

Metrics of population status for long-lived territorial birds: A case study of golden eagle demography

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ABSTRACT

The development of “snapshot” metrics that can serve as reliable diagnostic tools for rapidly assessing population status has great appeal. We used stochastic simulation modeling and recursive partitioning to evaluate the reliability of two proposed snapshot metrics in territorial raptors: the floater/breeder ratio and the rate of nest occupancy by immature subadults. A demographic model, parameterized with field data from an intensively studied population of golden eagle (*Aquila chrysaetos*), showed that neither metric, alone or together, is a good indicator of population status. However, one snapshot metric, the floater/breeder ratio, can help predict the risk of population decline when considered in combination with other information about the population or environment that may be quickly appraised in the field or literature. Specifically, qualitative knowledge of adult survival and whether the population is limited by prey or habitat availability can help with rapid risk assessment of raptor populations.

1. Introduction

Effective conservation of biodiversity depends on reliable monitoring of population trends and accurate assessments of risk. Adaptive management often requires rapid evaluation and re-evaluation of populations, placing a premium on short-term measures of population status. Although the demographic dynamics of long-lived species are difficult to capture in rapid monitoring efforts, this is often attempted in practice. For example, cetacean population sizes are commonly estimated from shore-based censuses that last only a few months (Reilly et al., 1983); and marine turtles are generally assessed by the number of eggs, tracks, nests, and nesting females counted on a beach in one or a few days (NRC, 2010). Similarly, the North American Breeding Bird Survey relies on a series of 3-min point counts, which provide an index of abundance for many species (Link and Sauer, 1998). However, these indices cannot be used to estimate past or projected population trends without repeated sampling events over many breeding seasons or years.

Earlier work has attempted to elucidate which life-history variables most influence population growth rate. Modeling studies have shown that population growth rate is most sensitive to changes in adult survival in long-lived animals with low reproductive rates. This pattern has been detected in mammals (Heppell et al., 2000; Oli and Dobson, 2003) and birds (Sæther and Bakke, 2000; Stahl and Oli, 2006). While the population status of many long-lived species might best be assessed by

measuring adult survival, estimation of survival rates usually requires long-term human and economic investment (Hernández-Matías et al., 2011). In the management of long-lived species, the need for rapid assessments has sometimes been filled by “snapshot” metrics based on the age or stage structure of populations. However, faster is not necessarily better and it is important to ask whether snapshots are truly indicative of population status or trends (Katzner et al., 2007). Uncovering which demographic traits are useful snapshot proxies of a longer term status remains a priority in conservation practice.

Two snapshot metrics commonly presented as indicators of population status or as early-warning signals of population decline for long-lived, territorial raptors are the floater/breeder ratio and the rate of nest occupancy by subadults. In the parlance of avian biology, floaters are adult birds without breeding territories that may be recruited into the breeding segment of the population when a territory or potential mate becomes available (Penteriani et al., 2011). The floater/breeder ratio is typically considered a measure of population robustness: a high floater/breeder ratio might indicate a surplus of mature birds available to fill empty nests, and a low floater/breeder ratio might indicate insufficient survival or productivity for population persistence. Thus, all else being equal, a high floater/breeder ratio may reveal both an elevated rate of recruitment to the adult stage and a greater capacity to buffer environmental insults (Hunt, 1998; Penteriani et al., 2011). In contrast, a high incidence of subadults occupying nests is typically

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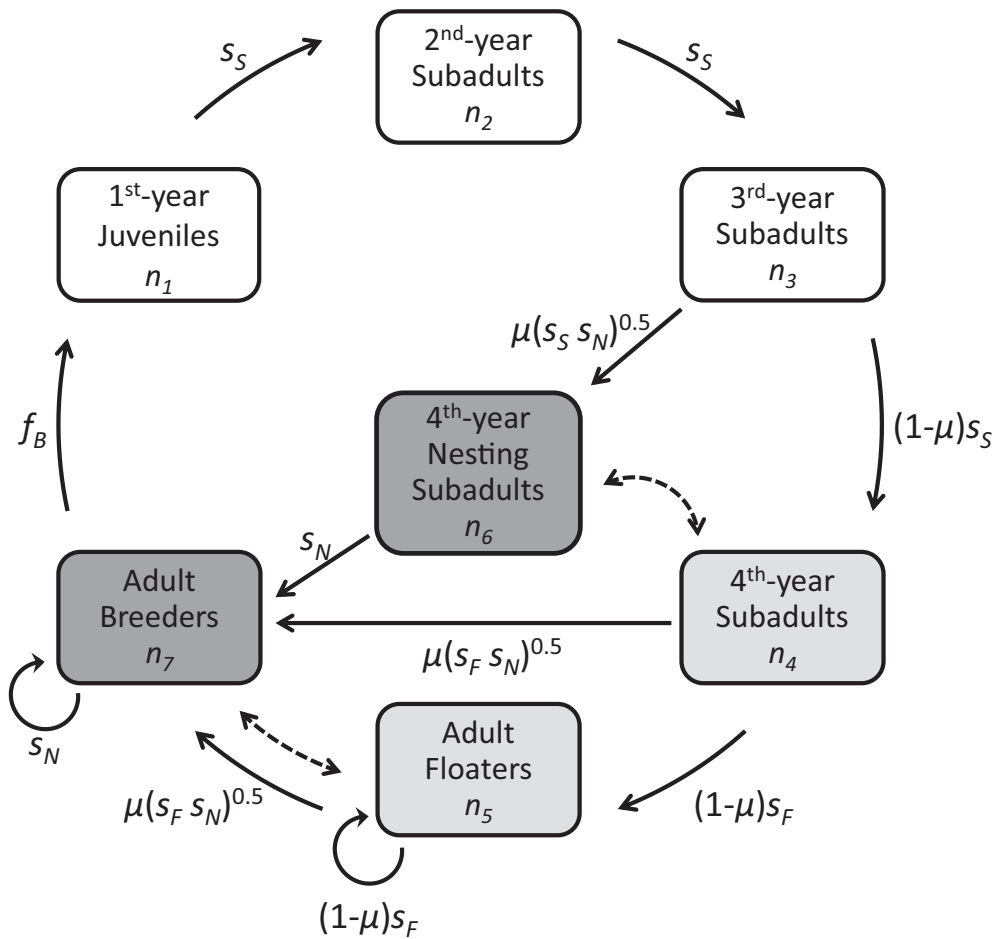


Fig. 1. Life cycle and density dependent model of golden eagle demography. Solid arrows represent annual transitions; dashed arrows represent sub-annual transitions to and from nesting (dark shade) and vagrant (light shade) stages as responses to territory availability (see text for conditional formulas). n_i : number of female eagles in stage i ; s_S, s_F, s_N : survival rates of subadults, floaters, and nesters, respectively; f_B : fecundity of breeders; μ = proportion of non-territorial adults or subadults expected to gain a territory based on current occupancy and mean breeder survival.

interpreted as a scarcity of adults and a diminished capacity to counter disturbance. Although immature individuals can occupy a territory, they usually cannot reproduce or do so with little success (Steenhof et al., 1983; Whitfield et al., 2004a). Therefore, a high incidence of subadults on nests might characterize a population in decline or at high risk of decline because it may be depleted of adult breeders and floaters (Balbontín et al., 2003; Ferrer et al., 2003).

