basado en territorios era un pobre indicador del tamaño y crecimiento poblacional del águila y que el monitoreo de la supervivencia podría proporcionar más información sobre estos parámetros. Sin embargo, estos parámetros tradicionalmente monitoreados con base en territorios fueron más poderosos que la supervivencia o la estructura de la población para detectar cambios en el tamaño de la población. Independientemente de los taxa considerados, las amenazas pueden tener impactos inmediatos (sobre el*

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tamaño y crecimiento de la población) y a mayor plazo (sobre la dinámica de la población). Programas de monitoreo diseñados prudentemente para cualquier especie detectarán los efectos demográficos de ambos tipos de amenazas.

Palabras Clave: Águila Imperial Oriental, *Aquila heliaca*, análisis de sensibilidades, análisis de simulación de etapa de vida, demografía, modelo de simulación estocástico, monitoreo de población

Introduction

Monitoring, “the process of gathering information about some system. . . at different points in time, for the purpose of assessing system state and drawing inferences about changes in state over time” (Yoccoz et al. 2001), is central to conservation. Scientifically oriented population monitoring is designed to provide ecological insights and it contrasts with monitoring geared specifically toward producing information for management (Yoccoz et al. 2001). In the realm of conservation monitoring can take either approach and usually has one of three goals—evaluating the status of biodiversity, of a single species, or of a single event (e.g., migration, spawning). Broad-scale biodiversity monitoring programs are often expensive and complex to design and maintain and, in developing countries, usually depend on external funding (Danielsen et al. 2003). In contrast, single-species or single-event monitoring can be low cost, straightforward, and internally funded. Consequently these programs can build long-term data sets that have high conservation value and great potential for retrospective analysis.

Considerable effort has been invested to improve data collection for population monitoring. The majority of this research has addressed sampling strategies, in particular accounting for variability due to spatial heterogeneity and detectability (Yoccoz et al. 2001; Pollock et al. 2002). In addition, a few studies have addressed issues of design and implementation (Danielsen et al. 2003). In spite of improved data collection, however, there are other potential problems with monitoring that remain unaddressed. Improving the accuracy of counts or designing better sampling schemes involves the implicit assumption that research is focused on the biological parameters most relevant to the conservation question being asked. In fact, this assumption is often violated, particularly for structured populations. This problem was demonstrated clearly by Doak (1995), who used models to show that detectable change in size of grizzly bear (*Ursus arctos*) populations would lag far behind degradation of their habitat. Thus, the response of bear populations would be detected only once the habitat was too degraded to support a viable bear population. Instead, Doak recommended monitoring habitat change and habitat-specific densities, rather than overall population size. In this situation improved sampling accuracy would not make population counts more indicative of long-term population trends.

Thus, there is a clear need to step back and, before improving our ability to collect data, to ask first whether the correct data are being collected for the conservation or monitoring questions being asked. Simulation models are a useful tool for addressing these questions (Peck 2004). Our goal was to develop a method to evaluate whether monitoring programs are gathering the correct information to allow accurate assessment of system state (population size and growth) and of changes in state (population size) over time. Our case study was one of the longest-term single-species raptor-monitoring programs in the world: a >25-year study of populations of Eastern Imperial Eagles at a nature reserve in north-central Kazakhstan in the former Soviet Union. This population has been monitored since 1977 by E.A.B., and in recent years also with T.E.K., to provide information about population size and trends. In the field we used traditional techniques that focus on territory occupancy, nesting success, and reproductive output (Bragin 2000; Bragin & Katzner 2004). Trends in these parameters are stable or increasing, but it is unclear whether these patterns accurately reflect population dynamics. In particular, because eagles are long-lived, lagged dynamics may inhibit our ability to evaluate population trends. The best way to address this problem is through experimentation (Krebs 1991), but such an approach is not feasible in this setting. Instead, we used demographic models to simulate eagle population dynamics under a range of plausible scenarios and to evaluate our monitoring.

Standard sensitivity analyses evaluate the relationship between changes in input parameters and population growth (λ). Here, by contrast, we evaluated the relationships between modeled population size and trends and the demographic parameters that can be observed and monitored in the field. We then used the outputs to identify what the current monitoring program really is saying about the size and trajectory of these eagle populations and whether there are other demographic parameters that would be more informative to monitor.

Methods

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 Eastern 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 and although many of those fields now are fallow, their outlines still are visible in satellite images, even as they are being recolonized by their original floral and faunal communities (T.K., personal observation). Interspersed within the steppe matrix are four woodland areas (Tersec, Sip-sin, north and south Naurzum) that comprise much of the protected reserve land. Because eagle ecology is different in each region, we considered data from each of them separately (Katzner et al. 2003). The forested areas are dominated by pine (*Pinus sylvestris* L.), birch (*Betula* spp.), and aspen (*Populus* spp.). The remaining protected area includes dry steppe and numerous permanent and ephemeral lakes with saline or freshwater.

