AVIAN NEST SURVIVAL IN POST-LOGGING COASTAL BUFFER STRIPS ON PRINCE OF WALES ISLAND, ALASKA

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ABSTRACT

Avian nest survival in post-logging coastal buffer strips on Prince of Wales Island, Alaska

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I examined the effect of forest buffer width and nest site characteristics on the nest survival of forest birds on Prince of Wales Island, Alaska. During 2002 and 2003, a total of 164 nests of three closed cup (Chestnut-backed Chickadee (*Parus rufescens*), Red-breasted Sapsucker (*Sphyrapicus ruber*) and Winter Wren (*Troglodytes troglodytes*)) and four open cup (Pacific-slope Flycatcher (*Empidonax difficilis*), Hermit Thrush (*Cartharus guttatus*), Swainson's Thrush (*Cartharus ustulatus*) and Varied Thrush (*Ixoreus naevius*)) species were monitored within forested buffers along the coastline. I modeled daily survival rate (DSR) of closed (DSR = 0.989) and open (DSR = 0.982) cup nesting species independently using variables at two spatial scales. For closed cup nests the model best describing variation in DSR included height of nest and species. Nests located higher from the ground had better nest success. Variation in DSR of open cup nests was best explained by species. Pacific-slope Flycatcher nests had the highest success (87%) whereas Varied Thrush nests had the lowest (21%). DSR of Hermit Thrush nests, the only species for which I had adequate data to analyze separately, was related to distance to the coastline. Species with low DSR had similar nest site characteristics including diameter of nesting substrate and average percentage concealment of nest. However, these nest site characteristics alone do not determine DSR of the species evaluated in my study. Width of coastal forested buffers appears to have a negligible effect on DSR,

however, some species exhibited low DSR within the buffers and further examination of these species is recommended.

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INTRODUCTION

The association between declines in songbird populations and forest fragmentation has received a great deal of attention in the last few decades. Songbird population declines have been associated with decreased forest tract size and increased forest edge (Wilcove 1985, Noss and Cooperrider 1994, Donovan and Flather 2002). Changes in forest structure may reduce productivity of nesting songbirds by increasing vulnerability of nests to predators (Herkert 1994, Robinson et al. 1995, Sherry and Holmes 1995, Helzer and Jelinski 1999). Most studies of the effects of habitat fragmentation on bird populations, however, have been conducted in eastern deciduous forests of North America. Few have been conducted in the Pacific Northwest, and even fewer have examined demographic differences between birds nesting near anthropogenic and natural edges (Ruefenacht 1998, Salabanks et al. 2001, George and Brand 2002, George and Dobkin 2002).

In the Pacific Northwest, timber harvesting has resulted in fragmentation of original old-growth forest and an increase in the amount of forest edge. A third of the Tongass National Forest consists of commercially managed timber (Schoen et al. 1988). Of this, approximately seven percent of the original old-growth forest has been logged, and another 16% is designated for harvest under the current Tongass Land Management Plan (USDA Forest Service 1997, USDA Forest Service 1999, Joy 2002). The Tongass National Forest implemented the Tongass Land Management Plan, which includes an aggressive conservation strategy designed to mitigate the effects of timber harvesting on habitat quality for terrestrial wildlife, including migratory and resident birds. This management plan requires a no-harvest buffer zone extending 305 m inland along all marine coastlines (USDA Forest Service 1997, USDA Forest Service 1999). This coastal buffer is intended to: (1) provide links between habitat reserves and watersheds, (2) maintain a functional interior forest condition, (3) contribute to overall landscape appearance, and (4) conserve habitat for resident and migratory species of wildlife (Suring et al. 1993, USDA Forest Service 1997).

Although studies of avian density within riparian buffers are extensive and have demonstrated a positive relationship between buffer width and abundance of forest associated birds (Stauffer and Best 1980, Keller et al. 1993, Darveau et al. 1995, Hagar 1999, Whitaker and Montevecchi 1999), little is known about avian density and productivity within coastal buffers. Ecological relationships in coastal buffers are most likely different than those in riparian buffers as nutrient and soil composition, light and wind intensity, and the avian predator community along the coastline may influence avian productivity differently compared to buffers adjacent to freshwater streams and rivers (Concannon 1995). Reproductive success of nesting songbirds may be a better measure of habitat quality than abundance because long-term persistence of a species in an area is dependent on recruitment into the local breeding population (Van Horne 1983, Robbins et al. 1989, Blake 1991, Vickery et al. 1992, Hagan et al. 1996, Vander Haegen and De Graaf 1996).

Nest predation has been shown to have a large negative effect on productivity of songbirds (Stauffer and Best 1980, Martin 1992). Numerous studies across various vegetation types have demonstrated that artificial and natural nests located near forest edges experience higher predation rates than those in forest interior (Brand and George 2000, De Santo and Willson 2001, Peak et.al. 2004, Albrecht 2004). Artificial nest studies in coastal redwood (*Sequioa sempervirens*) forests in northern California suggest that nest success is significantly lower within 115 m of natural and anthropogenic forest edges (Brand and George 2000). If similar effects occur in coastal Alaska, all birds nesting within coastal buffers less than 230 m wide would experience higher predation rates than those birds nesting in wider buffers which offer less forest edge and more forest interior.

My objectives were to: (1) determine stand-level and nest site factors affecting daily nest survival rate within coastal buffers of varying widths, and (2) compare stand-level and nest site characteristics among species nesting in coastal buffers to identify factors potentially related to observed differences in nest survival. These results will aid in establishing a long-term monitoring program for birds nesting in Tongass National Forest and help guide coastal forest management practices.

