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RESIDENTIAL EDGES AS ECOLOGICAL TRAPS: POSTFLEDGING SURVIVAL OF A GROUND-NESTING PASSERINE IN A FORESTED URBAN PARK

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Abstract.—Substantial offspring mortality can occur during the postfledging period of birds, but few postfledging survival studies have been conducted within the context of habitat suitability. We conducted a 2-year radiotelemetry study of Spotted Towhee (*Pipilo maculatus*) reproductive success and fledgling survival in a 24-ha forested park in a residential area of Lake Oswego, Oregon. In corroboration of previous research on this species, we found (1) that Spotted Towhees nested closer to the edge between the park and residential neighborhoods than expected by chance, and (2) that pairs nesting near edges produced the largest and most offspring. However, fates were reversed during the postfledging period. Thirty-six of 52 fledglings survived the 27-day tracking period, and although fledglings were more likely to be found near edges than in the interior, fledglings near edges had a far higher probability of dying. All deaths were from predation, and at least 11 of 16 predation events were attributable to Domestic Cats (*Felis catus*) and Western Screech-Owls (*Megascops kennicottii*). A stochastic model that incorporated probability of nest success, nestling production from successful nests, and fledgling survival showed that the number of independent offspring produced per nest was greatest in the park interior. Heavy use of, and apparent preference for, edge by nesting Spotted Towhees, coupled with high fledgling mortality near edges, created a severe ecological trap that was not apparent until the final stage of parental care. Hence, failure to document offspring survival in the late stages of reproduction may lead to incorrect assessment of habitat suitability and poor management decisions. *Received 26 July 2012, accepted 19 February 2013.*

Key words: Domestic Cat, ecological trap, edge, juvenile survival, *Pipilo maculatus*, radiotelemetry, severe trap, Spotted Towhee, urban.

Bordes Residenciales como Trampas Ecológicas: Supervivencia Posterior al Emplumamiento en un Paserino que Anida en el Suelo en un Parque Urbano Boscoso

Resumen.—Una mortalidad considerable de las crías puede ocurrir durante el periodo posterior al emplumamiento en las aves, pero se han desarrollado pocos estudios sobre la supervivencia en este periodo en el contexto de la idoneidad del hábitat. Hicimos un estudio de radio telemetría de dos años midiendo el éxito reproductivo y la supervivencia de volantones de *Pipilo maculatus* en un parque boscoso de 24 ha en un área residencial de Lake Oswego, Oregon. Corroboramos estudios previos hechos en esta especie al encontrar (1) que las aves anidaron más cerca al borde entre el parque y los barrios residenciales que lo esperado al azar, y (2) que las parejas que anidaron cerca de los bordes produjeron más crías y crías de mayor tamaño. Sin embargo, el destino de las aves se invirtió durante el periodo posterior al emplumamiento. De un total de 52 volantones, 36 sobrevivieron al periodo de rastreo de 27 días. Aunque fue más probable encontrar volantones cerca de los bordes que en el interior del bosque, los volantones tuvieron una probabilidad de muerte mucho mayor cerca al borde. Todas las muertes fueron por depredación y al menos 11 de 16 eventos de depredación pudieron ser atribuidos a gatos domésticos (*Felis catus*) y a búhos (*Megascops kennicottii*). Un modelo estocástico que incorporó la probabilidad de supervivencia de los nidos, la producción de volantones en nidos exitosos y la supervivencia de los volantones, demostró que el número de crías independientes producidas por nido fue máximo en el interior del parque. El uso continuo de los bordes y la aparente preferencia hacia éstos que demuestra *P. maculatus*, junto con la alta mortalidad de los volantones cerca de los bordes, resultó en el origen de una trampa ecológica severa que no se hizo evidente sino hasta las últimas etapas del cuidado parental. Por lo anterior, no documentar la supervivencia de las crías en las etapas finales de la reproducción puede llevar a una evaluación incorrecta de la idoneidad del hábitat y a la toma de decisiones inadecuadas sobre manejo.

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Gates and Gysel (1978) were among the first to use the term "ecological trap" to refer to situations in which animals seemingly preferred low-quality habitat over available higher-quality habitats. Robertson and Hutto (2006) described the poor habitats that were actively chosen as "severe traps" to distinguish them from habitats in which individuals settle without regard to suitability ("equal-preference trap"). Three mechanisms could lead to the existence of severe traps: (1) settlement cues change so that habitat becomes more attractive but suitability does not change; (2) a habitat's attractiveness is unchanged but suitability decreases; or (3) habitat attractiveness increases and suitability decreases simultaneously (Robertson and Hutto 2006).

Examples of severe traps abound in the literature. These range from the attraction of West Indian Manatees (*Trichechus manatus*) to waters artificially heated by power-plant effluent (only to die when the effluent is turned off; Packard et al. 1989) to the fatal attraction of adult dragonflies to crude oil (Horváth et al. 1988). More commonly, poor choices of nest sites create ecological traps, for example in insects (Kriska et al. 1998, Ries and Fagan 2003), turtles (Kolbe and Janzen 2002), and numerous avian taxa. Indeed, most studies of ecological traps examine nesting birds' use of anthropogenically altered habitats. Expansive hay fields (Bollinger et al. 1990) or grass fields near airports (Kershner and Bollinger 1996) often attract high densities of breeding grassland birds that then experience nest failure when the fields are mowed. Birds sometimes also appear to prefer nest sites in exotic vegetation, which, in some instances, leads to greater probability of nest predation (Remeš 2003), even if only for a portion of the nesting season (Rodewald et al. 2010).

