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Estimating Raptor Nesting Success: Old and New Approaches

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Abstract

Studies of nesting success can be valuable in assessing the status of raptor populations, but differing monitoring protocols can present unique challenges when comparing populations of different species across time or geographic areas. We used large datasets from long-term studies of 3 raptor species to compare estimates of apparent nest success (ANS, the ratio of successful to total number of nesting attempts), Mayfield nesting success, and the logistic-exposure model of nest survival. Golden eagles (*Aquila chrysaetos*), prairie falcons (*Falco mexicanus*), and American kestrels (*F. sparverius*) differ in their breeding biology and the methods often used to monitor their reproduction. Mayfield and logistic-exposure models generated similar estimates of nesting success with similar levels of precision. Apparent nest success overestimated nesting success and was particularly sensitive to inclusion of nesting attempts discovered late in the nesting season. Thus, the ANS estimator is inappropriate when exact point estimates are required, especially when most raptor pairs cannot be located before or soon after laying eggs. However, ANS may be sufficient to assess long-term trends of species in which nesting attempts are highly detectable.

Keywords

American kestrel; *Aquila chrysaetos*; *Falco mexicanus*; *Falco sparverius*; golden eagle; nest survival; nesting success; population monitoring; prairie falcon; raptors

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Nesting success is an important component of avian population dynamics (Johnson 2007a), and studies of nesting success can be valuable in assessing the status of bird populations and factors that influence them (Steenhof and Newton 2007). Increasing concerns about many raptor populations are renewing focus on their monitoring and management, yet assessment of raptor nesting success may not always be straightforward. Raptor monitoring protocols differ from those of ground-nesting birds in that many raptor nests are observed remotely, and investigators check raptor nests less often (sometimes only 2-3 times each season) because of logistical constraints and to minimize disturbance. Frequently, nesting success has been estimated as the raw proportion of raptor pairs that were observed to raise young to the age of fledging (Steenhof and Newton 2007).

However, avian ecologists have long been aware that simple ratios of successful to total nesting attempts detected (apparent nest success, or ANS) can be biased upwards if nesting attempts found late in the nesting stage are included in the calculations (Mayfield 1961, 1975, Johnson and Shaffer 1990). Nesting attempts discovered during the later stages of nesting are more likely to survive to the end of the nesting period simply because they have less time to fail (Johnson 2007b). Therefore, one strategy for avoiding bias is to apply the apparent estimator only to nesting attempts found at the onset of the breeding season (Steenhof and Kochert 1982, Johnson 2007b). The disadvantage of this approach is that sample sizes may be severely restricted and useful information omitted from consideration. Detection probabilities of nesting attempts are often unequal in raptors: unsuccessful pairs of many raptor species are less likely to be detected than successful pairs, as raptor nests with young are usually easier to locate because of audible vocalizations from the young and defending adults, or because of conspicuous fecal matter (whitewash) around the nest (Newton 1979:129, Steenhof and Newton 2007). We therefore might expect that ANS estimates from many raptor monitoring protocols overestimate nesting success because of these unequal detection probabilities, but this error may not be problematic when assessing long-term trends if the bias is predictable and consistent over time.

Mayfield (1961) developed an approach to estimate nesting success that incorporates data from nesting attempts detected at various (and sometimes unknown) stages of the nesting cycle. Mayfield's method calculates daily nest survival (DSR) during the time that a nest is under observation. Nesting success can then be calculated by assuming that DSR is the same for all nests and all days (Johnson 2007a). Many raptor studies have incorporated the Mayfield approach into their assessments of nesting success (e.g., VanCamp and Henny 1975, Barber et al. 1998, Griffin et al. 1998, Lehman et al. 1998).

Recently, more sophisticated models have been developed to estimate nest survival (Rotella et al. 2004, Shaffer 2004, Johnson 2007a, Schmidt et al. 2010). Unlike Mayfield's method, the newer nest survival models can include many categorical and continuous covariates and allow evaluation of the importance of a variety of spatial and temporal factors that might affect nest survival. Nest survival models also allow competing models to be assessed via likelihood-based information-theoretic methods (Akaike 1973, Burnham and Anderson 2002). If nest initiation dates (and therefore what modelers call nest ages; Shaffer 2004) can be estimated, nest survival models can provide insights into within-season variation in nest survival because they do not require Mayfield's assumption of constant daily survival

throughout the nesting period. Thus far, the newer nest survival models have been used mainly for waterfowl, shorebirds, and passerines that nest on or near the ground (Dinsmore et al. 2002, Jehle et al. 2004, Rotella et al. 2004, Shaffer 2004). To date, relatively few, mostly short-term, intensive studies of raptors have used nest survival models (Lantz and Conway 2009, Martin et al. 2010, Briggs et al. 2011, Brown and Collopy 2012, McIntyre and Schmidt 2012).

