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Assessing Nesting Success and Productivity

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INTRODUCTION

Studies of reproductive rates in raptors can be valuable in assessing the status of raptor populations and the factors that influence them. Estimates of nesting success and productivity provide insight into only one component of the demography of a raptor population. Individuals are added to local populations through reproduction, and they are subtracted through mortality. Together with immigration and emigration, these two demographic parameters determine the year-to-year trends in local populations. Reproductive rates usually are easier to evaluate than other aspects of demography, and properly designed studies will allow inferences to be made about relationships between the status of raptor populations and a variety of environmental influences. Unbiased data on reproductive rates allow comparisons among populations in different areas and different years that may reflect differences in land use, contaminant levels, human activity, or variations in natural phenomena, such as weather or prey supply. Such studies may be essential for identifying effective conservation measures for threatened and declining species. Data on reproduction can help predict the effects of land use changes on raptor nesting populations (U.S. Department of Interior 1979), document effects of contaminants (Newton 1979, Grier 1982), or measure whether a population is reproducing well enough to sustain itself, given existing rates of survival (Henny and Wight 1972). Information on reproductive rates can be useful in deciding whether to list or reclassify an endangered raptor species or whether to allow harvest of a more common species for falconry purposes. Investigations have limited value, however, if objectives are not considered when the study is designed and initiated. Year-to-year fluctuations in nest success and productivity are common in raptors, and short-term decreases in productivity need not affect the long-term stability of populations.

The main objectives of this chapter are to (1) establish standard definitions that will facilitate comparisons of data over time and space, (2) identify the types of information needed to estimate raptor nesting success and productivity, (3) evaluate the advantages and disadvantages of various field techniques, and (4) offer suggestions for procedural and analytical approaches that will minimize bias. We include a glossary of technical terms for reference (Table 1).

CONCEPTS AND DEFINITIONS

To produce young, a raptor must pass successfully through a number of stages. It must first settle in a particular area, establish a **nesting territory** (terms in **bold**

are defined in Appendix 1), and acquire a mate. It must then proceed through **nest** building, egg laying, and then to hatching and rearing of young. In this sequential process, birds can fail at any stage.

For the purpose of analyzing reproductive data, a nesting territory is an area that contains, or historically contained, one or more nests (or **scrapes**) within the home range of a mated pair. The term nesting territory should not be confused with the more restricted ethological definition of a territory as any defended area. A raptor nesting territory can be thought of as a confined area where nests are found, usually in successive years, and where no more than one pair is known to have bred at one time (Newton and Marquiss 1982). The concept holds even in colonial species, in which the same nest sites tend to be used year after year with the occupants often defending only a small area around their nest.

Individuals that are unable to secure a nesting territory are known as **floaters**. They are usually unpaired and do not reproduce (Postupalsky 1983). Because of the difficulty in counting non-territorial raptors, and their greater mobility, they usually are excluded from analyses of **nesting success** and **productivity**. However, it may sometimes become possible to consider these birds in analyses of population dynamics (e.g., Kenward et al. 1999, Newton and Rothery 2001).

Some individuals are able to secure a nesting territory but not a mate. Postupalsky (1983) recommended that lone territorial birds be excluded from tallies of nesting pairs, but this is seldom practical. Territories that truly have only one adult are difficult to distinguish from those in which the second adult was absent at the time of the nest check, perhaps hunting some distance away. They also often represent only a temporary situation, as a lone bird may soon acquire a mate.

Certain pairs may occupy a territory for only a few days or a few weeks, or may even build a nest, but the process stops here. Not all raptor pairs occupying nesting territories lay eggs every year. A major factor influencing egg laying is food supply and in poor food years, many territorial pairs in some populations fail to lay eggs (Newton 2002). The proportion of pairs that produce eggs in different years, therefore, can be an important measure of a population's response to changing food supplies (Steenhof et al. 1997).

Still other territory holders may lay and then desert their eggs or lose them to predation, weather, or other causes. Others may produce eggs that hatch, but then their young die due to a variety of causes and at a variety of ages. Pairs that raise at least one young that is nearly old enough to fly are usually considered **successful**. Of course, additional offspring mortality might occur after this stage (Marzluff and McFadzen 1996) when the young are free-flying, but still fed by their parents. Their death at this stage could be measured by a separate detailed study, or accounted for in estimates of juvenile survival, which is usually calculated as starting when the young are banded.