The floater/breeder ratio and incidence of subadults on nests have been used in the assessment of golden eagle (*Aquila chrysaetos*) population status (Hunt, 1998, 2002; Whitfield et al., 2004b) and are part of an emerging adaptive management framework in the United States (Millsap and Allen, 2006; USFWS, 2009, 2011, 2016). The golden eagle is a large, territorial bird of prey that can live more than 30 years in the wild (Fransson et al., 2010), typically developing its adult plumage and reaching reproductive maturity in its fifth year (Bloom and Clark, 2001). The golden eagle is endangered in South Korea and Japan, and critically endangered in the Czech Republic (<http://globalraptors.org>). While the regional population in western North America appears to be stable (Millsap et al., 2013), some local populations are undergoing a long-term decline (Kochert and Steenhof, 2002). Golden eagles east of the Mississippi River are also declining; most breeding pairs in New England have disappeared since the late 1990s (Katzner et al., 2012). Additionally, collisions with wind turbines have caused concern that continued wind energy development may have cumulative population-level impacts (Allison, 2012; New et al., 2015). In the United States, the golden eagle is federally protected by the Bald and Golden Eagle Protection Act and the Migratory Bird Treaty Act. These laws call for

continued monitoring and adaptive management of eagles, and in practice require decisions based on short-term monitoring studies (USFWS, 2009, 2011). Long life expectancy, delayed maturity, and a territorial breeding system are characteristic of many large raptor species worldwide, making the golden eagle a useful focus for the development of models and conservation metrics that can be applied more broadly.

The objective of this study is to evaluate whether snapshots could be effective indicators of risk of population decline if combined with information that might already be known about the population or environment under various ecological scenarios. We developed a stochastic model of a stage-structured territorial life history and parameterized it with data from an intensively studied golden eagle population. We explored scenarios that are experienced by real populations of golden eagle or other raptors worldwide, such as habitat loss or expansion (Pedrini and Sergio, 2001; Whitfield et al., 2007), population recovery (Ortega et al., 2009), and prey-dependent fluctuations of reproductive output (Mcintyre and Schmidt, 2012). Insights from this study should inform the management of golden eagles, other raptors, and other long-lived, territorial animals.

2. Methods

2.1. Demographic model

We developed a stage-structured model for a territorial life history, implemented as a custom density dependence function in RAMAS

Metapop 6.0, a Monte Carlo simulation program for structured population models (Akçakaya and Root, 2013). The model framework accommodates a generic territorial life history in which one or more stages are split between territory-holders and non-territory-holders. The structure of the model enabled differentiation of vital rates and their variability between the two classes of each stage. Rates of transition between the territorial and non-territorial split stages were determined dynamically by functions of abundance and the availability of empty territories.

We built a specific instance of the model for the golden eagle life history. Golden eagle nesting pairs provide biparental care of young, but an observed male-biased sex ratio makes females the limiting sex (Hunt et al., 1998); hence we modeled only the female component of the population, as has been done in various demographic models of raptors (Hernández-Matías et al., 2013; Katzner et al., 2006; LaHaye et al., 1994; Ortega et al., 2009). The model divides the golden eagle life history into seven stages corresponding to individual status in a pre-breeding survey (Fig. 1). Golden eagles typically live one year as juveniles, 3 years as immature subadults, and become sexually mature adults in their fifth year (Bloom and Clark, 2001; Hunt et al., 1998). Floaters are adult eagles lacking a breeding territory, and breeders are adult eagles defending a territory. The model also captured the ability of fourth-year subadults to occupy a nesting territory. We considered breeders and territorial subadults as nesting stages; we considered floaters and 4th-year, non-territorial subadults as vagrant stages because birds in these stages are not settled on a territory, but immediately occupy a territory if one becomes vacant. Vagrant and nesting stages could differ in their survival rates. In this pre-breeding, annual birth-pulse model, individuals were assigned to a stage on the day before that stage ends; e.g., individuals in the juvenile stage were one year less one day old. Thus, the transition probability to the second stage was the survival rate of 2nd-year subadults. All transitions occurred immediately after a hypothetical census, except transitions to nesting stages which we assumed occurred, on average, mid-year. Survival can vary substantially between territorial and non-territorial individuals (Hunt, 2002; Whitfield et al., 2004b). Hence, individuals taking territories were assigned the geometric average of nester survival and either subadult or floater survival.

A Metapop model file with baseline parameters and the territorial density dependence function described below can be downloaded from www.ramas.com/golden-eagles.

2.2. Density dependence

In many raptors, density dependence is primarily a result of competition for a limited number of nesting territories available in the landscape (Newton, 1988; Pedrini and Sergio, 2002; Tapia et al., 2008). In our stage-based model, the transition matrix, T , included a dynamic transition rate, μ , into nesting stages such that

$$T = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & f_B \\ s_S & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & s_S & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & (1 - \mu)s_S & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & (1 - \mu)s_F & (1 - \mu)s_F & 0 & 0 \\ 0 & 0 & \mu(\sqrt{s_S s_N}) & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \mu(\sqrt{s_F s_N}) & \mu(\sqrt{s_F s_N}) & s_N & s_N \end{pmatrix}$$

where s_S is the survival rate of subadults, s_F is the survival rate of adult floaters, s_N is the survival rate of nesters (adult breeders and territorial subadults), and f_B is the fecundity of adult breeders occupying nests. We assumed nesting subadults do not reproduce. Fecundity incorporated nest productivity, sex ratio of fledglings, and juvenile survival.