Thus far, long-term trends in raptor nesting success have not been evaluated with nest survival models such as logistic-exposure models or Program MARK. Not all long-term and large-scale raptor monitoring programs have collected and tabulated the data required for this approach. The nest survival models require, at a minimum, the date a nesting attempt was found and its status on that date, the last date the nesting attempt was checked and its status on that date, and the date the nest was last known to be viable if it had failed by the last check. For these reasons, adapting nest survival models to legacy raptor nesting studies presents challenges not typically encountered in studies of other taxa.

We used data from long-term studies of 3 species of raptors to compare apparent nesting success with estimates based on the Mayfield method and a more recent model of nest survival (Shaffer 2004). We selected the logistic-exposure nest survival (Shaffer model) because the approach is general and can be implemented with any software that allows user-specified link functions in generalized linear models (e.g., SAS, R). The methods we used to monitor reproduction were typical of approaches used to survey birds of prey (Steenhof and Newton 2007). The 3 species we studied, golden eagles (*Aquila chrysaetos*), prairie falcons (*Falco mexicanus*), and American kestrels (*F. sparverius*), differ in their breeding biology, and we used different methods to monitor reproduction in each species (Table 1). Our golden eagle surveys were typical of extensive aerial surveys that are used to monitor species with large, conspicuous nests and predictable nesting locations (Boeker 1970, Carrier and Melquist 1976, Fraser et al. 1983, McIntyre and Adams 1999). Prairie falcon surveys represented studies of species with inconspicuous nesting locations; nesting attempts were found throughout the nesting season, often in nestling stage rather than during incubation. Kestrel studies were typical of more intensive studies that involve frequent checks of species with highly detectable nests in boxes.

Our objective was to identify opportunities and limitations of using nest survival models to monitor raptor nesting success and to identify situations when old and new approaches are acceptable or inappropriate. Although model-based approaches can incorporate covariates, we analyzed our data without considering any covariates other than annual variation to simplify comparisons with annual estimates of apparent nest success. To the best of our knowledge, this is the first methodological review of nesting success estimation for raptors since Steenhof and Kochert (1982).

Study Area

We conducted our studies in southwestern Idaho, USA. We restricted our dataset to years in which we had consistent survey methods and reasonable sample sizes for the species in question: 1982–2005 for golden eagles; 1975–1987, 1990–1994, 1997, 2002–2003 for

prairie falcons; and 1992–2005 for American kestrels. We surveyed cliff-nesting golden eagles in the Morley Nelson Snake River Birds of Prey National Conservation Area (NCA; 42° 50′ N, 115° 50′ W) and an adjacent Comparison Area (U.S. Department of the Interior 1979). We surveyed prairie falcons on cliffs within the NCA, and monitored American kestrels in nest boxes within a 1000-km^2 study area (Steenhof and Peterson 2009) just north of the NCA (43° N, 116° W).

Methods

Field Procedures

Previous researchers had identified nearly all of the 56 golden eagle nesting territories when our study began (Hickman 1968, Beecham Jr. 1970, Kochert 1972). To evaluate golden eagle nesting success each year, we surveyed all known nesting territories from a Bell 206 Jet Ranger helicopter (Bell Helicopter, Hurst, TX) in late March and again in late May or early June. We used the first survey to determine if territories were occupied and if adults were incubating, and the second to assess the age and number of young in territories where we found incubating birds. We surveyed territories from the ground if we could not ascertain occupancy or breeding status during the first flight or if young had not reached 51 days of age during the second flight (more details of protocol in Steenhof et al. 1997). We surveyed nesting cliffs from a helicopter approximately 10–75 m from the cliff at speeds of 30–65 km/hr. Occasionally we hovered approximately 10–30 m from nests for 5–15 sec to view nest contents. We never attempted to flush incubating birds or count eggs.

The prairie falcons we studied nested in inconspicuous cavities on large cliffs at very high densities (Steenhof et al. 1999), and we did not have the resources to sample the entire population each year. Our sample included nesting attempts selected for intensive study prior to or early in the nesting season as well as nesting attempts found incidentally during occupancy surveys and other research activities. We approached and inspected some nesting sites for eggs, young, prey remains, or other signs of reproductive activity; we observed others only from a distance. We identified prairie falcon nesting attempts while walking along the canyon rim or below cliffs and during monthly 2-hour bouts at observation points in standardized 1-km segments of the canyon floor (see Steenhof et al. 1999 for details). Before each nesting season, we identified 20-50 nesting territories known to have been occupied in previous years. We tried to locate pairs at these “pre-selected” territories during courtship, ascertain their status when most pairs are typically incubating, and observe them as often as necessary to determine the fate of their nesting attempt. The nesting attempts in pre-selected territories comprised approximately 10-25% of all nesting attempts each year

We studied kestrels nesting in approximately 125 boxes in agricultural, rangeland, and rural residential habitats (Steenhof and Peterson 2009). Each year we checked all nest boxes in March, and re-visited all boxes in April, May, and June to check for occupancy and incubating birds. We re-visited boxes with kestrel eggs or young as often as necessary (1-10 times) to capture adults, age and band young, and ascertain the fate of each nesting attempt. We inspected all boxes while standing on a ladder.