The proportions of pairs that reach these various stages can form a useful basis for comparing different raptor populations or subsets within populations. The most useful comparisons are based on the proportions of territorial pairs (or occupied territories) that produce young, but for practical reasons many studies can only obtain information on the proportion of laying pairs that produce young. Researchers who have good historical information on species that show strong fidelity to well-defined nesting territories (e.g., eagles, Ospreys [*Pandion haliaetus*]) can report nesting success and productivity on the basis of territorial pairs or occupied territories in a particular year (Brown 1974, Postupalsky 1974). In short-term investigations or studies of more nomadic raptors, it may be necessary to report success and productivity on the basis of laying pairs. For polygynous or polyandrous species (e.g., harriers, Harris's Hawks [*Parabuteo unicinctus*], etc.), success and productivity are best reported per mated territorial female or per mated male.

Estimates of productivity based solely on the number of young produced per successful pair can be misleading because successful pairs often produce average numbers of young even in years when most pairs fail (Steenhof et al. 1997, 1999). However, **brood size at fledging** can be a useful measure in some calculations (Steenhof and Kochert 1982: see below), depending on the purpose of the study.

CRITERIA FOR CLASSIFYING REPRODUCTIVE EFFORTS

Measurement error occurs when investigators incorrectly interpret the status of a particular pair or nesting territory, or incorrectly count the number of eggs or young. The ability to determine correctly the status of nests and to count the number of young varies with many factors, including the field situation, observer experience, and weather. Because these factors cannot be held constant, it is sometimes difficult to determine whether differences in estimates reflect measurement

error or true differences in productivity. Fraser et al. (1984) analyzed the problem of measurement error in aerial surveys of Bald Eagles (*Haliaeetus leucocephalus*) in the Chippewa National Forest. By running three simulated two-stage surveys in the same year, they were able to compute an error rate caused by mistakes in counts of occupied territories, laying pairs, and fledglings. Using this information, they calculated an estimated standard error that allowed them to test for true differences in productivity among years. The use of simulated surveys to obtain an estimate of variability due to measurement error is a site-specific procedure that must be repeated for each study area and each population. It is most valuable in situations where all territorial pairs have been found.

Territory Occupancy

Evidence that a territory is occupied can be based on observation of two birds that appear to be paired or one or more adults engaged in territorial defense, nest affinity, or other reproductive-related activity. Any indications that eggs were laid or young were reared constitute clear evidence for territorial occupancy. In some species, the presence of a nest that has been recently built, repaired, or decorated may constitute evidence for territorial occupancy, providing that these activities can be ascribed to the species of interest unequivocally. Caution must be used in applying this criterion because of the occasional difficulty in distinguishing old and new nest material. Fresh greenery, several sticks with fresh breaks, or a distinct layer of new material on top of older, weathered sticks usually suggest recent nest repair.

Individuals of some species may occupy territories for short periods only (perhaps less than one day), before moving on to another territory or reverting to a "floating" lifestyle. Some birds can thus easily be missed during a survey, or double-counted if they move from one territory to another in the same study area. Harriers are particularly problematic in this regard, because different individuals may "sky-dance" on different days over the same piece of nesting habitat during migration (e.g., Hamerstrom 1969). Fortunately, this seems not to be an issue for most species, and once a territory is occupied, it seems to remain so at least until the nest fails or the young reach independence.

For long-lived species that re-use the same territories year after year, such as Golden Eagles (*Aquila chrysaetos*) (Watson 1957) and Peregrine Falcons (*Falco peregrinus*) (Mearns and Newton 1984), an estimate of the proportion of traditional territories occupied by pairs in any given year can be a useful index to the size and status of the nesting population. In species that show less fidelity to particular nesting territories among years, this measure can be misleading because it can grossly underestimate the status of species that normally use nesting territories intermittently or only once, such as Burrowing Owls (*Athene cunicularia*) (Rich 1984), Northern Hawk-Owls (*Surnia ulula*) (Sonerud 1997), Short-eared Owls (*Asio flammeus*) (Village 1987), and Ferruginous Hawks (*Buteo regalis*) (Lehman et al. 1998). For these and similar species, studies should be designed to sample all potential nesting habitat within a study area each year and not only previously occupied territories.