However, edges created as a consequence of habitat fragmentation because of either agriculture (Johnson and Temple 1990) or timber harvest (Flaspohler et al. 2001) are most often cited as responsible for the existence of ecological traps for birds. Gates and Gysel (1978), Chasko and Gates (1982), Johnson and Temple (1990), Flaspohler et al. (2001), and Weldon and Haddad (2005) found that birds preferred to nest near edges (based on age-class distribution of breeding adults, site fidelity, or nest density or abundance), but that nest success or number of young fledged was lowest near edges. Exceptions exist, especially for shrubland birds (e.g., Woodward et al. 2001), but the increased likelihood of nest failure near edges (i.e., the edge effect) seems especially pronounced among forest-breeding and ground-nesting birds (see review by Batáry and Báldi 2004). The cause of the low nest success across all studies was elevated rates of nest predation arising from an apparent high abundance or high activity of some nest predators in edge habitats. Although some mammalian predators appear to be equally abundant in edge and interior habitats (Heske 1995, Chalfoun et al. 2002), many snake species (Blouin-Demers and Weatherhead 2001, Chalfoun et al. 2002), Brown-headed Cowbirds (*Molothrus ater*; Howell et al. 2007), and corvids (Andrén 1992, Niemuth and Boyce 1997, Marzluff et al. 2004) appear to show preferences for forest edges.

An important caveat noted by Robertson and Hutto (2006) is that changes in habitat or settlement cues that reduce fitness at one stage of the life cycle may not necessarily be present or relevant at another stage. For example, a trap that exists for a species at the egg stage may equally affect, not affect, or more strongly affect individuals as adults. Rarely, if ever, has this caveat been acknowledged. All studies of ecological traps referenced above examined only one life-history stage; in birds, this was universally the nesting stage. Most studies of avian reproductive success conclude at the end of the nestling phase, but in recent years researchers have tracked survival during the postfledging period (e.g., Anders et al. 1997, Yackel Adams et al. 2001, Moore et al. 2010, Balogh et al. 2011). Other than Ausprey and Rodewald (2011), who failed to find evidence for the possibility that exotic shrubs might act as ecological traps for fledglings, no work on fledgling survivorship has been conducted within the framework of ecological traps.

The Spotted Towhee (*Pipilo maculatus*; hereafter "towhee") is a resident ground-nesting and ground-foraging inhabitant of early successional forests of the Pacific Northwest (Greenlaw 1996). Towhees are also common in urban parks and greenspaces, where they use multiple habitat types (Whittaker and Marzluff 2009). Research in parks and greenspaces in the Portland, Oregon, metropolitan region has shown that towhees nest in natural areas as small as 1 ha, and that populations in some parks appear to be sufficiently productive to be self sustaining (S. Bartos Smith and M. T. Murphy unpubl. data). Their use of parks of all sizes exposes towhees to both edge and interior habitats, and contrary to expectations based on their placement of nests on the ground in forests (see Batáry and Báldi 2004), Bartos Smith et al. (2012) showed that (1) the earliest-breeding female towhees nested near edges; (2) nests near park edges fledged significantly more young than nests in the interior of parks; and nests near park edges (3) produced heavier young and (4) were less likely to incur partial brood losses. These data suggest that food is more abundant near edges than in the habitat interior. Assuming that important nest predators are more common along edges, Bartos Smith et al.'s (2012) results suggest that food availability overrides possible negative influences of predators on decisions of where to nest. Nonetheless, towhees appear to be sensitive to habitat fragmentation (Patten and Bolger 2003), and higher nesting success near edges may be offset by reduced survival of fledglings.

We conducted a 2-year study of the reproductive ecology of Spotted Towhees at a residential park in the Portland metropolitan region. Our goals were to corroborate Bartos Smith et al.'s (2012) findings that nest success and productivity increased with proximity to edge, and to measure reproductive success in the postfledging period to evaluate whether fledgling survival varied in relation to use of habitat edges. To that end, we (1) measured nest success in relation to a nest's distance to a park edge, (2) quantified nesting productivity and nestling mass and size in relation to distance to edge, (3) determined whether fledglings were found primarily in edge or interior habitats, (4) documented survival of fledgling towhees in the immediate 30-day period of postfledging parental care in relation to distance to park edge, and finally, (5) modeled productivity of pairs up to the point of offspring independence to determine whether edges are ecological traps.

Methods

Study site.—Our study site, Springbrook Park, is a 24-ha urban park located near the border of Lake Oswego and Portland and is one of the four parks included in Bartos Smith et al.'s (2012) study. The park is separated from Lake Oswego High School on the north by a four-lane highway and is bordered on the east by mowed athletic fields associated with Lake Oswego Junior High School and Uplands Elementary School and by 12 homes. Ten homes and a neighborhood road border it on the south side, and 20 homes form the border on the west side. The average (± SE) distance of homes to the legal boundary of the park is 16 ± 1.7 m (range: 3–43 m; *n* = 44). The park's network

of recreational trails (up to ~2 m wide; Fig. 1) is used heavily by joggers and local recreational walkers. The dominant tree species are Bigleaf Maple (*Acer macrophyllum*), Paper Birch (*Betula papyrifera*), and Red Alder (*Alnus rubra*). Douglas-fir (*Pseudotsuga menziesii*) is locally common in portions of the park. The well-developed understory includes native Western Swordfern (*Polystichum munitum*), Salal (*Gaultheria shallon*), Indian Plum (*Oemleria cerasiformis*), Cascade Barberry (*Mahonia nervosa*), Beaked Hazelnut (*Corylus cornuta*), and Thimbleberry (*Rubus parviflorus*), as well as non-native Himalayan Blackberry (*Rubus armeniacus*), English Ivy (*Hedera helix*), and English Holly (*Ilex aquifolium*).