METHODS

STUDY AREA

This study was conducted on Prince of Wales Island, in the Alexander Archipelago of southeast Alaska , approximately 35 km northwest of Ketchikan, Alaska (56° 01′ N, 132° 51′ W). Prince of Wales Island is 5,778 km^2 and ranges 0-1,092 m above sea level. The landscape is characterized by steep, rugged topography and narrow inlets. Vegetation of the island is naturally heterogeneous because of mountainous terrain, wetlands, and various small-scale disturbances such as wind throw (Ott 1997).

All study sites bordered the ocean and were dominated by low elevation rain forest characteristic of the Tongass National Forest (Pojar and MacKinnon 1994). These stands were dominated by western hemlock (*Tsuga heteropylla*), Sitka spruce (*Picea sitchensis*), western red-cedar (*Thuja plicata*) and Alaska yellow-cedar (*Chamaecyparis nootkatensis*). Along streambeds and in areas of disturbed soils red alder (*Alnus rubra*) was common. Size class distributions of live trees for each study site are presented in Appendix A. The understory was dominated by devil's club (*Oplopanax horridum*), salmonberry (*Rubus. spectabilis*), blueberry (*Vaccinium* spp.) and rusty menziesia (*Menziesia ferruginea*) (Alaback 1982). Coverage of understory vegetation for each study site is presented in Appendix B. All study sites had structural features associated with old-growth forests such as, large snags, downed logs and live trees (Franklin et al. 1981).

I used aerial photography and US Forest Service vegetation classification maps to measure coastal buffer widths and identify seven sites with similar elevation (<350 m), timber size class (>150 years old), type of harvest adjacent to the site (clear-cut), date of cut (1983-1997), and accessibility. Locations for each study site are presented in Appendix C. Average area of sites was 12.3 ha (range 7.8-18.4 ha). Buffers widths of selected study sites ranged from 124-490 m. Specific study site characteristics are presented in Appendix D.

Potential predators observed at least once within the vicinity of the study sites included Common Raven (*Corvus corax*), Northwest Crow (*Corvus caurinus*), Steller's Jay (*Cyanocitta stelleri*), Barred Owl (*Strix varia*), Northern Pygmy-Owl (*Glaucidium gnoma*), Great Horned Owl (*Bubo virginianus*), Bald Eagle (*Haliaeetus leucocephalus*), Sharp-shinned Hawk (*Accipiter striatus*), Merlin (*Falco columbarius*), black bear (*Ursus americanus*), mink (*Mustela vison*), marten (*Martes Americana*), northern flying squirrel (*Glaucomys sabrinus*), gray wolf (*Canis lupus*), shrew (*Sorex spp*.), vole (*Microtus spp*.) and mouse (*Peromyscus* spp.). A usually ubiquitous nest predator in southeast Alaska, the red squirrel, does not occur on Prince of Wales Island (MacDonald and Cook 1996).

NEST SEARCHING

To standardize search effort among sites, I used a ratio of two search hours per hectare per nest searcher. Nest searching was conducted between 05:00-14:00 (AST) from May to August 2003 and 2004 following methods described by Martin and Geupel (1993). To minimize disturbance, we marked nests inconspicuously with flagging tape and avoided disturbing incubating or feeding adult(s) associated with the nest. Nests were monitored every one to four days until at least one nestling fledged or the nest failed. Nests were assumed to have failed if nest contents were missing > 2 days before the predicted fledge date. Initiation date was calculated for each nest found as the Julian date for when the first egg was laid or by back dating from hatch assuming incubation periods described by Ehrlich et al. (1988). Five nests were discovered with a full clutch and failed before hatching occurred. To estimate initiation date for these nests, I back calculated using the midpoint assumption as described by Mayfield (1975).

HABITAT MEASUREMENTS

I quantified habitat characteristics at the stand-level and nest site scales. To quantify stand-level characteristics, I used the Tongass National Forest Geographic Information System (GIS) library to obtain coverages of vegetation classification. Following the suggestion of McGarigal and McComb (1995) I examined stand-level characteristics within a 300 ha area surrounding each study site. The 300 ha area was used to maximize stand-level data collected while minimizing overlapping among study sites. Within the 300 ha area I used ARC GIS 9 software (Earth Systems Research Institute Inc., Redlands, California) to estimate percentage of area covered by young forest (trees <150 years), and density of roads (km ha^{-1}). I also calculated a buffer width for each site by averaging the width of forest between the coast and harvest edge every 75 m.

Nest site characteristics were measured in addition to stand-level variables to control for site level differences and to compare the influence of site and stand-level variables. Measurements were conducted after the completion of nesting and followed the protocol described by the Breeding Biology Research and Monitoring Database (Martin et al. 1997). I counted, identified to species, and estimated the diameter breast height (dbh) in 10 cm increments all trees in a 10 m radius around each nest. (Appendix E). I also counted all live saplings (>2 m tall and <10 cm dbh). Shrub cover greater than 0.5 m in height was estimated using the line intercept technique (Grieg-Smith 1964) along two 20 m perpendicular transects, orientated NW to SE and NE to SW, centered on the sample plot (Appendix F). I recorded height and type of nesting substrate (i.e., log, snag, stump, tip-up, tree or shrub). I also measured the height of the nest and distance between the nest and the center of the nesting substrate. I visually estimated nest concealment from 1 m above and 1 m below the nest and also at the four cardinal directions. I then averaged the six percentages to result in one value for nest concealment. I collected latitude and longitude for each nest and at 25 m intervals along the harvest and coastal edges at each site. I digitized a continuous line in ARC GIS 9 (GIS) software from the points collected along both edges (Earth Systems Research Institute Inc., Redlands, California). I calculated the shortest distance (to the nearest meter) between each nest and both edges using the distance command in GIS software (Earth Systems Research Institute Inc., Redlands, California).

