BioOne RESEARCH EVOLVED

Detection Probabilities of Woodpecker Nests in Mixed Conifer Forests in Oregon

Author(s): Robin E. Russell, Victoria A. Saab, Jay J. Rotella, and Jonathan G. Dudley
Source: The Wilson Journal of Ornithology, 121(1):82-88.
Published By: The Wilson Ornithological Society
https://doi.org/10.1676/08-026.1
URL: http://www.bioone.org/doi/full/10.1676/08-026.1

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

The Wilson Journal of Ornithology 121(1):82–88, 2009

DETECTION PROBABILITIES OF WOODPECKER NESTS IN MIXED CONIFER FORESTS IN OREGON

ROBIN E. RUSSELL,[1,5] VICTORIA A. SAAB,[2] JAY J. ROTELLA,[3] AND JONATHAN G. DUDLEY[4]

ABSTRACT.—Accurate estimates of Black-backed (*Picoides arcticus*) and Hairy Woodpecker (*P. villosus*) nests and nest survival rates in post-fire landscapes provide land managers with information on the relative importance of burned forests to nesting woodpeckers. We conducted multiple-observer surveys in burned and unburned mixed coniferous forests in Oregon to identify important factors influencing detection rates of woodpecker nests. We found 21 Black-backed Woodpecker nests and 38 Hairy Woodpecker nests in burned forest, and three Hairy Woodpecker nests in unburned forest. Competing models of detection probability in Program MARK indicated that nest-detection probability differed by nest stage. We found no evidence to indicate that detection rates of nests were associated with survey timing during the nesting season. Raw nest counts in burned coniferous forests may underestimate nest numbers, especially for nests in early stages of development. Black-backed Woodpecker nests were slightly more detectable than those of Hairy Woodpeckers in burned forests, and observers may differ in their abilities to detect nests. *Received 12 February 2008. Accepted 29 May 2008.*

The importance of estimating probabilities of detection for individuals, species, or age classes has been noted by many authors (Nichols 1992, Buckland et al. 2001, Williams et al. 2001, MacKenzie et al. 2006), and computer programs are available for estimating detection probabilities for a wide variety of sampling scenarios. Program MARK (White and Burnham 1999) and Program PRESENCE (MacKenzie et al. 2006), for example, are based on generating estimates of detection and/or recapture probabilities (p) to adjust observed counts of individual animals or occupied sites, and account for differences in detection probabilities (Nichols 1992). Despite the volume of literature emphasizing potential biases that can be induced by ignoring detection rates, few studies have quantified detection rates for nests of avian species. In the few cases where avian researchers have estimated detection probabilities for nests, p has varied by observer, species, or habitat type (Erwin 1980, Ferns and Mudge 1981, Wanless and Harris 1984, Rivera-Milán 2001, McPherson et al. 2003, Barbraud et al. 2004, Barbraud and Gélinaud 2005).

Woodpeckers perform an important ecosystem function by creating cavities which are subsequently used by a number of different wildlife species (Raphael and White 1984, Murphy and Lehnhausen 1998, Hutto 2006, Saab et al. 2007). Previous studies have identified post-fire forests as important nesting habitat for several woodpeckers and other cavity-nesting species (Bock et al. 1978, Raphael and White 1984, Saab and Powell 2005, Saab et al. 2007). Accurate counts of nests and estimates of productivity are necessary to provide land managers with information regarding the effects of management practices (such as salvage logging) on these species. We selected two woodpecker species, Hairy Woodpeckers (*Picoides villosus*) and Black-backed Woodpeckers (*P. arcticus*), as our focal species.

We conducted a study using a survey design with independent observers to examine whether probability of nest detection varied as a function of nesting stage, observer, species, season, and/or habitat (burned or unburned). Our objectives were to: (1) identify important factors affecting nest detection rates of the two woodpecker species, (2) quantify the detection rates of woodpecker nests and examine how the probability of detection increases from one to three surveys, and (3) provide recommendations to improve the probability of detecting woodpecker nests.

[1] Montana Fish, Wildlife, and Parks, 1400 South 19th Avenue, Bozeman, MT 59718, USA.

[2] USDA Forest Service, Rocky Mountain Research Station, 1648 South 7th Avenue, Bozeman, MT 59717, USA.

[3] Department of Ecology, Montana State University, Bozeman, MT 59717, USA.