We wrote density dependence functions that capture the nuanced dynamics of territoriality observed in long-lived raptors. First, to compute μ , the program calculates the total number of *nesters* (i.e., the

total abundance in nesting stages, $n_6 + n_7$) that would result with $\mu = 1$ (i.e., 100% transition to a nesting stage). If *nesters* is greater than the number of territories, K , the program iteratively reduces μ to yield *nesters* = K . To a first approximation, $\mu = 1 - \max[0, (1 - K/\text{nesters})]$. Errors arising from stochasticity or trends in vital rates and K are corrected retroactively by the direct manipulation of stage abundances, implying that territorial processes occur at a sub-annual time scale. Second, if *nesters* exceeds carrying capacity (i.e., number of territories, K), then surplus nesters instantaneously move to vagrant stages in proportion to the abundance in each nesting stage. Thus, adult breeders move to the adult floater stage and nesting subadults move to the youngest vagrant stage:

$$\text{If } \text{nesters} > K, \left\{ \begin{array}{l} n_i = n_i - \frac{n_i}{\text{nesters}}(\text{nesters} - K) \\ n_{i-2} = n_{i-2} + \frac{n_i}{\text{nesters}}(\text{nesters} - K) \end{array} \right\} \text{ where } i = 6, 7$$

Third, when there are vacant territories (i.e., *nesters* < K), vagrant eagles instantaneously move to nesting stages in proportion to the abundance in each vagrant stage, as long as there are individuals to move. Thus, adult floaters move to the adult breeder stage and 4th-year vagrant subadults move to the nesting subadult stage:

$$\text{If } \text{nesters} < K, \left\{ \begin{array}{l} n_i = n_i + \min \left[n_{i-2}, \frac{n_{i-2}}{\text{vagrants}}(K - \text{nesters}) \right] \\ n_{i-2} = n_{i-2} - \min \left[n_{i-2}, \frac{n_{i-2}}{\text{vagrants}}(K - \text{nesters}) \right] \end{array} \right\} \text{ where } i = 6, 7$$

Fourth, the annual transitions from non-nesting to nesting stages are reduced to make P_{nesters} , the projected *nesters* at the next time step, approximate carrying capacity:

$$\text{If } P_{\text{nesters}} > K, \left\{ \begin{array}{l} T_{i,j} = T_{i,j} \frac{K}{P_{\text{nesters}}} \\ T_{i-2,j} = T_{i-2,j} \left(1 - \frac{K}{P_{\text{nesters}}} \right) \end{array} \right\}$$

where $T_{i,j}$ is the element in the Leslie matrix that represents the transition probability from stage j to stage i , and

$$P_{\text{nesters}} = \sum_{j=1}^7 \sum_{i=6}^7 (T_{i,j} n_j)$$

These density dependence functions implicitly assume neither adults nor subadults have a competitive advantage in occupying vacant territories. This assumption is supported by the presence of adult floaters and subadults occupying nests in real populations of various raptors.

2.3. Demographic and environmental stochasticity

The model incorporated both demographic and environmental stochasticity to account for two sources of unpredictability inherent in all biological populations: the finite integer number of individuals that constitute a population, and the temporal variations in survival and reproductive rates (Akçakaya et al., 1999). RAMAS Metapop is a population-level model that implements demographic stochasticity using binomial random samples for survival and dispersal and Poisson random samples for fecundity (Akçakaya and Root, 2013). We modeled temporal environmental stochasticity in vital rates as lognormal with means given by the transition matrix and standard deviations defined by the corresponding elements of a matrix of the same size. Environmental stochasticity was further modeled by lognormal variation in carrying capacity. We used the “Pooled variance for survivals” advanced setting in RAMAS to avoid truncations in the simulations. See Section 2.4 for the actual values of the parameters and their standard deviations.

2.4. Parameterization of ecological scenarios

While our goals did not include the simulation of any specific golden eagle population, we parameterized a realistic model of population dynamics using data from a seven-year study of golden eagles in the Diablo Range of California (Hunt, 2002; Hunt et al., 1998). In the baseline model, we used survival rates calculated in the absence of wind turbine mortality. Survival rate of floaters and all subadult stages was 0.900, and survival rate of nesters was 0.924. Although the Diablo Range golden eagle study reported stage-specific survival rates, the authors did not report any temporal variability of survival. Hence, we parameterized environmental stochasticity by assuming a 10% year-to-year coefficient of variation in stage-specific mortality rates. Whitfield et al. (2004b) and Bekessy et al. (2009) made this same assumption in their demographic models of golden eagles and wedge-tailed eagles (*Aquila audax*), respectively.

We computed female breeder fecundity as the mean product of nest productivity (fledglings per female breeder), female fledgling sex ratio, and juvenile survival. We used annual estimates of nest productivity, but a single estimate of female fledgling sex ratio (0.366) and a single estimate of juvenile survival (0.840) from Hunt (2002). We estimated the variance in fecundity due to environmental stochasticity by removing variance due to demographic stochasticity from total observed variance, as described by Akçakaya (2002). Table 1 summarizes the demographic vital rates and their variability used in the baseline model.

We altered the baseline model assumptions to simulate a total of 12 ecological scenarios representing all combinations of six backgrounds and two levels of adult survival. The six backgrounds reflected conditions of habitat and demographic stability (the “baseline background”), habitat loss, habitat expansion, prey-limited population recovery, prey-dependent cyclical fecundity, and high fecundity (Table 2). In the habitat loss and habitat expansion backgrounds, we assumed a changing landscape in which one territory every two years was lost or gained, respectively. In the recovery background, we assumed a small founding population of 10 females, of which 5 were resident breeders and 5 were newly arriving floaters. In the cyclical fecundity background we modeled the cyclicity in reproduction due to prey abundance as sinusoidal functions of breeder productivity and juvenile survival, the two components of fecundity. Specifically, we assumed a period of 10 years, as is typical for jackrabbit (*Lepus californicus*; Steenhof et al., 1997) and snowshoe hare (*Lepus americanus*; Rohner, 1996) population cycles. The amplitude of breeder productivity was 0.26, the difference between the maximum and average productivity reported by Hunt (2002). The amplitude of juvenile survival was 0.11, the difference between average juvenile survival reported by Hunt (2002) and a minimum value assuming a 13% decrease in survival related to low prey densities (Rohner, 1996). The cyclical productivity was multiplied with the cyclical juvenile survival (in the same phase) and average female fledgling sex ratio to get a cyclical fecundity. Finally, in the high-fecundity

Table 1

Model input parameters and their estimates for the baseline background. Mean survival and reproductive rates taken from a seven-year study of golden eagles in the Diablo Range of California, USA (Hunt, 2002).