Imperial Eagle Ecology at the Naurzum Reserve

Eastern Imperial Eagles in northern Kazakhstan are migratory and initiate the on-territory component of their breeding cycle in March (E.B., personal observations). There are approximately 40 breeding territories distributed throughout the reserve and breeding is attempted at 20–35 territories of these each year (Bragin & Katzner 2004). Nests are built in pine, birch, and occasionally aspen trees; conspecific nearest-neighbor distances among active nests average 2.9–3.9 km (Katzner et al. 2003). Eagles at Naurzum forage on a variety of primarily steppe-living prey, and nesting density is correlated with 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.), small mammals (Muridae), and birds including corvids (*Corvus corone*, *C. frugilegus*, *Pica pica*), Little 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 correlate with regional patterns in dietary diversity (Katzner et al. 2005). When breeding is successful, Eastern Imperial Eagles at Naurzum produce 1–3 chicks that fledged in early to mid August. Fledglings stay in the general area of the nest for 30–60 days, gradually moving farther away. Eventually they

migrate south. One bird marked as a nestling at the reserve was observed on the Arabian Peninsula during winter (T. K. and E.B., unpublished data). Once fledged, Eastern Imperial Eagles go through a prolonged (3–5 year) “subadult” phase, during which their plumage is different than adults and they do not hold territories. Every year many subadult Eastern Imperial Eagles summer at Naurzum, foraging primarily on susliks and roosting communally between breeding territories (T.K. and E.B., unpublished data). Preliminary genetic analyses suggest that a few (<5%) of these birds were originally born at the reserve (J. Rudnick, unpublished data). In addition to these subadults, an unknown number of adult floaters (birds that are capable of reproducing but that do not hold a territory) are present (Hunt 1998).

Field Monitoring

Population monitoring of raptors has focused historically on nest-related parameters (Fuller & Mosher 1987). In general monitoring consists of surveys of known or suitable sites and identification of occupancy rates, nesting status, and fledging success. Surveys for nests are conducted on foot or from a vehicle or airplane (Ayers & Anderson 1999). Determination of occupancy and nesting status is usually accomplished by climbing to and looking in nests. This approach has been used for the majority of monitoring programs for eagles and other raptors (e.g., Ferrer & Calderon 1990; Green 1996; Kochert & Steenhof 2002). Other monitoring schemes also include migration studies to elucidate larger-scale demographic and regional trends (Viverette et al. 1996; Miller et al. 2002). In a few studies, population-wide marking or telemetry programs have allowed for more detailed study of other aspects of avian demographics, especially population turnover and movement and age-specific survival and fecundity (Green et al. 1996; Newton & Rothery 1997; Kenward et al. 1999; Ferrer & Bisson 2003; Sandvik et al. 2005).

From 1978 to the present the entire reserve has been searched each year for nesting eagles; the majority of nesting territories were identified by 1980. Any area where a single adult eagle is repeatedly observed in one or more years is considered an eagle territory. A territory is considered occupied if we regularly observe a pair of adult or subadult birds or if we observe signs of territory defense, nest building, or other reproductive activity. Occupied territories are mapped annually and, since 1998, nest locations were determined with a GPS. Nests at which breeding occurred are monitored at least twice a year, once in the second half of April and again in late July or early August. The first survey is designed to determine whether territories are occupied, and the second is designed to determine breeding success. Many nests are 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 Eastern 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 subadult survivorship.

The Demographic Model

We built an age-structured demographic model of the female component of the Eastern Imperial Eagle population at the Naurzum Reserve (Fig. 1). We briefly outline our model here; a detailed description is provided in Katzner et al. (2006). The model reflects age-related behavior patterns observed at Naurzum and shown by other *Aquila* eagles (Watson 1997; Ferrer 2001). The model reflects spatial structure in the environment by performing most calculations at the level of the four regions within the reserve, but it is not strictly spatially explicit.

Demographic effects due to age, stochasticity, population density, and long-distance movements can all influence raptor populations. Our model is age-structured because survivorship, the likelihood of breeding, and reproductive output of raptors are all age related (Newton & Rothery 1997; 1998, Ferrer & Bisson 2003; Penteriani et al. 2003). We assumed that adult birds, if present, occupy territories ahead of subadults and that birds younger

than 4 years old never breed. We modeled the effects of stochastic fluctuations on eagle demography by drawing, from binomial or normal random distributions, variables describing survival, territory occupancy and re-occupancy, probability of breeding, probability of breeding success, and annual chick production at successful nests. Density dependence is included in our model in an absolute way because population growth is limited by the cap on the maximum number of territories at the reserve and because the potential for subadult breeding depends on the number of adults in the population. We did not explicitly model the impact of density dependence within the population because previous research and observation at Naurzum give no indication that eagle productivity is density dependent and we have no knowledge of potential density effects on survival (Katzner et al. 2005; E.B. & T.K., personal observations). 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 & Manosa 1997; Whitfield et al. 2004).

Model parameters were estimated either from data collected during long-term field monitoring described above or from a combination of published data on similar species and preliminary field data. More detail on parameter estimation is provided elsewhere (Katzner et al. 2006). We simulated population dynamics over 100 years and averaged output parameter values over the last 5 years (hereafter called “5-year mean” parameter values or outputs).