DATA ANALYSIS

I used logistic-exposure models (Rotella et al., 2004, Shaffer 2004) to estimate nest daily survival rates (DSR). Logistic-exposure models are a class of generalized linear models used to estimate parameters by associating explanatory variables with DSRs. Due to small sample sizes only one species, the Hermit Thrush *(Cartharus guttatus*), could be analyzed individually. Therefore, I lumped all species into two functional groups based on nest types (i.e., open cup and closed cup; Ehrlich et al. 1988) and analyzed each functional group separately.

Prior to analysis I developed a set of *a priori* biological hypotheses in the form of candidate models (Burnham and Anderson 2002) based on existing literature and personal experience to explain the variation in DSR of nests in coastal forests. I created one set of candidate models for each functional group, open cup and closed cup, and one set for Hermit Thrush. For each set, I included only the variables and combination of those variables that I believed could reasonably explain variation in nest survival. For example, I did not include average concealment for closed cup nesting species as this variable did not differ among closed cup nests. I emphasized additive models to keep the number of parameters low enough for sufficient statistical power given small sample sizes. This resulted in a total of 23 models for closed cup nests, 31 models for open cup nests and 16 models for Hermit Thrush nests (Table 1). Variables included in the candidate models and their predicted relationship to nest survival included:

Buffer width (Buffer), *Percent young forest* (Young Forest), *Road density* (Roads), *Distance from coastal edge* (Coast Edge), *Distance from harvested edge* (Harvest Edge). Generalist predators may be attracted to higher prey abundances associated with smaller patches (Gates and Gysel 1978), travel corridors (Fritzell 1978), or edges (Ibarzabal and Desrochers 2004).

Average nest concealment (Concealment): Nest concealment may prevent detection by predators (Martin and Roper 1988, Cresswell 1997, Weidinger 2002).

Nest height (Height): Nest height may limit accessibility to nests by certain predators (De Santo et al. 2003, Remeš 2005).

Initiation Date (Initiation). Seasonal effects on nest survival have shown a decrease as the breeding season progresses. This trend is possibly due to inexperienced birds attempting to nest later in the season when there is a decrease in food availability (Hochachka 1990, Davis 2005).

Year (Year). Annual variation in nest survival is common (Greenwood et al. 1995). Mechanisms of this variation are uncertain but food availability, predator numbers and weather patterns can all affect nest survival. By including year, I attempted to capture these sources of variation that were not measured directly.

Species (Species). I included this variable to help account for the variation among species. This variable was added to all *a priori* models except the single species models for Hermit Thrush.

To determine the best approximating model, I compared each set of candidate models using Akaike's Information Criterion (AIC) with small sample bias adjustment to choose the best approximating model (AICc; Burnham and Anderson 2002). Model(s) with values of $\Delta AIC \leq 2.0$ and high Akaike's weights ($w_i \geq 0.05$) were considered when making inferences. If model selection statistics indicated that one model was not strongly supported over all other models ($w_i > 0.9$), a multi-model approach was used to estimate coefficients and variances to obtain more accurate estimates (Burnham and Anderson 2002). Actual DSR values were calculated by back transforming logit-scale regression equations.

NEST SITE CHARACTERISTICS

I used a Chi-square goodness of fit to test the distribution of nesting substrates used among species (Hintze 2001). As an exploratory analysis, I compared all continuous stand level and nest site measurements among species with an analysis of variance test in an attempt to make coarse comparisons of nest site characteristics among species. If variance among species was significantly different, I used the Tukey Kramer multiple comparison method to control for experimentwise error in NCSS (Hintze 2001).

RESULTS

PATTERNS OF NEST SURVIVAL

A total of 164 nests of seven species was found in 2003 (n = 62) and 2004 (n = 102; Table 2). Closed and open cup nests were under observation for 703 and 1154 days, respectively. Eighty-five percent (139/164) of nests successfully fledged young. The primary cause of nest failure was predation; 92% (23/25) of nests failed due to predation and 8% (2/25) of failures were caused by abandonment. Daily nest survival was higher for closed cup nests (0.989, 95% CI 0.819-0.999) than for open cup nests (0.942, 95% CI 0.797-0.985).

Closed cup nesting species. None of the candidate models explained a large proportion of the variance in DSR of closed cup nesting birds including those models containing variables relating to buffer width. Model selection uncertainty was high, as all 21 models were within six AIC_c units, and thus model averaging was used. The model which included both nest height and species received the most support (Table 3). Parameter estimates for the variables buffer, coast edge, harvest edge, height, and initiation had a positive effect on DSR, whereas, young forest and road density had a negative effect. However, the 95% CI for all parameter estimates, excluding the intercept, included zero.

Open cup nesting species. Again there was no strong empirical evidence that any one model captured a large proportion of the variance in DSR for open cup nesting birds and therefore model averaging was employed (Table 3). The best model included only species, however this model had a low model weight (w_i = 0.16). Varied Thrush (*Ixoreus naevius*) and Swainson's Thrush (*Cartharus ustulatus*) nests had the lowest DSR, whereas, the Pacific-slope Flycatcher (*Empidonax difficilis*) had the highest (Table 2). The second best approximating model was within 1 AIC_c unit and included both variables of species and roads. However, the parameter estimate for the effect of roads was negligible (<0.001) and confidence interval included zero (Table 4). Only one model which included variables related to buffer width had an $AIC_c < 2$, however, this model included the species variable and all models which included the species variable performed better than those without.

Hermit Thrush. The logistic-exposure model best describing daily nest-survival rates included the distance from coast variable (coast edge). Of the remaining 15 candidate models, only one (coast edge + concealment) had a $\Delta AIC_c < 5$ and $w_i > 0.05$ (Table 5). Based on model-averaging from 15 *a priori* candidate models the DSR of Hermit Thrush was positively affected by distance from coastline edge $\beta\ (_{\text{coast edge}}) =$ 0.017, 95% CI = (-0.009-0.430; Figure 1) and negatively affected by increasing average concealment, however, this estimate was negligible $(_{\text{concealment}}) = 0.002$, and confidence interval was centered over zero 95% CI = (-0.009-0.009).