[4] USDA Forest Service, Rocky Mountain Research Station, 322 East Front Street, Suite 401, Boise, ID 83702, USA.

[5] Corresponding author; e-mail: RRussell@mt.gov

We expected nest detection would be highly associated with nest stage. Late-stage nestlings close to fledging are often more conspicuous and vocal (Best and Petersen 1982, Pietz and Granfors 2000). Johnson and Shaffer (1990) noted the number of Mallard (*Anas platyrhynchos*) nests found increased with age, indicating nests were missed in early stages for this species. Mayfield (1961, 1975) methods for estimating nest success were developed because successful nests have a higher probability of being detected than failed nests due to longer exposure times, and estimates of apparent nest success are biased high.

We expected the day in the season the survey was conducted should be related to nest stage (more late stage nests found later in the season), and potentially would be associated with increasing nest detection rates later in the season. Hairy and Black-backed woodpeckers are similar with regard to calling rates, size, foraging behavior, and visual appearance (Dixon and Saab 2000, Jackson et al. 2002), and we expected detection rates to be similar for both species. We also expected nest detection probability to be lower in unburned landscapes due to denser vegetation than in forests burned by wildfire, and that detection probability would vary by observer.

METHODS

Study Area.—We conducted this study in burned and unburned coniferous forests in south-central Oregon. We selected one unburned 250-ha study unit on The Nature Conservancy's Sycan Marsh Reserve, and one on the Fremont-Winema National Forest. Both locations were subjected to similar management regimes prior to the implementation of our study. Burned sites were in the Toolbox fire complex on the Fremont-Winema National Forest, which burned 34,400 ha in 2002 (USDA 2002). We selected study units within the Toolbox fire using remotely-sensed data. We selected units with a mixed conifer overstory with >40% pre-fire crown closure that had been moderately-severely burned following the wildfire to ensure that study units were relatively uniform. Eight units were selected within the burned area and protected from logging. Units ranged in size from 23 to 106 ha. Dominant tree species were ponderosa pine (*Pinus ponderosa*), lodgepole pine (*P. contorta*), and white fir (*Abies concolor*). Elevations on the burned study sites ranged from 1,500 to 1,800 m, and on the unburned sites from 1,500 to 2,000 m.

Field Methods.—We used standard field protocols to estimate the probability of nest detection and to evaluate factors affecting those probabilities (p) for Hairy and Black-backed woodpeckers in burned and unburned forests. We used repeated independent observer surveys to estimate the probability (p) of detecting a nest. This survey design allowed us to calculate the probabilities of nest detection after one, two, or three visits, by independent observers, and to estimate total number of nests missed by all three observers.

Observers alternated between surveying burned and unburned areas during the season to allow us to separate seasonal changes in p from habitat differences in p. Survey effort (observer hours) was equal in both burned and unburned areas; however, low nest densities in the unburned areas allowed observers to survey longer transects and more area. We surveyed 435 and 241 ha in unburned and burned forests, respectively.

Transects were 200 m apart and placement was designed to cover the entire area of the study unit without overlap. The 200-m wide transects ranged in length from 0.5 to 2.0 km, depending on study unit size. Three observers systematically surveyed the full length and width of each transect. All three surveys occurred within 3–5 days from May to June 2006. A short interval was used to minimize the probability that nests would advance from one stage to another (i.e., eggs to nestlings). Surveys ceased at noon and were not conducted during inclement weather conditions (raining or extreme wind). The order in which observers surveyed each transect varied, and one observer was not always the first observer to survey a transect line. The order in which transects were surveyed was random.

Observers played calls of Black-backed and Hairy woodpeckers along a transect line every 200 m following the protocols of Dudley and Saab (2003). When observers detected a Hairy or Black-backed Woodpecker, they spent ≤90 min attempting to follow the bird and locate its nest. If a nest was found, the observer recorded the spatial coordinates of the nest, how long it took to locate the nest,

the bird species, and any behavioral cues that indicated the stage of the nesting attempt. When possible, observers used a treetop-peeper (video camera) (TreeTop II System, Sandpiper Technologies Inc., Manteca, CA, USA) to further establish the stage of the nesting attempt (Dudley and Saab 2003).