Parameter	Symbol in Fig. 1	Estimate ^a ($\bar{x} \pm SD$)
Juvenile survival	–	0.840 \pm 0.016
Subadult survival	s_S	0.900 \pm 0.010
Floater survival	s_F	0.900 \pm 0.010
Nester survival ^b	s_N	0.924 \pm 0.008
Breeder fecundity ^c	f_B	0.196 \pm 0.037

^a Environmental stochasticity was modeled by standard deviations of means of vital rates. For survival rates, $SD = 10\% \times (1 - \text{survival})$.

^b Nester survival refers to survival of breeders and 4th-year nesting subadults.

^c Breeder fecundity = nest productivity \times proportion of female offspring \times juvenile survival.

Table 2

Six backgrounds, each simulated for 50 years with 10,000 replications. Each background was simulated with high or low adult survival, for a total of 12 scenarios. Nester survival, s_N , was decreased by 3% in scenarios of low adult survival.

Background	Parameter altered	Mode of limitation
Baseline	None	Habitat-limited
Habitat loss	$K = 50 - 0.5/\text{year}$	Habitat-limited
Habitat expansion	$K = 50 + 0.5/\text{year}$	Habitat-limited
Recovery	$K - \text{nesters} = 45$	Prey-limited
Cyclical fecundity	f_B trended cyclically (see text)	Prey-limited
High fecundity	$1.2 \times \text{baseline } f_B$	Habitat-limited

background, we increased fecundity by 20% to account for a more equal female fledgling sex ratio (0.5), instead of the male-biased fledgling sex ratio observed in the Diablo Range population (Hunt, 2002).

The population in each of the six backgrounds was simulated assuming adult survival was either high or low. In the scenarios of low adult survival, we reduced s_N by 3%, consistent with the estimate of additional adult mortality in persecuted populations (Whitfield et al., 2004b). All simulations began with a carrying capacity of 50 territories varying temporally with a standard deviation of 2. All simulations started with 110 individuals at stable age distribution, except for the recovery scenario, which started with only 5 breeders and 5 floaters. We simulated each of the 12 scenarios for 50 years using 10,000 replications.

2.5. Data analysis

To assess the predictive value of the floater/breeder ratio and subadult nest occupancy on population status, we documented the risk of a 20% population decline over 50 years from the RAMAS output of each modeled scenario. This level of decline was sufficiently moderate to be observed in all scenarios. An emphasis on relatively small declines (rather than extinction) is also appropriate given the apparent long-term stability of the North American golden eagle population (USFWS, 2016). We explored the association of floater/breeder ratio or subadult nest occupancy with decline risk using conditional inference trees. Specifically, we sampled floater/breeder ratio and subadult nest occupancy in a random subset of 2000 data points from each scenario after the 10th time step to create a dataset of 24,000 points. We then used recursive partitioning to construct classification trees with risk as the response variable and floater/breeder ratio or subadult nest occupancy as a predictor variable. In initial analyses using raw risk data, we found the regression trees difficult to interpret because they were cluttered and featured branches that differentiated similar outcomes. The distribution of decline risks produced by the 12 scenarios had three distinct modes. Categorization of the data into risk levels enclosing these three modes - low risk (0–0.5), medium risk (0.5–0.8), and high risk (0.8–1.0) - divided the 24,000 samples equally among categories and produced qualitatively similar classification trees that were easier to interpret.

To assess the relative predictive value of various demographic and environmental factors simultaneously, we grew a random forest of 1000 conditional inference trees with risk category as the response variable and floater/breeder ratio, subadult nest occupancy, total nest occupancy, adult survival (high vs. low), and mode of limitation (prey-limited vs. habitat-limited) as predictor variables. We computed the relative importance of each predictor variable from the random forest using conditional permutation tests. We then constructed various conditional inference trees with floater/breeder ratio plus one or more predictor variables and evaluated the fit of each model using Cohen's kappa, a statistic that measures the agreement between the predicted risk and the true risk. This approach differs from traditional sensitivity and elasticity analyses which perturb the parameters of the transition