General Terminology

Our evaluation included only those nesting pairs that we suspected laid at least 1 egg and thereby initiated a "nesting attempt" in a given year. We excluded known re-nesting attempts from all analyses. We confirmed viable nesting attempts by observing fresh eggs, live young, or an adult in incubating or brooding position. For prairie falcons, we also confirmed nesting attempts to be viable if we recorded an adult inside a nesting cavity for ≥1 hour.

We estimated the length of the nesting period for each species based on data in the literature on pre-laying behavior, egg-laying intervals, modal clutch size, incubation period, and ages at fledging (Table 1). The nesting period for prairie falcons and American kestrels began with laying of the first egg. The nesting period for golden eagles included a 5-day pre-laying period because golden eagles typically assume incubation posture 5 days before laying their first egg (Ellis 1979). The nesting periods for all species ended when at least one young reached a minimum acceptable fledging age (Steenhof and Newton 2007; i.e., 80% of the age at which young typically leave their nest of their own volition): 51 days for golden eagles, 30 days for prairie falcons, and 22 days for American kestrels (Steenhof 1987). We estimated nestling ages using aging keys (Hoechlin 1976, Moritsch 1983, Griggs and Steenhof 1993) and assigned median hatching dates to all broods based on nestling ages. We considered the status of a nesting attempt at the end of the nesting period to be its fate. We considered daily nest survival (DSR) to be the probability that a nesting attempt would survive a single day (Dinsmore et al. 2002), and defined nesting success as the proportion of nesting attempts that raised at least 1 young to the minimum acceptable age for fledging (Steenhof and Newton 2007).

Data Analysis

We defined apparent nest success (ANS) as the number of successful nesting attempts divided by the total number of nesting attempts with known fates. We calculated ANS on three subsets of data for each species. The first set, typical of most raptor surveys, included all nesting attempts with known fates. The second dataset included only nesting attempts confirmed during incubation, an approach recommended by Steenhof and Kochert (1982) to reduce the bias induced by including nesting attempts found late in the nesting season. The third dataset was most similar to the dataset used for the logistic-exposure and Mayfield models in that it included only those nesting attempts for which the viability of the attempt was checked at least once after nest discovery. We calculated standard errors and confidence intervals using the normal approximation for the binomial distribution, that is, the square root of $(p(1-p))/n$, where p is the proportion of successful nesting attempts and n is the sample size (full set or year, depending on analysis).

The datasets used for the Mayfield and logistic-exposure analyses did not include every date a nest was checked and determined to be viable because our datasets were created before the requirements of the new models were known, and not all nest visits were transcribed from the original hand-written field notes to the computer database. We recorded information required by the Mayfield method: the first and last check dates during incubation, the first and last checks after hatching, and for failures, the date that a nesting attempt was last

known to be viable. For successful nesting attempts, we estimated the end of the last observation interval as the estimated date by which at least 1 nestling reached minimum acceptable fledging age (Steenhof and Newton 2007). For failed nests, the end of the last observation interval was the first date when we confirmed failure. If we confirmed failure after the nesting period should have ended, we truncated the last observation interval to the end of the estimated nesting period. In cases where researchers manipulated nesting attempts by adding or removing young for the purposes of an ancillary study, we considered the date of the manipulation to be the last check date, censoring survival days that occurred beyond that date. We calculated nesting success (the probability that at least 1 young survived the nesting period) from the Mayfield and logistic-exposure analyses by taking the product of DSR estimates across total length of the nesting period (Table 1, Johnson 1979). We suspected that nesting success varied across years because of underlying factors such as prey abundance, but such data were not available for direct analysis. Therefore we modeled inter-annual variation directly to describe any temporal patterns that may exist, by considering year as a categorical variable (hereafter, year), effectively modeling DSR separately for each year. We report all results with ± 95% confidence intervals.

We estimated DSR using the Mayfield method following Mayfield (1961, 1975) and Johnson (1979). We assumed nesting attempts that failed did so at 40% of the length of the interval between nest checks. We calculated standard errors for the complete nesting period following Johnson (1979).

We described DSR as a function of time using generalized linear models developed in R (R Version 2.6.1, www.r-project.org, accessed 24 June 2012). These logistic-exposure models are similar to logistic regression models in that the response variable is binomial (success or failure of nest occurred between nest checks), but the link function is modified from the logit link to consider nest exposure days (Shaffer 2004). We presented final parameter estimates as means with 95% confidence intervals.

