Predicting Nest Success From Habitat Features in Aspen Forests of the Central Rocky Mountains

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Abstract—We collected nesting data on bird use of aspen stands in the Routt and Medicine Bow National Forests between 1987 and 1989. We found active nest sites of 28 species of small nongame birds on nine study plots in undisturbed aspen forests. We compared logistic regression models predicting nest success (at least one nestling) from nest-site or stand-level habitat predictors. Most common species used nest sites in aspen trees in forest interior locations (distance to edge >100 m), with dense trees (opening >100 m away) despite no apparent positive correlation with use of these habitat features and nest success rates. Further investigation may demonstrate that these forest interior sites do not experience lower predation and cowbird parasitism rates than nest sites near openings. We recommend adaptive management experimental treatments, including carefully planned cutting and controlled burns, that should benefit most birds in western aspen forests.

Several studies have examined nesting habitat relationships by exploring patterns in nest success of forest birds. Predation was the major cause of failure in several studies of birds nesting in forests (Hartley and Hunter 1998; Hannon and Cotterill 1998; Donovan et al. 1997; Robison et al. 1995; Martin 1992, 1993; Ricklefs 1969). Finch (1989) studied nesting habitat of house wrens (*Troglodytes aedon*) using nest boxes in southeastern Wyoming and found that success was higher on relatively open habitats that were actively selected by the birds. Predation by foliage climbing bullsnakes (*Pituophis melanoleucus sayi*) was the major cause of nest failure in this study. Open habitats were thought to hinder predator access to nests and allow early detection and deterrence of predators by the wrens (Finch 1989). Yahner (1991) found an overall inverse relationship between nest height and nest success in aspen forests of central Pennsylvania; higher nests had a significantly higher predation rate. Conversely, Li (1989) found that cavity-nesting birds on the Mogollon Rim in Arizona preferred to nest in aspen trees, and failed nests had greater concealment, shorter distances to conifers, and lower nest height. Li also found that excavators had a significantly higher success rate than secondary cavity nesters. Schmidt and Whelan (1998) found that both predation and competition influenced avian community patterns.

In the current study, we predicted that nest success would relate strongly to nest-site characteristics that are associated with nest predation, as in Christman and Dhont (1997), Yahner (1991), Finch (1989), and Martin (1998), parasite loads (Moller 1989), or disease and thermoregulation costs (Walsberg 1985). In addition, nest success could be influenced by the availability and abundance of some invertebrates or plant foods selected by adults during nesting (Winternitz 1980; Ehrlich et al. 1988; Martin 1987). Because of their association with specific host plants, some invertebrate species may have a patchy distribution associated with certain habitat conditions (Jones et al. 1985; Bernays and

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Chapman 1994; Jolivet 1998). The presence of abundant food near the nest could reduce foraging costs for parents feeding young by reducing travel costs (Dobkin et al.1995). Reducing travel associated with foraging away from the nest could increase energy and time available for egg incubation or predator and cowbird deterrence.

Study Area

The study area was located in the Routt and Medicine Bow National Forests on both sides of the Colorado-Wyoming border in the Southern Rocky Mountain (SRM) vegetation zone (2,300 to 2,700 m elevation) (Mueggler 1985). The average annual precipitation within the study area was 42.4 cm (Jones and Debyle 1985a). Aspen trees were typically over 50 years old and many were over 100 years old. Tree sizes were highly variable (d.b.h. = 2–215 cm with mean approximately 28 cm), depending on the clone, and were not closely related to age across clones. The topography included flat to mild slopes in the Medicine Bow National Forest to hillsides with up to 35% slope on the Routt National Forest. Disturbances to the area at the time of data collection included sheep herding during the nonbreeding season for birds and some small-scale historical tree harvesting. Around the turn of the century and through the late 1800s, the sites in the Medicine Bow National Forest were used as cattle runs (grazed during summer months).

Nine study plots were chosen in aspen stands about 40 ha in size. Six plots were located in the Battle Mountain area about 15 miles from the Sandstone work station in the Medicine Bow National Forest, and three plots were located in the California Park area of the Routt National Forest. Aspen comprised about 90% of all trees in these study plots with mixed understories of shrubs, grasses, and forbs. Aspen stands were mature to late seral with decay in more than 50% of the stems. Three aspen plots had grass-forb understories dominated by *Calamogrostis rubescens*, *Carex* spp., *Thalictrum fendleri*, *Lupinus argenteus*, and *Geranium* spp. Three aspen plots had small shrub understories dominated by *Symphoricarpos oreophilus* and a variety of forbs. Three aspen plots had tall shrub understories composed of *Amelanchier alnifolia, Prunus virginiana*, and *S. oreophilus*.

Methods

General Data Collection

Grids were used for vegetation sampling and locating bird nest sites. Study stands selected as examples of unfragmented aspen forests were: (1) large-sized (>40 ha) and mature, with forest openings of <2 acres; (2) accessible by 4-wheel drive vehicle, snowmobile, or motorbike; and (3) relatively level (slope <40%). Within each stand, 30 stations were established along E-W grid lines with 100 m between stations. Study plots were variable in length and width, depending on the shape and size of the stand, but all plots were approximately 36 ha (90 acres) in size with a buffer zone between plots of >450 m. Grids were laid out from a random start. Stations were located using a staff compass and measuring tape, and distances were measured along the ground surface. Each station was flagged and staked, and each stake was painted orange for visibility,

numbered, and lettered with grid coordinates (e.g., A1, A2, B1, B2, etc.) Habitat structure was estimated at the 30 sampling stations on each plot. At each sampling station, a variety of habitat variables were measured following recommendations of Noon (1981) for tree habitats.

Habitat Features

Several spatial scales of vegetation measures were recorded, including stand, tree, and cavity characteristics. Nesting habitat features measured included: distance to water, distance to edge, nest plant height, snag decay, nest height, tree d.b.h. or shrub cd, cavity diameter, tree diameter at nest site, distance of nest from tree trunk, nest substrate, nest plant position within the forest, forest opening size, compass direction of nest within tree, nest plant species, and cavity location within tree. Vertical foliage density (Noon 1981) was measured in the shrub-sapling vegetation layer by counting hits of vegetation against a vertical rod marked off in increments of 0–0.3 m, 0.3–1 m, 1–2 m, 2–5 m, >5 m.