We defined the park's edge as where the tree cover thinned markedly and understory vegetation disappeared. This sometimes extended several meters beyond the park's legal boundary. The location of the edge was recorded using a GeoXT GPS receiver (Trimble Navigation, Sunnyvale, California) with 90% of readings accurate to <2 m. To map the park's perimeter, the park's edge locations were projected onto a regional land-use map available from the Regional Land Information System (Metro 2004) using ARCGIS, version 9.2 (ESRI, Redlands, California). Data on habitat composition at the edge, and in the surrounding landscape in buffers that expanded outward from the edge at distances of 50 m, 250 m, 500 m, 1,000 m, 1,500 m, and 2,000 m, were extracted using ARCGIS and

FRAGSTATS (Lichti 2004). At the park boundary, undeveloped forest (i.e., natural forest with undeveloped ground surface) covered 91.9% of the ground surface (Fig. 2). Another 5.7% of the land area was covered by tree canopy, but with a developed ground surface (i.e., developed forest [>5% of land surface covered by roads, driveway, or a built structure]). The remaining 2.4% was split between grassland and light urban development (i.e., residential homes). The proportion of the landscape covered by undeveloped and developed forest, grassland (athletic fields, golf courses, and residential backyards without trees), wetland (marshes and small ponds with emergent vegetation), urban areas (private homes, apartment buildings, or light industry, all without tree cover), and open water (i.e., Lake Oswego) remained relatively constant at regular intervals out to 2 km (Fig. 2). Averaged over the six distance categories (see above), just over half of the land surface (52.5 ± 1.88%, $n = 6$; Fig. 2) in the landscape was covered by trees (developed + undeveloped forest), followed by urban development (28.6 ± 0.87%, $n = 6$).

Nest location and transmitter attachment.—Many of the adult towhees in the park already had a unique combination of color bands when we began the study in 2008 because the population had been continuously monitored since 2004 (Bartos Smith et al. 2012). In any given year, 25 to 30 towhee pairs defend territories and breed. We attempted to locate all nests in the park in 2008 and 2009. Towhees often raise two or three broods per year, which necessitated near daily searches throughout the park from late March through August. We tried to capture and mark all unmarked adult towhees with a federal leg band and a unique combination of three colored leg bands. Males were captured by playing a towhee song near a taxidermic mount that was set behind a mist net in the male's territory. Adult females were captured by playing a recording of a fledgling towhee distress call near a mist net when her young were ≥7 days old.

We used female behavior to find nests during nest construction (e.g., carrying nesting material) and incubation (e.g., prolonged
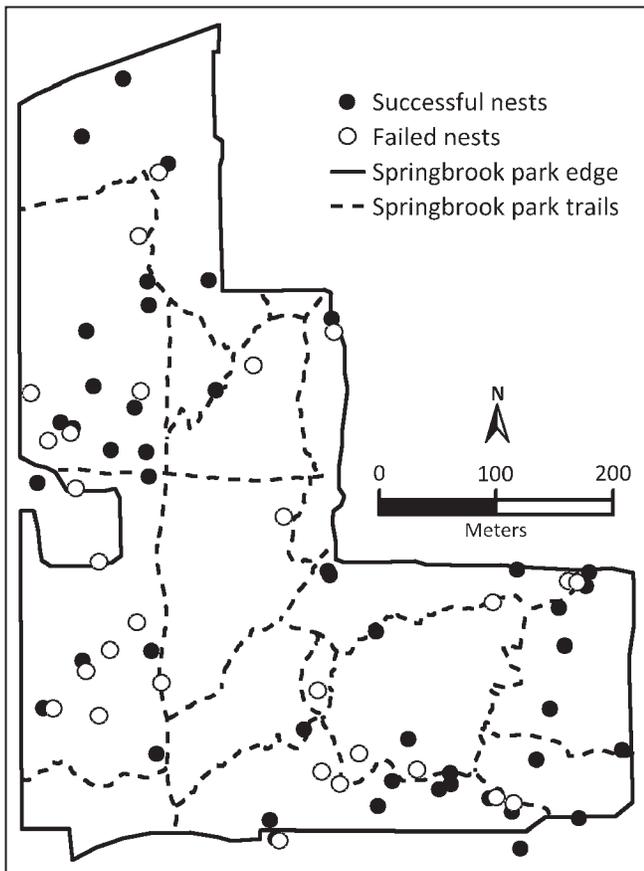

Fig. 1. Successful ($n = 45$) and failed ($n = 28$) Spotted Towhee nests from 2008 and 2009 in Springbrook Park, Lake Oswego, Oregon. Vegetation extends slightly beyond the park's official boundaries and, therefore, some pairs also placed nests outside the park's official edge.
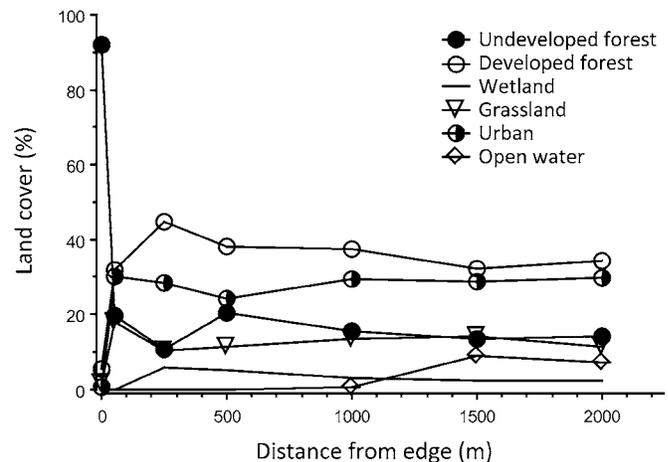

Fig. 2. Landscape composition beginning at the edge of Springbrook Park, Lake Oswego, Oregon, and at buffer distances of 50 m, 250 m, 500 m, 1,000 m, 1,500 m, and 2,000 m from the park's edge. Landscape categories included undeveloped forest, developed forest (>5% of ground surface underneath the canopy was developed), wetlands, grassland, urban, and open water. "Urban" in this setting was principally private homes, apartment complexes, and otherwise paved surfaces.