We defined and assigned each nest to one of three nest stages depending on nest status (i.e., eggs, recently hatched, or older nestlings). If we observed eggs or incubation behavior (adults returning to the cavity without food and remaining in the cavity for a long period of time), the nest was considered an ''early'' stage nest. ''Middle'' stage nests were those where we observed nestlings or feeding behavior inside the nest cavity. If we observed nestlings feeding or perched at the cavity entrance (i.e., near fledging), the nest was classified a ''late'' stage nest.

Statistical Analyses.—We treated each observed nest as an individual in Program MARK and constructed a detection history of zeros and ones indicating detection by particular observers. For example, a nest found by observer #1 but not observers #2 or #3 would receive a detection history of ''100''. A closed capture Huggins estimator with a logit-link function in Program MARK (Huggins 1989) enabled us to estimate population sizes from initial capture and recapture probabilities (in our case detection probabilities), and allowed inclusion of individual covariates to model detection probabilities.

Closed-capture models assume that survival probability is 1.0 for all individuals for short time intervals between sampling occasions (White and Burnham 1999). Given previous research indicating that daily nest survival rates are high for these two species (Saab et al. 2007), we assumed the nest did not fail over the short time period during which the three observers surveyed each transect. Previous estimates of daily nest survival in an unlogged post-fire landscape of Idaho were 0.995 (95% CI [0.982–0.999]) for Black-backed Woodpeckers and 0.989 (95% CI [0.979–0.994]) for Hairy Woodpeckers (Saab et al. 2007). Thus, probability of nest failure within a 5-day period was 0.05 for Hairy Woodpeckers and 0.02 for Black-backed Woodpeckers; we believe we were justified in choosing a closed-capture model for this study.

We generated an *a priori* list of candidate models of detection probability including a model of constant detection as well as models that varied across burned and unburned forest, nest stages, and species. We selected top models of nest detection probability using information theoretic approaches (Burnham and Anderson 2002). Day in season the survey occurred was calculated as a continuous covariate with the first day of the first survey equal to day 1. We did not include day in season and nest stage in the same model because these variables were confounded with one another. We used the delta method (Seber 1982) to estimate 95% confidence limits for probabilities of detection as functions of variables in the best models.

TABLE 1. Model selection results based on closed capture Huggins models of detection probability for two woodpecker species in burned and unburned forests in south-central Oregon. Models are ranked from most plausible ($\Delta AIC_c = 0$) to least plausible; k is the number of parameters. Forty-one Hairy Woodpecker and 21 Black-backed Woodpecker nests were included in the analyses.

Model	ΔAIC_c	AIC_c *wt*	k
Stage	0.0	0.55	3
Stage and species	1.6	0.24	4
Observer and stage	2.0	0.20	5
Observer, species, stage	8.0	0.01	8
Constant	14.2	0.00	1
Species	16.1	0.00	2
Day in season	16.1	0.00	2
Day in season and species	16.2	0.00	3
Observer	18.0	0.00	3
Observer and day	18.2	0.00	4
Observer and species	22.4	0.00	6

RESULTS

Searchers located 21 Black-backed Woodpecker (21 in burned and zero in unburned forest) and 41 Hairy Woodpecker nests (38 in burned and 3 in unburned forest). We did not include habitat as a factor in our candidate models due to small sample sizes in the unburned landscape. Detection probabilities varied as a function of nest stage, species, and observer (Table 1). Later stage nests were more detectable than early stage nests, and Black-backed Woodpecker nests were slightly more detectable than those of Hairy Woodpeckers. Fifty-five percent of the model weight was associated with the model con-

TABLE 2. Parameter estimates from best models of nest detection probability for two woodpecker species in a mixed conifer forest in south-central Oregon. Estimates are the probability that an observer will locate a nest on one survey.

Detection probability	Estimate	95% C.I.
Black-backed Woodpecker		
Early stage	0.4	0.23–0.60
Middle stage	0.6	0.36–0.75
Late stage	0.9	0.75–0.96
Hairy Woodpecker		
Early stage	0.3	0.18–0.53
Middle stage	0.5	0.36–0.64
Late stage	0.9	0.71–0.95

taining nest stage only, 24% was associated with the model that also included a species effect, and 20% was associated with a model including both observer and nest stage effects. The probability of detecting a nest with only one survey was <0.50 for early stage nests of both species, but increased to >0.90 for late stage nests of both species (Table 2).