Avifauna

We designed our avian nest sampling methods to enable location of many small nongame species' nests in an unbiased way with respect to survival, and then to record nest survival. Observers visited each of the 30 stations within a plot each morning to collect bird count data for a related study (Finch and Reynolds 1987). Each afternoon during the nesting period (May–July), observers searched for nests of all small nongame bird species during 2-hour walks through the plot and sampling effort was carefully recorded. Adults observed carrying nesting material or food were followed to locate some nests. Others were located where adults had been flushed or began calling excitedly. Bird species, grid locations, nest sites, and behavior of all birds at nests were recorded. Nest observation sheets were used to record nest status over time. Nest trees were flagged so new observers could record nesting progress. Each station was visited five times per season, and the time interval between visits to each nest to check progress was usually 3 days but varied from 1 to 43 days. In addition, nest-site characteristics were recorded at the time of nest discovery.

Preliminary Analyses

Our main objective when conducting analyses was to identify relationships between nest success and habitat features for small nongame birds in aspen forests of the central Rocky Mountains. The first step in this process was to group avian species into clusters based on ecology and life history. These guilds were used to examine nest success-habitat relationships because they provided a way to examine whether patterns existed within and between groups of similar species and increased sample size.

We grouped all the species found in our study other than raptors and species with extremely small sample sizes (less than five nests found during the entire study) into nest guilds (open cup on ground, open cup in tree, primary cavity, and secondary cavity) and seven life-history guilds. To group birds into life-history guilds, we used a cluster analysis and principal components analysis (SYSTAT 9 1999) based on life-history traits recorded in the literature for the species found in this study. Grouping bird species into guilds increased the sample size for analysis and allowed us to make inferences concerning species with similar niches that may be affected in similar ways by conifer encroachment and anthropogenic habitat alterations.

Data Preparation

Nesting outcome was directly recorded for 126 nests out of 614 nests observed throughout this 3-year study. No outcome was recorded for 488 nests because no direct observations of success or failure were made. For example, the nest contents may have been empty yet no fledglings or signs of mortality were observed in the area. Therefore, we created a macro in Minitab that assigned nesting outcomes based on logic. The developmental stage of the offspring at the second-to-last visit was determined either from a direct record or from the adult behavior that was recorded. If a time interval elapsed that was shorter than the normal amount of time required for the young to fledge (Brown et al. 1992; Calder and Calder 1992; Dobbs et al. 1997; Ingold and Galati 1997; Power and Lombardo 1996; Robertson et al. 1992; Smith 1993) between visits and the observers noted an empty nest on the last visit, the nest was classified as a failure. We used a relatively conservative rule set which tended to assign a class of failure more often than would occur under other rule sets. This decision was based on knowledge suggested in the literature that a majority of nests of most birds fail (Murphy et al. 1997; Paton 1994; Yahner 1991; Martin 1998; Finch 1990). We chose to assume that the young were close to the beginning of each nesting stage (incubation or nestling) at the second-to-last observation. This assumption increased the amount of time required to reach fledging compared to the assumption that the young were at the center of each stage at the second-to-last observation. Therefore, nests were coded as failures more frequently using this logic. If adult behavior indicated the young reached at least the nestling stage, the nest was recorded as a success.

Logistic Regression

We used logistic regression (SYSTAT 9, Systat Inc. 1999) to elucidate relationships between nest success and habitat features for common species and guilds. Models predicting nest success from habitat features were fit and evaluated according to the advice of Hosmer and Lemeshow (1989). The overall significance of each model predicting nest success from habitat was evaluated using the G statistic. We interpreted each significant model predicting nest success from habitat features using odds ratios. The predictive ability of each model was evaluated using the total correct rate and success index values. We used Akaike's Information Criterion to compare the predictive ability of nest-site habitat features to that of stand-level habitat components.

Data Screening

Species, guilds, and variables with small sample sizes (less than 10 nests and less than 50% of the maximum possible sample size for the data set, respectively) were excluded from logistic regression analyses. In addition, after running the Minitab macro described above, we did not further analyze data for species with only one failure observed, only one success observed, no failures observed, or no successes observed.

Nest Site Analyses

Prior to evaluating nesting success and nest-site habitat relationships using logistic regression, we created a rank correlation matrix (SYSTAT 9, Systat Inc. 1999) to enable us to eliminate correlated variables that measured similar biological parameters. Each of the continuous habitat variables left in the set was evaluated for its potential contribution in explaining nest success patterns using univariate logistic regression analysis. Habitat variables with an insignificant

relationship to nesting success were excluded from the complete model as recommended by Hosmer and Lemeshow (1989). The reduced set of habitat factors produced by these techniques was then used to create a logistic regression model of nest success patterns for common species and guilds (years pooled). The most parsimonious logistic regression models that still explained nest success patterns were chosen for each species or guild.

To further explore potential nest success and nest-site habitat relationships, we summarized the data using frequency tables and compared median values of continuous habitat variables between successful and failed nests to allow tentative conclusions regarding nest-site use by each common species or guild. To create frequency tables, we calculated the percent of nests that were successful for each species within each habitat feature used. We considered a nesting attempt within a habitat feature successful if the birds had at least one egg survive. These values were compared tentatively without using statistics such as chi-square analyses because many cells had low sample sizes (many were zero). We used the nonparametric Mann-Whitney U statistic (where overall comparisons were significant, $p < 0.05$, using the Kruskal-Wallis statistic) to compare median successful values to median failed values for the continuous nest-site habitat features.

Stand-Level Analyses

Stand-level vegetation data were collected using the same grid points to locate each sampling station as the grid points used to relocate a nest. Stand-level data collection sites were <100 m from each nest associated with that site. We calculated the mean value for continuous stand-level parameters measured within 100 m of each grid point and assigned these values to nest sites within 100 m of the same grid point. We analyzed stand data for three abundant species: American robins (*Turdus migratorius*), house wrens, and tree swallows (*Tachycineta bicolor*).

The logistic regression analysis described for nest-site habitat and success patterns was conducted once using only nest-site habitat parameters and once using only stand-level habitat parameters for each of the most abundant species. Since the only stand-level models that converged were insignificant, they could not be compared using Akaike's Information Criterion as planned.

Results

We found active nests of 28 small avian species (table 1) and assigned them to seven life-history guilds (table 2). Possible sources of mortality included predators, inclement weather, ectoparasites, nest parasites, and nest desertion due to disturbance and/or death of adults. Potential nest predators included northern flickers (*Colaptes auratus*), black-billed magpies (*Pica pica*), Clark's nutcrackers (*Nucifraga columbiana*), martens (*Martes americana*), striped skunks (*Mephitis mephitis*), red squirrels (*Tamiasciurus hudsonicus*), raccoons (*Procyon lotor hirtus*), and bull snakes (*Pituophis melanoleucus sayi*).