stationary behavior), and parental behavior (e.g., carrying food and defensive behavior) to find nests with hatched young. Locations of all nests were recorded using a Garmin 72 GPS receiver (Garmin, Olathe, Kansas) that was accurate to ≤10 m. We checked and recorded nest contents at intervals of ~2 days (2.1 ± 0.05 days, n = 407; range: 1–5 days) and measured (body mass and tarsus length) and banded young 7 days after hatching. Nests were checked daily after the nestlings were banded to determine age at fledging (usually day 10 or 11 posthatch). Spotted Towhees fledge prematurely if handled after day 8 (A. A. Shipley pers. obs.), and preliminary study indicated that attaching transmitters to 7- to 8-day-old nestlings often proved fatal (M. T. Murphy unpubl. data). Therefore, to ensure that the young were large enough to carry radiotransmitters to measure postfledging survival, we postponed transmitter attachment until 3 days after the young fledged. We then captured 1 or 2 fledglings from a brood by hand or by using a butterfly net, recorded body mass and tarsus length, and attached a Holohil BD-2 radiotransmitter with a figure-eight leg harness (Rappole and Tipton 1991). As recommended (Fair et al. 2010), all transmitters and harnesses were ≤5% of fledgling body mass. At banding, neither body mass nor tarsus length differed between fledglings that were fitted with transmitters (mass = 23.9 ± 0.5 g, tarsus = 25.5 ± 0.23 mm) as compared to all nestlings from the nest (mass = 23.7 ± 0.56 g; tarsus = 25.4 ± 0.28 mm; mass: t = 0.302, P = 0.76; tarsus: t = 0.403, P = 0.69; n = 35 nests for all comparisons). Adult and nestling towhees were banded, and fledglings were fitted with transmitters under permits from the Oregon Department of Fish and Wildlife (no. 089-08 to A.A.S.) and the U.S. Geological Survey Patuxent Wildlife Research Center Bird Banding Laboratory (subpermit no. 22230-M to A.A.S. under M.T.M.).

Radiotracking and survival.—We used a three-element folding Yagi antenna and an FM100 receiver (Advanced Telemetry Systems, Isanti, Minnesota) to locate all transmittered fledglings once daily between 0700 and 1900 hours PST until they reached 30 days postfledge. Fledglings remain with and are largely dependent on their parents for food and protection over this period (Greenlaw 1996, A. A. Shipley pers. obs.). The order in which we located fledglings during the day was haphazard, and fledglings were approached only as close as necessary to determine identity and location, to avoid pushing them from where they were found. After locating a bird, we marked the location with flagging and recorded the location with a Garmin 72 GPS receiver. If the bird was found alive in a backyard or otherwise outside the park boundaries, we recorded the bird as "out of park." Fledglings that died outside of the park were found by searching at sites where signal locations remained stationary for >1 day. Cause of death was determined by examining transmitter location and condition. Predation was attributed to Western Screech-Owls (*Megascops kennicottii*) or Cooper's Hawks (*Accipiter cooperii*) when the transmitter and/or fledgling remains were found associated with an active nest of either species. Predation was assigned to Domestic Cats (*Felis catus*) when the transmitter and/or fledgling remains were found in a backyard with either a cat sitting nearby or with a homeowner testimonial that his or her cat had killed the bird. If there was no direct evidence of the predator species, we recorded the fledgling as killed by an unknown predator if there were fledgling towhee feathers, body parts, or a partial carcass with bite marks found near the transmitter. Additionally, if no fledgling carcass or body part was near the transmitter, we recorded the fledgling as killed by an unknown predator if the transmitter

was damaged and was found well outside of the parents' territory before the fledgling could have become independent. At 30 days out of the nest, we recaptured and removed transmitters from survivors by "herding" each one into a long line of mist nets, or by occasionally capturing a bird at night using a mist net at its roost location.

The GPS coordinates of nests and daily fledgling locations were projected onto a map of the park using ARCGIS. Random locations within the park were generated in ARCGIS using the Create Random Points tool. We then used the Near Tool in ARCMAP to calculate the shortest distance from each nest, every fledgling location, and all random locations to the nearest park edge.

Statistical analyses.—We used a two-sample t-test to test the null hypothesis that towhee nests and random locations were, on average, equal distances from park edges. We estimated nest success (≥1 young fledged) using the logistic exposure models (Shaffer 2004) to account for exposure time while simultaneously testing for possible associations between nest fate and distance to park edge, year, and the date the nest was found (seasonality) using the GENMOD procedure in SAS (SAS Institute, Cary, North Carolina). We used an information-theoretic approach with Akaike's information criterion (AIC) corrected for small sample size (AIC$_c$) to evaluate model fit, and considered models within two AIC$_c$ units of the top model (ΔAIC$_c$ = 0) as potentially informative and included them in the calculation of model-averaged parameter estimates. Linear regression was used to test for relationships between distance of nest to edge and (1) clutch size, (2) brood size, (3) average nestling mass and tarsus length, and (4) number of fledglings per nest. A nest's mean nestling mass and tarsus length were used for analyses. For each fledgling, all distances to edge were averaged over the 27-day observation period (days 4 to 30 postfledging) so that we had one estimate per individual. We used t-tests as described above to determine whether fledgling locations were closer to edges than random locations, and whether fledgling survival was related to their average distance to edge.