The estimated percentage of early stage nests that was missed for three visits by independent observers was 21.3% for Black-backed Woodpeckers and 29.6% for Hairy Woodpeckers (Table 3). Confidence limits on these estimates ranged from 6 to 55%, suggesting that substantial numbers of early stage nests were potentially missed. The estimated percentage of middle stage nests missed was lower than for early stage nests (8.0% for Black-backed Woodpeckers and 12.8% for Hairy Woodpeckers). We estimated the percentage of late stage nests missed was small (<1%) for both species (Table 3).

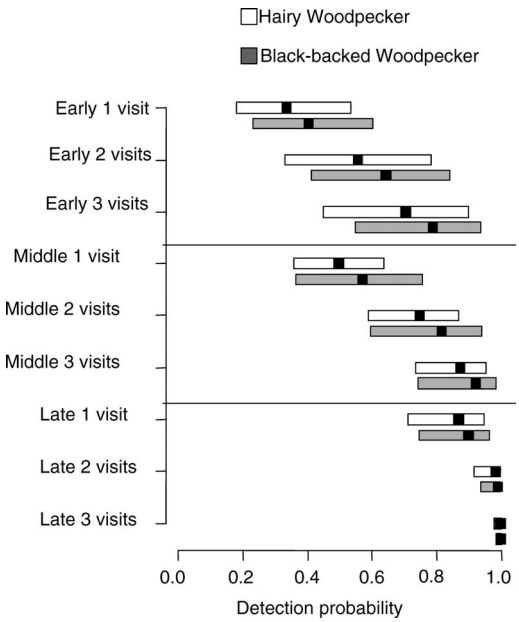

FIG. 1. Estimates of detection probabilities (probability of a nest being detected after 1, 2, or 3 visits) for each nest stage from the closed capture Huggins model in Program MARK for 41 Hairy Woodpecker nests and 21 Black-backed Woodpecker nests in south-central Oregon. Bars indicate 95% confidence intervals, boxes indicate average detection probability.

The probability of nest detection increased in the early nesting stage from 0.4 (95% CI [0.23–0.60]) for one visit to 0.8 (95% CI [0.55–0.94]) for three visits for Black-backed Woodpeckers and from 0.3 (95% CI [0.18–0.53]) to 0.7 (95% CI [0.45–0.90]) for Hairy Woodpeckers (Fig. 1). A similar increase was observed for middle stage nests of both species. The detection probabilities of late stage

TABLE 3. Estimates of nest numbers ($\hat{N}$) from closed-capture Huggins model in Program MARK for two woodpecker species in a mixed conifer forest in south-central Oregon. Estimates of nest numbers are based on three surveys.

Species and stage	Count	$\hat{N}$ (95% C.I.)	% Missed
Black-backed Woodpecker			
Early Stage	10	12.7 (10.7–18.3)	21.3 (6.3–45.3)
Middle Stage	6	6.5 (6.1–8.1)	8.0 (1.5–25.8)
Late Stage	5	5.0 (5.0–5.1)	0.2 (0.0–1.7)
Hairy Woodpecker			
Early Stage	10	14.2 (11.1–22.2)	29.5 (10.2–55.0)
Middle Stage	21	24.1 (22.1–28.6)	12.8 (4.9–26.5)
Late Stage	10	10.0 (10.0–10.3)	0.2 (0.0–2.4)

nests of both species was greater than 0.8 for one visit and approached one for three visits (Fig. 1).

Differences between probabilities of detection for early versus late stages and middle versus late stages were large (>0.3) for both species, indicating that late stage nests were more detectable than early and middle stage nests. Estimated differences between detection probabilities for Hairy versus Black-backed woodpeckers for all nest stages were small (<0.1) with non-significant differences between Black-backed and Hairy woodpeckers (Fig. 1). Estimates of differences in detection for Black-backed versus Hairy Woodpecker nests were 0.07 (95% CI [−0.197–0.335]) for early stage nests, 0.07 (95% CI [−0.177–0.325]) for middle stage nests, and 0.03 (95% CI [−0.121–0.182]) for late stage nests.

One observer (observer A) was slightly better at finding nests in all stages of development than the other two observers; however, confidence limits for each observer by stage were wide and overlapped considerably (Fig. 2). Overall, observer A found ~69% of all nests, while observer B located ~60% and observer C, ~56% (Table 4). This difference was consistent across nest stages and species. Observer B appeared to be slightly better at detecting Black-backed Woodpecker nests (67% of total) than Hairy Woodpecker nests (56% of total).

