J. Field Ornithol., 69(2):244–256

ASSESSING RELATIVE ABUNDANCE AND REPRODUCTIVE SUCCESS OF SHRUBSTEPPE RAPTORS

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Abstract.—From 1991–1994, we quantified relative abundance and reproductive success of the Ferruginous Hawk (*Buteo regalis*), Northern Harrier (*Circus cyaneus*), Burrowing Owl (*Speotyto cunicularia*), and Short-eared Owl (*Asio flammeus*) on the shrubsteppe plateaus (benchlands) in and near the Snake River Birds of Prey National Conservation Area in southwestern Idaho. To assess relative abundance, we searched randomly selected plots using four sampling methods: point counts, line transects, and quadrats of two sizes. On a per-sampling-effort basis, transects were slightly more effective than point counts and quadrats for locating raptor nests (3.4 pairs detected/100 h of effort vs. 2.2–3.1 pairs). Random sampling using quadrats failed to detect a Short-eared Owl population increase from 1993 to 1994. To evaluate nesting success, we tried to determine reproductive outcome for all nesting attempts located during random, historical, and incidental nest searches. We compared nesting success estimates based on all nesting attempts, on attempts found during incubation, and the Mayfield model. Most pairs used to evaluate success were pairs found incidentally. Visits to historical nesting areas yielded the highest number of pairs per sampling effort (14.6/100 h), but reoccupancy rates for most species decreased through time. Estimates based on all attempts had the highest sample sizes but probably overestimated success for all species except the Ferruginous Hawk. Estimates of success based on nesting attempts found during incubation had the lowest sample sizes. All three methods yielded biased nesting success estimates for the Northern Harrier and Short-eared Owl. The estimate based on pairs found during incubation probably provided the least biased estimate for the Burrowing Owl. Assessments of nesting success were hindered by difficulties in confirming egg laying and nesting success for all species except the Ferruginous hawk.

DETERMINANDO LA ABUNDANCIA RELATIVA Y EL ÉXITO REPRODUCTIVO DE AVES RAPACES DE ESTEPAS ARBUSTIVAS

Sinopsis.—Entre 1991 y 1994, cuantificamos la abundancia relativa y el Vexito reproductivo de *Buteo regatis, Circus cyaneus Speotyto cunicularia* y *Asio flammeus* en las planicies de estepas arbustivas en y cerca del "Area Nacional de Conservació, de Aves de Rapiña en el Rio Snake" en el suroeste de Idaho. Para determinar la abundancia relativa, buscamos parcelas seleccionadas al azar usando euatro métodos de muestreo: puntos de conteo, transectos lineares, y cuadrantes de dos tamaños. En base a un esfuerzo pre-muestreo, los transectos fueron más efectivos que los otros métodos para localizar nidos de aves rapaces (3.7 parejas defectadas/100 horas de esfuerzo vs. 2.2–2.6 parejas). Muestreos al azar usando cuadrantes fallaron en detectar un aumento poblacional en *Asio flammeus* entre 1993 y 1994. Para evaluar el éxito de nidos, tratamos de determinar el producto de todos los intentos de anidaje localizados en búsquedas aleatorias, históricas e incidentales. Comparamos los estirnados del éxito en anidar basados en todos los intentos por anidar, en intentos hallados durante la incubación, y según el modelo de Mayfield, La Mayoria de las parejas usadas para evaluar el éxito fueron halladas incidentalmente. Las visitas a logares históricos de anidaje produjeron el mayor número de parejas por esfuerzo de muestreo (14.6/100 horas), peros las tasas de reocupación para la mayoria de las especies decreció a través del tiempo. Los estimados basados en todos los intentos tuvieron los mayores tamaños de muestra pero probablemente sobreestimaron el éxito para todas las especies excepto para *Buteo regalis.* Estimados de exito basados en intentos de anidar hallados durante la incubación tuvieron el menor tamaño de muestra. Los tres métodos mostraron estimados de éxito de anidaje viciados para *Circus cyaneus* y *Asio flammeus.* El estimado basado en parejas halladas durante la incubación probablemente proveyó el estimado menos viciado *Speotyto cunicularia.* La determinación del éxito en anidar se afectó por dificultades en confirmar la deposición de huevos y el éxito de anidaje para todas las especies con excepción de *Buteo regalis.*

Raptor nest surveys often are used to compare numbers of nesting pairs and reproductive success of breeding birds among years or locations (Fuller and Mosher 1987, Steenhof 1987). When conducting surveys, biologists must decide among several possible measures to evaluate a nesting population. For example, relative abundance often is the most convenient measure to compare numbers of pairs occupying nesting areas because there is no need to find every nesting pair (as required for absolute abundance or density estimates). Estimates of productivity (the number or percentage of young that reach fledging age) require complete counts of young at nests, whereas estimates of nesting success (the number or percentage of pairs in a population that raise young to fledging age) require only a determination that young of a certain age were or were not produced at each nest (Steenhof 1987).