In many species, it is unusual to find all previously known territories occupied in any given year. Over a period of years, some territories may be used every year (or almost every year), whereas others are used irregularly, or very infrequently. In other words, certain territories are used much more often than expected by chance at the population levels found, and others are used much less often. This has led some long-term researchers to distinguish categories of territories, such as "regular and irregular." Typically, occupants of "regular" territories are more often successful than are occupants of less used territories, giving a correlation between occupancy and nest success (Newton 1991, Sergio and Newton 2003). It seems that many raptors are capable of selecting those particular territories where their chances of raising young are high.

Egg Laying

Not all raptor pairs occupying nesting territories lay eggs every year (see above). Evidence of laying may be based on observations of eggs, young, an incubating adult, fresh eggshell fragments, or any other field sign that indicates eggs were laid. However, be aware that some species, such as the Bald Eagle, may assume incubation posture without actually having laid an egg (Fraser et al. 1983).

Laying Date

The laying date of the first egg usually is taken as a measure of the timing of breeding in birds. Laying date is useful because it often correlates with nest success; birds laying earliest in the season usually are the most

successful. Laying date also is a critical data element required for some **nest survival** models (Dinsmore et al. 2002). As nests are seldom visited on the very day that the first egg is laid, laying date is usually calculated indirectly, by backdating from some later stage in the cycle. Allowances are then made for the intervals between laying of successive eggs (two days in most raptor species), the **incubation period**, and, in the case of nests found during the **nestling period**, age of the young. Ages of nestlings can be estimated from weights or measurements in some species (e.g., Petersen and Thompson 1977, Bortolotti 1984). Photographic aging keys (e.g., Hoechlin 1976, Moritsch 1983a,b, 1985; Griggs and Steenhof 1993, Boal 1994, Priest 1997, Gossett and Makela 2005) also are useful tools for aging young. Repeated checks during the laying period can help to estimate the date of onset of incubation (Millsap et al. 2004). Otherwise, it is usually difficult to estimate laying date for pairs that fail during incubation. Investigators often assume that nest failure occurred at some specific stage, most typically in mid-incubation, or midway between successive nest checks, the latter check being the one in which failure was discovered. If deserted eggs are present, their stage of development sometimes can be estimated by candling (Weller 1956) to determine the stage of embryo growth, but the observer may still not know how long the eggs have lain unincubated in the nest.

Clutch Size

The number of eggs laid by each pair is useful, but not crucial, in assessments of overall productivity (Brown 1974). Because many raptor species nest on cliffs or in trees, not all nests are readily accessible, and clutch sizes may be difficult or impossible to record. In addition, some raptors are affected adversely by visits to nests during incubation. Because of this, counts of eggs at close range are sometimes associated with increased failure rates (Luttich et al. 1971, Steenhof and Kochert 1982, White and Thurow 1985, Chapter 19). For these reasons, a traditional measure of avian nesting success, the proportion of eggs that hatch and ultimately develop into fledglings, often is not attainable. Data on clutch sizes, however, can provide further insight into the mechanisms of a population's response to food supply or other environmental influences.

Nesting Success and Productivity

Nesting success is defined as the proportion of nesting or laying pairs that raise young to the age of **fledging** (i.e., the age when a fully-feathered offspring voluntarily leaves the nest for the first time). The difference between success per territorial pair and success per laying pair can be large in species that have relatively high rates of non-laying, including Golden Eagles and Tawny Owls (*Strix aluco*) (Southern 1970, Steenhof et al. 1997). It is less important for species in which all or most territorial pairs lay eggs (Steenhof and Kochert 1982).

In many studies, it is impossible to visit each nest on the exact day that young take their first flight; and after young have left the nest, they may be difficult to locate. Once young approach fledging age they become liable to flee from the nest prematurely if approached too closely. As they cannot fly at this stage, they usually flutter to the ground, and unless retrieved, could be vulnerable to predation or drowning. For this reason, it is sensible to check nests a week or more before young are likely to fledge. Most studies of raptors, therefore, consider pairs to be successful when well-grown young are observed in the nest at some point prior to fledging. Studies that consider nests with young of any age to be successful will overestimate nest success because they fail to consider mortality that may occur late in the brood-rearing period. Researchers should consider nest survival models (see below) when it is impossible to check an adequate number of nests at or near fledging.