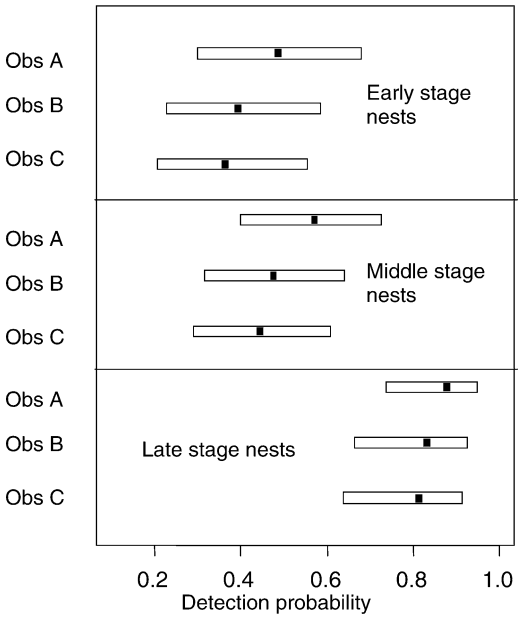

FIG. 2. Estimates of detection probabilities of each nest stage (early, middle, and late) from the closed capture Huggins model in Program MARK for 62 woodpecker nests (Hairy and Black-backed) in south-central Oregon for three different observers. Bars indicate 95% confidence intervals, boxes indicate average detection probability.

DISCUSSION

The probability of a single observer detecting a woodpecker nest in a burned forest was <1 for all observers, both species, and all nest stages. These results have implications regarding the validity of treating single-survey nest counts as census data. We believe our results are relevant to other avian species and urge caution when interpreting single-survey nest counts as census data. Depending on the specific goals of the work, the results of nest detection studies can be used to improve survey design by correcting for biased count data.

Observer and species differences in detection of nests are expected. Nichols et al. (2000) concluded that observer and species differences account for a large portion of the variability in detection probability. Studies surveying for multiple species of cavity-nesting birds may find larger differences between detection rates of different species than we found for the two similar species in this study. Our results indicated that although Black-backed Woodpecker nests were slightly more detectable than Hairy Woodpecker nests, confidence limits overlapped for probabilities of detection in each nest stage. This result may have been due to the relatively small sample sizes of nests.

Multiple surveys were effective at finding successful nests (i.e., late stage nests), and these nests were more likely to be included in the data set than nests that failed before reaching later developmental stages. Differences in probabilities of detection between nest stages for woodpecker nests in the mixed-coniferous forests of Oregon may have consequences for estimates of nest survival if nest survival varies as a function of nest stage (Grant et al. 2005). Numerous methods exist for incorporating effects of nest stage or age on nest survival including methods that are appropriate when nest age is unknown (Dinsmore et al. 2002, Jehle et al. 2004, Rotella et al. 2004,

TABLE 4. Number of nests found, and percentage of total nests found for each species and nest stage for each of three independent observers. All three observers surveyed the same area within 3–5 days. The order in which the observers surveyed the area was random.

Species	Early	Middle	Late	Totals	%
Black-backed Woodpecker					
Observer A	8	3	4	15	71.4
Observer B	5	5	4	14	66.7
Observer C	5	3	4	12	57.1
Hairy Woodpecker					
Observer A	6	10	12	28	68.3
Observer B	5	6	12	23	56.1
Observer C	4	9	10	23	56.1
Both species					
Observer A	14	13	16	43	69.4
Observer B	10	11	16	37	59.7
Observer C	9	12	14	35	56.5

Stanley 2004). Rotella (2007) cautioned that methods of Dinsmore et al. (2002) and Rotella et al. (2004) do not account for detection rate, are contingent on the data set, and assume the sample of nest data is representative of the population of nest data. If researchers are aware of important factors influencing nest detection, they may be able to adjust search effort to improve their ability to locate difficult to detect nests, or detection rate could be incorporated into estimates of nest survival (McPherson et al. 2003).