Biologists also must consider potential biases of each measure used. Estimates of raptor reproductive rates are particularly sensitive to survey timing and the method used to select pairs for analysis (Fraser 1978, Steenhof and Kochert 1982). Surveys that begin early in the nesting season may cause nesting failures because investigator disturbance during incubation and early brood-rearing is more likely to cause egg and nestling mortality (Fyfe and Olendorff 1976). As a result, reproductive rates estimated from early surveys may be lower than natural rates. Surveys that begin late miss pairs that failed early and, therefore, may overestimate reproductive rates (Steenhof and Kochert 1982).

Steenhof and Kochert (1982) outlined three ways to overcome error associated with inclusion of conspicuous, successful nests found late in the nesting season. First, estimates of nesting success can be based on a group of nesting areas selected prior to the nesting season. If all known nesting areas cannot be surveyed a sample of nesting areas should be selected randomly. Second, nesting success can be based only on pairs found during incubation to ensure that successful pairs found late in the breeding period are not included. Finally, estimates of nesting success can be based on the Mayfield model (Mayfield 1961, 1975). The Mayfield model requires that the viability of a nesting attempt (eggs or young) be confirmed during at least two visits to a nesting area, and assumes that laying pairs will fail at a constant rate during the nesting season. This allows an estimate of a daily nest failure rate based on the known number of failures during the observation period and the total number of days nests were observed.

From 1991–1994, we quantified relative abundance and nesting success of the Ferruginous Hawk (*Buteo regalis*), Northern Harrier (*Circus cyaneus*), Burrowing owl (*Speotyto cunicularia*), and Short-eared Owl (*Asio flammeus*) on the shrubsteppe plateaus (hereafter, the benchlands) in and near the Snake River Birds of Prey National Conservation Area (NCA) in southwestern Idaho. Our research was part of a larger study of the effects of habitat alterations in the NCA (U.S. Dep. Inter. 1996), and was the first systematic effort to assess abundance and reproductive success of benchland raptors in the NCA. In this paper, we compare detection rates and potential biases for four random and two non-random sampling methods used to estimate relative abundance of nesting raptors, and we evaluate three methods used to estimate nesting success.

STUDY AREA

Our research was conducted on the benchlands north of the Snake River Canyon, Ada and Elmore counties (43°N, 116°W). Topography on the 160,541-ha study area is flat to slightly rolling with scattered, isolated cinder cones and buttes. Elevation ranges from 920 m at the canyon rim to 1066 m at the highest point.

In undisturbed areas, vegetation is dominated by big sagebrush (*Artemisia tridentata*), shadscale (*Atriplex confertifolia*), winterfat (*Krascheninnikovia lanata*), and other shrub species (Kochert and Pellant 1986). In areas where surface-disturbing activities or wildfires have occurred, vegetation is dominated by cheatgrass (*Bromus tectorum*), Russian thistle (*Salsola kali*), and other non-native annual plants (Yensen 1982). Native perennial grasses occur in both disturbed and undisturbed habitats, and include Sandberg's bluegrass (*Poa secunda*), bottlebrush squirreltail (*Elymus elymoides*), and bluebunch wheatgrass (*Pseudoroegneria spicatum*) (U.S. Dep. Inter. 1995).

Primary land uses in the study area are grazing, hunting, and other forms of recreation (U.S. Dep. Inter. 1995). Military training, including artillery firing, armored vehicle training, and small arms firing, occurs in a 56,002-ha Idaho Army National Guard training site contained entirely within the study area (U.S. Dep. Inter. 1996).