We also used Cox proportional hazards regressions in PASW STATISTICS for Windows, version 19.0 (SPSS, Chicago, Illinois; Cox 1972, Whittaker and Marzluff 2009), to estimate the cumulative survival probability of fledglings in relation to proximity to edge. Cox models are well suited to studies in which individuals are relocated daily and the probability of detection is 1.0 (Manolis et al. 2002, Berkeley et al. 2007, Kaiser and Lindell 2007, Whittaker and Marzluff 2009). Ample evidence from other species indicate that survival of young after leaving the nest is often lower late in the season and in light-weight young from large broods. We therefore began with a Cox proportional hazards regression that included brood size, fledge date, and body mass at banding, along with year and the proportion of days the birds were found outside the park as covariates of survival. Distance to edge was then entered into the model in a second step to determine whether its entry led to a measurable improvement in our ability to account for variation in survival. Distance to edge was included as a categorical variable with three distance-to-edge categories based on the observed distribution of fledgling distances to edge: below the first quartile (≤20 m; "near"), in the middle 50% (21–41 m; "intermediate"), and above the third quartile (>41 m; "far"). We used distance to edge as a categorical variable to assist with the visualization of results, but note that analyses conducted with distance to edge as a continuous variable yielded identical qualitative results and were significant. We used an information-theoretic approach to evaluate model fit and

the importance of distance to edge for survival by comparing AIC_c between the first and second models. We also reduced model complexity by eliminating covariates until we obtained the model with the minimum AIC_c. All models within two AIC_c of the top model ($\Delta AIC_c = 0$) were considered competitive.

To explore the possibility that edges are ecological traps for towhees, we used STELLA to construct a stochastic model to predict the number of young per pair per nesting attempt to survive to an age of 30 days after fledging using (1) model-based estimates of nest success, and observed measurements of (2) the number of offspring to fledge from successful nests and (3) the probability of fledgling survival. In all three cases, estimates and measurements were obtained for nests and fledglings that fell within the near (≤20 m), intermediate (21–41 m), and far (>41 m) categories as described above. For each simulated nest (1,000 per distance category), we used a Monte Carlo simulation based on the predicted probability of nest success for that distance-to-edge category to determine whether or not it fledged young. If successful, we determined the number of young to fledge by drawing randomly from a normal distribution based on the observed mean (and standard deviation) of nests at that distance-to-edge category. We then assumed that each fledgling had an independent probability of survival, and used Monte Carlo simulation based on the observed probability of fledgling survival at that distance-to-edge category to determine whether or not each fledgling survived to 30 days postfledging. The sum of the number of survivors from each simulated nest equaled the number of young per pair per nesting attempt, which we compared among near ($n = 1,000$), intermediate ($n = 1,000$), and far nests ($n = 1,000$) using analysis of variance (ANOVA). Statistics are reported as means ± SE.

RESULTS

Nesting productivity.—Fourteen and 31 of the 27 and 46 towhee nests found in 2008 and 2009, respectively, were successful (Fig. 1). Given the daily nest survival rates in 2008 (0.9594) and 2009 (0.9694), and a 27-day period of nest occupancy (from egg 1 to fledging), nest success was 32.7% (95% CI: 2.5–72.0%) in 2008 and 43.2% (95% CI: 25.5–59.7%) in 2009. Combining years, 38.9% of nests fledged young (95% CI: 25.7–51.9%).

Distance of nests to the nearest park edge in 2008 (41.3 ± 5.38 m) and 2009 (38.9 ± 4.06 m) did not differ ($t = 0.357$, df = 71, $P = 0.722$), and therefore we pooled years for analyses. Nests were closer to park edges (39.8 ± 3.22 m) than were random locations (54.1 ± 3.14 m; $t = -3.140$, df = 166, $P = 0.002$), but distance to park edge did not differ between successful (37.6 ± 3.78 m) and failed nests (43.3 ± 5.83 m; $t = 0.85$, df = 71, $P = 0.397$). The top model from the logistic exposure analysis ($AIC_c = 204.074$, number of parameters [k] = 2) included only date of nest discovery. Model combinations of date and year ($\Delta AIC_c = 1.371$, $k = 3$); date and distance to edge ($\Delta AIC_c = 1.457$, $k = 3$); and date, year, and distance to edge ($\Delta AIC_c = 2.786$, $k = 4$), although within two AIC units of the best-fit model, included uninformative parameters (Arnold 2010). Distance to edge by itself also produced a poor fit ($\Delta AIC_c = 7.857$, $k = 2$). Confidence limits (95%) of model-averaged parameter estimates for distance to edge ($-0.002 ± 0.004$) and year ($-0.105 ± 0.216$) included zero, but that of date did not ($-0.022 ± 0.009$). Proximity of a nest to edge thus had no influence on the likelihood of nest success.

Linear regression analyses also showed that neither clutch size (coefficient [β] = 0.031, $t = 0.216$, df = 51, $P = 0.830$) nor brood
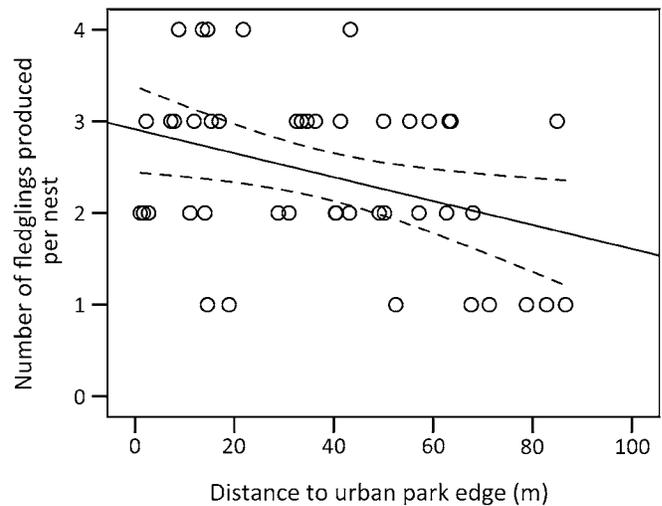

FIG. 3. The relationship between the number of fledgling Spotted Towhees produced per nest and the distance from the nest to the nearest edge of Springbrook Park, Lake Oswego, Oregon, 2008–2009. Dashed lines indicate 95% confidence intervals.

size near fledging (β = -0.096, $t = -0.647$, df = 46, $P = 0.521$) varied with distance to edge. After excluding complete nest failures, number of young to fledge from successful nests was greater for nests located near park edges than in the interior (β = -0.360; $t = -2.530$, df = 44, $P = 0.015$; Fig. 3). Nestlings fledged from nests near the park edge were also heavier (β = -0.342, $t = -2.600$, df = 52, $P = 0.012$; Fig. 4) and had longer tarsi (β = -0.285, $t = -2.127$, df = 52, $P = 0.038$) than nestlings raised in the park interior.