If investigators wish to compare nest success among years, areas, or treatments, they should establish a standard minimum nestling age at which they consider nests to be successful. This age should be when young are well grown but not old enough to fly and at a stage when nests can be entered safely and after which mortality is minimal until actual fledging. Steenhof (1987) recommended that nests of diurnal raptors be considered successful only if at least one nestling has reached 80% of the average age at first flight. Mortality after this age until first flight is usually minimal (Millsap 1981). Furthermore, young are usually large enough to count from a distance at this stage. For Prairie Falcons (*F. mexicanus*), Golden Eagles, and Red-tailed Hawks (*B. jamaicensis*) nesting in the Snake River Canyon, 80% of fledging age corresponds with the age at which most young are banded (Steenhof and Kochert 1982). The 80% of first-flight age criterion has been used to determine nesting success in studies of several additional raptors, including Ferruginous Hawks, Northern Harriers (*Circus cyaneus*) (Lehman et al.

1998), Snail Kites (*Rostrhamus sociabilis*) (Bennetts et al. 1998), and Northern Goshawks (*Accipiter gentilis*) (Boal et al. 2005). A lower criterion for evaluating nest success (70 or 75% of the age at which young first leave the nest) might be more appropriate for species in which age at fledging varies considerably (i.e., highly sexually dimorphic raptors such as Cooper's Hawks [*A. cooperii*]) or for species that are more likely to leave the nest prematurely when checked. Millsap et al. (2004) considered Bald Eagle nests to be successful if young reached eight weeks of age or approximately 70% of first flight age, and the U.S. Fish and Wildlife Service (2003) considers Peregrine Falcon pairs to be successful when their young are at least 28 days old, or approximately 65% of first flight age. Information about fledging ages of most North American raptors can be found online at the Birds of North America website (http://bna.birds.cornell.edu/BNA/) (Poole 2004). Data on fledging ages of raptors from other parts of the world are in Newton (1979; Table 18) and Cramp et al. (1980). Investigators should consult more recent sources about their study species and use the best available information about variation in fledging ages and susceptibility to disturbance when they define and adopt a minimum age to evaluate success.

Productivity, which refers to the number of young that reach the minimum acceptable age for evaluating success, is usually reported on a per pair basis. In situations with a juvenile sex ratio of 1:1, the number of young per pair is equivalent to **fecundity** (number of females produced per female), a measure that can be incorporated into broader evaluations of a population's demography (e.g., Blakesley et al. 2001, Seamans et al. 2001). After leaving the nest, young normally continue to depend upon their parents (or one parent) for several weeks or months, before becoming independent and dispersing away from the nest vicinity. During the **post-fledging period**, young are sometimes difficult to locate (Fraser 1978). Counts after young have left the nest are unreliable because they tend to miss birds and underestimate the number of young produced. Owls present a special challenge in this regard because the young of many species leave the nest long before they can fly (Forsman et al. 1984) and often at staggered intervals (Newton 2002). Investigators should be aware that the number of young that leave the nest does not always correlate with the number of young that survive to disperse from the nesting territory (Marzluff and McFadzen 1996).

Nest failures. Evidence found at the nest may be helpful in determining the proximate cause of a nest failure. Such signs might include intact, cold eggs, broken eggs, shell fragments, dead nestlings, nestling body parts, or hairs and feathers from likely nest predators. Unhatched eggs can be used for analyses of fertility or contaminant levels. Although a cause of failure often can be assigned in this way, it is important to remember that it may only be the proximate, and not the ultimate, cause. Thus, a female may be short of food, so desert her clutch, which might then be eaten by a predator, leaving shell fragments behind. In this case, the ultimate cause of failure was food shortage, but the proximate cause may be recorded as desertion or predation, depending on whether the observer happened to visit the nest before or after the predator. Nevertheless, assessing proximate causes of nest failure often has proved useful in defining conservation problems, including pesticide-induced shell thinning and egg-breakage (Ratcliffe 1980).

