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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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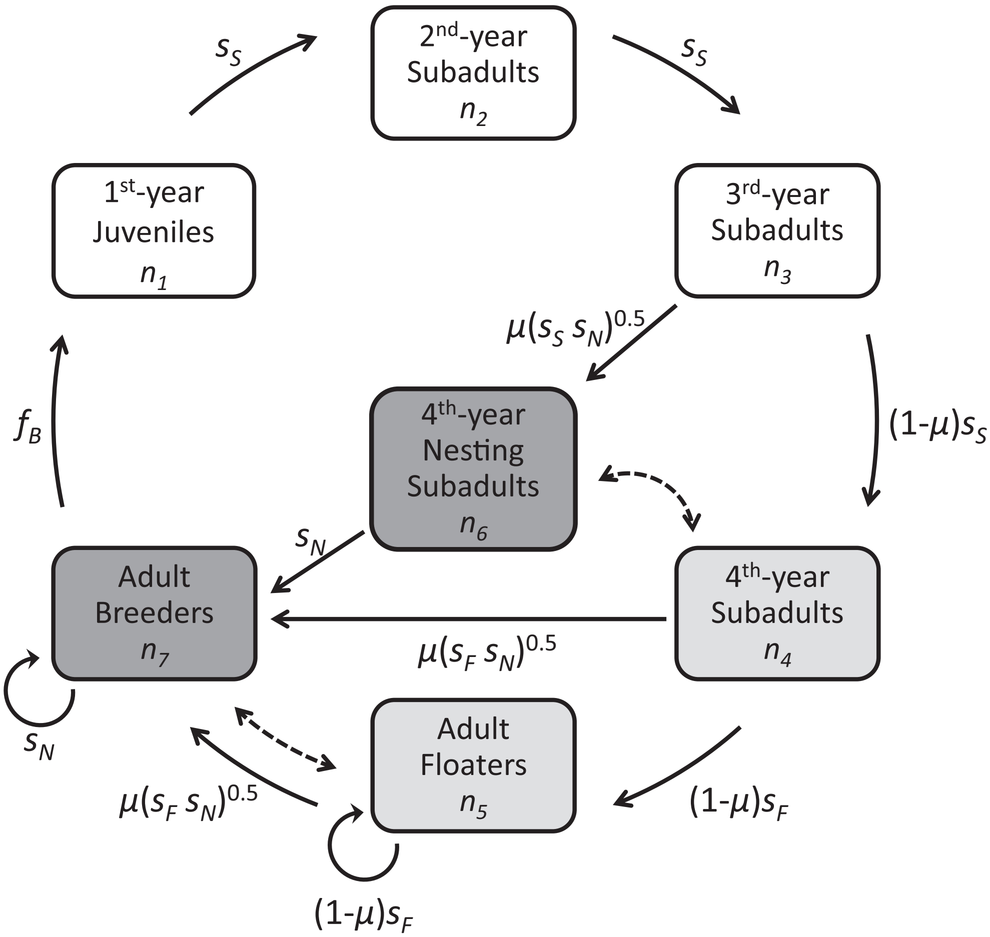

Fig. 1. Life cycle and density dependent model of golden eagle demography. Solid arrows represent annual transitions; dashed arrows represent sub-annual transitions to and from nesting (dark shade) and vagrant (light shade) stages as responses to territory availability (see text for conditional formulas). 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