Fledgling survival and causes of mortality.—Thirty-six of the 52 fledglings that we radiotracked (69.2%) survived the 27-day tracking period (i.e., days 4 to 30 postfledging; daily survival rate [S] = 0.9865; Fig. 5). Of the 16 deaths, 7 occurred during days 4 to 7 out of the nest ($S = 0.9640$), 3 during the second week ($S = 0.9902$), 4 during the third week ($S = 0.9858$), and 2 during the fourth week
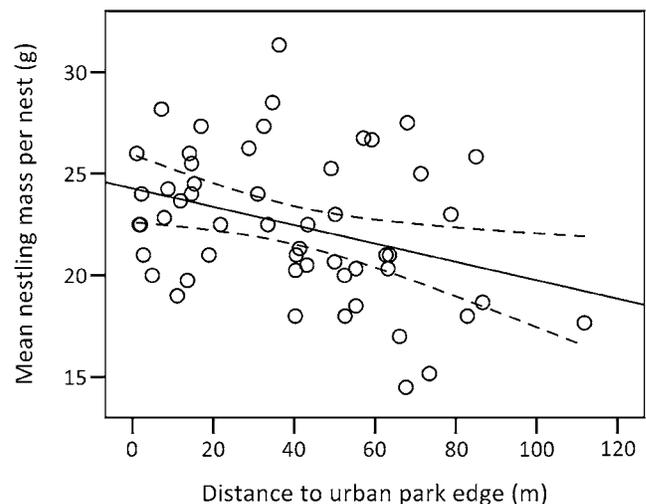

FIG. 4. The relationship between mean nestling mass just prior to fledging and distance from the nest to the nearest edge of Springbrook Park, Lake Oswego, Oregon, in 2008 and 2009. Dashed lines indicate 95% confidence intervals.

df = 2, P = 0.132). Based on the locations of dead fledglings in different backyards, and assuming that a cat would not leave the carcass of a fledgling it killed in the territory (i.e., backyard of homes) of another cat, 3 to 4 cats killed fledglings. Five of six fledglings killed by unidentified predators died between days 4 and 7, and in two of these cases, cats were the most likely predator because the fledglings' remains were found in the same homeowner's driveway, one in each year. Predators other than cats would be unlikely to deposit the carcasses in the same driveway, and, therefore, in all probability at least 6 of 16 dead fledglings (37.5%) were killed by cats.

There was no difference in the distance to edge for fledglings from 2008 (38.0 ± 4.14 m; t = 1.014, df = 52, P = 0.315) and 2009 (32.2 ± 2.89 m; t = 1.014, df = 52, P = 0.315) and, thus, data were pooled for analyses of fledgling survival. Fledglings were located closer to park edges (33.6 ± 2.42 m) than random locations (54.1 ± 3.14 m; $t_{\text{unequal variance}}$ = −5.17, df = 146.9, P < 0.001). However, the average location of fledglings that died was closer to park edges (23.5 ± 2.80 m) than that of survivors (37.8 ± 3.02 m; t = −2.89, df = 50, P = 0.006). Average distance to edge did not differ among fledglings killed by cats (27.6 ± 3.89 m), raptors (21.3 ± 4.70 m), or unidentified predators (23.0 ± 5.61 m; ANOVA, F = 0.360, df = 2 and 49, P = 0.704).

Our base model for the Cox proportional hazards regression that included year, brood size, fledging date, nestling body mass, and time spent outside the park was a poor fit to the data (Table 2). Adding distance to edge to the model as a three-category variable—near (first quartile), intermediate (middle 50%), and far (fourth quartile)—improved the fit. However, the top model included just fledging date, time spent outside the park, and distance to edge (Table 2 and Fig. 6). Young that fledged later in the year (β = −0.028 ± 0.012), spent more time outside the park (β = −0.028 ± 0.017), and were farther from the park edge (β = −1.135 ± 0.382) were most likely to survive. The parameter estimate for time spent out of park included zero, and the model of fledge date and distance to edge was the only other competitive model. Neither fledge date nor distance to edge were competitive as single variables (Table 2). Fledge date did not differ among near (mean fledge date = 163.6 [1 = 1 January], range: 128–202), intermediate (mean = 162.9, range: 132–201), and far fledglings (mean = 157.8, range: 133–178;
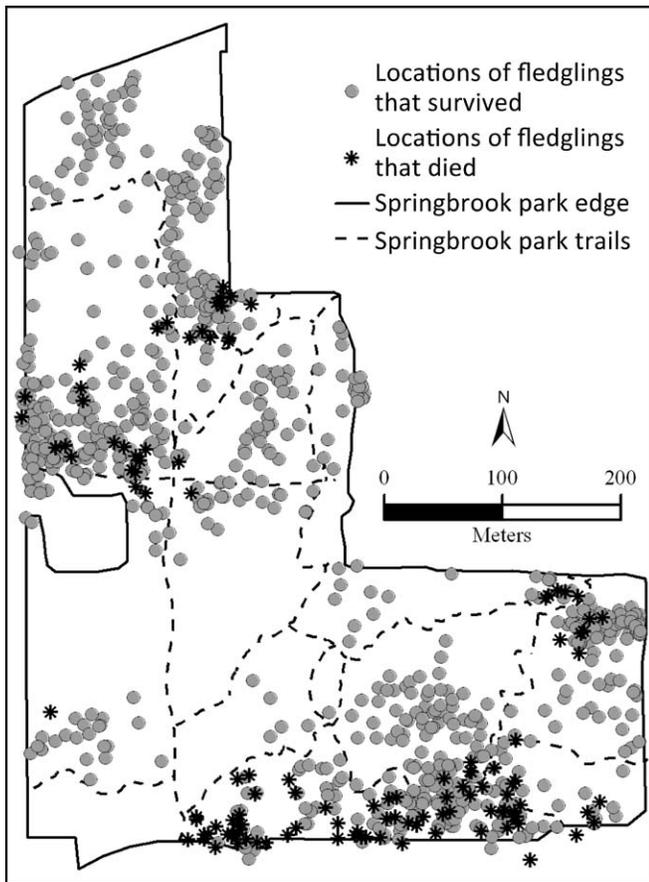