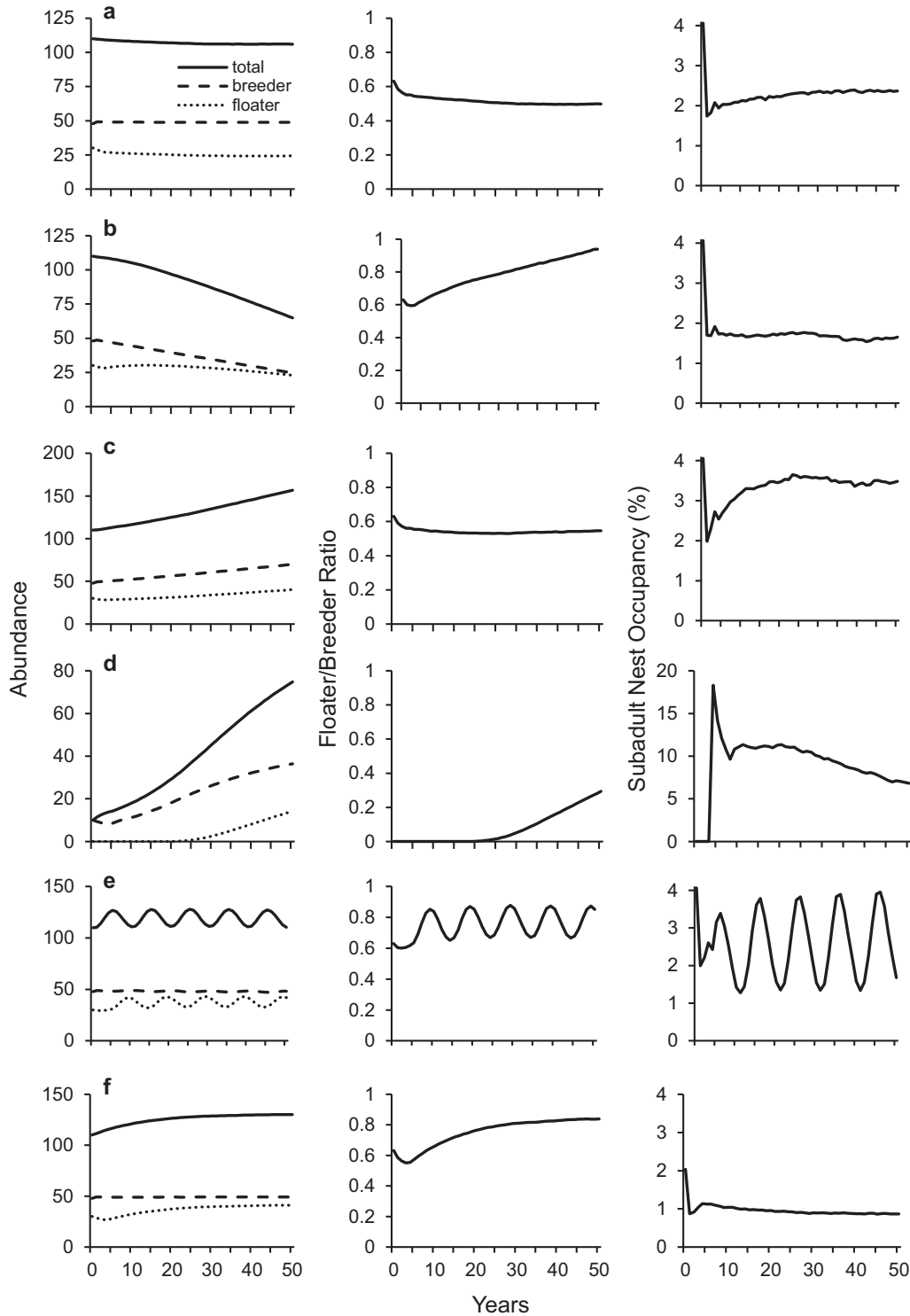


Fig. 2. Averages of 10,000 stochastic simulation replicates of a population with high adult survival in six background scenarios: a) baseline, b) habitat loss, c) habitat expansion, d) recovery, e) cyclical fecundity, and f) high fecundity. See [Methods](#) and [Table 2](#) for details of each background. Abundance (total, breeder, and floater), floater/breeder ratio, and subadult nest occupancy are plotted for each background.

matrix to examine how the population growth rate responds. Instead, our approach was to treat the demographic model output as hypothetical real-world data and then examine how observable demographic and environmental factors related to population decline. This global sensitivity test of the predictive model accounted for correlations among predictors. [Shoemaker et al. \(2014\)](#) took a similar approach, using a random forest algorithm to assess the relative importance of several environmental variables as predictors of black-footed ferret

(*Mustela nigripes*) extinction risk. The conditional inference trees and random forest were constructed using the *ctree* and *cforest* functions ([Hothorn et al., 2006](#); [Strobl et al., 2008](#)), respectively, built into the *party* package for R (R Core Team, 2016).

3. Results

The baseline scenario of habitat and demographic stability ([Fig. 2a](#))

highlighted the effect of stochasticity on projected population structure and size. Mean total abundance under stochastic simulation declined slightly from its deterministic equilibrium. This decrease was concentrated in the floater class. The reduction in non-territorial adults led to a modest decline in mean floater/breeder ratio from an initial value of 0.63 to about 0.5 after 30 years. Subadult nest occupancy stabilized at 2–3 females (2.3%) after an immediate decrease from the initial value of 4 nesting subadult females.

The habitat loss scenario (Fig. 2b) clearly demonstrated that simple snapshot metrics (i.e., floater/breeder ratio and subadult nest occupancy) are unreliable indicators of population status. The loss of breeding territories reduced population growth rate and caused a shift to floating behavior among adults. Mean floater abundance was stable for about one generation before trending downward with total population size. Despite a reduction in population growth rate and size, the floater/breeder ratio increased steadily as the number of territories decreased. Mean subadult nest occupancy remained below 2%. In exploratory simulations of more rapid habitat loss (not shown), floater abundance increased sharply as the time lag between birth and maturity cause recruitment to the adult class to decline more slowly than territories were lost. In all cases, the population became a non-reproductive pool of adults that declined due to mortality once all nesting habitat was gone. Consequently, the floater/breeder ratio surpassed unity quickly, and continued to increase sharply until there were no breeders.

Snapshot metrics were also unreliable in the habitat expansion scenario (Fig. 2c). In contrast to habitat loss, habitat expansion increased the mean number of breeders continually as territories became available. The floater class also increased, maintaining the floater/breeder ratio with little change over 50 years. Subadult nesting rose slightly to between 3 and 4 females. Additional simulations of more rapid habitat expansion (not shown), confirmed that the floater/breeder ratio could decline dramatically, potentially to zero, and subadult nesting could rise even higher, often exceeding 7%, when recruitment to the adult class was insufficient to fill the increasing number of territories.

The recovery scenario, in which conditions affecting vital rates have recently improved, was another case in which snapshot metrics fail to describe the current population trend, though they do positively indicate recent stress (Fig. 2d). At the beginning of the recovery all adults acquired territories. Consequently, the floater/breeder ratio was 0 until about the 25th year despite population growth of 3% annually. Subadult nest occupancy increased sharply after four years when the first cohort of young matured in a landscape with many unoccupied territories. Subadult nest occupancy remained relatively high, ~10%, for most of the 50-year simulation.

When reproduction followed prey cycles (Fig. 2e), total and stage-specific abundances cycled accordingly. The floater/breeder ratio oscillated between 0.6 and 0.9, while subadult nesting oscillated between 1% and 4%. Importantly, both metrics lagged the changes in prey cycles. In the case of the floater/breeder ratio, peaks in the metric corresponded with troughs in prey availability, reinforcing the lesson of the recovery scenario that snapshots in a population of long-lived individuals are likely to reflect past rather than present conditions.

When fecundity was high due to a more balanced sex ratio (Fig. 2f), the abundance of the floater class increased, thus raising the floater/breeder ratio. Due to the constant recruitment into the adult class but relative stability in the number of territories, the rate of subadult nesting remained low at about 1% throughout the 50-year simulation. In this scenario, a growing population was associated with a high floater/breeder ratio and a low subadult nest occupancy rate.

Repeating the above simulations but with a lower survival rate substantially increased the risk of decline in all scenarios, except the habitat loss scenario, which already was almost guaranteed to decline (Table 3). The recursive partitioning analysis revealed that a high floater/breeder ratio ($FBratio > 0.94$) is mostly associated with high

Table 3

Risk of 20% decline for each combination of background and adult survival (s_w), based on 10,000 replications. Shading indicates level of risk: no shading = low risk, light gray = medium risk, dark gray = high risk.