We assessed whether the annual estimates of raptor nesting success suggested long-term directional trends with beta regression models of nesting success estimates versus time. Beta regression models are more appropriate than Gaussian linear regression models for proportional data, because such data are bounded by 0 and 1, and are often strongly heteroskedastic (Ferrari and Cribari-Neto 2004). We constructed models using the R package betareg with the predictor variable of time and response variable of nesting success (for all 3 species, ANS of full data set, Mayfield method, and logistic-exposure; for prairie falcons only, also ANS from nests found during incubation), and used a likelihood-ratio test (LRT) to compare the time models to null models which lacked any time variable (Cribari-Neto and Zeileis 2010). If the LRT test statistic was significant at alpha=0.05, we interpreted this result as evidence for a long-term time trend in our data, and examined the predicted parameter estimates to determine the direction of the trend.

Results

Sample sizes for golden eagles and American kestrels were similar for each analytical method, whereas sample sizes for prairie falcon datasets varied markedly (Table 2). The

prairie falcon ANS dataset had the largest sample size because by including all nesting attempts with known fates, it included many nesting attempts found incidentally (and checked only once) late in the nesting season. Only 50% of the full set of prairie falcon nesting attempts were found during incubation. The sample sizes for Mayfield and logistic-exposure prairie falcon datasets included nesting attempts found incidentally only if they were checked more than once.

Mayfield and logistic-exposure estimates of nesting success pooled across years were very similar to each other, but were less than all of the ANS estimates for each species (Fig. 1; difference of means from 0.215 to 0.080). For prairie falcons, ANS estimates differed with the dataset analyzed; the highest estimate was generated from the full dataset of all nesting attempts with known fates, whereas the lowest estimate (and the estimate most similar to the Mayfield and logistic-exposure estimates) came from the sample of nesting attempts found during incubation (differences of means 0.215 and 0.087, respectively). For all species, yearly nesting success estimates from the Mayfield and logistic-exposure methods also were similar and less than ANS estimates based on all nesting attempts with known fates (Fig. 2). The differences between ANS and model estimates were relatively consistent across years for eagles and kestrels; however the magnitude of the difference for prairie falcons varied considerably across years (Fig. 2). The differences between ANS and model estimates were more consistent across years for prairie falcons when the ANS estimate was based on nesting attempts found during incubation (Fig. 3).

For both golden eagles and kestrels, we found no evidence of long-term trends in nesting success regardless of estimation method. For prairie falcons, however, when ANS from the full data set was assessed, nesting success decreased over the course of the study from a high mean value of 0.874 in 1975 to 0.724 in 2003 (Fig. 3; LRT of beta regression model considering time vs. null model, χ^2=3.897, P=0.04837). In contrast, we did not find support for time trends in prairie falcon nesting success estimates from the Mayfield method, logistic-exposure, or ANS from the data set of nesting attempts found during incubation.

Discussion

Apparent nest success has been the most common measure used by researchers to estimate raptor reproductive success; however, our analysis confirmed previous findings that ANS usually overestimates nesting success (Mayfield 1961, Dinsmore et al. 2002, Shaffer 2004). Even when ANS samples were restricted to nesting attempts found during incubation, ANS estimates were greater than model-based estimates in all 3 species. The magnitude of the overestimate was most severe for prairie falcons, the species with the lowest nest detectability and for which we monitored only a small portion of the entire nesting population for reproduction.

Apparent nest success estimators tracked with model estimates of annual variation in nesting success in golden eagles and American kestrels, but not in prairie falcons. Similarly, both ANS and model-based methods suggested no long-term trends in nesting success existed for eagles and kestrels, whereas ANS estimates suggested a long-term trend in prairie falcon nesting success that was not supported by estimates from other methods. For a species with

lesser nest detectability, the prairie falcon, the ANS estimator provided plausible yearly estimates only when the sample was restricted to nesting attempts found during incubation (Fig. 3). Because the ANS estimator is particularly sensitive to inclusion of nesting attempts first found late in the nesting season, as long as surveying is adequate to yield multiple checks of each nest, the Mayfield or logistic-exposure models are more appropriate than ANS in situations when most pairs cannot be located before (or soon after) laying or cannot be checked at the end of the nesting period.

Mayfield and logistic-exposure models generated similar estimates of nesting success for all species, with similar levels of precision. We recommend use of either the Mayfield method or logistic-exposure model when a point estimate of nesting success is important. An advantage of using Mayfield or logistic-exposure models is that data can be used from all nesting attempts checked for viability at least twice, regardless of when the attempt was found and whether it was followed to completion. Either the Mayfield method or logistic-exposure model may be used to consider categorical variables, but sample sizes may be too small within each category for effective estimation with the Mayfield method.

The main advantage of the logistic-exposure model over the Mayfield method is that it allows evaluation of the influence of continuous covariates on nesting success. In particular, logistic-exposure models allow modeling of the variation in nesting success over time, both within and between seasons, when time is considered as a continuous variable. Analyses of within-season variation in nesting success require estimates of nest initiation dates or nest age. This can be a challenge for raptor studies, particularly for nests that fail before the age of nestlings can be determined. Moreover, studies with long intervals between nest checks may be limited in their ability to evaluate the effects of time-specific variables (e.g., weather). When nest initiation dates cannot be estimated reliably for all nesting attempts, the logistic-exposure model may be constrained to assume constant daily survival throughout the entire nesting period. Seasonal effects may be modeled without knowing nest initiation dates, but interpretation of the effects of day of year warrants caution because the variable contains information from both the nest initiation date and extrinsic seasonal effects.