Bird nests were observed on all study sites. The most common nesting species in order of descending abundance were house wrens, American robins, tree swallows, warbling vireos (*Vireo gilvis*), western wood-pewees (*Contopus sordidulus*), northern flickers, red-naped sapsuckers (*Sphyrapicus nuchalis*), and dark-eyed juncos (*Junco hyemalis*). In a related study, none of these common species were more common in one aspen understory type than another except

Table 1—Bird species and number of observations of nests from 1987 to 1989 in aspen stands of the Routt and Medicine Bow National Forests of Wyoming and Colorado.

spp code	Common name	Scientific name	Number of observations
AMRO	American robin	*Turdus migratorius*	61
TRSW	Tree swallow	*Tachycineta bicolor*	54
WAVI	Warbling vireo	*Vireo gilvus*	44
WWPE	Western wood-pewee	*Contopus sordidulus*	25
NOFL	Northern flicker	*Colaptes auratus*	23
RNSA	Red-naped sapsucker	*Sphyrapicus nuchalis*	20
DEJU	Dark-eyed junco	*Junco hyemalis*	18
YRWA	Yellow-rumped warbler	*Dendroica coronata*	14
DOWO	Downy woodpecker	*Picoides pubescens*	13
MOBL	Mountain bluebird	*Sialia currucoides*	13
MOCH	Mountain chickadee	*Parus gambeli*	13
BCCH	Black-capped chickadee	*Parus atricapillus*	10
HAWO	Hairy woodpecker	*Picoides villosus*	9
HAFL	Hammond's flycatcher	*Empidonax hammondii*	6
BTHU	Broad-tailed hummingbird	*Selasphorus platycercus*	5
LISP	Lincoln's sparrow	*Melospiza lincolnii*	5
WETA	Western tanager	*Piranga ludoviciana*	4
WCSP	White-crowned sparrow	*Zonotrichia leucophrys*	4
DUFL	Dusky flycatcher	*Empidonax oberholseri*	3
VGSW	Violet-green swallow	*Tachycineta Thalassina*	3
YBSA	Yellow-bellied sapsucker	*Sphyrapicus varius*	3
CAFI	Cassin's finch	*Carpodacis cassinii*	2
EVGR	Evening grosbeak	*Coccothraustes vespertinus*	2
MGWA	MacGillivray's warbler	*Oporornis tolmiei*	2
WISA	Williamson's sapsucker	*Sphyrapicus thyroideus*	2
HETH	Hermit thrush	*Catharus guttatus*	1
PISI	Pine siskin	*Carduelis pinus*	1

Table 2—Bird species and guild assignments used to analyze data on nest success from 1987 to 1989 in aspen stands of the Routte and Medicine Bow National Forests of Wyoming and Colorado.

Common name	Nest guild	Life-history guild
Western wood-pewee	Open cup in tree	1 = Intermediate migrants and residents
Yellow-rumped warbler	Open cup in tree	1
Hammond's flycatcher	Open cup in tree	1
Western tanager	Open cup in tree	1
Cassin's finch	Open cup in tree	1
Dusky flycatcher	Open cup in tree	1
Pine siskin	Open cup in tree	1
Warbling vireo	Open cup in tree	1
Dark-eyed junco	Open cup on ground	1
Lincoln's sparrow	Open cup on ground	1
White-crowned sparrow	Open cup on ground	1
Hermit thrush	Open cup on ground	1
MacGillivray's warbler	Open cup on ground	1
Downy woodpecker	Primary cavity	1
Yellow-bellied sapsucker	Primary cavity	2 = intermediate migrants and occasionals
Williamson's sapsucker	Primary cavity	2
Red-naped sapsucker	Primary cavity	2
Tree swallow	Secondary cavity	2
Mountain bluebird	Secondary cavity	2
Violet-green swallow	Secondary cavity	2
Mountain chickadee	Secondary cavity	3 = small migrants and residents
House wren	Secondary cavity	3
Black-capped chickadee	Secondary cavity	3
Evening grosbeak	Open cup in tree	4 = large residents
Hairy woodpecker	Primary cavity	4
American robin	Open cup in tree	5 = large migrant
Broad-tailed hummingbird	Open cup in tree	6 = smallest migrant
Northern flicker	Primary cavity	7 = largest resident

the dark-eyed junco that was more common in small shrubs than tall shrubs (Finch and Reynolds 1987). All of these species only used aspen overstories for nesting except the American robin and dark-eyed junco that also used mixed aspen-conifer overstories and all overstories present in the forest (Struempf 2000).

Nest Site as Success Predictor

Most nests of the common species and life-history guilds were in forest interior locations (distance to edge >100 m) and oriented northeast of the aspen tree center (tables 3 and 5). This pattern in nest-site use was not positively correlated with nest success rates; birds using forest interior nest sites were not more successful than those nesting near edges (tables 3 and 5). However, comparisons of nest success rates are tentative because estimates with greater sample sizes have narrower confidence intervals. Northern flicker successful nests occurred in smaller diameter trees than did failed nests (table 4). In contrast, house wren successful nest sites were found near (26–100 m) small forest openings (£25 m radius), large forest openings (>200 m radius), or over 100 m away from an opening. Another deviation was found for tree swallow and red-naped sapsucker successful nests that were located near large openings or over 100 m away from an opening. Successful nests of most life-history guilds were placed in decayed or live trees that were not broken (table 5). However, the largest resident had success in broken trees that were decayed more than the nest sites of other birds.

Some patterns can be discerned in nest-site use as it relates to nest success in tree swallows (tables 3 and 4–6). Successful nests were usually located northwest of the nest tree center and all nest trees were aspen (table 3). Tree swallows placed most of their relatively successful nests in forest interior locations with dense trees near edges (£50 m) where forest openings were over 200 m in radius. Cavity diameter and nest tree height influenced tree swallow nest success (tables 4 and 6). More specifically, for every 1 cm increase in hole diameter, the nest was 0.12 times less likely to succeed. For every 1 m increase in nest plant height, the nest was 1.35 times more likely to succeed.

Nest success for small migrants and residents slightly decreased with an increase in distance to water and hole diameter while the pattern for snag decay was more complex (table 6). If distance to water increased by 1 m, the chance of success decreased by 0.99 times. If hole diameter increased by 1cm, the chance of success decreased by 0.55 times. Nests were 0.15 times less likely to succeed if they were in trees that were decayed and falling apart, or dead but not yet falling apart, than when they were in living trees. Nests were 0.01 times less likely to succeed if they were in living trees with dead wood at the cavity than nests in living trees with living wood at the cavity. Relatively successful nests were located in forest interiors over 100 m from an edge, northeast of the nest tree center (table 5). If these successful nests were in cavities, they were located in the central tree stem of an intact aspen tree (table 5).