Repeat and double layings. In raptor species that have relatively short breeding cycles and long nesting seasons, pairs that fail early in the breeding cycle (during laying or early incubation) sometimes recycle, and lay another clutch. This usually occurs in a different nest within the same territory. The observer should be aware of this possibility, and check for repeat layings in likely circumstances. Repeat laying does not normally occur in pairs that fail at the nestling stage, presumably because by that stage in the season, pairs would not have time to raise the resulting young before the season ended. However, in at least 15 temperate zone species (Curtis et al. 2005), including Harris's Hawks (Bednarz 1995), American Kestrels (*F. sparverius*) (Steenhof and Peterson 1997), Barn Owls (*Tyto alba*) (Marti 1992), and Long-eared Owls (*A. otus*) (Marks and Perkins 1999), pairs sometimes produce more than one brood in a year. Snail Kites do not necessarily remain paired for successive nestings, but one partner remains to raise the young, while the other moves on, sometimes to re-pair and nest elsewhere (Beissinger and Snyder 1987). Each of these situations requires special attention and interpretation.

FIELD TECHNIQUES

Surveys for raptors may be conducted on foot or from ground vehicles, fixed-wing aircraft, helicopters, or boats (see Chapter 5). The value and accuracy of each of these techniques for locating breeding raptors and

their nests depends on the species being surveyed, the nesting substrate, observer experience, the topography and vegetation of the survey area, and the objective of the study. A combination of survey techniques may be most appropriate for specific situations.

Once found, nests on cliffs or trees can be checked from the ground in one of three ways: (1) remote observation, using telescopes or binoculars, (2) close inspection, accessing the nest using ropes or ladders, or (3) inspecting the nest from a short distance, perhaps using a mirror on a telescopic pole (Parker 1972). Mirrors mounted on 15-m poles proved useful in examining the contents of woodland raptor nests (Millsap 1981). Shorter mirror poles (up to 5 m) were used effectively to assess reproductive success of Ospreys nesting on navigational posts (Wiemeyer 1977). Binoculars or telescopes are ideal for cliff situations, but are not as useful where topography or dense vegetation prevents looking down into the nest from above. Observations from a distance may be adequate to confirm the presence of an incubating bird or of young, but they may be less useful in counting young, especially if the full contents of a nest are not visible.

Counts of nestlings from a distance can be particularly difficult if adults stay on the nest to brood or shade young. Climbing to nests is the best way to reduce error in counting young, but it also can be time-consuming and hazardous (see Chapter 10). Climbing requires special training, and the act of climbing to nests sometimes affects the birds adversely (Ellis 1973, Kochert et al. 2002, Chapter 19). Aerial surveys to assess reproduction are most appropriate for large raptors that build large nests in exposed locations. Aerial surveys of productivity have been effective for Ospreys (Carrier and Melquist 1976), Bald Eagles (Postupalsky 1974, Fraser et al. 1983), and Golden Eagles (Boeker 1970, Hickman 1972). In certain situations, helicopter surveys of Osprey reproductive success and productivity can be more cost-effective than ground surveys (Carrier and Melquist 1976), and fixed-wing aerial surveys of Osprey breeding pairs and numbers of fledged young can be as accurate as ground counts (Poole 1981). Both fixed-wing and helicopter surveys of nesting Golden Eagles may be more efficient and cost-effective than ground assessments (Boeker 1970, Hickman 1972, Kochert 1986).

It is easier to age and count young accurately from a slow-flying aircraft than from a fast, fixed-wing airplane (Hickman 1972, Carrier and Melquist 1976). For surveying Golden Eagle productivity, for example, slow-flying aircraft, such as the Piper Super-Cub, which can travel at speeds of 70 to 120 kmph, are more economical than faster aircraft such as the Cessna 180 series (which travels 110 to 180 kmph) (Hickman 1972). Watson (1993) recommended quieter turbine-engine helicopters to minimize disturbance to Bald Eagles. Even with helicopters, investigators may not always be able to obtain complete brood counts, and ground-based surveys may be necessary to supplement aerial surveys. Most small fixed-wing or rotor-winged aircraft are acceptable for locating nesting pairs early in the season, but slow-flying Super-Cubs or helicopters are preferable during surveys conducted to count young. The accuracy of data can be increased if flights are scheduled for times when low winds improve maneuverability (Carrier and Melquist 1976). To minimize disturbance to Bald Eagles and to maximize safety and data reliability, Watson (1993) recommended conducting helicopter flights on calm, dry days, spending <10 seconds at each nest, staying at least 60 m from the nest, and using binoculars when necessary.