One notable limitation of typical nest survival models is that they do not consider survival of individual eggs or young and therefore do not estimate productivity, which is often an important component of raptor population monitoring (Thompson et al. 2001). Another reason that raptor researchers have not embraced nest survival models is that the models typically address only part of the raptor reproductive cycle. Not all raptor pairs that occupy nesting territories lay eggs every year (Steenhof and Newton 2007), and the proportion of pairs that produce eggs in different years can be an important measure of a population's response to changing food supplies (Steenhof et al. 1997). Another concern is that models of raptor nesting success do not typically include the post-fledging stage (Rosenfield pers. comm.). However, only the most intensive surveys could assess survival after fledging, and it would be difficult to define a standard length for the post-fledging period because there is considerable individual variation in the length of the post-fledging period within species (Newton 1979:118).

Future research should involve analyses of simulated raptor populations to evaluate how well the estimators perform when reproductive parameters are known (Johnson and Shaffer 1990). By varying the sample sizes, probabilities of detecting nest attempts, frequency and number of nest status checks, and the underlying true daily nest survival rate, the performance of nest survival models in plausible scenarios could be more rigorously evaluated.

Management Implications

The new generation of nest survival models appears to be ideal for intensive, short-term investigations of raptor breeding biology. Extensive, long-term monitoring efforts, especially those that involve legacy datasets, may not be able to take full advantage of nest survival models and may be forced to rely on more traditional measures of nesting success. Investigators should be aware of biases when using old approaches. In some cases, these biases are neither consistent nor predictable. Traditional measures of nesting success tend to be unreliable for species whose nesting attempts are difficult to locate and for situations in which a small proportion of the population is sampled. The ANS estimator could be sufficient for assessing long-term trends of species with highly detectable nests. Traditional measures may be adequate for studies with extensive background data on nesting territories, but they are not suitable for studies in new areas with limited background information. We recommend that biologists design future surveys to collect data necessary for newer nest survival models. A minimum monitoring effort would include at least 2 visits to the nest. At minimum, biologists should record the date, the stage and viability of nesting attempt on, and age of the young if present. If sampling from a larger population, we recommend that the biologist implement a stratified random sampling approach.

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Literature Cited

Akaike, H. Information theory and an extension of the maximum likelihood principle. In: Petran, BN.; Csaki, F., editors. International symposium on information theory. Second. Akademiai Kiado; Budapest, Hungary: 1973. p. 267-281.

Barber JD, Wiggers EP, Renken RB. Nest-site characterization and reproductive success of Mississippi Kites in the Mississippi River floodplains. Journal of Wildlife Management. 1998; 62:1373–1378.

Beecham, JJ, Jr. Nesting ecology of the golden eagle in southwestern Idaho. University of Idaho; Moscow, ID, USA: 1970.

Bird, DM.; Palmer, RS. American Kestrel. Palmer, RS., editor. Handbook of North American birds Vol 5 Diurnal Raptors Pt 2 Yale Univ Press; New Haven, CT, USA: 1988. p. 253-290.

Boeker EL. Use of aircraft to determine Golden Eagle, Aquila chrysaetos, nesting activity. Southwestern Naturalist. 1970; 15:136–137.

Briggs CW, Collopy MW, Woodbridge B. Plumage polymorphism and fitness in Swainson's hawks. Journal of Evolutionary Biology. 2011; 24:2258–68. [PubMed: 21767320]

Brown JL, Collopy MW. Bayesian hierarchical model assessment of nest site and landscape effects on nest survival of Aplomado Falcons. Journal of Wildlife Management. 2012; 76:800–812.

Burnham, KP.; Anderson, DR. Model selection and inference: a practical information-theoretic approach. Second. Springer-Verlag New York; New York, NY, USA: 2002.

Carrier WD, Melquist WE. The use of a rotor-winged aircraft in conducting nesting surveys of Ospreys in northern Idaho. Raptor Research. 1976; 10:77–83.

Cribari-Neto F, Zeileis A. Beta regression in R. Journal of Statistical Software. 2010; 34:1–24.

Dinsmore SJ, White GC, Knoff FL. Advanced techniques for modeling avian nest survival. Ecology. 2002; 83:3476–3488.

Ellis DH. Development of behavior in the Golden Eagle. Wildlife Monographs. 1979; 70:1–94.

Enderson JH. An account of Prairie Falcons bred in captivity. Raptor Research News. 1971; 5:44–47.

Ferrari SLP, Cribari-Neto F. Beta regression for modelling rates and proportions. Journal of Applied Statistics. 2004; 31:799–815.

Fraser JD, Frenzel LD, Mathisen JE, Martin F, Shough ME. Scheduling Bald Eagle reproduction surveys. Wildlife Society Bulletin. 1983; 11:13–16.