Secondary cavity nest success decreased with increasing distance to water and hole diameter (table 6). Conversely, success increased near edges. If distance to water increased by 1 m, the chance of success decreased by 0.99 times. If hole diameter increased by 1 cm, the probability of nest success decreased by 0.50 times. A secondary cavity nest was 13.6 times more likely to succeed if it was in a location £100 m away from an edge than a nest further away.

A logistic regression model predicting nest success from nest-site habitat features was not calculated for some species because the data did not meet all

Table 3—Percent of nests successful for each nesting habitat feature used by each of the eight most common species in aspen of the Medicine Bow and Routt National Forests, 1987–1989.

Species	American robin	n	Dark-eyed junco	n	House wren	n	Northern flicker	n	Red-naped sapsucker	n	Tree swallow	n	Warbling vireo	n	Western wood-pewee	n
Nest plant position																
Isolated	unused	0	unused	0	100.00	1	unused	0	unused	0	0.00	1	unused	0	unused	0
Open	50.00	2	unused	0	100.00	4	unused	0	100.00	2	100.00	2	unused	0	0.00	1
Marginal	50.00	2	100.00	1	100.00	16	100.00	1	100.00	4	100.00	5	unused	0	0.00	1
Interior	41.03	39	75.00	8	0.82	142	41.67	12	76.92	13	64.71	17	58.82	17	20.00	5
Distance to edge																
>100 m away	26.92	26	0.00	1	82.65	98	57.14	7	87.50	8	20.00	5	60.00	10	77.78	9
£25m	33.33	3	100.00	2	100.00	9	unused	0	100.00	2	75.00	4	100.00	1	0.00	1
26£ x £50 m	100.00	1	unused	0	80.00	15	unused	0	77.78	9	100.00	3	unused	0	unused	0
51£ x £100 m	25.00	4	100.00	1	82.35	17	0.00	4	unused	0	0.00	1	50.00	2	0.00	1
Opening size																
£25m radius	unused	0	100.00	2	80.95	21	unused	0	0.00	2	50.00	4	unused	0	0.00	1
26£ x £100 m	50.00	2	unused	0	66.67	9	100.00	2	unused	0	unused	0	0.00	2	100.00	1
101£ x £200 m	100.00	1	unused	0	62.50	8	0.00	2	100.00	1	unused	0	100.00	1	unused	0
>200m radius	40.00	5	unused	0	100.00	16	33.33	3	100.00	9	83.33	6	0.00	1	unused	0
Opening >100 m away	23.08	26	75.00	4	84.71	85	25.00	4	85.71	7	25.00	4	66.67	9	75.00	8
Compass direction																
ne	33.33	18	87.50	8	83.00	100	33.33	9	80.00	15	57.14	14	83.33	6	0.00	1
nw	42.86	7	100.00	1	94.12	17	100.00	1	100.00	2	75.00	4	66.67	3	50.00	2
se	25.00	4	unused	0	100.00	13	unused	0	unused	0	100.00	4	50.00	4	0.00	1
sw	40.00	5	unused	0	94.12	17	50.00	2	100.00	2	100.00	3	33.33	3	0.00	3
Nest plant species																
AMAL	0.00	1	unused	0	unused	0	unused	0	unused	0	unused	0	unused	0	100.00	1
POTR	52.94	34	66.67	3	84.94	166	50.00	14	84.21	19	72.00	25	58.82	17	0.00	6

model assumptions. These unmet assumptions included noncolinearity among explanatory variables (despite the use of data screening techniques including correlation matrices), few missing values for explanatory variables, or some other unmet assumptions that prevented convergence. Only three of the models that converged were significant overall (p <0.05) and had significant coefficients (p <0.05).

Nest Site Versus Stand-Level Habitat

Only a tentative qualitative comparison is possible between stand-level and nest-site level habitat parameters as predictors of nest success. This is because most of the models predicting nest success from stand-level habitat features did not converge and others were not significant.

Discussion

Nest Site and Success Relationships
Forest interior

Most birds in this study used nest sites in forest interior locations despite no apparent positive correlation with nest success rates (tables 3 and 5). Similarly, Yahner (1991) found that bird nest success in aspen stands of Pennsylvania was independent of distance from edge. Tewksbury et al. (1998) discovered that avian nest predation rates in western Montana were higher in forested landscapes than in fragmented landscapes dominated by agriculture, while brood parasitism by brown-headed cowbirds decreased with increasing forest cover. In their

Table 4—Comparisons of median values for each continuous nest site parameter between successful (first line) and failed nests (second line) within each of the most common bird species in aspen stands of the Routt and Medicine Bow National Forests 1987-1989. Values of successful medians and failed medians for the same variable and species with the same letter following them are not significantly different (Mann-Whitney U, P-value <0.05).