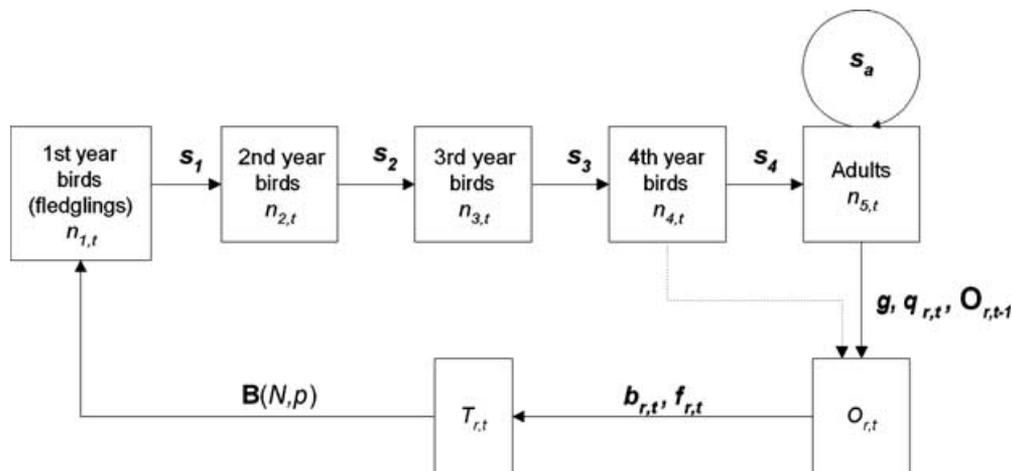


Figure 1. Model of Eastern Imperial Eagle demography at the Naurzum Zapovednik, Kazakhstan. Symbols are as follows: n , number of individuals in each age class (subscripted by age class and year $[t]$); s , age-specific survivorship; g , probability that a previously unoccupied territory will become occupied; q , probability that a previously occupied territory will remain occupied; O , number of occupied territories; b , probability that birds at an occupied territory will attempt to breed; f , probability that a breeding territory will fledge chicks; T , number of territories fledging chicks; and $B(N,p)$, number of chicks produced at successful territories picked from binomial distributions where sample size $N = T_{r,t}$ with region-specific probabilities p . Reproductive and territory-related parameters are subscripted by region (r), year (t), or both. The dotted line indicates that fourth-year birds only occupy territories when no adults are present to occupy those territories.

Model Evaluation

We derived our approach to model evaluation in part from sensitivity analysis, specifically life-stage simulation analysis (LSA; Wisdom & Mills 1997; Mills & Lindberg 2002; Gerber et al. 2004). Life-style simulation 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 matrices (input conditions) whose key components are randomly picked from a bounded uniform probability distribution. In some cases composite values are used in place of single-parameter manipulations (Wisdom & Mills 1997). Population growth rates are estimated analytically from eigenvalues. This permits consideration of relationships among parameters over a wide range of conditions.

We modified the LSA approach to suit our goal of evaluating relationships among simulated demographic parameters. First, as in classical LSA, we randomly picked 1000 sets of initial parameter values and, for each set, ran our model to completion 10 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 the proportion of territories breeding and successful from 0.5 to 1.0, for annual juvenile survivorship from 0.20 to 0.80, and for annual adult survival from 0.75 to 1.0. We evaluated the relationships among parameters by plotting different combinations of 5-year mean parameter values output from the simulations (output values) against each other. Our stochastic simulation-based approach differs and produces different results from a classical LSA that considers relationships among time-invariant input parameter values and analytically estimated λ values.

Static Analyses

Standard sensitivity analyses and model evaluation focus on population growth (λ). In conservation, however, total population size (N) often is as important as population growth. Nevertheless, because populations of birds of prey often have many nonbreeding floaters whose numbers are difficult to estimate (Hunt 1998), the size of raptor populations is almost impossible to count accurately. Thus, most monitoring focuses on estimable parameters as surrogates for population size. Because our goal was to evaluate the utility of these estimable parameters as surrogates, our analyses compared 5-year mean values of both time-specific population growth rate, λ (calculated as $N(t+1)/N(t)$) and total population size N with the 5-year mean of the following output parameters: the proportion of territories that were occupied; the proportion of territories where breeding was attempted; the proportion of territories where breeding was successful; the number of chicks produced in the reserve; the average number

of chicks produced per territory; subadult survival; adult survival; the ratio of preadult to adult birds; the ratio of breeders to preadult birds; the proportion of the breeding population made up of subadult birds.

The first five of these parameters are currently monitored at our study site. The two survivorship parameters are often cited as the most sensitive parameters in demographic models of raptors (Lande 1988; Hiraldo et al. 1996). The three other parameters have been proposed as indicators of raptor demographics in other settings (Ferrer et al. 2003; Balbontin et al. 2003).

Power to Detect Change

We evaluated the power of all parameters to detect change in population size by regressing change in monitored parameter value against time over the last 25 years of a 35-year simulation run. To understand whether change in monitored parameters accurately reflected change in population size, we compared the slopes of these regressions with those from regressions of the change in population size over the same time period (Hatfield et al. 1996). We used an F test to evaluate whether slope was significantly different than zero and we calculated the coefficient of determination (r^2) for each regression (Zar 1999). We ran the model as before (10 times for each of 1000 different initial parameter combinations) and evaluated the frequency with which the monitored parameters correctly reflected change in population size. We separately considered scenarios where the slope describing population change over 25 years was negative and significantly non-zero, where slope was positive and significantly non-zero, and where slope was not significantly different than zero.

Results

Static Analysis

Five-year mean values of the five parameters that we are currently monitoring generally had a weak relationship with, and were thus poor indicators of, 5-year means of both N and λ (Fig. 2; because proportional breeding and success rates showed nearly identical relationships to λ and N , breeding rates are not shown). Only the reserve-wide total number of chicks produced appeared somewhat linearly related to population size. Nevertheless, the great variability in possible population sizes across the range of chick production made this parameter a poor proxy for population size. No parameter was a particularly good indicator of λ , but low per-territory productivity and success rates were nearly always indicative of low λ s.