COMPARISON OF NEST SITE CHARACTERISTICS

Closed cup nests. Type of nesting substrate differed significantly among species (χ^2_8= 42.3, *P*= <0.001). Sixty-nine percent of Chestnut-backed Chickadee (*Parus rufescens*) and 96% of Red-breasted Sapsucker nests were found in snags whereas Winter Wren (*Troglodytes troglodytes*) nests were discovered in all substrates but were most often in logs (42%). Nest height, substrate dbh and substrate height also were significantly different among closed cup nesting species (Table 6). On average Red-breasted Sapsucker nests were located nearly four times higher than Chestnut-backed

Chickadee nests and 13 times higher than Winter wren nests. Winter wrens preferred to nest in shorter and narrower substrates than the two other closed cups nesting species. Vegetation measurements surrounding the nest site were not significantly different among species.

Open cup nests. Type of nesting substrate significantly differed among species (χ^2_{15}= 41.7, *P*= <0.001). Pacific-slope Flycatcher (55%), Swainsons Thrush (88%) and Varied Thrush (95%) nested more often in live trees than other substrates. Hermit Thrush nests were found in snags (37%) and live trees (35%). Nest height, substrate dbh, substrate height, distance to center of nest substrate, average cover around nest and distance to coastline edge were significantly different among open cup nesting species (Table 7). Pacific-slope Flycatcher nests were located in larger diameter substrates, higher off the ground and closer to the coast edge than the other open cup nesting species. On average both Pacific-slope Flycatcher and Hermit Thrush nests were less visible than either the Swainson's or Varied Thrush.

Comparison of vegetation measurements surrounding the nest site showed a significant difference only in density of saplings (F-ratio= 3.25, df= 3, P= 0.025); however the Tukey-Kramer multiple comparison procedure did not result in any one species being significantly different from another.

DISCUSSION

Width of coastal forested buffers appears to have no direct effect on daily survival rates for both closed and open cup nesting species. Compared to other studies conducted in the Pacific Northwest, daily survival rates were similar or higher for all but two, Swainson's and Varied Thrush, of avian species monitored in this study (Willson and Gende 2000, George and Brand 2002 and De Santo et al. 2003).

A possible reason for high survival rates in my study area is the lack of a well documented nest predator, red squirrel (Sieving and Willson 1998, De Santo et. al. 2003), on Prince of Wales Island (MacDonald and Cook 1996). However, Varied Thrush nests on Prince of Wales Island did experience lower daily survival rates compared to those near Juneau, Alaska (Willson and Gende 2000). Previous research in redwood forests has shown that relative density of Varied Thrushes increased further from forest edge (Brand and George 2001) and with increasing patch size (Hurt 1996). Predation risk might explain avoidance of forest edges by some species (Brittingham and Temple 1983). Brand and George (2000) found that predation on artificial nests, which mimicked Varied Thrush nests, declined with distance from edge in redwood forests patches. However, Kissling (2003) found relative density of Varied Thrushes to be highest in the narrowest buffers (< 100 m) and higher in forested buffers than contiguous forests within coastal forests of southeast Alaska. This finding coupled with the low daily nest-survival rate found in this study suggests coastal forested buffers may be ecological traps for Varied Thrushes. I recommend further evaluation of forest management guidelines and nest survival estimates for the Varied Thrush in southeast Alaska. This species appears to be particularly susceptible to predation and may be negatively impacted by forest management actions that result in increased edge or a lack of midstory structure.

In order to increase sample size, I combined species into functional groups to model effects of nest-site and stand-level characteristics on daily survival rates. The method of combining species into functional groups has proven useful when applied in a management context (Rodewald and Yahner 2001, Shirley 2005). However, data from this study suggest that researchers should use caution, particularly in southeast Alaska, when grouping multiple avian species for analysis. In coastal buffers variation in daily survival rates among species was more important than any stand-level or nest site level variables measured for open cup nesting species. Species-specific studies should be considered when evaluating factors that affect reproductive success of avian species in this region.

Hermit Thrush nest survival was associated with habitat characteristics at the nest scale. Hermit Thrush nest survival was negatively related to proximity to the coast edge. On Prince of Wales Island, the productive inter-tidal zone attracts many generalist predators such as black bears, mustelids, eagles, and corvids. Kissling (2003) found the highest relative density for this species within the widest (251-400 m) coastal forested buffers and positively related to amount of old growth forest habitat. In Southeast Alaska, nesting Hermit Thrush may avoid natural forest edges to minimize predation risk and increase nest survival.

The effect of proximity to coast edge was not consistent among all species, thus some species may have the ability to mitigate high predator densities along forest edges either through active nest defense (Montgomerie and Weatherhead 1988, Pietz and

Granfors 2005) or nest site selection (Willson and Gende 2000, Weidinger 2002, De Santo et al. 2003, Remeš 2005). For example, I found that within coastal buffers Pacific-slope Flycatchers nested closer to the coast than any other species; however, this species had high nest survival. High nest survival despite close proximity to forest edges may be related to nest defense behavior. During nest checks, Pacific-slope Flycatchers frequently exhibited vigorous nest defense when their nests were checked compared to other species (personal observation).

Although very speculative, a comparison of nest site attributes to DSR estimates of open cup nesting species does reveal some interesting patterns. Varied and Swainson's Thrushes had lower daily survival rates compared to other open cup nesting species. I also found that Varied and Swainson's Thrush nests were less concealed, situated in smaller diameter nesting substrates, and placed farther from the center of the nest tree, shrub or snag. These habitat attributes suggest that their nests were more exposed and more likely to be detected by predators that use visual cues, particularly raptors. Nestling diet for Northern Goshawks (*Accipiter gentilis*) in southern southeast Alaska was comprised mostly of birds (85%) of which 11% were adult Varied Thrushes and 10% were unknown passerines (Lewis 2001). Poorly concealed nests, particularly those with incubating or feeding adults, situated in the sub-canopy may be easily located by raptors.