We believe it is unlikely that we missed late-stage nests of Black-backed Woodpeckers in the unburned forest given the high probability of detecting their late stage nests in burned forests. Our results support previous findings that burned forests are important nesting habitat for this species compared to unburned forest (Bock et al. 1978, Raphael and White 1984, Hutto 1995, Dixon and Saab 2000, Hoyt and Hannon 2002, Saab et al. 2007). Additional studies confirming the scarcity of Black-backed Woodpeckers in unburned forests would be useful; however, obtaining data on use of unburned forests by these species would likely be difficult and expensive.

Recent literature has emphasized the importance of estimating detection rates when conducting presence/absence studies (Dorazio et al. 2006, MacKenzie et al. 2006, Royle and Kéry 2007). Our results suggest that multiple surveys and different observers are required throughout the nesting season to ensure the majority of nests are counted. Researchers interested only in the total number of successful nests may need to only focus on surveying during the late nesting season (if the species nests synchronously and renesting rates are low). We recommend evaluating detection probability in all habitats of interest for studies of habitat-specific comparisons where habitats might have different detection rates. However, in habitats where the species is scarce, estimates of detection may not be possible. By quantifying detection probability, researchers can have more confidence in their conclusions regarding woodpecker population dynamics and will be less likely to report misleading results on habitat preferences.

ACKNOWLEDGMENTS

We acknowledge Amy Markus and Craig Beinz for providing logistical support. Funding was provided by the USDA, National Fire Plan and Forest Service, Rocky Mountain Research Station. William Thompson, Rudy King, and Kevin Podruzny provided valuable suggestions on an earlier version of the manuscript. Chris Forristal helped with implementing project design and collected data along with observers Scott Daniels, Michelle Anderson, and Kim Prosek.

LITERATURE CITED

BARBRAUD, C. AND G. GÉLINAUD. 2005. Estimating the sizes of large gull colonies taking into account nest detection probability. Waterbirds 28:53–60.

BARBRAUD, C., Y. KAYSER, D. COHEZ, M. GAUTHIER-CLERC, AND H. HAFNER. 2004. Detection probability of nests of Squacco Herons in southern France. Journal of Field Ornithology 75:172–175.

BEST, L. B. AND K. L. PETERSEN. 1982. Effects of stage of the breeding cycle on Sage Sparrow detection probability. Auk 99:788–791.

BOCK, C. E., M. RAPHAEL, AND J. H. BOCK. 1978. Changing avian community structure during early post-fire succession in the Sierra Nevada. Wilson Bulletin 90:119–123.

BUCKLAND, S. T., D. R. ANDERSON, K. P. BURNHAM, J. L. LAAKE, D. L. BORCHERS, AND L. THOMAS. 2001. Introduction to distance sampling. Oxford University Press, Oxford, United Kingdom.

BURNHAM, K. P. AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second Edition. Springer-Verlag, New York, USA.

DINSMORE, S. J., G. C. WHITE, AND F. L. KNOPF. 2002. Advanced techniques for modeling avian nest survival. Ecology 83:3476–3488.

DIXON, R. D. AND V. A. SAAB. 2000. Black-backed

Woodpecker (*Picoides arcticus*). The birds of North America. Number 509.

DORAZIO, R. M., J. A. ROYLE, B. SÖDERSTRÖM, AND A. GLIMSKÄR. 2006. Estimating species richness and accumulation by modeling species occurrence and detection probability. Ecology 87:842–854.

DUDLEY, J. G. AND V. A. SAAB. 2003. A field protocol to monitor cavity-nesting birds. USDA, Forest Service, Research Paper RMRS-RP-44. Rocky Mountain Research Station, Fort Collins, Colorado, USA.

ERWIN, R. M. 1980. Censusing waterbird colonies: some sampling experiments. Transactions of the Linnaean Society of New York 9:77–86.

FERNS, P. N. AND G. P. MUDGE. 1981. Accuracy of nest counts at a mixed colony of Herring and Lesser Black-backed gulls. Bird Study 28:244–246.

GRANT, T. A., T. L. SHAFFER, B. ELIZABETH, M. MADDEN, AND P. J. PIETZ. 2005. Time-specific variation in passerine nest survival: new insights into old questions. Auk 122:661–672.

HOYT, J. S. AND S. J. HANNON. 2002. Habitat associations of Black-backed and Three-toed woodpeckers in the boreal forest of Alberta. Canadian Journal of Forest Research 32:1881–1888.