Variable	AMRO median	AMRO SD	AMRO n	DEJU median	DEJU SD	DEJU n	HOWR median	HOWR SD	HOWR n	NOFL median	NOFL SD	NOFL n	RNSA median	RNSA SD	RNSA n	TRSW median	TRSW SD	TRSW n	WAVI median	WAVI SD	WAVI n	WWPE median	WWPE SD	WWPE n
Nest plant height (m)	20.0A	11.9	18	0.0A	18.2	12	13.0A	6.7	12	10.0A	6.6	141	16.0A	4.8	9	14.8A	4.3	15	2.0A	7.9	18	3.5A	*	1
	17.0A	10.3	25	0.0A	*	1	11.0A	10.0	1	10.0A	7.1	24	18.0A	6.4	7	9.0B	6.4	3	9.0A	5.2	7	20.5A	10.2	6
Distance from trunk (cm)	0.0A	22.8	19	0.0A	6.2	8	0.0A	12.5	8	0.0A	0.0	128	0.0A	0.0	9	0.0A	10.0	15	65.0A	90.8	16	150.0A	*	1
	0.0A	26.0	25	0.0A	*	1	0.0A	0.0	1	0.0A	0.0	21	0.0A	0.0	7	0.0A	0.0	3	25.0A	39.9	4	0.0A	10.5	6
Nest height (m)	4.0A	7.5	19	0.0A	0.0	17	3.8A	4.3	17	6.5A	2.8	140	5.0A	3.1	9	6.8A	2.5	15	3.8A	6.5	18	2.5A	*	1
	2.0A	4.6	25	0.0A	0.0	2	3.0A	2.3	2	8.5A	3.8	25	31.0A	5.9	7	7.0A	2.1	3	5.5A	4.8	7	8.5A	3.3	6
Tree d.b.h. or shrub cd (cm)	29.5A	11.4	19	0.0A	61.5	9	26.0A	9.5	9	25.2A	10.3	140	30.0A	6.9	9	29.5A	22.6	16	7.0A	11.3	18	3.0A	*	1
	30.0A	34.1	25	3.0A	*	1	26.0A	5.3	1	29.3B	9.0	25	4.5A	3.3	7	30.5A	7.7	3	12.3A	3.8	7	24.0A	10.8	6
Hole diameter (cm)	n/a	n/a	n/a	n/a	n/a	n/a	4.0A	1.8	n/a	6.0A	1.7	136	4.3A	4.7	9	4.0A	0.9	18	n/a	n/a	n/a	n/a	n/a	n/a
	n/a	n/a	n/a	n/a	n/a	n/a	4.0A	2.2	n/a	6.0A	0.45	21	4.5A	1.9	5	6.0B	1.0	7	n/a	n/a	n/a	n/a	n/a	n/a
Site diameter (cm)	43.0A	619	3	n/a	n/a	n/a	23.0A	14.3	n/a	13.8A	6.2	112	25.0A	3.9	16	25.0A	28.6	9	n/a	n/a	9	n/a	n/a	n/a
	30.0A	*	1	n/a	n/a	n/a	23.0A	5.0	n/a	27.0B	6.7	21	27.0A	5.0	3	21.4A	8.0	6	n/a	n/a	6	n/a	n/a	n/a

Table 5—Percent of nests successful for each nesting habitat feature used by each of the life-history guilds in aspen of the Medicine Bow and Routt National Forests, 1987-1989.

Guild	Intermediate migrants and residents	n	Intermediate migrants and occasionals	n	Small migrants and residents	n	Large residents	n	Large migrant	n	Smallest migrant	n	Largest resident	n
Nest plant position														
Isolated	unused	0	66.67	3	100.00	1	unused	0	unused	0	unused	0	unused	0
Open	0.00	1	100.00	4	100.00	4	unused	0	50.00	2	unused	0	unused	0
Marginal	66.67	3	84.62	13	100.00	16	100.00	1	50.00	2	100.00	1	100.00	1
Interior	55.00	60	64.58	48	80.92	152	88.89	10	41.03	39	75.00	4	41.67	12
Distance to edge														
≤25 m	80.00	5	66.67	9	100.00	9	100.00	1	33.33	3	unused	0	unused	0
26≤ x ≤50 m	100.00	1	84.62	13	80.00	15	unused	0	100.00	1	unused	0	unused	0
51≤ x ≤100 m	42.86	7	60.00	5	82.35	17	100.00	1	25.00	4	unused	0	0.00	4
>100m	58.33	24	55.56	27	80.37	107	100.00	7	26.92	26	100.00	2	57.14	7
Opening size														
Opening >100 m away	42.86	35	59.26	27	81.91	94	100.00	8	23.08	26	100.00	2	25.00	4
≤25 m radius	75.00	4	37.50	8	80.95	21	100.00	1	unused	0	unused	0	unused	0
26≤ x ≤100 m	50.00	4	0.00	1	66.67	9	unused	0	50.00	2	unused	0	100.00	2
101≤ x ≤200 m	unused	0	100.00	1	62.50	8	unused	0	100.00	1	unused	0	0.00	2
>200 m radius	100.00	3	88.24	17	100.00	16	unused	0	40.00	5	unused	0	33.33	1
Compass direction														
ne	70.00	30	60.47	43	80.73	109	87.50	8	33.33	18	0.00	1	33.33	9
nw	61.54	13	87.50	8	94.12	17	100.00	1	42.86	7	unused	0	100.00	1
se	57.14	7	85.71	7	100.00	13	100.00	2	25.00	4	100.00	1	unused	0
sw	22.22	9	90.91	11	94.12	17	unused	0	60.00	5	100.00	1	50.00	2
Cavity location														
Trunk	28.57	7	64.81	54	84.13	126	100.00	8	100.00	2	unused	0	36.36	11
Branch	unused	0	unused	0	66.67	9	unused	0	unused	0	unused	0	unused	0
Other	0.00	1	100.00	1	100.00	3	unused	0	0.00	1	unused	0	unused	0
Nest plant species														
ABLA	unused	0	unused	0	unused	0	unused	0	0.00	8	unused	0	unused	0
AMAL	100.00	3	unused	0	unused	0	unused	0	0.00	1	unused	0	unused	0
POTR	48.08	52	71.01	69	83.52	176	90.91	11	52.94	34	80.00	5	50.00	14
SYOR	75.00	4	unused	0	unused	0	unused	0	unused	0	unused	0	unused	0
Tree type														
Intact	12.50	8	77.50	40	83.33	96	100.00	8	66.67	3	100.00	5	33.33	3
Broken	100.00	1	16.67	12	81.25	48	unused	0	unused	0	unused	0	37.50	8
Snag decay														
Decayed snag	100.00	1	37.50	8	85.71	28	unused	0	100.00	1	unused	0	50.00	4
Dead tree and dead at cavity	40.00	10	64.00	25	81.03	58	100.00	4	100.00	1	unused	0	37.50	8
Live tree and dead at cavity	0.00	2	100.00	2	63.64	22	unused	0	75.00	4	unused	0	unused	0
Live tree and live at cavity	80.00	10	82.35	34	93.33	60	83.33	6	80.00	5	66.67	3	100.00	2

Table 6—Logistic regression models for predicting nest success from habitat variables collected at bird nests in the Medicine Bow and Routt National Forests, 1987–1989.

Logistic regression model variables	G[a](p–value)	Total correct rate[b]	Success index[c]
Tree swallow	13.85(0.0010)	0.7929	0.1362
8.15constant – 2.13hole diameter + 0.30nest plant height			
Small migrants and residents	28.75(0.00001)	0.8830	0.0531
9.61constant – 1.84snag_DC – 1.90snag_DD – 4.23snag_LD – 0.01distance to water – 0.61hole diameter			
Secondary cavity nesters	21.12(0.0001)	0.8325	0.0367
7.43constant – 0.007distance to water – 0.69hole diameter + 2.61distance to edge			

[a]Tests the null hypothesis that all the coefficients associated with the predictors equal zero versus these coefficients not all being zero (SYSTAT9 1999).
[b]The ratio of the sum of correctly predicted observations divided by the total number of observations (SYSTAT9 1999).
[c]The gain that this model shows over a purely random model that assigned the same probability of success to every observation in the data (SYSTAT9 1999).

study, forest cover was not the best predictor of cowbird parasitism; the abundance of human development on the landscape and the density of cowbird host species were the best predictors of parasitism. Cowbirds were present in the current study but sample sizes were too low to analyze. In contrast, Donovan et al. (1997) found that landscape fragmentation patterns interacted with edge effects to create nest predation and cowbird parasitism patterns.