Artificial Nest Sites

Many raptor species breed in areas where a shortage of nesting sites limits nesting density. Provision of artificial sites (boxes or platforms, depending on species) can increase density, and also allow data on nesting success and productivity to be collected in an efficient manner. This is because the locations of all artificial sites are known, and they can be placed in accessible situations, so that nest contents can be easily inspected at every visit. Artificial nest sites, therefore, provide an extremely efficient means of data collection (for a study of more than 100 pairs of Common Kestrels (*F. tinnunculus*) nesting in boxes, see Cavé 1968). However, nesting success in artificial sites may not be the same as that in natural sites, which may be less secure or less sheltered, or vice versa.

Timing of Data Collection

Visits to raptor nests can yield useful information at any stage of the nesting cycle, but for adequate information on numbers and productivity, at least two visits are needed, one at the start of the nesting cycle (ideally around the time of egg-laying) and a second in the late nestling period (ideally just before young fledge). Because not all pairs start nesting at the same time, and, therefore, are out of phase with one another, the ideal

time for a survey is a compromise. When surveys of nesting raptors are conducted from aircraft, all pairs can be checked in a short period, but with ground-based surveys, nest checking may have to occur throughout much of the **breeding season**. The objective of the first series of checks is to count the number of pairs associated with nesting territories and (if conducted after laying) the number of pairs with eggs. Some researchers have made these checks after the last clutch has been laid, but before the first brood hatches (Fraser et al. 1983) and before many failures have occurred. In deciduous woodlands, initial surveys made before leaf-out allow nests to be seen more easily (Fuller and Mosher 1981).

The goal of the second set of observations is to count the number of successful pairs and the number of well-grown young. Timing is again a compromise — in this case, between the date that the last brood reaches the minimum acceptable age for success and the date that the earliest brood leaves the nest. In checks that involve close-range observation, care is needed so that frightened young do not leave the nest prematurely. Checks from aircraft or distant vantage points should be scheduled just prior to fledging so that young are large enough to be counted accurately.

Information on the nesting chronology of local raptor populations must be considered when scheduling all nest checks. Some species show wide variations in laying dates within populations, particularly in regions with warmer climates and extended breeding seasons. When there is considerable variation in nesting chronology, more than two surveys may be necessary (Postupalsky 1974). Similarly, when several species are being inventoried, more than two surveys may be needed to accommodate their separate chronologies. When nesting chronology is unknown or highly variable within a species, an intermediate survey after the young hatch, but before they leave the nest, may be necessary to age nestlings and determine when to schedule the final survey.

ANALYTICAL TECHNIQUES TO AVOID BIASED ESTIMATES

In many studies, estimates of nesting success and productivity are based on a sample of pairs rather than the entire nesting population in a defined area. **Sampling error** is the error that occurs when the pairs observed are not representative of the entire population. Obtaining a sample large enough to yield an unbiased estimate of the parameters of interest is the researcher's greatest challenge. Because nests of most raptor species are relatively inaccessible and widely spaced, there has been a tendency to base productivity estimates on all pairs detected regardless of when or how they were found. The problem with this approach is that the probability of finding a pair is often related, directly or indirectly, to its position or reproductive status. For example, nests low in trees or near roads and openings may be easier to find (Titus and Mosher 1981), but their productivity may be affected by factors related to nest height (e.g., accessibility to predators) or proximity to roads (e.g., availability of road-killed prey).

A more serious problem, common to all studies designed to assess avian reproduction, is that non-laying or early-failing pairs are less likely to be detected than successful pairs (Newton 1979, p. 129). Non-layers spend less time near their nest sites than laying pairs, and unsuccessful pairs spend less time near their nests as the breeding season progresses (Fraser 1978). Non-nesters and unsuccessful pairs have larger home ranges (Marzluff et al. 1997), and unsuccessful pairs may even leave the area altogether soon after failure, especially in migratory populations. Nests with young are usually easier to locate because of audible vocalizations from the young and defending adults, or because of conspicuous "whitewash" or fecal matter around the nest. Because surveys that begin late in the nesting season tend to miss pairs that fail early, they may overestimate nesting success and productivity. Similarly, surveys that simply pool data from nests found at any stage throughout the nesting season also overestimate nest success (Mayfield 1961, 1975; Miller and Johnson 1978). In these situations, the ratio of the number of successful pairs to the total number of all pairs found is clearly of limited value and is equivalent to **apparent nest success** (Jehle et al. 2004).