Subadult (year 2–4) survivorship had a reasonable relationship with population size, and high population sizes occurred only when the value of this parameter was high

(Fig. 3a). Nevertheless, as was the case with many other variables, high levels of subadult survivorship alone did not guarantee high population sizes and there were many cases where this parameter was high but population size

was low. Subadult survival generally had a weak relationship with λ (Fig. 3b).

Adult survival had a reasonable relationship with both population size and with λ , especially when adult survival

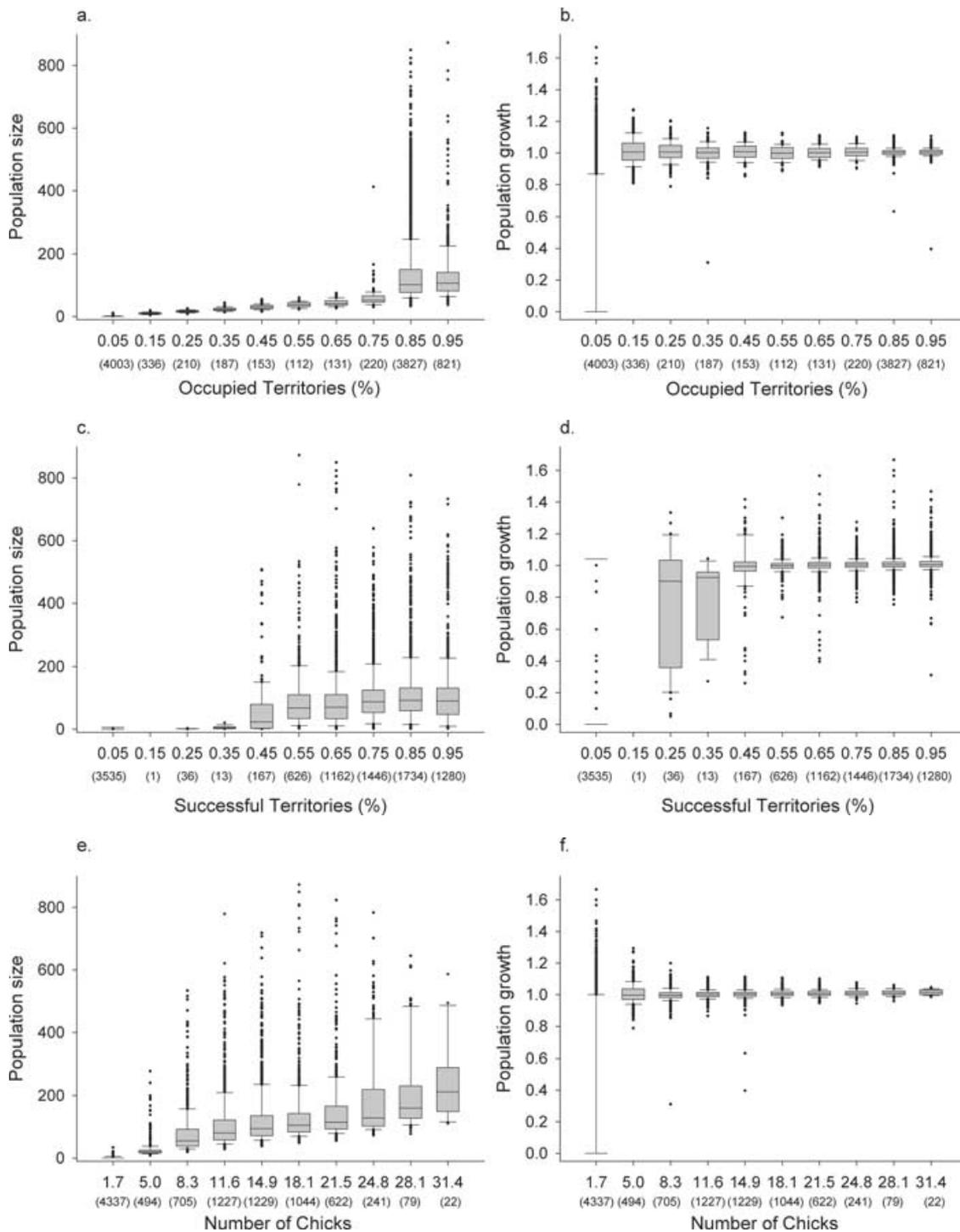


Figure 2. Relationships between 5-year means of demographic parameters currently monitored and 5-year means of population size (N) and population growth (λ) for Eastern Imperial Eagles at the Naurzum Zapovednik, Kazakhstan (static analysis, a-b). The x-axes are divided into intervals of 10% of the range of the x value. Box plots show median, first and third quartiles, 95% range, and outliers within each interval. The number of observations in each interval is shown below the x-axis.