METHODS

Random sampling.—From 1991 to 1994, we used four random sampling techniques to estimate relative abundance of nesting raptors: point counts and line transects in 1991 (Fuller and Mosher 1987), 9-km^2 quadrats (3 × 3 km) in 1992, and 6-km^2 quadrats (2 × 3 km) in 1992 and 1994 (Schmutz 1984). Our goal was to locate as many occupied nesting area as possible within the sampling units each year.

In 1991, we randomly selected 192 points from Universal Transverse Mercator grid lines using an ARC/INFO (Environ, Sys. Res. Inst 1993) Geographic Information System (GIS). Each point was the starting point of a transect pattern configured as two 800-m parallel lines spaced 400 m apart. We randomly selected the orientations of parallel transects. Each point also served as the center of a point count plot. Points were located in the field using a Global Positioning System.

We sampled each plot four times during the nesting period (March–July), twice using point counts and twice using transects. Survey type was assigned randomly to each plot for the first survey, with half the plots surveyed by transects and half by point counts. Survey type was then alternated each month at each plot. We sent different observers to each sampling plot during the four surveys. During point counts, we observed all areas visible from the center point for 30 min. During transect surveys, we observed all areas visible while walking the two 800-m transects. There was no time limit while walking transects, but they were usually completed in <1.5 h.

In 1992, we surveyed 9 km^2 quadrats and set a maximum survey duration of 8 h for each quadrat. Large quadrats were difficult to survey efficiently in one day, so in 1993 and 1994 we reduced quadrat size to 6 km^2. We increased quadrat coverage by setting a minimum survey period of 6 h and extending the maximum period to 12 h. In 1994, we changed the starting point for the grid overlay to avoid duplicating 1993 quadrat boundaries. Otherwise, we did not attempt to avoid overlap of sampling plots from year to year.

To select quadrats, we superimposed 9-km^2 and 6-km^2 cell grids on the study area using the GIS, and randomly selected quadrats from cells on the grid. We sampled 44 quadrats in 1992, 49 in 1993, and 50 in 1994. Depending on the size and number of quadrats surveyed, 18–24% of the study area was sampled each year.

We sampled each quadrat twice during the nesting period using different observers each time. During all 3 years, we conducted the first survey from late March to mid or late April. In 1992, we conducted the second survey from mid April to mid May. Because nesting areas were more easily detected late in the breeding period, in 1993 and 1994 we scheduled the second survey later than in 1992 (late April to early June in 1993; late May to early July in 1994).

During surveys, we used maps and compasses and focused on geographic features to remain inside quadrats. We did not mark quadrat boundaries in the field. We usually drove, and sometimes walked, all roads within each quadrat, and walked areas within quadrats not visible from roads. Observers walked line transects through quadrats spaced 100–200 m apart in areas with dense shrubs, and 300–400 m apart in open areas. To improve detection of owls, ≥1 survey began at dawn or ended at dusk.

During sampling, we noted the location and behavior of all raptors observed. We defined an occupied nesting area as any area where we observed territorial defense, courtship, or nest attendance by a pair of raptors. In this paper, we use the terms nesting pair and occupied nesting area interchangeably.

Nonrandom sampling.—In addition to random sampling, between 1991–1993 we checked all nesting areas known to have been occupied at least once during previous years. In 1994, time limitations prevented visits to all historical nesting areas, so we selected only those occupied during the previous two years. We checked 63 historical nesting areas in 1991, 116 in 1992, 142 in 1993, and 205 in 1994. Each year we also searched areas where there were incidental observations of nesting activity of the four target species. We classified nesting areas found inside random sampling plots as incidental or historical if they were missed during random sampling.

Initial visits to nesting areas occurred during the incubation period. We considered a historical nesting area to be vacant if we detected no signs of occupancy by the end of the brood-rearing period, after ≥3 nest visits. We spent 0.5–1.5 h during each visit, and occasionally watched nesting areas from a distance for nest-building activity, prey deliveries, or other behaviors that would help pinpoint a nest. We visited owl nesting areas during early morning or late evening at least once to improve detection rates.

Analysis of survey methods.—To quantify the effectiveness of survey methods used to locate nesting pairs, we calculated search times for all years and the number of pairs found per 100 h of effort for each method. For historical nest surveys we included only the time required to confirm occupancy. To estimate the number of pairs found per unit effort for incidental observations, we subtracted the total time spent conducting random plot and historical nest surveys from the total time spent on the benchland study.