Fig. 5 Daily radiotelemetry locations of all fledgling Spotted Towhees in Springbrook Park, Lake Oswego, Oregon, that either survived or died during the postfledging period in 2008 and 2009.

(S = 0.9929; Table 1). We assumed that the probability of dying was equal for all days of the first week after fledging, and after applying the daily fledgling survival rate for days 4 to 7 to the first 3 days we estimate that 3.7 (~4) fledglings would have died had we begun tracking from the point of fledging. Thus, 64.3% (36/[52 + 4]) of young would have survived the 30-day period (S = 0.9854). Four of 36 (11.1%) transmittered fledglings that survived to 30 days were observed on the study site in the next year.

Predation was the cause of all 16 deaths (Table 1). Age at death (number of days postfledging) did not differ among fledglings killed by raptors (11.8 ± 3.17 days, n = 6), Domestic Cats (17.0 ± 4.14 days, n = 4), or unidentified predators (7.0 ± 2.30 days, n = 6; F = 2.37,

Table 1. Numbers of fledgling Spotted Towhees killed by different predators during the first 4 weeks postfledging in Springbrook Park in Lake Oswego, Oregon, 2008 and 2009. Raptors include Cooper's Hawks and Western Screech-Owls.

Predator	2008; 2009			
	Week 1	Week 2	Week 3	Week 4
Domestic Cat	0; 0	0; 1	0; 2	0; 1
Raptor	1; 1	0; 2	0; 1	0; 1
Unknown	1; 4	0; 0	1; 0	0; 0

Table 2. Model selection results from the Cox proportional hazards analysis of fledgling Spotted Towhee survival to 30 days posthatching for 2008 and 2009 at Springbrook Park, Lake Oswego, Oregon. Number of parameters (k, change in AIC_c from the top model (ΔAIC_c), and model weights (w_i) are reported. Date refers to the date young left the nest, and mass and brood size equal nestling body mass and brood size at banding, respectively, 2 to 3 days before fledging.

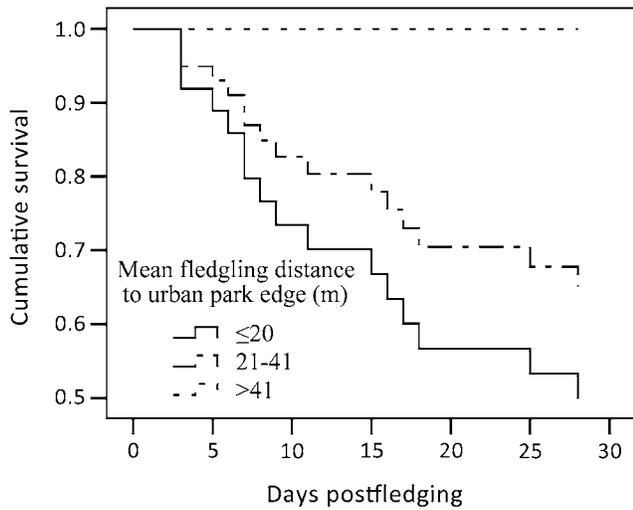| Model	k	ΔAIC_c	w_i
Year + brood size + date + mass + time outside park	6	8.484	0.008
Year + brood size + date + mass + time outside park + distance to edge	7	3.816	0.079
Date + time outside park + distance to edge	4	0.000 [a]	0.534
Date + distance to edge	3	1.220	0.290
Date	2	6.241	0.024
Distance to edge	2	4.179	0.066

[a] Minimum AIC_c = 115.129.

Fig. 6. Cox proportional hazards regression describing the survival of fledgling Spotted Towhees over the first 30 days out of the nest. Fledglings were placed into one of three categories of distance from the park edge on the basis of whether they were within the lower 25%, middle 50%, or upper 25% of all fledglings' observed distance to edge in Springbrook Park, Lake Oswego, Oregon, in 2008 and 2009.

ANOVA, $F = 0.269$, df = 2, $P = 0.765$), and, thus, the association of survival with distance to edge was unrelated to fledge date.

The latter analyses were based on the location of fledglings and not nests, which raised the question of whether fledged young remained near their nest locations. Young that fledged from nests ≤20 m from the edge tended to move away from the edge (16.4 ± 3.77 m) so that the mean distance of fledglings to edge (26.3 ± 3.93 m) put them into the area occupied by young that fledged from nests located at intermediate distances (i.e., 21–41 m) from the edge. The latter young moved little (mean distance moved from nest = 3.3 ± 3.85 m; mean distance of fledglings to edge = 29.5 ± 3.99 m). Young that fledged from far nests (i.e., >41 m from the edge) remained significantly farther ($F = 5.10$, df = 2 and 49, $P = 0.010$) from the edge (mean = 42.4 ± 3.94 m) than young from both other distance categories (Tukey's test, $P < 0.05$), but they moved an average of 18.9 m (± 3.62 m) from their nests closer to the edge.