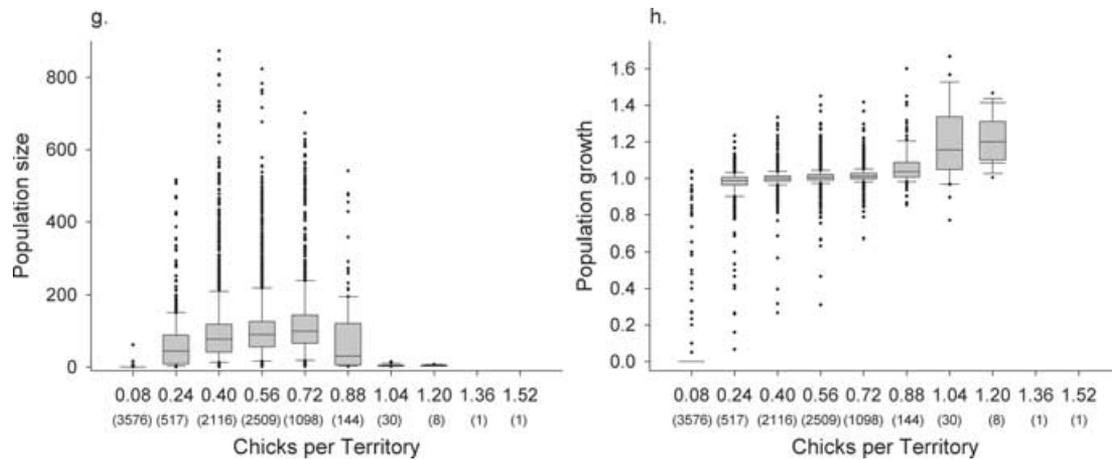


Figure 2. (continued)

was >0.70 (Figs. 3c & 3d). Below that level, populations were always small and either declining or extinct. Adult survivorship was more closely related to λ than was any other single parameter and, as survivorship values trended up, an increasing proportion of λ values was above 1. In spite of this even at the highest levels of adult survivorship, population growth rates could be below one.

The ratio of preadults to adults was reasonably well correlated with N (Fig. 4a). Furthermore, the “tail” of this distribution has less scatter than any other parameter—especially below ratios of about 1.75, where the majority of observations occurred. This ratio, however, was not especially informative of population growth, and λ values could be large or small over a range of preadult: adult ratios (Fig. 4b). The relationship between the ratio of breeders to preadults and N had a similar shape as that for the preadult:adult ratio, but the distribution is more variable and less informative (Fig. 4c). This parameter had an even poorer relationship to λ than did the adult:preadult ratio (Fig. 4d).

The proportion of breeders that were subadults was strongly related to N (Fig. 4e). There was never a subadult breeder when population size was more than 132, and the only situations in which 5% or more of the breeders were subadults occurred when total population size was <102 . Nevertheless, of 5065 model runs when average population size was >0 but <132 , subadults only rarely bred (31%). Thus, although this parameter had a good relationship with population size, it was an imperfect indicator of N because of the many situations in which subadults did not breed. The proportion of breeders that were third-year birds was weakly and inversely related to λ (Fig. 4f).

Power to Detect Change

Because we evaluated power to detect change only in situations where the slope of the regression for change in

population size was not exactly equal to zero, 9,900 to 10,000 model simulations were included for most parameters. There were only 5461 cases, however, where the slope of the proportion of breeders that were subadults was not zero. For most parameters population decline occurred in 55–56% of simulations, population increase occurred 25% of the time, and the population size remained essentially unchanged 20% of the time. Nevertheless, the total population decreased in 76% of the 5461 simulations where the proportion of breeders that were subadults changed over the 25 years of the study. Populations increased in 7% of those simulations and remained stable in 17% of simulations. Trends in the three ratios (preadult to adult; breeders to preadults; the proportion of the breeding population made up of subadult birds) were considered from two perspectives: when the trend positively correlated to trends in population size (e.g., population size increased and the value of the ratio increased) and when the trend was inverse to the trend in population size (e.g., population size increased and the value of the ratio decreased).

Most parameters that we are monitoring or that we could be monitoring were more accurate reflections of population stability or of population decline than they were of population increase (Table 1). Change in the percentage of occupied territories most accurately reflected both overall change in population size and declines in population over the 25-year period considered. The coefficient of determination for this parameter was generally high, suggesting that these regression lines fit the model data well. Of the other parameters, when population size decreased only the number of chicks produced was accurate in $>25\%$ of model runs. Increase in population size was reflected poorly by change in the potentially monitored parameters, and only negative change in the preadult to adult ratio corresponded well to increase in population size. Finally, although most parameters reasonably accurately reflected no significant change in population size, the two parameters that had the best relationships to