HUGGINS, R. M. 1989. On the statistical analysis of capture-recapture experiments. Biometrika 76: 133–140.

HUTTO, R. L. 1995. Composition of bird communities following stand-replacement fires in Northern Rocky Mountain (USA) conifer forests. Conservation Biology 9:1041–1058.

HUTTO, R. L. 2006. Toward meaningful snag-management guidelines for post-fire salvage logging in North American conifer forests. Conservation Biology 20:984–993.

JACKSON, J. A., H. R. OUELLET, AND B. J. S. JACKSON. 2002. Hairy Woodpecker (*Picoides villosus*). The birds of North America. Number 702.

JEHLE, G., A. A. YACKEL-ADAMS, J. A. SAVIDGE, AND S. K. SKAGEN. 2004. Nest survival estimation: a review of alternatives to the Mayfield estimator. Condor 106:472–484.

JOHNSON, D. H. AND T. L. SHAFFER. 1990. Estimating nest success: when Mayfield wins. Auk 107:595–600.

MACKENZIE, D. I., J. D. NICHOLS, J. A. ROYLE, K. H. POLLOCK, L. L. BAILEY, AND J. E. HINES. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, Amsterdam, The Netherlands.

MAYFIELD, H. F. 1961. Nesting success calculated from exposure. Wilson Bulletin 73:255–261.

MAYFIELD, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456–466.

MCPHERSON, R. J., T. W. ARNOLD, L. M. ARMSTRONG, AND C. J. SCWARTZ. 2003. Estimating the nest-success rate and the number of nests initiated by radiomarked Mallards. Journal of Wildlife Management 67:843–851.

MURPHY, E. C. AND W. A. LEHNHAUSEN. 1998. Density and foraging ecology of woodpeckers following a stand-replacement fire. Journal of Wildlife Management 62:1359–72.

NICHOLS, J. D. 1992. Capture-recapture models: using marked animals to study population dynamics. BioScience 42:94–102.

NICHOLS, J. D., J. E. HINES, J. R. SAUER, F. W. FALLON, J. E. FALLON, AND P. J. HEGLAND. 2000. A double-observer approach for estimating detection probability and abundance from point counts. Auk 117:393–408.

PIETZ, P. J. AND D. A. GRANFORS. 2000. Identifying predators and fates of grassland passerine nests using miniature video cameras. Journal of Wildlife Management 64:71–87.

RAPHAEL, M. G. AND M. WHITE. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. Wildlife Monographs 86.

RIVERA-MILÁN, F. F. 2001. Transect surveys of columbid nests on Puerto Rico, Vieques, and Culebra islands. Condor 103:332–342.

ROTELLA, J. J. 2007. Modeling nest-survival data: recent improvements and future directions. Studies in Avian Biology 34:145–148.

ROTELLA, J. J., S. J. DINSMORE, AND T. L. SHAFFER. 2004. Modeling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. Animal Biodiversity and Conservation 27:187–204.

ROYLE, J. A. AND M. KÉRY. 2007. A Bayesian state-space formulation of dynamic occupancy models. Ecology 88:1813–1823.

SAAB, V. A. AND H. D. POWELL. 2005. Fire and avian ecology in North America: process influencing pattern. Studies in Avian Biology 30:1–13.

SAAB, V. A., R. E. RUSSELL, AND J. G. DUDLEY. 2007. Nest densities of cavity-nesting birds in relation to post-fire salvage logging and time since wildfire. Condor 109:97–108.

SEBER, G. A. F. 1982. The estimation of animal abundance and related parameters. Second Edition. Macmillan Publishing, New York, USA.

STANLEY, T. R. 2004. Estimating stage-specific daily survival probabilities of nests when nest age is unknown. Auk 121:134–147.

U.S. DEPARTMENT OF AGRICULTURE (USDA). 2002. Toolbox Fire Recovery Project, Fremont-Winema National Forest, Lake County, OR. Federal Register 67:66604–66605.

WANLESS, S. AND M. P. HARRIS. 1984. Effect of data on counts of nests of Herring and Lesser Black-backed gulls. Ornis Scandinavica 15:89–94.

WHITE, G. C. AND K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–138.

WILLIAMS, B. K., J. D. NICHOLS, AND M. J. CONROY. 2001. Analysis and management of animal populations. Academic Press, San Diego, California, USA.