Fyfe R. Nelson RW. Breeding behavior of captive and wild Prairie and Peregrine Falcons. Special conference on captivity breeding of raptors, Part C Behavioral considerations to egg-laying. Raptor Research 6 (Supplement). 1972:43–52.

Griffin CR, Paton PWC, Baskett TS. Breeding ecology and behavior of the Hawaiian Hawk. Condor. 1998; 100:654–662.

Griggs, GR.; Steenhof, K. Photographic guide for aging nestling American Kestrels. Boise, ID, USA: 1993.

Hickman, GL. The ecology and breeding biology of the Golden Eagle in southwestern Idaho and southeastern Oregon. Washington, D.C., USA: 1968.

Hoechlin DR. Development of Golden Eaglets in southern California. Western Birds. 1976; 7:137–152.

Jehle G, Yackel Adams AA, Savidge JA, Skagen SK. Nest survival estimation: a review of alternatives to the Mayfield estimator. Condor. 2004; 106:472–484.

Johnson DH, Shaffer TL. Estimating nest success: when Mayfield wins. Auk, The. 1990; 107:595–600.

Johnson DH. Estimating nest success: the Mayfield method and an alternative. Auk. 1979; 96:651–661.

Johnson DH. Estimating nest success: a guide to the methods. Studies in Avian Biology. 2007a; 34:65–72.

Johnson DH. Methods of estimating nest success: an historical tour. Studies in Avian Biology. 2007b; 34:1–12.

Kochert, MN.; Steenhof, K.; McIntyre, CL.; Craig, EH. Golden eagle (Aquila chrysaetos). Poole, A.; Gill, F., editors. The Birds of North America The Birds of North America, Inc.; Philadelphia, PA, USA: 2002.

Kochert, MN. Population status and chemical contamination in Golden Eagles in southwestern. Idaho University of Idaho; Moscow, ID, USA: 1972.

Lantz SJ, Conway CJ. Factors affecting daily nest survival of Burrowing Owls within black-tailed prairie dog colonies. Journal of Wildlife Management. 2009; 73:232–241.

Lehman RN, Carpenter LB, Steenhof K, Kochert MN. Assessing relative abundance and reproductive success of shrubsteppe raptors. Journal of Field Ornithology. 1998; 69:244–256.

Martin JM, Branch LC, Raid RN, Beyeler SC. Temporal instability of agricultural habitat reduces reproductive success of barn owls (Tyto alba). Auk, The. 2010; 127:909–916.

Mayfield HF. Nesting success calculated from exposure. Wilson Bulletin. 1961; 73:255–261.

Mayfield HF. Suggestions for calculating nest success. Wilson Bulletin. 1975; 87:456–466.

McIntyre CL, Adams LG. Reproductive characteristics of migratory Golden Eagles in Denali National Park, Alaska. Condor. 1999; 101:1115–123.

McIntyre CL, Schmidt JH. Ecological and environmental correlates of territory occupancy and breeding performance of migratory Golden Eagles Aquila chrysaetos in interior Alaska. Ibis. 2012; 154:124–135.

Moritsch, MQ. Photographic guide for aging nestling Prairie Falcons. Boise, ID, USA: 1983.

Newton, I. Population ecology of raptors. Buteo Books; Vermillion, SD, USA: 1979.

Porter RD, Wiemeyer SN. Reproductive patterns in captive American Kestrels (Sparrow Hawks). Condor. 1972; 74:46–53.

Rotella JJ, Dinsmore SJ, Shaffer TL. Modeling nest-survival data; a comparison of recently developed methods that can be implemented in MARK and SAS. Animal Biodiversity and Conservation. 2004; 27:187–204.

Schmidt JH, Walker JA, Lindberg MS, Johnson DS, Stephens SE. A general Bayesian hierarchical model for estimating survival of nests and young. Auk. 2010; 127:379–386.

Shaffer TL. A unified approach to analyzing nest success. Auk. 2004; 121:526–540.

Smallwood, JA.; Bird, DM. American Kestrel (Falco sparverius). In: Poole, A.; Gill, F., editors. The Birds of North America Volume 602. The Birds of North America, Inc.; Philadelphia, PA: 2002.

Steenhof K, Kochert MN, Carpenter LB, Lehman RN. Long-term Prairie Falcon population changes in relation to prey abundance, weather, land uses, and habitat condition. Condor. 1999; 101:28–41.

Steenhof K, Kochert MN, McDonald TL. Interactive effects of prey and weather on Golden Eagle reproduction. Journal of Animal Ecology. 1997; 66:350–362.

Steenhof K, Kochert MN. An evaluation of methods used to estimate raptor nesting success. Journal of Wildlife Management. 1982; 46:885–893.

Steenhof, K.; Newton, I. Assessing raptor nest success and productivity. In: Bird, DM.; Bildstein, KL., editors. Raptor Management and Research Techniques. Hancock House; Blaine, WA, USA: 2007. p. 181-192.