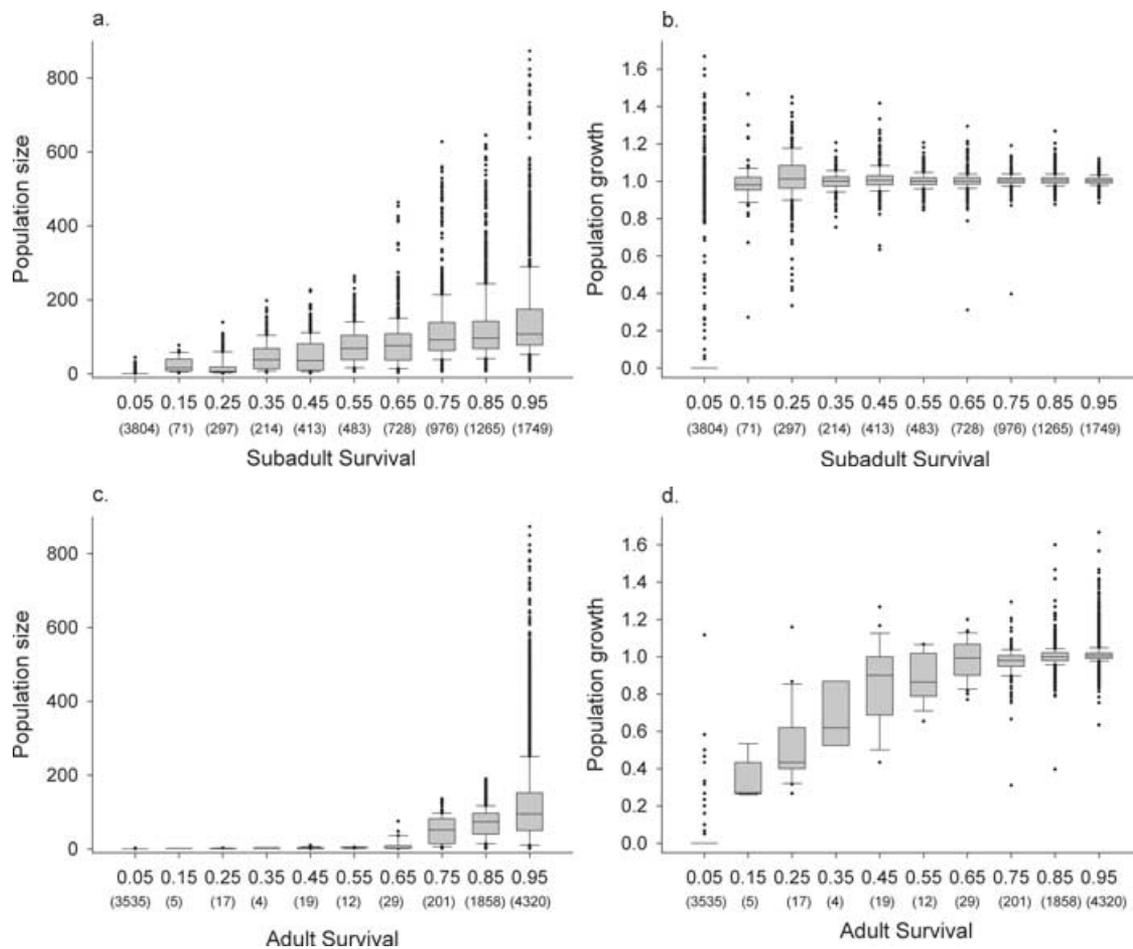


Figure 3. Relationships between 5-year means of potentially monitored demographic parameters (survivorship) and 5-year means of population size (N) and population growth (λ) of Eastern Imperial Eagles at the Naurzum Zapovednik, Kazakhstan (static analysis, a-d). The x-axes are divided into intervals of 10% of the range of the x value. Box plots show median, first and third quartiles, 95% range, and outliers within each interval. The number of observations in each interval is shown below the x-axis.

population increase and decline (proportion of territories occupied and preadult to adult ratio) most frequently incorrectly suggested change in population size when none existed.

Discussion

Our goals were to assess our current monitoring program, to try to understand what it would take to improve that program, and to put these results in a larger context that included other populations and species. We designed our approach to evaluate the effectiveness of current and potential parameters for monitoring in assessing both system state (5-year mean population size and growth rate) and change in system state (change in population size over 25 years; Yoccoz et al. 2001). To our knowledge this is the first attempt to use simulation models in this way to investigate the relative values of different approaches to monitoring.

Our static analysis suggested that currently monitored parameters are generally poor indicators of system state. Furthermore, the proportion of breeders that are subadults, a parameter that field data suggest should be useful in evaluating decline (e.g., Ferrer et al. 2003; Balbontin et al. 2003), was not a good indicator of either population size or population growth. Nevertheless, other parameters better reflected system state. The most useful among these were adult survival and the preadult to adult ratio. Incorporating either (or both) of these into our monitoring program would provide a great deal of additional information about the status of eagle populations. That these two parameters were so important is consistent with current theory, especially that derived from modeling and sensitivity analyses for a variety of raptor species (Lande 1988; Hiraldo et al. 1996; Real & Manosa 1997; Whitfield et al. 2004; Katzner et al. 2006). It is therefore all the more surprising and counterintuitive that the best indicator of long-term change in population size was the change in the proportion of territories that was occupied.