Orientation within a tree

Most bird nests in this study were oriented northeast of the center of the nest tree or shrub (tables 3 and 5). Finch (1985) also found that Abert's towhees (*Pipilo aberti*) in Colorado oriented their nests in different directions, depending on whether it was early or late in the nesting season. In the current study, the dominant slope direction in the study area could have been such that a northeast nest plant location decreased thermoregulatory costs or allowed early detection and repulsion of nest predators.

Nest plant species

The use of aspen as the nest plant (tables 3 and 5) was probably in proportion to availability and related to susceptibility to heart rot and thus ease of cavity excavation for the cavity nesters as in Daily (1993). Another possible reason for a bird to use aspen as its nest plant is the abundance and diversity of associated plants it could use as cover from weather and predators.

Snag decay

Most successful nests were located in intact and living trees in this study (tables 3 and 5). This could be due to an increase in cover from weather and predators over that surrounding broken snags. It could also be due to a greater diversity and abundance of insect or plant food sources over that found near broken snags. However, this result should be interpreted with caution because over 50% of aspen stems (including living stems) in the study area were infested with heart rot that probably increased ease of cavity excavation as in Winternitz (1980). In contrast to the overall nest-site use pattern, northern flicker successful nests were on broken snags (table 5). Similarly, Daily (1993) found a correlation between the placement of red-naped sapsucker nests and the spread of heart rot through a tree.

Tree diameter at cavity

Northern flicker successful nest trees were smaller in diameter than those of failed nests in aspen-dominated stands (tables 4 and 6). This is contrary to the results of Loose and Anderson (1995) who found that woodpeckers nested in

aspen trees of south-central Wyoming with an average d.b.h. of 26.7 cm, and this diameter was larger than the mean d.b.h. of available aspen (11.8 cm or snags, 9.0 cm). Dobkin et al. (1995) found that living trees and snags with d.b.h. >4 cm were favored as nest sites by all bird species in aspen of southeastern Oregon. In the current study, perhaps trees with a larger diameter were more likely to have been excavated in previous years and thus provided search cues to predators that could remember nest locations from year to year as in Sonerud (1985, 1989).

Cavity diameter

Secondary cavity nesting birds' nest success decreased as hole diameter increased (table 6). These results correspond with the conclusion by Roberston and Rendell (1990) that greater cavity entrance area (mean = 32.4 +/− 0.3) at natural cavities (than in nest boxes) resulted in increased interspecific competition for tree swallow nest sites in Ontario. Nest sites with smaller entrance diameters probably gave birds an advantage by reducing the risk of nest depredation.

Proximity to standing water

Distance to water influenced nest success of small migrants and residents and secondary cavity nesters. Nest success decreased as distance to water increased (tables 5 and 6). It makes sense that birds at an intermediate distance from water would have the greatest nest success relative to birds over 300 m from water because predation (Wilcove 1985; Donovan et al. 1997) may be greater closer to water (an edge), yet the presence of water may increase forage availability (insect abundance).

Another possible explanation for increased success near water could be increased food availability. Insects are commonly more abundant (Schimpf and MacMahon 1970) and aspen usually have a faster growth rate closer to water within suitable habitats. Loose and Anderson (1995) observed that woodpeckers in Wyoming used larger than average trees for foraging. They concluded this foraging pattern could be due to an increase in foraging efficiency as larger trees and snags contain higher concentrations of insects.

Nest plant height

Tree swallow nest success increased with nest plant height (table 6). Similarly, Li (1989) found that failed nests of cavity-nesting birds on the Mogollon Rim in Arizona were closer to the ground than successful nests. Conversely, Yahner (1991) found an overall inverse relationship between nest height and nest success in aspen forest of central Pennsylvania. These differences may be explained by differences in the most common predator search strategies. Avian predators may be more likely to find taller nests while terrestrial mammalian predators may be more likely to find shorter nests.

Nest Site Versus Stand-Level Habitat

Nest success may be more strongly correlated with nest-site characteristics than it is with stand characteristics since none of the stand-level logistic regression models that converged were significant and contained more than one explanatory variable (table 6). Similarly, Martin (1998) found that microhabitat parameters of nesting birds in aspen forests of Arizona are under selection and adaptive. However, other studies such as Tewksbury (1998) and Donovan (1997) have found large-scale habitat features good predictors of forest bird nesting success.

Importance of Aspen Nesting Habitat

When the results of the current study are considered along with those of a related study (Struempf 2000), one can see that the value of aspen forests as a major landscape component should not be underestimated. We reached this conclusion because Struempf (2000) found that most birds and guilds had lower mortality rates in aspen forests than they had in nearby mixed or conifer forests. Therefore, a decline in aspen on the landscape could lead to significant declines in nest success for birds that experienced greater nest success in aspen than they did in mixed or conifer forests. The next logical step toward elucidating relationships between habitat and avian survival rates in aspen forests and wintering grounds would be to investigate overall population trends for residents and migrants and create models to determine the most important life-history transition to population persistence.

Management Implications

Avian habitat and nest success relationships in aspen forests of the Western United States are still poorly understood. Therefore, an adaptive management approach to maintain nesting bird diversity in aspen forests would probably be best until more is known. In all of the significant logistic regression models for cavity nesters, smaller hole diameters experienced greater nest success. This suggests that management actions should provide and maintain suitable habitat for a variety of primary cavity excavators who build several sizes of nest holes to allow the secondary cavity nesters to thrive. We hypothesize that birds more susceptible to predation (primary cavity nesters in Struempf 2000 and Martin 1993) should exhibit greater nesting survival rates as the area of contiguous habitat increases than birds less susceptible to predation (ground nesters in Struempf 2000 and Martin 1993). Furthermore, a greater diversity of primary cavity excavators should exhibit increased nest success in forested landscapes with more variation in aspen seral stage, stem size, clone age, and degree of heart rot infestation than more homogenous landscapes.