Background	s_{yhigh}	s_{ylo}
Baseline	0.537	0.988
Habitat loss	0.999	1.000
Habitat expansion	0.163	0.765
Recovery	0.209	0.471
Cyclical fecundity	0.545	0.989
High fecundity	0.057	0.629

risk of decline, and an absence of floaters (i.e., $FBratio = 0$) was associated with low risk of decline (Fig. 3a). This is because the floater/breeder ratio was highest in the habitat loss scenarios, in which breeders lost their territories and were relegated to the floater stage, and maturing subadults were unable to acquire territories and became floaters. Also, the lack of floaters was a phenomenon only observed in the recovery scenarios, in which floaters did not appear until the 25th year of the simulation when all the territories were occupied. Intermediate values of the floater/breeder ratio ($0 < FBratio < 0.94$), which characterized the majority of observations, were not associated with any particular risk category. The single-variable regression using subadult nest occupancy as a predictor revealed that a high incidence of subadult nesting ($SubNest > 12\%$) is associated with low risk of decline (Fig. 3b). This is because subadult nesting was highest in the low-risk recovery scenarios (Fig. 2d, Table 3). The vast majority of observations maintained subadult nesting rates of $< 12\%$, but these typified scenarios of low, medium, and high risk in equal proportions.

Growing a forest of 1000 random conditional inference trees allowed us to evaluate the relative importance of several predictor variables that may be known about a population, as well as the relative goodness of fit of models with various combinations of predictor variables. Adult survival was the most important variable in predicting risk of decline, followed by mode of limitation, floater/breeder ratio, and total nest occupancy (Fig. 4a). Subadult nest occupancy had little predictive value. Accordingly, the models that most accurately predicted the three levels of risk were the models with the three or four most important predictor variables (Table 4). The models that only had floater/breeder ratio and subadult nesting alone or together performed well in predicting medium-risk scenarios, but performed poorly in predicting low- and high-risk scenarios. The addition of subadult nesting to floater/breeder ratio actually worsened the ability to predict a high risk of decline. The addition of adult survival greatly augmented the predictive ability of the floater/breeder ratio for low- and high-risk scenarios. Incorporating mode of limitation and total nest occupancy as variables further enhanced the predictive ability of the model, especially for medium-risk scenarios. Fig. 4b illustrates the best-fitting model with the four most important predictor variables. It shows that the interpretation of snapshot information depends on context. For instance, consider a population with high adult survival. With a low floater/breeder ratio (≤ 0.19), the population is very likely at low risk of decline. Meanwhile a high ratio (> 0.67) indicates that decline risk is quite uncertain. With low adult survival, the floater/breeder ratio is not informative; under prey limitation it is not a predictor and under habitat limitation the population is at a moderate to high risk of decline irrespective of ratio (Fig. 4b). Total nest occupancy as a metric of risk is even more contextual, adding value only when adult survival is low and the population is prey-limited (Fig. 4b).

4. Discussion

We find that the floater/breeder ratio and the rate of subadult nest occupancy as snapshot metrics are not by themselves useful measures of population health or reliable predictors of risk of decline. These snapshots must be combined with other information to be useful. Adult

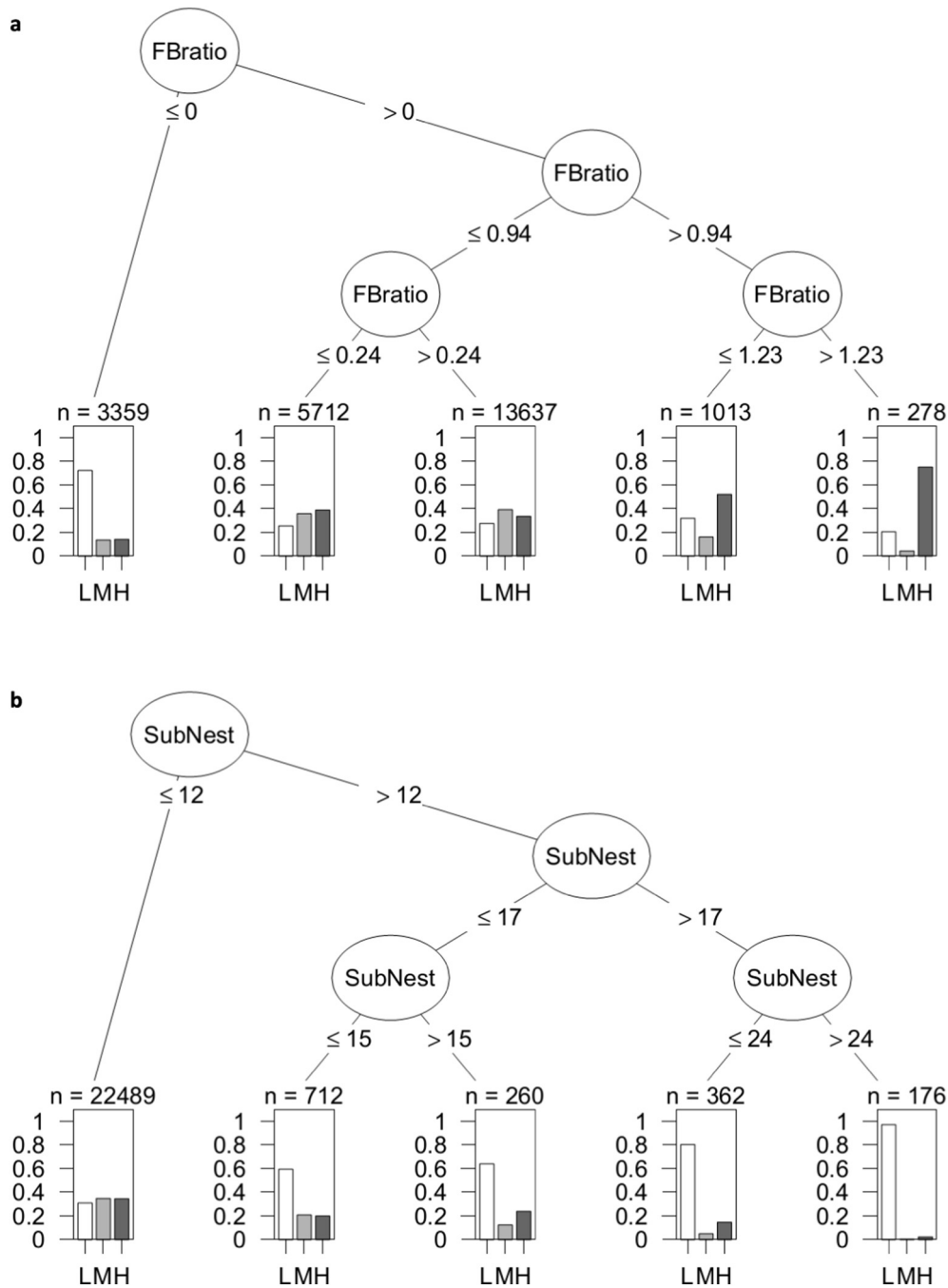


Fig. 3. Conditional inference trees with (a) floater/breeder ratio (FBratio), and (b) subadult nest occupancy (SubNest) as individual predictor variables of population status. Frequency plots at tips of trees correspond to three levels of risk: L = low, M = medium, H = high (see text). n = number of observations meeting conditions of the branches.