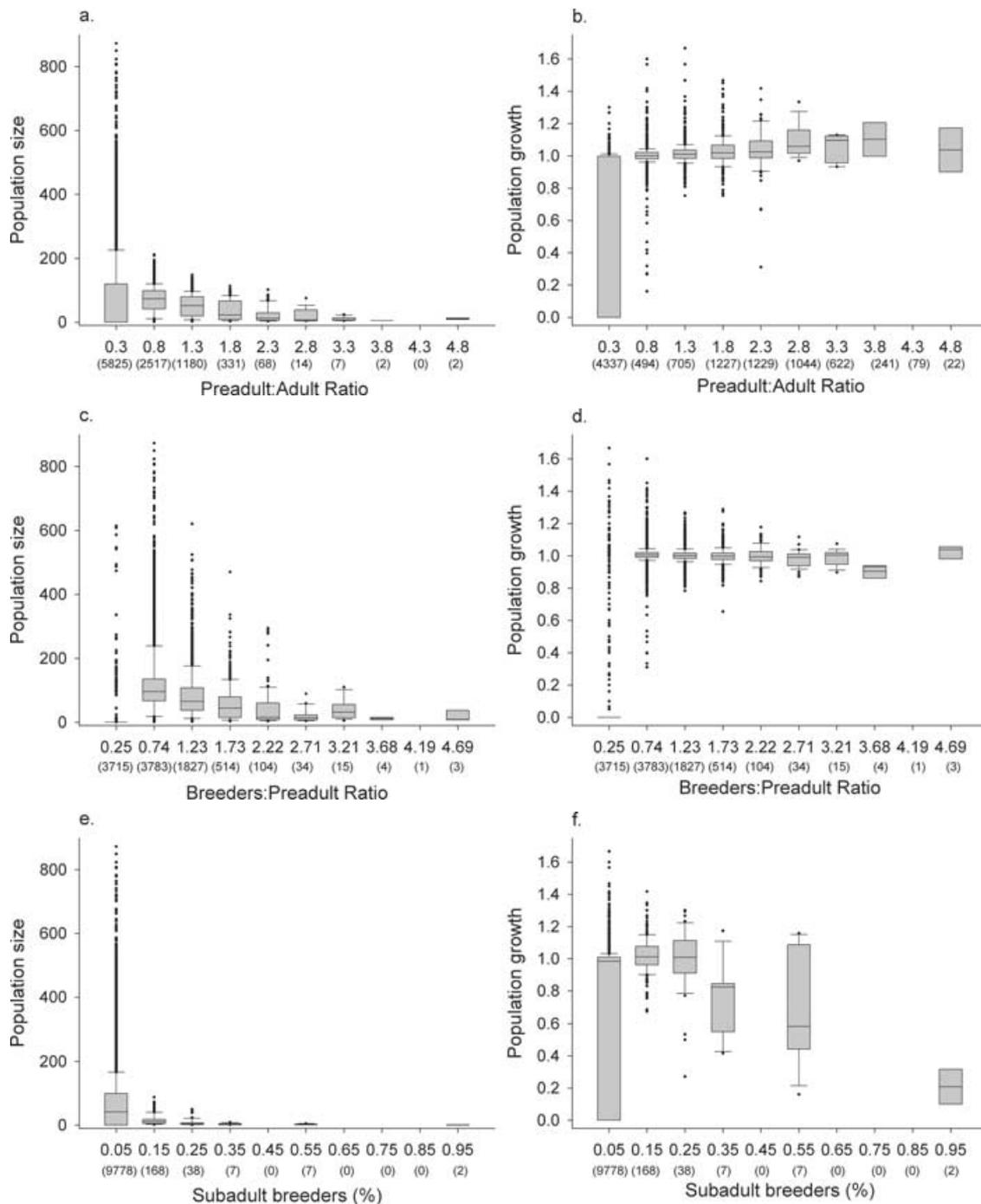


Figure 4. Relationships between 5-year means of potentially monitored demographic parameters (ratios between age classes) and 5-year means of population size (N) and population growth (λ) of Eastern Imperial Eagles at the Naurzum Zapovednik, Kazakhstan (static analysis, a-f). The x-axes are divided into intervals of 10% of the range of the x value. Box plots show median, first and third quartiles, 95% range, and outliers within each interval. The number of observations in each interval is shown below the x-axis.

Thus, although our current monitoring program provides a relatively poor snapshot of population status, it may provide a relatively good reflection of longer-term population dynamics.

These seemingly contradictory results lead us to consider a number of questions. First, why is it that field data suggest that the proportion of the breeding pop-

ulation composed of subadults may be an “early warning” of population decline, but our model shows this to be a surprisingly poor indicator of either population size, population growth, or long-term change in population size? Second, why is it that parameters such as adult survival, which perform well in sensitivity analysis and as indicators of population size, apparently have low power

Table 1. Frequency with which the slope *and* sign of the regression for change in monitored parameters corresponded with the slope *and* sign of change in modeled Eastern Imperial Eagle population size over the last 25 years of a 35-year simulation (change detection analysis).

Parameter	Percent correct of total ^a	Mean r^2	Percent correct, population decreasing ^b	Mean r^2	Percent correct, population increasing ^b	Mean r^2	Percent correct, population stable	Mean r^2
	Territories occupied (%)	0.58	0.60 ± 0.31	0.85	0.73 ± 0.19	0.11	0.29 ± 0.13	0.81
Successfully breeding (%)	0.22	0.21 ± 0.21	0.19	0.39 ± 0.16	0.03	0.21 ± 0.06	0.96	0.03 ± 0.04
Total number of chicks	0.50	0.34 ± 0.22	0.68	0.44 ± 0.16	0.04	0.22 ± 0.06	0.96	0.03 ± 0.04
Chicks per territory	0.19	0.15 ± 0.16	0.14	0.31 ± 0.12	0.04	0.21 ± 0.06	0.96	0.03 ± 0.04
Subadult survival	0.20	0.15 ± 0.13	0.16	0.26 ± 0.09	0.03	0.21 ± 0.05	0.94	0.03 ± 0.04
Adult survival	0.22	0.26 ± 0.26	0.20	0.48 ± 0.18	0.03	0.21 ± 0.05	0.95	0.03 ± 0.04
PreAd:Ad (same trend) ^c	0.19	0.25 ± 0.19	0.21	0.36 ± 0.15	0.05	0.30 ± 0.11	0.68	0.05 ± 0.05
PreAd:Ad (opposite trend) ^c	0.28	0.29 ± 0.21	0.14	0.30 ± 0.12	0.53	0.43 ± 0.18	0.68	0.05 ± 0.05
Brd:Ad (same trend) ^d	0.22	0.25 ± 0.20	0.23	0.38 ± 0.16	0.07	0.27 ± 0.10	0.82	0.04 ± 0.04
Brd:Ad (opposite trend) ^d	0.20	0.18 ± 0.15	0.11	0.28 ± 0.10	0.19	0.29 ± 0.11	0.82	0.04 ± 0.04
Subadult breeders (%; same trend) ^e	0.09	0.07 ± 0.08	0.02	0.21 ± 0.06	0.00	0.21 ± 0.06	0.91	0.04 ± 0.04
Subadult breeders (%; opposite trend) ^e	0.12	0.10 ± 0.09	0.04	0.22 ± 0.06	0.07	0.21 ± 0.06	0.91	0.04 ± 0.04

^aThe percent correct of total is the frequency with which the slope of the regression for change in parameter value accurately reflected the slope of the regression for change in population size, disregarding significance of the F test for $\beta = 0$ ($F_{0.05(1),1.23} = 4.28$).