A few studies investigating disturbance and area effects on bird assemblages in western conifer and aspen forests have produced preliminary results that need further investigation (Johns 1993; Scott et al. 1982; and Scott and Crouch 1988). Scott et al. (1982) and Scott and Crouch (1988) found that clearcuts in subalpine forests of Colorado had little to no effect on breeding bird densities. Johns (1993) found that avian species richness in aspen parklands of Saskatchewan was positively correlated with aspen grove area, and densities of some species were positively or negatively correlated with aspen grove isolation. However, further investigation is required because presence and density data do not adequately indicate the quality of a habitat. Survival data are needed because birds may be forced to use substandard habitat at high densities due to low availability of quality habitat.

Possible treatments that could be used in adaptive management experiments include carefully planned cutting and controlled burns, and monitoring of natural disturbances such as fungal infestations, fires, and avalanches. These treatments should benefit most birds by maintaining aspen on the landscape and increasing overstory complexity and understory diversity (Bartos et al. 1991; Shepperd and Smith 1993; Turchi et al.1995). Further support for this conclusion was found in a related study (Struempf 2000) where most birds had

greater nest success in aspen forests than they experienced in adjacent mixed or conifer forests. Pilot studies using these treatments should be conducted and the effects of habitat manipulations on nesting success and adult survival closely monitored.

Acknowledgments

References

Baker, W.L., J.A. Munroe, and A.E. Hessl. 1997. The effect of elk on aspen in the winter range in Rocky Mountain National Park. Ecography 20:155-165.

Bartos, D.L. and R.B. Campbell, Jr. 1998. Decline of quaking aspen in the interior west examples from Utah. Rangelands 20(1):17-23.

Bartos, D.L., W.F. Mueggler, and R.B. Campbell Jr. 1991. Regeneration of aspen by suckering on burned sites in western Wyoming. Research paper INT-448. Ogden, UT: USDA Forest Service.

Bernays, E.A. and R.F. Chapman. 1994. Host plant selection in phytophagous insects. Chapman & Hall, Inc. New York, NY.

Brown, C.R., A.M. Knott, and E.J. Damrose. 1992. The Birds of North America. Life Histories for the 21st Century No. 14.

Calder, W.A. and L.L. Calder. 1992. The Birds of North America. Life Histories for the 21st Century No. 16.

Christman, B.J. and A.A. Dhondt. 1997. Nest predation in Black-capped chickadees: how safe are cavity nests? The Auk 114(4):769-773.

Crouch, G.L. 1983. Aspen Regeneration After Commercial Clearcutting in Southwestern Colorado. Journal of Forestry May:316-319.

Daily, G.C. 1993. Heartwood decay and vertical distribution of red-naped sapsucker nest cavities. Wilson Bulletin 105(4):674-679.

DeByle, N.V. 1981. Songbird populations and clearcut harvesting of aspen in northern Utah. USDA Forest Service Intermountain Forest and Range Experiment Station. Research Note INT-302.

Dobbs, R.C., T.E. Martin, and C.J. Conway. 1997. The Birds of North America. Life Histories for the 21st Century No. 285.

Dobkin, D.S., A.C. Rich, J.A. Pretare, W.H. Pyle. 1995. Nest-site relationships among cavity-nesting birds of riparian and snowpocket aspen woodlands in the northwestern great basin. The Condor 97:694-707.

Donovan, T.M., P.W. Jones, E.M. Annand, F.R. Thompson III. 1997. Variation in local-scale edge effects: mechanisms and landscape context. Ecology 78(7):2064-2076.

Dowdy, S, and S. Weardon. 1991. Transformations. Pages 352-356 *In* Statistics for research. John Wiley & Sons, Inc. New York.

Ehrlich, P.R., D.S. Dobkin, and D. Wheye. 1988. The Birder's Handbook. A field guide to the natural history of North American Birds. Simon and Schuster Inc. New York, NY.

Finch, D.M. 1985. Multivariate analysis of early and late nest sites of Abert's towhees (*Pipilo aberti*). Southwestern Naturalist 30(3): 427-432.

Finch, D.M. 1989. Relationships of surrounding riparian habitat to nest-box use and reproductive outcome in House Wrens. The Condor 91:848-859.

Finch, D.M. 1990. Effects of predation and competitor interference on nesting success of House Wrens and Tree Swallows. The Condor 92:674-687.

Finch, D.M. 1991. House wrens adjust laying dates and clutch size in relations to annual flooding. Wilson Bulletin 103(1):25-43.

Finch, D.M., and R.T. Reynolds 1987. Bird response to understory variation and conifer succession in aspen forests. In*:* Issues and technology in the management of impacted wildlife. Thorne Ecological Institute, Boulder, CO: 87-96.

Hannon, S.J., and S.E. Cotterill. 1998. Nest predation in aspen woodlots in an agricultural area in Alberta: the enemy from within. The Auk 115:16-26.

Hartley, M.J., and M.L. Hunter. 1998. A meta-analysis of forest cover, edge effects, and artificial nest predation rates. Conservation Biology 12:465.

Hosmer, D.W. and S. Lemeshow. 1989. Applied logistic regression. John Wiley and Sons Inc. New York, NY: 88-91.

Ingold, J.L., and R. Galati. 1997. The Birds of North America. Life Histories for the 21st Century No. 301.

Johns, B.W. 1993. The Influence of grove size on bird species richness in aspen parklands. Wilson Bulletin 105(2): 256-264.

Jolivet, P. 1998. Interrelationship between insects and plants. CRC Press, Washington, DC.

Jones, J.J. 1985. Distribution. In: Aspen ecology and management in the Western United States. Rocky Mountain Forest and Range Experiment Station. USDA Forest Service. RM-119.

Jones, J.J., and DeByle, N.V. 1985a. Genetics and Variation. In: Aspen ecology and management in the Western United States. Rocky Mountain Forest and Range Experiment Station. USDA Forest Service. RM-119.

Jones, J.J., and DeByle, N.V. 1985b. Fire. In: Aspen ecology and management in the Western United States. Rocky Mountain Forest and Range Experiment Station. USDA Forest Service. RM-119.

Jones, J.R., and G.A. Schier. 1985. Growth. In: Aspen: ecology and management in the Western United States. N.V. DeByle and R.P. Winokur, editors. USDA Forest Service GTR RM-119: 21.

Jones, J.R., N.V. DeByle, and D.M. Bowers. 1985. Insects and other invertebrates In: Aspen: ecology and management in the Western United States. N.V. DeByle and R.P. Winokur, editors. USDA Forest Service GTR RM-119: 21.

Kay, C.E. 1997. Is aspen doomed? Journal of Forestry May:4-11.