survival is of primary importance in accurately assessing the risk of decline (Fig. 4). This is consistent with theoretical and empirical work on various other bird species (Hernández-Matías et al., 2013; Katzner et al., 2007; Lande, 1988; Newton et al., 2016; Ortega et al., 2009; Stahl and Oli, 2006; Tauler et al., 2015; Whitfield et al., 2004b). Adult survival in our simulations was a binary variable: high or low. As such, it was not sufficient to parse three levels of decline risk. Thus, anecdotal evidence for low or high adult survival may not on its own permit accurate assessments of risk. For instance, the risk of decline can be low or high in a scenario of low adult survival, depending on the mode of population limitation and total nest occupancy (Fig. 4b). However, its high importance in our models demonstrates that even a relative and qualitative understanding of adult survival should be considered when interpreting snapshots of population size and structure. In the starkest

example from our simulations, adult survival reverses the meaning of a low floater/breeder ratio: the raptor population with a low floater/breeder ratio is at low risk under high adult survival, but at medium or high risk under low adult survival. Overall, our best-fit model emphasizes that combining other information, such as the mode of population limitation and a snapshot of total nest occupancy, can help improve the assessment of population health (Fig. 4b).

A floater/breeder ratio of one has been proposed as a threshold above which a population is healthy, stable, and buffered against declines (Hunt, 1998; Hunt and Hunt, 2006; Penteriani et al., 2011). But under the assumption of this rule of thumb, a high floater/breeder ratio can give a false sense of security when the population is actually declining (Fig. 2b). Conversely, a low floater/breeder ratio can give a false sense of alarm when the population is actually expanding or recovering

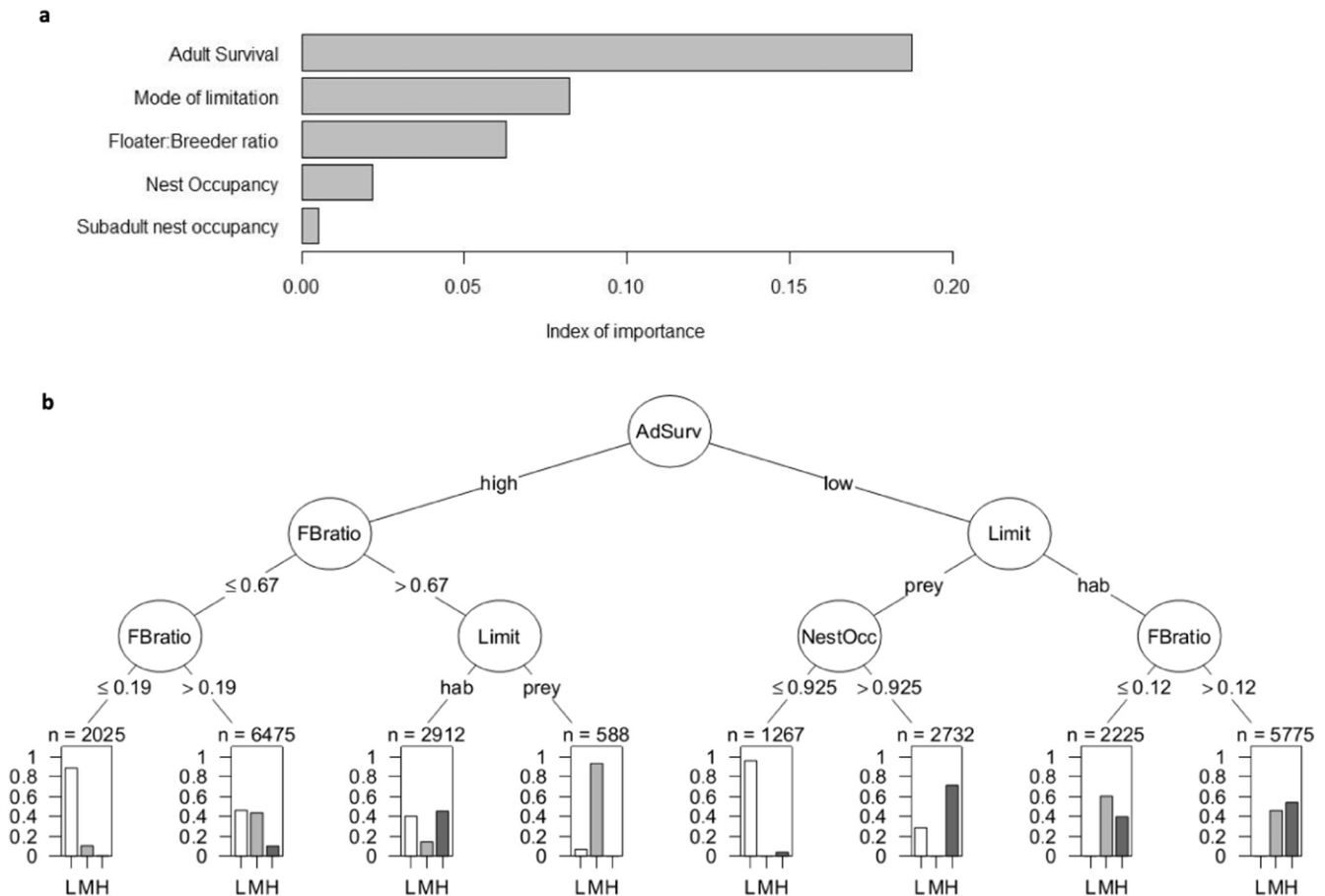


Fig. 4. (a) Index of relative importance of predictor variables, assessed from a forest of 1000 random conditional inference trees. (b) Conditional inference tree of the best model with adult survival (AdSurv), mode of limitation (Limit), floater/breeder ratio (FBratio), and total nest occupancy (NestOcc) as predictor variables, and risk category as response variable. Frequency plots at tips of tree correspond to three levels of risk: L = low, M = medium, H = high (see text). n = number of observations meeting conditions of the branches.