^bSlope significantly different from 0 ($F > 4.28$).

^cRatio of preadults (PreAd) to adults (Ad), considered when the trend positively correlates to trends in population size (i.e., pop. size increases and the value of the ratio increases) and when the trend is inversely correlated to that of population size (i.e., pop. size increases and the value of the ratio decreases).

^dRatio of breeders (Brd) to adults (Ad), considered separately when trends positively and inversely correlate to trends in population size.

^eProportion of breeders that are subadults, considered separately when trends positively and inversely correlate to trends in population size.

to detect longer-term change in population size? Third, when designing monitoring, is it more important to get a moment-in-time snapshot of population size and growth or a long-term continuous picture of change in population size? The answers to these questions deal with the objectives of monitoring, with the threats to populations, and with our modeling approach and its assumptions.

To assess our monitoring we simulated population dynamics under 1000 different conditions in which we hypothesized populations may exist. These conditions were randomly picked from a uniform distribution, thus implying that all scenarios could occur with equal frequency. In reality each time and location presents different threats to birds and, thus, all causes for decline are not equally probable. In Spain, where mortality of adult territorial birds is the primary threat to Booted Eagles (*Hieraaetus fasciatus*), the relative number of subadults breeding apparently is a reliable indicator of significant population decline and, by implication, of severe depletion of the pool of nonbreeding floaters (Balbontin et al. 2003). Our results indicate that if the causes of decline are different, this ratio may be a less useful indicator of population size or decline. Therefore, because other demographic parameters provide more information than this one, subadult breeding is a poor choice for monitoring, except in those situations—such as that with the Booted Eagles—where mortality of territorial adults is certain to be a primary cause of population decline. From a broader perspective, this means that when the causes of decline

are fully known, the most effective monitoring will be that focused on demographic parameters most reflective of the life stage the decline influences.

Connecting causes of population decline and parameter behavior is also important when considering why parameters perform differently in sensitivity, static, and change detection analyses. Sudden changes in adult survivorship will almost certainly cause population decline. Nevertheless, survivorship seems most likely to resemble a categorical state variable, being relatively high in a stable or growing population and relatively low in a declining population. If this is the case, then when state changes, survivorship will jump (not gradually progress) between relative highs and lows. If adult survival is considered a state variable, it becomes clear why model outcomes can be highly sensitive to changes in adult survivorship and why adult survivorship is a very good indicator of population size but also why long-term changes in adult survivorship are a poor indicator of long-term changes in population size.

Although the specific details of our results are most relevant to species with life histories and conservation threats similar to Naurzum's eagles, our conclusions also have implications for the way monitoring is conducted more broadly, especially for other structured populations. First, our findings indicate that the most appropriate parameters for monitoring will vary, depending on the demographics and threats to the species of interest. Although this seems obvious, it is rare to see monitoring programs

devised in the context of the vulnerability to threats in each of the species' life stages (in contrast, effective management is often geared toward specific life stages). Second, if there is a poor knowledge of the threats a population faces, it is not appropriate to monitor one parameter or one life stage for one type of threat. Proactive management depends on simultaneously monitoring from multiple perspectives. Thus, classical territory-based nest monitoring, such as we conduct, is effective at capturing long-term changes in eagle demography. Nevertheless, it poorly reflects population size or growth and therefore it is slow to inform about severe change in population size caused by sudden increased mortality.

These findings can guide us toward a conceptual framework for the design of monitoring programs, for raptors and for other species, so that they are more effective. Our analysis shows that the parameters that are most informative about system state and dramatic changes to system state may be different from those best suited to inform about long-term system trends. Likewise, threats to species are not homogeneous and occur at widely varying temporal scales. Threats that have immediate-term impacts (e.g., shooting pressure on adult eagles) will rarely be captured by monitoring continuous-type variables such as occupancy rates. Threats that are long-term (e.g., habitat degradation) are unlikely to be captured by changes in continuous parameters such as adult survival that, from a demographic perspective, behaves as a categorical state variable. A prudently designed monitoring program will detect the effects of both types of threats and this requires monitoring combinations of parameters. Because the details required to capture two types of threats will vary with species, population structure, study site, and local logistical constraints and cost-benefit ratios, simulation modeling can be important in identifying which parameters are best suited to address each type of threat. Such modeling allows one to assess which data are the most appropriate to address the demographic questions of interest, and these models are relevant whether they are supported by years of field data (as was the case here) or whether demographic parameters must be estimated from closely related and better-studied species. For Naurzum's Eastern Imperial Eagles, simulation modeling suggests that prudent monitoring entails maintaining our current territory-based approach to monitor long-term population trends, but it also suggests it would be good to develop a program for monitoring of adult survivorship to keep track of sudden demographic shifts.

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