One approach to minimize bias is to restrict analysis to pairs found prior to the nesting season, or if enough background data are available, to a set of pairs randomly selected prior to the nesting season (Steenhof and Kochert 1982). This approach requires that the success of all selected pairs be determined, but it is not necessary to distinguish non-laying pairs from unsuccessful laying pairs. It is practical only in situations where there is enough historical information on a species that tends to re-use traditional nesting territories (e.g., Golden Eagles). It is inappropriate for many other species of raptors and for most short-term investigations that lack previous information on territories. Some investigators

have tried to minimize bias by estimating nesting success only from laying pairs found early in the nesting season (Steenhof and Kochert 1982). However, this approach may greatly reduce sample size. When it is not possible to find all pairs before laying, researchers should consider using nest survival models to estimate the success of laying pairs.

Mayfield (1961) developed an approach to estimate nest success that incorporates data from nests found at various (and sometimes unknown) stages of the nesting cycle. By calculating **daily nest survival** during the time that a nest is under observation and by assuming a constant daily survival rate for all nests, Mayfield's model estimates the probability that all nests will survive over an entire **nesting period**. Several raptor studies have incorporated the Mayfield approach into their assessments of nesting success (e.g., Percival 1992, Bennetts and Kitchens 1997, Barber et al. 1998, Griffin et al. 1998, Lehman et al. 1998). Recently, more sophisticated models of nest survival have been developed that do not require Mayfield's assumption of constant daily survival throughout the nesting period (Dinsmore et al. 2002, Rotella et al. 2004, Shaffer 2004). Unlike Mayfield's original model, the newer models can include many categorical and continuous covariates that allow researchers to evaluate the importance of a variety of spatial and temporal factors that might affect nest survival. The new methods also allow competing models to be assessed via likelihood-based information-theoretic methods (Akaike 1973, Burnham and Anderson 2002). Nest survival models can be implemented in Program MARK (White and Burnham 1999) and in SAS (Rotella et al. 2004).

Nest-survival models allow data to be used from nests found at various times during the nesting season so long as the status of the nest was determined on at least two separate dates within the nesting period. If possible, nest checks should collectively span all stages of the nesting cycle. To use nest survival models, investigators need at least the following information: (1) the date the nest was found and its status on that date, (2) the last date the nest was checked and its status on that date, and, (3) the date the nest was last known to be viable if it had failed by the last check. Investigators also need to know the duration of the "nesting period" for their study species, which can be defined as the time from the laying of the first egg until the first young reaches the **minimum acceptable age for assessing success**. To calculate an appropriate nesting period for a given species, researchers should consider the length of the laying and incubation periods in addition to the average age at first fledging. Information on each of these parameters is available in Newton (1979; Table 18), Cramp et al. (1980), and Poole (2004). 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). Raptor studies involving tree and cliff-nesting species differ from studies of ground-nesting birds in that many nests are observed remotely. Nest contents are not always inspected and there often is no way to estimate the age of nests that fail during incubation. In addition, many raptors have a longer nesting season, and many offspring continue to stay at or near the nest after they have made their first flight. Typically, investigators check raptor nests less often (sometimes only 2–3 times each season), and intervals between nest checks are usually longer than in studies of passerines, shorebirds, and waterfowl. For these reasons, adapting the new nest-survival models to raptors can be challenging, and nest survival models that require investigators to know the age of the nest when it is first found (e.g., Dinsmore et al. 2002) may not be useful for raptors. Moreover, studies with long intervals between nest checks may be limited in their ability to evaluate the effects of time-specific variables, including weather. Finally, nest survival models should only be used to estimate nesting success of laying pairs, because it is difficult to define when the nesting period begins for non-laying pairs.

Nest survival models currently available do not estimate survival of individual eggs or young. Therefore, estimates of productivity must be calculated differently. To estimate productivity, the estimate of nesting success must be combined with average brood size at fledging. To estimate productivity per territorial pair, this result must be combined with an independent estimate of the percentage of pairs laying eggs (Steenhof and Kochert 1982). Variances of productivity estimates obtained as products can be calculated using formulas available in Goodman (1960).