Reoccupancy rates.—To determine if historical nesting areas can be used to monitor long-term abundance and nesting success, we evaluated reoccupancy rates for each species for the consecutive years 1993–1994 and the 3-yr interval 1991–1994. We considered nesting areas used in 1991 and 1993 to be reoccupied if we observed territorial defense, courtship, or nest attendance in 1994.

Nesting success.—From 1992 to 1994, we tried to determine the outcome of nesting attempts of all pairs found during random plot surveys, at historical nesting areas, and at nesting areas found incidentally. We defined a nesting attempt as one where pairs laid eggs. Evidence for a nesting attempt included eggs, young, adults in incubating posture, or eggshell fragments in fresh nesting material. Except for the Ferruginous Hawk all nest visits to confirm egg laying or success occurred on the ground. Ferruginous Hawk nests on transmission towers were checked at least twice each year from a helicopter.

We did not include non-laying pairs or pairs for which we could not confirm egg laying in any analyses of nesting success for the Ferruginous Hawk, Northern Harrier, or Short-eared Owl. However, we could not confirm egg laying for Burrowing Owl pairs because we were unable to inspect their underground nests. Therefore, our estimates of Burrowing Owl success were based on pairs instead of nesting attempts, and we may have included non-laying pairs.

We did not assess productivity (number of young per pair) because we could not obtain a complete count of young at many nests. We considered Ferruginous Hawk and Burrowing Owl nesting attempts to be successful if young reached 31 and 28 days of age, respectively (Smith and Murphy 1978, Zarn 1974). We used photographic keys (Moritsch 1985, J. Priest, Humane Society of Santa Clara, California, unpubl. data) to age nestlings of both species. We considered Short-eared Owl and Northern Harrier nesting attempts successful if young reached 20 and 24 days, respectively (Clark 1975, Steenhof 1987). We used descriptions of feather development to age nestlings of both species (Bent 1961, Watson 1977 for the Northern Harrier; Johnsgard 1988, Karalus and Eckert 1987 for the Short-eared Owl).

To determine if estimates of nesting success for the Ferruginous Hawk, Northern Harrier, and Short-eared Owl were biased upward by including pairs found late in the nesting season (Steenhof 1987, Steenhof and Kochert 1982), we pooled years and compared success rates of all nesting attempts with those attempts found during incubation. Because we could not determine the state of nesting when we first located Burrowing Owl pairs, we backdated from age estimates of young after young had emerged from their burrows to determine if pairs were found during incubation. If no young were observed at a nest, we included the pair if it was found before the median hatch date for the year.

We used contingency table analysis (*G*-tests) to compare estimates of nesting success based on all nesting attempts with estimates based on attempts found during incubation. We also compared estimates of nesting success based on these two methods with those obtained using the Mayfield model (Mayfield 1961, 1975; Steenhof 1987).

RESULTS

Effectiveness of random sampling.—The total number of occupied nesting areas found in the study area (all methods combined) increased each year from 64 in 1991 to 151 in 1994 (Table 1). For all but one year, we found the fewest nesting areas by random sampling (<25% of each year's total) (Table 2). More nesting pairs were found incidentally than by any other method during all 4 years of the study.

Each year we found some pairs during historical nest searches or incidentally inside random plots that we missed during random sampling. We missed at least 3 pairs at random plots in 1991 (transects and point

TABLE 1. Number of occupied raptor nesting areas found on the benchlands in and near the Snake River Birds of Prey National Conservation Area, southwest Idaho, by year and species (all methods combined).

Species	1991	1992	1993	1994
Ferruginous Hawk	8	17	14	18
Northern Harrier	8	9	10	11
Burrowing Owl	30	44	71	87
Short-eared Owl	18	24	11	35
Totals	64	94	106	151

counts), 9 pairs in 1992 (large quadrats, 3 pairs in 1993 (small quadrats), and 6 pairs in 1994 (small quadrats).

The number of Short-eared Owl pairs found tripled from 1993 to 1994 from 11 to 35 pairs (Table 1). However, data from random sampling showed no change in the number of Short-eared Owl pairs (five pairs were found each year) and a decrease in the total number of raptor pairs found inside sampling plots between 1993 and 1994 (Table 2).

Comparison of random sampling methods.—On a per-sampling-effort basis, transects were more effective than point counts and quadrats for locating raptor nests (Table 3). In 1991, we found twice as many nesting pairs by walking transects than by point counts, probably because of the tendency of raptors to flush when we walked by their nests. Although transects required more time to complete than point counts ($\bar{x}$ = 0.9 vs. 0.5 h), the greater number of nests we found on transects compensated for the additional effort.