Knight, D.L. 1994. Mountains and plains. Yale University Press, New Haven: 171-173.

Li, P. 1989. Nest site selection and nesting success of cavity-nesting birds on the Mogollon Rim, Arizona. MS Thesis. Arizona State U.

Loose, S.S., and S.H. Anderson. 1995. Woodpecker habitat use in the forests of southeast Wyoming. Journal of Field Ornithology 66(4):503-514.

Madson, C. 1996. Trees born of fire and ice. National Wildlife 34(6):28-36.

Martin, T.E. 1987. Food as a limit on breeding birds: a life-history perspective. Annual Review of Ecology and Systematics 18:453-487.

Martin, T.E. 1988. Habitat and area effects on forest bird assemblages: is nest predation an influence? Ecology 69(1):74-84.

Martin, T.E. 1992. Breeding productivity considerations: what are the appropriate habitat features for management? In: J.M. Hagan and D.W. Johnston, eds. Ecology and conservation of neotropical migrant land birds. Smithsonian Institution Press, Washington, DC: 455-473.

Martin, T.E. 1993. Nest predation among vegetation layers and habitats: revising the dogmas. American Naturalist 141:897-913.

Martin, T.E. 1998 Are microhabitat preferences of coexisting species under selection and adaptive? Ecology 79(2):656-670.

Mitton, B.J., and M.C. Grant. 1996. Genetic variation and the natural history of quaking aspen. Bioscience 46:25-31.

Moller, A.P. 1989. Parasites, predators and nest boxes: Facts and artefacts in nest box studies of birds? Oikos 56:421-423.

Mueggler, W.F. 1985. Vegetation Associations. In: Aspen ecology and management in the Western United States. Rocky Mountain Forest and Range Experiment Station. USDA Forest Service. RM-119.

Murphy, M.T., C.L. Cummings, and M.S. Palmer 1997 Comparative analysis of habitat selection, nest site and nest success by Cedar Waxwings and Eastern Kingbirds. American Midland Naturalist 138:344-356.

Noon, B.R. 1981. Techniques for sampling avian habitats. In: D.E. Capen (ed.). The use of multivariate statistics in studies of wildlife habitat. Rocky Mountain Forest and Range Experiment Station. USDA Forest Service Gen. Tech. Rep. RM-87: 42-52.

Paton, P.C. 1994. The effect of edge on avian nest success: how strong is the evidence? Conservation Biology 8(1):17-26.

Power, H.W., and M.P. Lombardo. 1996. The Birds of North America. Life Histories for the 21st Century No. 222.

Reimoser, F., H. Gossow. 1996. Impact of ungulates on forest vegetation and its dependence on the silvicultural system. Forest Ecology and Management 88:107-119.

Ricklefs, R.E. 1969. An analysis of nesting mortality in birds. Smithson. Contrib. Zool. 9:1-48.

Robertson, R.J. and W.B. Rendell 1990 A comparison of the breeding ecology of a secondary cavity nesting bird, the Tree Swallow, in nest boxes and natural cavities. Canadian Journal of Zoology 68:1046-1052.

Roberston, R.J., B.J. Stutchbury, and R.R. Cohen. 1992. The Birds of North America. Life Histories for the 21st Century No. 11.

Robichaud, P.R. 1997 Forest fire: friend or foe? Experts say fires have their place in nature. Engineering & Technology for a Sustainable World 4(5):7-9.

Robison, S.K., F.R. Thompson, T.M. Donovan, D.R. Whitehead, J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987-1991.

Romme, W. H., M.G. Turner, L.L. Wallace, J.S. Walker. 1995. Aspen, elk, and fire in northern Yellowstone National Park. Ecology 76(7):2097-2106.

Schmidt, K. A. and C.J. Whelan. 1998. Predator-mediated interactions between and within guilds of nesting songbirds: experimental and observational evidence. The American Naturalist 152:393-403.

Schimpf, D.J. and J.A. MacMahon. 1970. Insect communities and faunas of a Rocky Mountain subalpine sere.

Scott, V.G. and G.L. Crouch. 1988. Breeding birds in uncut aspen and 6- to 10-year-old clearcuts in southwestern Colorado. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station RM-485.

Scott, V.G., G.L. Crouch, and J.A. Whelan. 1982. Responses of birds and small mammals to clearcutting in a subalpine forest in central Colorado. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station RM-422.

Shepperd, W.D. and F.W. Smith. 1993. The role of near-surface lateral roots in the life cycle of aspen in the central Rocky Mountains. Forest Ecology and Management 61: 157-170.

Smith, G.A. 1993. The Birds of North America. Life Histories for the 21st Century No. 39.

Sonerud, G.A. 1985. Nest hole shift in Tengmalm's owl, *Aegolius funereus*, as a defence against nest predation involving long-term memory in the predator. Journal of Animal Ecology 54:179-192.

Sonerud, G.A. 1989. Reduced predation by pine martens on nests of Tengmaml's owls in relocated boxes. Animal Behavior 37:332-334.

Struempf, H. 2000. Comparing nest failure rates of common nesting birds and guilds in 3 aspen forests of the central Rocky Mountains. In: Nesting bird community response to natural habitat variation in aspen forests of the central Rocky Mountains. MS Thesis. University of Wyoming.

SYSTAT 9. Statistical software. Systat, Inc. 1999.

Tewksbury, J.J., S.J. Hejl, and T.E. Martin. 1998 Breeding productivity does not decline with increasing fragmentation in a western landscape. Ecology 79(8):2890-2903.

Turchi, G.M., P.L. Kennedy, D. Urban, and D. Hein. 1995. Bird species richness in relation to isolation of aspen habitats. Wilson Bull. 107(3):463-474.

Walsberg, G.E. 1985. Physiological consequences of microhabitat selection. In: M.L. Cody (ed.), Habitat selection in birds. Academic Press, New York. 389-413.

Wiens, J.A. 1989. The ecology of bird communities. Cambridge University Press. New York, NY: 349-359.

Wilcove, D.S. 1985 Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66:1211-1214.

Winternitz, B.L. 1980. Birds in aspen. U.S. Forest Service General Technical Report INT-86: 247-257. WR199.

Wirth, T., P. Maus, J. Powell, and H. Lachowski. 1996. Monitoring aspen decline using remote sensing and GIS. In: Forest Service Remote Sensing Applications Conference April 1996 Denver, CO American Society for Photogrammetry and Remote Sensing: 174-183.

Yahner, R.H. 1991 Avian nesting ecology in small even-aged aspen stands. Journal of Wildlife Management 55(1):155-159.