However, there are a number of potential predator species which use different habitats and different hunting strategies to locate prey. Without documentation of nest predators, it is impossible to determine which predators are most detrimental to avian nest success in a particular location. Understanding the mechanism which brings predators in contact with nests could provide land mangers the knowledge to help minimize predation risk of highly susceptible nesting species, such as the Varied Thrush.

Currently, the Tongass Land Management Plan uses “indicator species” to assess the effects of timber harvest on wildlife habitat. At this time, there are no open cup nesting avian indicator species. I suggest including an open cup nesting species because closed cup nesting species appear to be more robust to predation risk caused by habitat alterations. Due to the low DSR of the Varied Thrush nests I suggest further evaluation of this species in relation to management guidelines. By including the Varied Thrush the Tongass Land Management Plans would improve its efforts to mitigate the effects of timber harvesting on habitat quality for avian species and ensure a more complete policy of ecosystem management.

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Figure 1. Daily survival rate of Hermit Thrush nests in relation to distance from coastal edge on Prince of Wales island Alaska, 2003-2004. Horizontal dashed line indicates 152 m the management guideline for coastal buffer width used prior to 1997.

Figure 1.

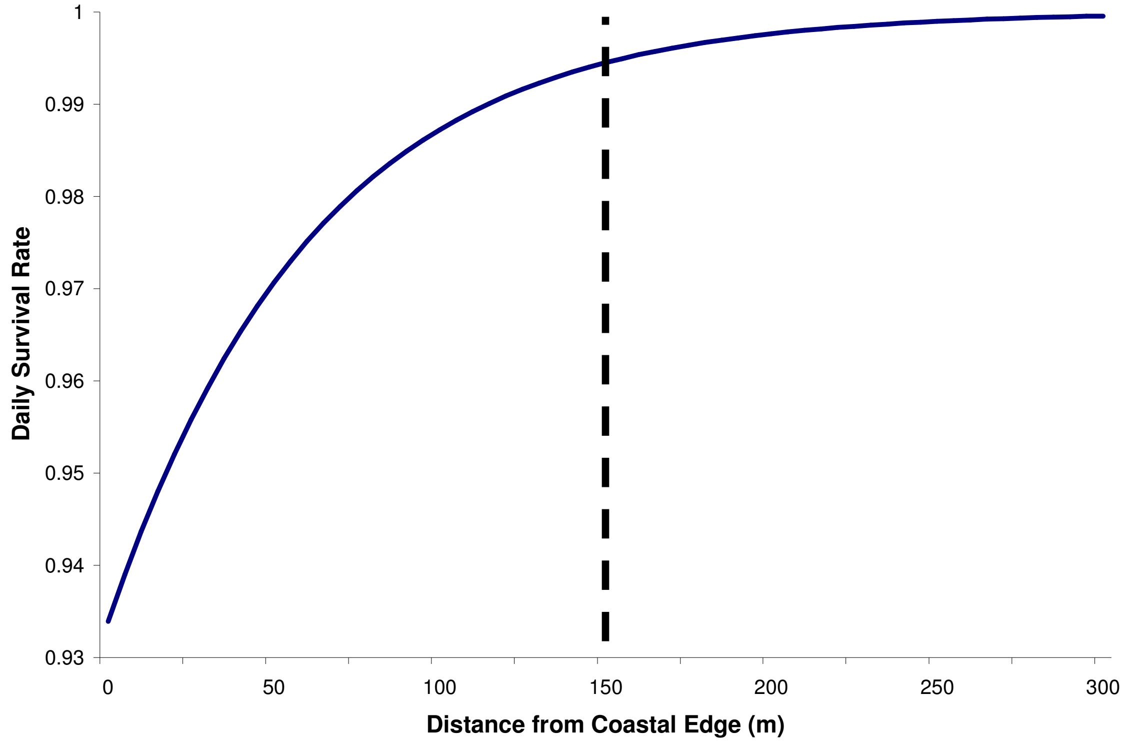
1
0.99
0.98
0.97
0.96
0.95
0.94
0.93
Daily Survival Rate
0
50
100
150
200
250
300
Distance from Coastal Edge (m)

Table 1. Candidate model sets used in the logistic exposure analysis for closed cup, open cup and Hermit Thrush nests. In addition to the models listed the variable Species was added to all closed cup and open cup models, resulting in a total of 23 and 31 models respectively.

Model	Closed Cup[a]	Open Cup	HETH
Buffer	X	X	X
Buffer + Year	X	X	X
Buffer * Year	X	X	X
Coast Edge	X	X	X
Coast Edge + Concealment		X	X
Concealment		X	X
Concealment + Harvest Edge		X	X
Concealment + Height		X	X
Global		X	X
Harvest Edge	X	X	X
Height	X	X	X
Initiation	X	X	X
Null	X	X	X
Roads	X	X	X
Species	X	X	
Year	X	X	X
Young Forest	X	X	X

[a] Generalized linear models cannot correctly estimate parameters or fit of models when values are zero or one. Therefore, Red-breasted Sapsuckers (*Sphyrapicus ruber*) were removed from the logistic exposure analysis because this species did not experience any depredation.

Table 2. Number of nests monitored and daily survival rates (DSR, 95% CI) for nest of seven species in coastal buffers on Prince of Wales Island, Alaska 2003-2004.