From 1992 to 1994, we found more nesting areas during quadrat surveys than we found using either point counts or transects (Table 3), but the greater number of nesting areas did not compensate for the additional effort required to conduct quadrat surveys. Quadrats required on average 8.3 h to complete; thus, the return per sampling effort was lower than point counts and transects. Starting the second quadrat survey 2 wk later than in 1992 may have contributed to a higher return rate in 1993 (Table 3). Starting the second survey 1 mo later than in 1992 may have lowered the return rate in 1994 (Table 3).

Comparison of all sampling methods.—Each year, we found most nesting pairs as a results of incidental encounters outside random plots of histor-

TABLE 2. Percent of occupied raptor nesting areas found on the benchlands in and near the Snake River Birds of Prey National Conservation Area, southwest Idaho, using three survey methods. Sample sizes are in parentheses.

Survey type	1991	1992	1993	1994
Historical surveys	17 (11)	34 (32)	37 (39)	36 (54)
Random sampling	24 (15)	17 (16)	22 (23)	12 (19)
Incidental observations	59 (38)	49 (46)	41 (44)	52 (78)

TABLE 3. Relative effectiveness of random sampling methods used to assess relative abundance of benchland raptors in and near the Snake River Birds of Prey National Conservation Area, southwest Idaho.

Year	Method	No. plots	$\bar{x}$ h/plot	Total h	No. pairs found	No. pairs/ 100 h
1991	Point count	381	0.5	192	6	3.1
1991	Transect	387	0.9	348	12	3.4
1992	Quadrat (9 km^2)	87	7.5	652	17	2.6
1993	Quadrat (6 km^2)	97	8.8	854	25	2.9
1994	Quadrat (6 km^2)	100	8.6	860	19	2.2

ical nesting areas (Table 1). Incidental encounters occurred during follow-up visits to confirmed nesting areas or while traveling between survey sites. We spent approximately 9780 h in these activities, compared to 3820 hrs for the other two survey methods combined. Thus, we found only 1.6 nesting pairs per 100 h of observation as a result of incidental encounters, the lowest of the three methods used to locate pairs. We found 2.7 pairs per 100 h during random plot surveys, and 14.6 pairs per 100 h during historical nest surveys.

Reoccupancy rates.—Reoccupancy rates were high only for the Ferruginous Hawk (Table 4). Seventy-five percent of Ferruginous Hawk nesting areas used in 1991 were still being used in 1994, and 71% of nesting areas used in 1993 were occupied in 1994. Less than 25% of Northern Harrier and Short-eared Owl nesting areas and less than 45% of Burrowing Owl nesting areas used in 1993 were occupied in 1994; for all three species, reoccupancy after 3 years was below 15%.

Nesting success.—Estimates of nesting success based on all nesting attempts were consistently higher than those based only on attempts found during incubation (Table 5). Estimates of nesting success based on attempts found during incubation tended to be intermediate between those for all attempts and those for the Mayfield model, but were usually closer to Mayfield estimates. Sample sizes for evaluating success were always highest when we used all pairs or attempts, and except for the Mayfield estimate for the Burrowing Owl, were lowest when we used only those attempts or pairs found during incubation.

Each year there were some pairs that could not be used in any evalu-

TABLE 4. Percent of nesting areas used by benchland raptors in 1991 and 1993 that were reoccupied in 1994 in and near the Snake River Birds of Prey National Conservation Area, southwest Idaho. Sample sizes are in parentheses.

Species	1991	1993
Ferruginous Hawk	75 (8)	71 (14)
Northern Harrier	12 (8)	22 (9)
Burrowing Owl	11 (28)	42 (71)
Short-eared Owl	14 (14)	20 (10)

TABLE 5. Comparison of percent nesting success for benchland raptors in and near the Snake River Birds of Prey National Conservation Area, southwest Idaho, 1992–1994 (all years pooled), using 3 methods. All estimates are based on laying pairs (percent of attempts successful), except as indicated. Sample sizes are in parentheses.