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Appendix 1. Glossary of terms frequently used in assessing nesting success.*

Active. An ambiguous term, originally defined by Postupalsky (1974) to describe nests where pairs laid eggs, but used subsequently in many different ways by other authors. The term is now best avoided (S. Postupalsky, pers. comm.), unless clearly defined.

Apparent Nest Success. The ratio of number of successful pairs to the total number of known pairs in a population.

Breeding Season. The period from the start of nest building (refurbishment) or courtship to independence of young.

Brood Size at Fledging. The number of young produced by successful pairs.

Clutch Size. The number of eggs laid in a nest.

Daily Nest Survival. The probability that at least one young or egg in a nest will survive a single day.

Fecundity. The number of female young produced per female. Equivalent to number of young produced per pair, assuming a 1:1 sex ratio among offspring.

Fledging. A fully-feathered young voluntarily leaving the nest for the first time.

Floaters. Birds in either subadult or adult plumage that are not associated with specific nesting territories and do not reproduce. Floaters may be physiologically capable of breeding, but are prevented from doing so by lack of a territory or nesting site. They are usually unpaired.

Incubation Period. The time between the start of incubation and the hatching of an egg, during which the egg is kept at or near body temperature by the parent.

Irregular Territory. Known nesting location occupied only in certain years out of many.

Measurement Error. Misclassification of the status of a particular pair or nesting territory or an inaccurate count of the number of eggs or young.

Minimum Acceptable Age for Assessing Success. A standard nestling age at which a nest can be considered successful. An age when young are well grown but not old enough to fly and at a stage when nests can be entered safely and after which mortality is minimal until actual fledging: 80% of the age that young of a species normally leave the nest of their own volition for many species, but lower (65–75%) for species in which age at fledging varies considerably or for species that are more likely to leave the nest prematurely when checked. Often the same as age at banding.

Nest. The structure made or the place used by birds for laying their eggs and sheltering their young.

Nesting Period. The time from laying of the first egg to the time when at least one young reaches the minimum acceptable age for evaluating success in a given species. This interval can be used to calculate nesting success from estimates of daily survival rates. It can be calculated as the sum of the minimum acceptable age for assessing success, the mean incubation period, and the mean time between laying of the first egg and the onset of incubation.

Nestling Period. The time between hatching of the first egg and the time the first young leaves the nest of its own accord.

Nesting Success. The proportion of pairs that raise at least one young to the minimum acceptable age for assessing success (see above) in a given season, even if it takes >1 attempt. Usually reported per territorial pair or per laying pair.

Nesting Territory. An area that contains, or historically contained, one or more nests (or scrapes) within the home range of a mated pair: a confined locality where nests are found, usually in successive years, and where no more than one pair is known to have bred at one time.

Nest Survival. The probability that a nesting attempt survives from initiation (laying of the first egg) to completion and has at least one offspring that reaches the minimum acceptable age for assessing success.

Nonbreeders. A collective term to describe both floaters and territorial pairs that do not produce eggs.

Post-fledging Period. The time between when young leave the nest (i.e., fledge) and their becoming independent of parental care. Sometimes measured from the time young are banded or are old enough for nests to be considered successful.

Pre-incubation Period. The time between laying of the first egg and onset of incubation.

Productivity. The number of young that reach the minimum acceptable age for assessing success; usually reported as the number of young produced per territorial pair or per occupied territory in a particular year.

Regular Territory. Known nesting territory, in use every, or almost every, year.

Sampling Error. Error that occurs when the pairs observed are not representative of the entire population.

Scrape. A site where falcons, owls, and New World vultures (species that do not construct nests) lay eggs; the depression in substrate (rotting wood chips, old pellets, dust, sand, or gravel) where eggs are deposited.

Successful (nest or pair). One in which at least one young reaches minimum acceptable age for assessing success.

* Although definitions in this Glossary are widely accepted among raptor researchers, not everyone uses particular terms in exactly the same way. Therefore, care is needed in making comparisons among studies. It is important to avoid using a familiar term in a different context, and it is equally important to define your terms carefully in your methods section. Doing so will make it easier for others to assess your findings, and to compare them with those of other researchers.