Common name	Genus species	n	DSR	95% CI
Closed Cup Nesting Species				
Chestnut-backed Chickadee	*Parus rufescens*	13	0.980	0.890-0.997
Red-breasted Sapsucker	*Sphyrapicus ruber*	23	1.00	------
Winter Wren	*Troglodytes troglodytes*	26	0.992	0.967-0.998
Open Cup Nesting Species				
Pacific-slope Flycatcher	*Empidonax difficilis*	18	0.995	0.963-0.999
Hermit Thrush	*Cartharus guttatus*	49	0.989	0.970-0.996
Swainson's Thrush	*Cartharus ustulatus*	16	0.980	0.938-0.994
Varied Thrush	*Ixoreus naevius*	19	0.947	0.902-0.972

Table 3. Model selection results for the eight most supported models for closed cup (Chestnut-backed Chickadee, Winter Wren) and open cup (Pacific Slope Flycatcher, Hermit Thrush, Swainson's Thrush, Varied Thrush) nesting species on Prince of Wales Island, Alaska, 2003-2004. *K* is the number of parameters in the model; deviance is the difference in -2 log-likelihood of the current model and -2 log-likelihood of the saturated model. Models are listed beginning with the best-fitting model and sorted by the lowest ΔAIC_c. Models with the lowest ΔAIC_c and the greatest Akaike weight (w_i) have the most support. The remaining candidate models had $\Delta AIC_c > 2$ and $w_i < 0.05$.

Nest type	Model	K	Deviance	ΔAIC_c	w_i
Closed cup	Height + Species	3	42.4	0.00	0.129
	Constant Survival	1	46.7	0.30	0.111
	Harvest Edge	2	45.7	1.32	0.067
	Buffer	2	45.8	1.37	0.065
	Species	2	45.8	1.42	0.063
	Roads	2	46.2	1.79	0.053
	Initiation	2	46.3	1.87	0.051
	Height	2	46.3	1.90	0.050
	Global	11	31.2	5.47	0.008
Open cup	Species	4	153.2	0.00	0.163
	Roads + Species	5	151.8	0.64	0.118
	Initiation + Species	5	152.3	1.12	0.093
	Young Forest + Species	5	152.6	1.39	0.081
	Coast Edge + Species	5	152.7	1.52	0.076
	Buffer + Species	5	153.0	1.81	0.066
	Height + Species	5	153.2	1.97	0.061
	Harvest Edge + Species	5	153.2	2.00	0.060
	Global	14	146.8	13.92	<0.001

Table 4. Model-averaged parameter estimates from logistic-exposure models relating daily survival rate of open cup nests. Confidence intervals reflect both uncertainty in parameter estimates from a given model and uncertainty in selecting that model (Burnham and Anderson 2002).

Effect	Parameter estimate	95% CI
Intercept	2.773	1.337-4.209
Species		
PSFL	2.315	-0.075-4.704
HETH	1.492	0.200-2.784
SWTH	0.924	-0.421-2.269
VATH	0	0
Roads	<0.001	-0.000-0.000
Initiation	0.001	-0.004-0.006
Young forest	-0.001	-0.008-0.005
Coast edge	<0.001	-0.001-0.002
Height	-0.011	-0.118-0.096
Buffer	<0.001	-0.001-0.002

Table 5. Model selection results for the two most supported models of daily survival rate of Hermit Thrush nests on Prince of Wales Island, Alaska, 2003-2004. *K* is the number of parameters in the model; deviance is the difference in -2 log-likelihood of the current model and -2 log-likelihood of the saturated model. Models are listed beginning with the best-fitting model and sorted by the lowest ΔAIC_c. Models with the lowest ΔAIC_c and the greatest Akaike weight (w_i) have the most support. The remaining candidate models had $\Delta AIC_c > 2$ and $w_i < 0.6$.

Model	K	Deviance	ΔAIC_c	w_i
Coast edge	2	46.6	0.00	0.5651
Coast edge + Concealment	3	46.6	2.00	0.2082

Table 6. Mean (±1 SE) values for nest substrate characteristics for three closed cup nesting species, Prince of Wales island Alaska 2003-2004. Columns sharing the same letter were not significantly different (Tukey-Kramer test).

	Nest Height (m)	Substrate dbh (cm)	Substrate height (m)
Red-breasted Sapsucker	26.12 ± 1.24^{a}	98.39 ± 6.91^{a}	34.69 ± 2.09^{a}
Chestnut-backed Chickadee	7.35 ± 1.66^{b}	77.97 ± 8.98^{a}	21.33 ± 2.79^{b}
Winter Wren	1.68 ± 1.15^{c}	48.12 ± 7.24^{b}	5.33 ± 1.93^{c}
P	<0.001	<0.001	<0.001

Table 7. Mean (±1 SE) values for nest characteristics for the four open cup nesting species, Prince of Wales Island, Alaska. Columns sharing the same letter were not significantly different (Tukey-Kramer test).

	Nest Height (m)	Substrate dbh (cm)	Distance to Center (cm)	Average Concealment (%)	Saplings	Distance to Harvest edge (m)	Distance to Coast (m)
Pacific-slope							
Flycatcher	9.3±0.8[a]	70.1±7.5[a]	27.6±21.1[a]	70.7±5.0[a]	18.7±4.2[a]	150.2±18.9[a]	82.8±19.8[a]
Hermit Thrush	2.3±0.5[b]	43.7±4.8[b]	16.2±13.2[a]	68.8±2.9[a]	30.3±2.6[a]	147.9±11.5[a]	144.7±11.9[b]
Swainson's Thrush	3.6±0.9[b]	14.7±8.3[c]	59.5±24.0[ab]	48.5±5.5[b]	17.9±4.8[a]	143.6±20.1[a]	109.9±21.0[ab]
Varied Thrush	3.8±0.8[b]	21.3±7.3[bc]	109.5±21.1[b]	36.1±4.7[b]	30.6±4.2[a]	153.6±18.4[a]	156.6±19.3[b]
P	<0.001	<0.001	0.003	<0.001	0.025	0.986	0.022

Appendix A. Size class distribution and average diameter of dominant live tree species and of standing dead wood within each study site on Prince of Wales Island, Alaska. A stratified random method was used within each study site to select six points. At each point, vegetation was sampled within four separate, 10 m radius, plots. The first plot was located at the point location itself; the remaining three were located 30 m from the grid point at 120 degrees from each other. Direction of the first subplot was chosen randomly. Vegetation measurements followed the protocol described by the Breeding Biology Research and Monitoring Database (BBIRD; Martin et al. 1997).