Species	All attempts[a]	Attempts found during incubation[c]	Mayfield estimate[d]
Ferruginous Hawk	67 (40)	61 (26)	59 (36)
Northern Harrier	45 (20)	23 (13)	16 (15)
Burrowing Owl	71 (189)[b]	64 (108)[b]	100 (37)
Short-eared Owl	62 (34)	8 (12)	8 (20)

[a] Includes pairs found after the incubation period.
[b] Estimates may include nonlaying pairs (percent of pairs successful).
[c] Estimates differed significantly from those of all pairs only for the Short-eared Owl ($G = 11.56$, $P < 0.001$). For all other species: $Gs \leq 1.69$, $Ps \geq 0.19$.
[d] Based on Mayfield (1961, 1975).

ation of nesting success. The number of pairs not used varied among species, and reflected difficulties in confirming if eggs had been laid, young were produced, or both. From 1992 to 1994, we could not confirm whether eggs were laid at any of the occupied Burrowing Owl nesting areas we found, at 7 of 49 Ferruginous Hawk nesting areas (14%), 10 of 30 Northern Harrier nesting areas (33%), and 31 of 70 Short-eared Owl nesting areas (44%). In addition, we were unable to confirm whether young were produced at 2 of 49 Ferruginous Hawk, 7 of 30 Northern Harrier, 27 of 202 Burrowing Owl, and 28 of 70 Short-eared Owl nesting areas (4%, 23%, 13%, and 40%, respectively).

DISCUSSION

Relative abundance.—The increase in total number of pairs found during the study using all methods was due primarily to the fact that we were working in areas that had never been surveyed. Each year, previously unrecorded pairs were added to pairs that reoccupied nesting areas from earlier years. Consequently, we expected cumulative increases during the first few years.

Each year random sampling provided proportionately fewer pairs for assessing relative abundance than the other methods we used, and quadrat sampling did not detect a Short-eared Owl population increase from 1993 to 1994. However, in 1994, many Short-eared Owl nesting areas were clumped in the northwest and central portions of the study area, whereas quadrats fell in the westcentral and eastern portions. Thus, the failure to detect the increase was an artifact of our random sampling. If we had reduced the size of quadrats and increased the number of plots, the increase may have been apparent. We also may have detected the increase if we had used transects in 1994 rather than quadrats.

Our 1994 survey data (all methods combined) suggest that mean raptor abundance on the benchlands was <1 pair per 10 km^2. Low abundance and the fact that random sampling provided relatively few pairs for analysis suggests that inferences about relative abundance using random techniques alone may always be limited by low sample sizes. Sample sizes presumably would increase if more of the study area was included inside sampling plots, but the number of additional pairs found might not justify the increase in time and expense.

Visits to historical nesting areas provided the highest return per sampling effort and incidental observations the greatest number of pairs; however, with these methods there is no way to ensure a random sample or that relative efforts among years or locations are equal. Historical nest surveys every 1–3 years would yield questionable data about population trends because most pairs do not return to a previously used nesting area. Low reoccupancy rates for the Northern Harrier, Burrowing Owl, and Short-eared Owl indicate that long-term monitoring of abundance should not be based on historical surveys. Monitoring only historical nesting areas would be misleading even for the Ferruginous Hawk, the species with the highest reoccupancy rate, because 25% of pairs will not return to nesting areas used in previous years. Without searches of other suitable habitats to determine if these pairs occupied new nesting areas, conclusions about abundance would not be reliable. Periodic searches of other habitats also would be necessary to detect population increases.

Nesting success.—Estimates of nesting success for the three methods varied least for the Ferruginous Hawk (59–67%). The species usually nested in conspicuous places in our study area (rock outcrops, transmission towers, and other artificial structures) and were observed easily from the ground or from a helicopter. We confirmed egg laying and success for most occupied nesting areas; thus, all three estimates appear to be relatively free of bias. The best approach for the Ferruginous Hawk is to preselect all historical nesting areas or a random sample of these nesting areas, begin nest surveys early in the breeding period, and use all confirmed nesting attempts. This approach will provide the largest sample size.

Estimates of success for the Northern Harrier and Short-eared Owl varied widely among methods, and probably were not accurate because the status of too many pairs could not be classified properly. Egg laying was difficult to confirm for these species because of problems locating nests. Both species nest on the ground in our study area and had very short flush distances at their nests. Typically, we had to pass within 2 m to flush an incubating or brooding adult, and often could not find nests even though we knew pairs were present.