Steenhof K, Peterson B. American Kestrel reproduction in southwestern Idaho: annual variation and long-term trends. Journal of Raptor Research. 2009; 43:283–290.

Steenhof, K. Assessing raptor reproductive success and productivity. In: Pendleton, BG.; Millsap, BA.; Cline, KW.; Bird, DM., editors. Raptor management techniques manual. National W National Wildlife Federation; Washington, D.C., USA: 1987. p. 157-170.

U.S. Department of the Interior. Snake River Birds of Prey Special Research Report to the Secretary of the Interior. Boise, ID, USA: 1979.

VanCamp LF, Henny CJ. The Screech Owl: its life history, population ecology in northern Ohio. North American Fauna. 1975; 71:1–65.

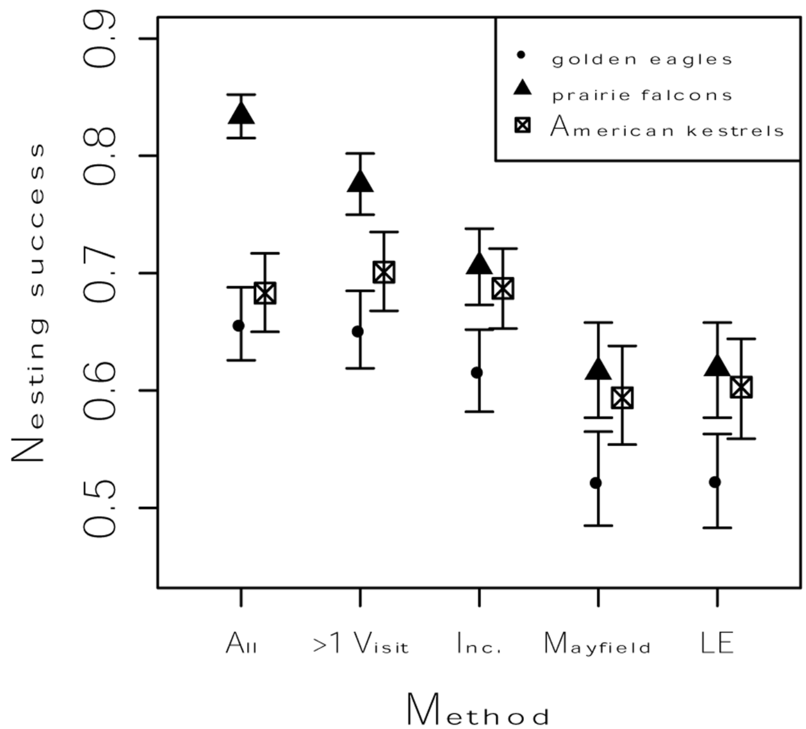

Figure 1.
Nesting success by species pooled across years (range: 1975-2005 for all species) and modeled without covariates in southwestern Idaho. Estimation methods include 3 variants of apparent nest success (ANS) estimates (all nesting attempts with known fates [all], nesting attempts visited at least twice [>1 visit], and nest attempts initially found during incubation [inc.]), Mayfield method, and logistic-exposure model (LE), presented with 95% confidence intervals.

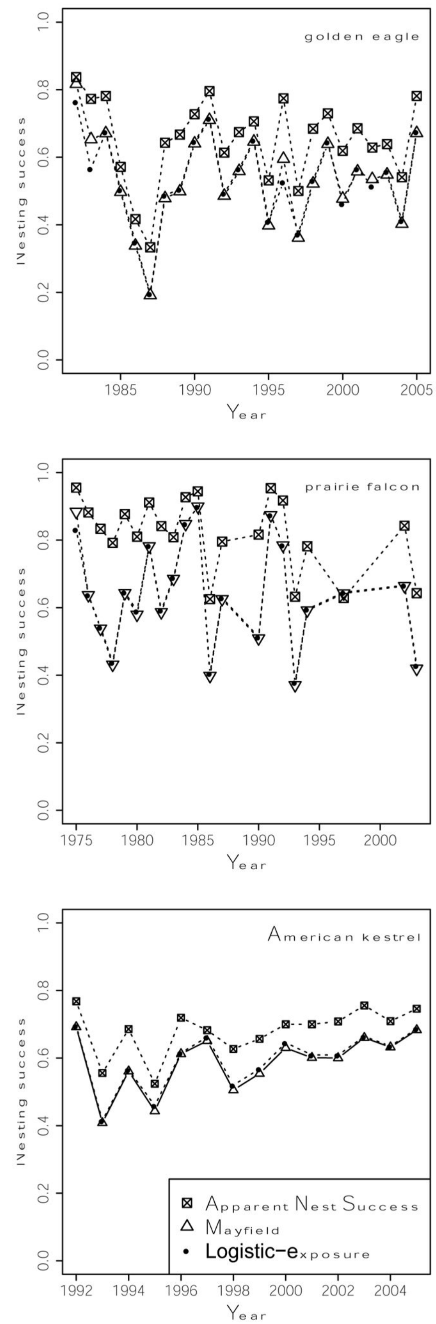

Figure 2.