(Fig. 2c–d). Our model shows that a recovering population may be completely lacking in floaters for many years until all suitable territories are occupied. It also demonstrates that there need not be as many floaters as breeders in a stable population (Fig. 2a).

A snapshot of the floater/breeder ratio may also not be an easy measure to obtain. Few attempts have been made to empirically appraise the size of the non-breeding component of bird populations. Kenward et al. (2000) estimated the breeding rate (breeders/total) of a population of common buzzards (*Buteo buteo*) and found that non-breeders were 3 to 5 times more prevalent than breeders, but this ratio of non-breeders to breeders is not equivalent to the ratio of adult floaters to breeders because the authors included juveniles and

subadults in the tally. When the floater/breeder ratio has been characterized, it has not been diagnostic. In a population of Eurasian sparrowhawk (*Accipiter nisus*), the number of female floaters fluctuated greatly from year to year, but averaged 0.28 per female breeder, a low ratio that suggests high risk of decline by its traditional interpretation, yet the population remained stable over a 20-year period (Newton and Rothery, 2001). We conclude that there is no empirical or theoretical basis for supposing that a healthy population of territorial birds should have one or more floaters for every breeder.

We acknowledge that the floater segment can buffer a population from extinction risk and that an imminent or ongoing population decline may go unnoticed in the absence of information on the dynamics

Table 4

Ability of single or multiple variables to accurately predict a population's risk of decline in a nonparametric, tree-structured regression model. FBratio = floater/breeder ratio, SubNest = subadult nest occupancy, NestOcc = total nest occupancy, Limit = mode of limitation (habitat or prey), AdSurv = adult survival (high or low). Models are sorted by increasing weighted Kappa, a statistic that measures the agreement between the predicted risk and the true risk.

Predictor variables in regression model	Proportion correct prediction of risk			Kappa	
	Low	Med	High	Unweighted	Weighted
SubNest	0.13	0.98	0.00	0.05	0.07
FBratio + SubNest	0.30	0.91	0.11	0.16	0.19
FBratio	0.30	0.67	0.37	0.17	0.20
FBratio + NestOcc	0.25	0.97	0.12	0.17	0.21
FBratio + Limit	0.30	0.84	0.39	0.26	0.25
AdSurv	0.75	0.00	0.75	0.25	0.33
FBratio + AdSurv	0.87	0.00	0.77	0.32	0.43
FBratio + AdSurv + Limit	0.77	0.24	0.78	0.39	0.46
FBratio + AdSurv + Limit + NestOcc	0.75	0.24	0.80	0.39	0.46

of floaters (Penteriani et al., 2011; Penteriani et al., 2006). For example, a traditional territory-based survey may fail to detect a decline due to adult mortality because nest occupancy would consistently be high until the floater buffer is depleted. Adult survival in long-lived, territorial species is usually high, but human sources of mortality may disproportionately affect adult breeders (e.g., poisoning, shooting, or trapping of nesters; Whitfield et al., 2004a, 2004b) or adult floaters (e.g., wind turbine collisions; Hunt, 2002). If such a mortality-related population decline is sustained, the floater segment will be the first to disappear (Wilcove and Terborgh, 1984). However, our results show that the floater segment is the last to disappear if the decline is caused by a sustained loss of habitat (Fig. 2b).

The rate of subadult nest occupancy is also not, by itself, an accurate diagnostic tool of population status. Ferrer et al. (2003) considered > 10% of immature breeders as an early warning signal that anticipates population decline. But under the assumption of this other rule of thumb, a low rate of immature nesting may give a false sense of security when the population is actually declining (Fig. 2b). Conversely, a high proportion of subadult nesters may characterize a healthy, recovering population (Fig. 2d). Indeed, during the recovery of the Spanish imperial eagle (*Aquila adalberti*), the periods of population increase coincided with high values (> 10%) of subadult nesting (Margalida et al., 2008; Ortega et al., 2009). During the recovery of an Italian golden eagle population, 4.5% of territorial pairs involved one subadult (Fasce et al., 2011). Long-term monitoring of Bonelli's eagles (*Hieraetus fasciatus*) in southern Spain has shown that the population remained stable despite a sharp increase in the frequency of territory occupation by subadults (Balbontín et al., 2003). In the Scottish population of golden eagles, which is often subject to persecution, subadult nesting increased from 7.2% to 9.3% in a decade, yet the population remained stable (Whitfield et al., 2004a, 2004b). The results from these field studies of various species of long-lived raptors, and of modeling efforts (this study and Katzner et al., 2007) do not support the hypothesis that a high rate of subadult nesting can be interpreted as a reliable early-warning signal of imminent population decline (Ferrer et al., 2003). The utility, if any, of subadult nesting as a diagnostic tool of population status depends on the overall context. For example, subadult nest occupancy alone does a good job at predicting medium risk of decline (Table 4). Also, the ratio of subadult to adult nesters may be used to indirectly estimate adult survival in one breeding season, as long as the bias in the method is corrected (Hernández-Matías et al., 2011).

5. Conclusion

The logic behind snapshots as indicators of future risk to a population relies on the assumption of a largely static environment at equilibrium (Hunt, 1998). However, stochastic modeling suggests that the snapshot metrics we evaluated – floater/breeder ratio and subadult nest occupancy – can be misleading or indiscriminate indicators of long-term trends in raptor populations. It is not possible to know, for instance, how many floaters there should be per breeder without some knowledge of the vital rates of the population and trends in habitat availability. Even if the complete schedule of survival and fecundity can be estimated or borrowed from other studies, the relationship between stage structure and population status is obscured by environmental variation or trends.

In conclusion, assessments of raptor populations should not rely solely on the ratio of adult floaters to breeders or on the rate of nest occupancy by subadults. The utility of these snapshot measures can be greatly enhanced with qualitative knowledge of adult survival and mode of limitation, which themselves may be appraised rapidly. For example, Hernández-Matías et al. (2011) showed how adult survival in age-distinguishable territorial birds may be rapidly and reliably estimated in one or two breeding seasons. While these measures should be especially useful in short-term monitoring, ultimately, there is no substitute for longitudinal studies that aim to derive accurate estimates of

the means and temporal variations of vital rates. Yet, snapshots and qualitative knowledge may be the best information available to managers facing time-sensitive decisions and may have a role in the regulatory permitting of take associated with development activities such as wind energy projects.

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