Short-eared Owl nestlings tended to wander from the nest on foot up to a week before reaching fledging age. Occasionally, they left the nest as early as 12 days of age. As a result, nestlings were difficult to find, and nesting success often was difficult to determine. The fact that two methods provided the same estimate for this species (Table 5) may mean that biases in both cases were similar. Low estimated nesting success for the Short-eared Owl also suggests investigator disturbance during early visits to nesting areas caused failures.

For the Burrowing Owl, confirming the viability of nesting attempts was possible only at nesting areas where young had emerged from their burrows. During our study, all of these turned out to be successful; thus, the Mayfield estimate for this species (100%) was inflated. The estimate based on all pairs may have been inflated by including successful pairs found late, and the estimate based only on pairs found during incubation was probably more accurate. However, because nestling owls move from their natal burrows to the burrows of other pairs (Henny and Blus 1981), some pairs classified as successful during our study may not have produced young of their own, and pairs seen without young may have been successful.

The principal advantage of the Mayfield model is that estimates are not biased upward by including conspicuous successful nesting attempts (Steenhof 1987), but the model has several other useful features. First, data from all nesting areas checked more than once can be used if viability of nesting attempts is confirmed each time. This is important when nests are scarce or difficult to locate. Also, nesting attempts need not be followed through the entire breeding period, reducing survey time and scheduling problems.

The Mayfield model has limitations, however. It may underestimate success rates of populations whose failure rates are high but extremely variable (Green 1977). In our study, this may have been the case with the Northern Harrier and Short-eared Owl. When the entire nesting population has been surveyed, the Mayfield model may underestimate success because it assumes that some unsuccessful attempts have been missed. Finally, the Mayfield model is sensitive to sample size. Hensler and Nichols (1981) suggested that the Mayfield model not be used for fewer than 20 nesting attempts. Because of this limitation, we were unable to estimate annual nesting success for any of our populations, and the reliability of the Mayfield estimate for the Northern Harrier is questionable, even when we pooled years (Table 5).

In summary, all methods we used to assess relative abundance and nesting success presented practical difficulties or had potential biases for most species. Random sampling provided small sample sizes for estimating abundance, and historical nest surveys and incidental observations were inappropriate for estimating abundance because they could not be randomized and because of low reoccupancy rates at historical nesting areas. Given low returns from random sampling and low reoccupancy rates at nesting areas used in previous years, monitoring of nesting success on the benchlands will require a combination of methods to maximize sample sizes. In this study, we pooled nesting areas found during random, historical, and incidental nest searches and pooled years to ensure adequate sample sizes for comparing three methods of computing nesting success. Long-term monitoring will require annual estimates of nesting success for comparison among years. Even if methods are combined each year, estimates of nesting success may be hindered by small sample sizes for all species except the Burrowing Owl. In the future, random sampling of a larger proportion of the study area using many small plots, preferably transects, may increase sample sizes for estimating relative abundance and nesting success. Intensive observations at Northern Harrier and Short-eared Owl nesting areas may be necessary to ensure that egg laying and nesting success are confirmed for most pairs. This will help to maximize the number of pairs used to analyze nesting success.

ACKNOWLEDGMENTS

Funding for this study was provided by the Idaho Army National Guard (IDARNG) under an agreement with the U.S. Army Edgewood Research Development, and Engineering Center, U.S. Bureau of Land Management (BLM), and National Biological Service (NBS)-Raptor Research and Technical Assistance Center (RRTAC). The study was part of the cooperative BLM/IDARNG Research Project conducted from 1990–1994. Numerous scientists and managers participated in planning workshops that resulted in the final study design. We thank Mark Fuller, John Rotenberry, Jim Bednarz, and Mark Bechard for additional suggestions on our study design, and the more than 50 BLM and NBS seasonal technicians who collected data in the field during all years of the research. Logistical and administrative support for the field effort was provided by the BLM Boise District Office and RRTAC. Thanks go to Gerry Griggs, Dave Dyer, and Elna Black for field support; Tom Zarriello and Deanna Dyer for GIS support; Genna Ashley and Deana Parrish for data automation; and Steve Knick for statistical advice. Additional administrative and logistical support was provided by the U.S. Fish and Wildlife Service Region II office, Portland, Oregon, the Boise State University Raptor Research Center, and IDARNG. We thank referees Mike Collopy and Joni Ward for their constructive criticism of the manuscript

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Received 23 Jan. 1997; accepted 3 Jul. 1997.