Annual estimates of nesting success for golden eagles, prairie falcons, and American kestrels in Idaho, USA, from apparent nest success (ANS) calculations on all nesting attempts with known fates, the Mayfield method, and logistic-exposure models.

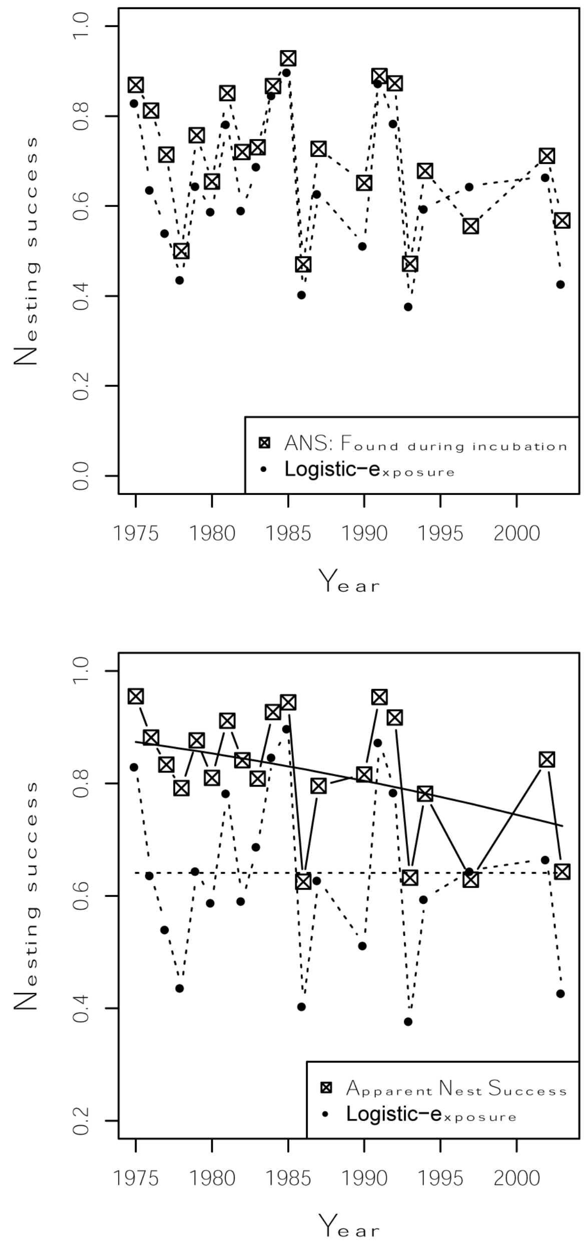

Figure 3.

Annual estimates of nesting success for prairie falcons in Idaho, USA. Top panel shows estimates from the logistic-exposure model and apparent nest success (ANS) calculations on nesting attempts found during incubation. Bottom panel shows estimates from the logistic-exposure model and ANS estimates from the full data set, along with the decreasing time trend (solid line) suggested by beta regression. Dotted horizontal line indicates overall time-invariant average nesting success of 0.64 indicated by beta regression of logistic-exposure estimates.

Table 1

Characteristics of raptors studied in southwestern Idaho and procedures used to monitor their reproduction.

Species	Nesting period[a]	Detectability of nesting attempts	No. of visits	% of nesting pairs sampled	% of nesting attempts found during incubation
Golden eagle[b]	101	High	≥2	>80%	88%
Prairie falcon[c]	79	Low	≥3	<25%	74%
American kestrel[d]	64	Very high	≥4	>90%	98%

[a] Duration in days

[b] Based on a 5-day pre-laying period (Ellis 1979), a 45 day incubation period (Kochert et al. 2002), and a 51-day minimum acceptable fledging age (80% of the mean fledging age; Kochert et al. 2002).

[c] Based on a modal clutch size of 5 (Steenhof et al. 1997), a 2-day laying interval (Enderson 1971), a 39-day incubation period (Fyfe 1972), and a 30-day minimum acceptable fledging age (Steenhof et al. 1997).

[d] Based on a modal clutch size of 5 (Smallwood and Bird 2002), a 2.4-day laying interval (Porter and Wiemeyer 1972), a 30 day incubation period (Bird and Palmer 1988), and a 22-day minimum acceptable fledging age (Steenhof and Peterson 2009).

Table 2

Sample sizes (number of nesting attempts) for estimating nesting success of raptors using apparent nest success (ANS), Mayfield method, and logistic-exposure models. All studies included in the analysis were conducted in southwestern Idaho between 1975 and 2005.

	Golden eagle	Prairie falcon	American kestrel
ANS (known fates)	889	1522	733
ANS (at least two visits)	816	968	713
ANS (found during incubation)	731	768	716
Mayfield	830	1019	719
Logistic-exposure	830	1019	719