	Tree Species				
Study ID 877	*Alnus rubra*	*Picea sitchensis*	*Thuja plicata*	*Tsuga heteropylla*	Standing dead wood
DBH Class					
10-20 cm	0	9	1	65	8
20-30 cm	0	1	1	59	4
30-40 cm	0	0	0	32	13
40-50 cm	0	1	0	11	15
50-60 cm	0	2	0	16	12
60-70 cm	0	0	1	7	4
70-80 cm	0	0	1	3	2
80-90 cm	0	0	0	3	2
90-100 cm	0	0	1	2	2
>100 cm	0	6	3	1	5

Average DBH	0	55.4	76.6	47.5	38.9
883					
DBH Class					
10-20 cm	0	1	0	74	14
20-30 cm	0	0	1	46	12
30-40 cm	0	0	1	21	9
40-50 cm	0	2	1	30	13
50-60 cm	0	2	6	15	11
60-70 cm	0	0	3	12	5
70-80 cm	0	2	0	4	6
80-90 cm	0	0	0	5	6
90-100 cm	0	0	1	2	3
>100 cm	0	2	3	0	0
Average DBH	0	45.8	67.9	32.8	32.1
3749					
DBH Class					
10-20 cm	0	0	0	155	8
20-30 cm	0	1	0	41	6
30-40 cm	0	1	1	24	7
40-50 cm	0	0	0	14	9
50-60 cm	0	1	1	14	5
60-70 cm	0	0	2	11	8
70-80 cm	0	0	0	10	4

80-90 cm	0	0	0	4	3
90-100 cm	0	0	1	3	2
>100 cm	0	1	6	2	5
Average DBH	0	59.5	96.6	28.4	41.1
856					
DBH Class					
10-20 cm	0	4	2	105	20
20-30 cm	0	2	4	49	11
30-40 cm	0	3	4	25	11
40-50 cm	0	4	4	18	8
50-60 cm	0	4	7	18	10
60-70 cm	0	1	4	7	4
70-80 cm	0	1	5	4	1
80-90 cm	0	3	4	3	3
90-100 cm	0	1	1	0	3
>100 cm	0	0	3	2	1
Average DBH	0	48.0	58.5	29.0	27.5
3760					
DBH Class					
10-20 cm	0	4	0	58	6
20-30 cm	0	1	0	42	7
30-40 cm	0	1	0	25	4
40-50 cm	0	1	0	8	5

50-60 cm	0	0	0	12	3
60-70 cm	0	3	0	9	5
70-80 cm	0	0	0	6	7
80-90 cm	0	1	0	5	5
90-100 cm	0	0	0	12	11
>100 cm	0	2	0	9	9
Average DBH	0	56.7	0	40.3	52.6
3803					
DBH Class					
10-20 cm	0	0	4	47	4
20-30 cm	0	0	9	17	9
30-40 cm	0	0	3	13	8
40-50 cm	0	4	5	17	10
50-60 cm	0	2	4	18	6
60-70 cm	0	2	6	14	7
70-80 cm	0	1	2	8	2
80-90 cm	0	1	5	14	1
90-100 cm	0	2	2	6	3
>100 cm	0	3	3	2	3
Average DBH	0	62.0	56.3	43.8	39.4
887					
DBH Class					
10-20 cm	1	1	1	44	8

20-30 cm	0	1	1	23	9
30-40 cm	0	2	1	23	15
40-50 cm	0	3	2	19	6
50-60 cm	0	3	1	22	4
60-70 cm	0	3	7	14	3
70-80 cm	0	4	4	11	3
80-90 cm	0	1	0	4	2
90-100 cm	0	1	1	3	1
>100 cm	0	9	3	2	5
Average DBH	15.0	72.1	72.6	46.4	40.1

Appendix B. Coverage and species composition of vegetation at random sites within each study site. Within each study site a stratified random method was used to select six points. At each point, vegetation was sampled within four separate, 10 m radius, plots. The first plot was located at the point location itself; the remaining three were located 30 m from the grid point at 120 degrees from each other. Direction of the first subplot was chosen randomly. Vegetation measurements followed the protocol described by the Breeding Biology Research and Monitoring Database (BBIRD; Martin et al. 1997). Values are a percent of coverage by each shrub species over the total distance measured, 960 m, for each site.

	Site ID						
Species	877	883	3749	856	3760	3803	887
Oplopanax horridum	6%	1%	0%	0%	0%	1%	3%
Rubus spectabilis	12%	1%	1%	1%	0%	0%	3%
Vaccinium spp	28%	31%	21%	18%	32%	19%	17%
Menziesia ferruginea	1%	1%	2%	2%	1%	2%	0%

Appendix C. Latitude and longitude for the corners of each study site on Prince of Wales Island, Alaska.

	Latitude and Longitude							
Site ID	NW		NE		SE		SW	
877	55.19251	132.28400	55.19244	132.28307	55.19082	132˚28232	55.19063	132.28352
883	55.19551	132.28036	55.19577	132.27537	55.19400	132.27406	55.19375	132.27535
3749	55.46466	133.13406	55.46456	133.13269	55.46323	133.13256	55.46326	133.13387
856	55.23334	132.30234	55.23294	132.30088	55.23124	132.30242	55.23181	132.30335
3760	55.48254	133.10586	55.48197	133.10423	55.48125	133.10442	55.48183	133.11038
3803	55.53373	133.09575	55.53343	133.09331	55.53248	133.09285	55.53224	133.09503
887	55.20395	132.28290	55.20437	132.20810	55.20289	132.27556	55.20248	132.28177

Appendix D. Average buffer width, number of closed and open cup nests monitored, area and time searched for the seven study sites used to examine the daily survival rate of birds on Prince of Wales Island, Alaska

	Site ID						
Site Characteristics	877	883	3749	856	3760	3803	887
Average buffer width (m)	183	204	211	243	350	367	386
Number of closed cup nests	11	17	9	9	6	19	3
Number of open cup nests	9	6	7	17	15	11	21
Area (ha)	10.9	12.0	9.0	12.6	7.8	15.2	18.4
Time spend nest searching							
(hr x number of searchers)	353	387	299	396	303	470	600

Appendix E. Size class distribution and average diameter of live tree species and of standing dead wood within a 10 m radius around closed and open cup nests on Prince of Wales Island, Alaska.

	Tree Species				
Avian species Chestnut-backed Chickadee (n=13)	*Alnus rubra*	*Picea sitchensis*	*Thuja plicata*	*Tsuga heteropylla*	Standing dead wood
DBH Class					
10-20 cm	0	4	2	50	6
20-30 cm	0	0	0	14	3
30-40 cm	0	0	0	4	8
40-50 cm	0	1	1	10	6
50-60 cm	1	2	0	13	6
60-70 cm	0	1	2	3	3
70-80 cm	0	2	2	0	1
80-90 cm	0	0	2	4	5
90-100 cm	0	1	1	1	1
>100 cm	0	1	1	0	3
Average DBH	55.0	56.3	76.5	30.3	51.1
Red-breasted Sapsucker (n=23)					

DBH Class					
10-20 cm	0	10	1	90	6
20-30 cm	0	0	2	24	11
30-40 cm	0	0	3	25	12
40-50 cm	0	1	1	13	15
50-60 cm	0	2	1	11	10
60-70 cm	0	8	1	5	11
70-80 cm	0	1	1	7	5
80-90 cm	0	0	1	5	13
90-100 cm	0	0	1	1	4
>100 cm	0	1	2	6	7
Average DBH	0	45.8	58.8	32.7	57.8
Winter Wren (n=26)					
DBH Class					
10-20 cm	31	7	3	124	24
20-30 cm	9	3	6	54	26
30-40 cm	0	2	5	32	20
40-50 cm	1	1	6	17	11
50-60 cm	1	2	0	7	11
60-70 cm	1	1	3	10	8
70-80 cm	0	2	3	2	8
80-90 cm	0	1	1	3	5

90-100 cm	0	0	3	4	4
>100 cm	0	2	5	2	11
Average DBH	19.9	45.1	58.3	27.9	48.4
Pacific Slope Flycatcher (n=18)					
DBH Class					
10-20 cm	0	2	0	82	8
20-30 cm	3	3	1	36	3
30-40 cm	3	0	0	27	8
40-50 cm	2	2	0	11	7
50-60 cm	0	1	1	4	8
60-70 cm	0	0	1	7	4
70-80 cm	0	0	3	3	5
80-90 cm	0	1	1	6	0
90-100 cm	0	1	2	4	5
>100 cm	0	0	7	1	3
Average DBH	33.8	42.0	97.6	30.1	53.4
Hermit Thrush (n=49)					
DBH Class					
10-20 cm	11	6	2	165	22
20-30 cm	9	3	2	71	23

30-40 cm	4	2	5	43	21
40-50 cm	1	4	3	35	19
50-60 cm	0	7	5	26	26
60-70 cm	0	4	3	16	14
70-80 cm	0	1	5	8	13
80-90 cm	0	6	4	14	15
90-100 cm	0	0	1	5	5
>100 cm	0	2	8	6	15
Average DBH	23.0	52.0	70.0	32.7	56.2
Swainson's Thrush (n=16)					
DBH Class					
10-20 cm	0	6	0	34	3
20-30 cm	0	1	0	11	3
30-40 cm	0	1	0	12	5
40-50 cm	0	2	1	11	3
50-60 cm	1	0	1	3	8
60-70 cm	0	0	0	6	2
70-80 cm	0	2	0	6	2
80-90 cm	0	1	0	1	2
90-100 cm	0	0	0	4	1
>100 cm	0	2	1	2	3

Average DBH	55.0	49.5	72.0	38.3	57.4
Varied Thrush (n=19)					
DBH Class					
10-20 cm	0	2	0	73	5
20-30 cm	5	0	1	25	8
30-40 cm	2	1	1	10	5
40-50 cm	0	3	2	13	1
50-60 cm	0	2	8	14	7
60-70 cm	0	6	0	10	6
70-80 cm	0	2	1	0	0
80-90 cm	0	1	4	7	2
90-100 cm	0	2	3	3	2
>100 cm	0	5	2	2	1
Average DBH	27.9	74.2	70.0	32.6	46.1

Appendix F. Coverage and species composition of vegetation for nest sites monitored. Vegetation measurements followed the protocol described by the Breeding Biology Research and Monitoring Database (BBIRD; Martin et al. 1997). Values are a percent of coverage by each shrub species over the total distance measured, 40 m, for each nest site.

	Vegetation species			
Avian species	*Oplopanax horridum*	*Rubus spectabilis*	*Vaccinium* spp	*Menziesia ferruginea*
Chestnut-backed Chickadee	4%	12%	44%	1%
Red-breasted Sapsucker	5%	8%	51%	3%
Winter Wren	3%	9%	43%	4%
Pacific-slope Flycatcher	2%	5%	41%	2%
Hermit Thrush	1%	6%	34%	2%
Swainson’s Thrush	8%	9%	44%	1%
Varied Thrush	5%	10%	35%	1%