Is edge habitat an ecological trap?—The probability that a nest fledged at least one nestling did not vary with distance to edge (see above, and Table 2), but the average number of young to fledge from successful nests was significantly lower for far than for near and intermediate nests (Table 3). As a result, the number of young fledged

per nesting attempt for far nests was only 73% and 78% that of near and intermediate nests, respectively (Table 2). However, the very large difference in the probability of postfledging survival for near (<21 m), intermediate (21–41 m), and far (>41 m) fledglings resulted in a progressive decline in number of young per pair per nesting attempt, such that pairs with nests located far from the edge had significantly more young alive at 30 days after fledging than intermediate nests, which likewise had more young survive to 30 days postfledging than nests located closest to the edge (Table 3).

Discussion

Our results showed a striking correspondence to those of Bartos Smith et al. (2012) in that (1) the likelihood of total nest failure did not vary with distance to the edge of the park, but (2) among successful nests, number of fledglings per nest increased as nests were located closer to the edge of the park and away from the interior. Bartos Smith et al. (2012) and we also found that (3) neither clutch size nor brood size varied with distance to edge, and thus the greater number of young to fledge from nests near the edge must have been due to greater partial brood loss during the nestling period for nests located in the interior. That this was attributable mainly to starvation is suggested by the fact that nestlings from interior nests were both lighter and smaller (i.e., shorter tarsi) than nestlings from edge nests, despite there being fewer young to fledge from interior nests.

The absence of an edge effect during nesting (i.e., an increased probability of nest failure near edges; Gates and Gysel 1978, Flaspohler et al. 2001, Manolis et al. 2002) suggests that edges are not inherently poor habitat. Indeed, that nests were located closer to edges than random points suggests that towhees prefer edge to interior habitat. Edges have often been suggested to be attractive to birds because of enhanced food resources (e.g., Gates and Gysel 1978), and our results on nesting productivity and nestling size are consistent with this view. Towhee nests at Springbrook were significantly more likely to fledge young than were towhees from Sacramento, California (Small 2005; 13.3%), but predators were the cause of nearly all nest failures at both locations. That the success or failure of a nest at Springbrook was unrelated to distance to edge suggests that nest-predator activity was spread evenly throughout the park. Studies conducted elsewhere indicate that the abundance of some small to medium-sized mammals varies little with distance to edge in fragmented forest landscapes (Heske 1995, Chalfoun et al. 2002), but that brood-parasitic Brown-headed Cowbirds (Howell et al. 2007), corvid nest predators (Andrén 1992, Niemuth and Boyce 1997, Marzluff et al. 2004), and

Table 3. Simulated number of Spotted Towhee young per nesting attempt that survived to 30 days postfledging in relation to distances to park edge. The simulated estimate was based on the empirically determined probability of nest success, number of young fledged per successful nest, and probability of postfledging survival in an urban park in Lake Oswego, Oregon, 2008–2009. Values are reported as means ± SE.

Distance to edge (m)	Probability of nest success	Fledglings per successful nest [a,b]	Simulated number of young to fledge per nest attempt [a]	Probability of fledgling survival [a]	Simulated number of young per nest alive 30 days postfledging [a]
≤20	0.424	2.62 ± 0.239 A	1.09 ± 0.0457 A	0.50 A	0.55 ± 0.0283 C
21–41	0.363	2.67 ± 0.236 A	1.02 ± 0.0446 A	0.64 A	0.67 ± 0.0335 B
>41	0.351	2.15 ± 0.209 B	0.80 ± 0.0376 B	1.00 B	0.80 ± 0.0376 A

[a] Estimates that share the same letters do not differ significantly ($P < 0.05$).
[b] Sample sizes are 16, 9, and 20 for number of fledglings per successful nest for nests ≤21 m, 21–41 m, and >41 m from edge, respectively.

especially snakes (Blouin-Demers and Weatherhead 2001, Chalfoun et al. 2002) show high activity along edges. Not a single Springbrook towhee nest was parasitized by cowbirds in 2008 or 2009. Snake diversity is low in northwest Oregon (Nussbaum et al. 1983, St. John 2002), and snakes were rarely seen. Snakes are often cited as a primary cause of nest loss in many studies (see above), and their near absence from our study site (and from other parks in the urban landscape) may explain why neither Bartos Smith et al. (2012) nor we detected an increased probability of nest failure along habitat edges.

Fledgling survival and causes of mortality.—Evidence from the condition and/or location of recovered transmitters indicated that predators appeared to be responsible for all fledgling towhee deaths. The failure of the Cox proportional hazards model to find an association of survival with nestling body mass just prior to fledging also suggests that starvation was not a factor. Of the nearly third of fledglings to die, Domestic Cats and Western Screech-Owls were the primary predators. Whittaker and Marzluff (2009) also reported that predators were the sole cause of death for fledgling Spotted Towhees in Seattle, Washington, but their estimate of survival for fledglings still dependent on parents (83.5% when adjusted to a 30-day observation period) was higher than in Portland (64.3%), possibly because of an apparent absence of predation by Domestic Cats on young towhees at the Seattle study sites (K. Whittaker, University of Washington, pers. comm.). Although lower than in Seattle, our estimate of fledgling survival was possibly an overestimate. Our attempt to adjust survival for the first 3 days out of the nest before young were captured assumed that mortality was the same for the entire first week out of the nest, but Ausprey and Rodewald (2011) showed that the first few days may be a period of especially high mortality. Our estimate of fledgling survival came from a short-term study at one site, and whether it or Whittaker and Marzluff's (2009) estimate represents typical values awaits further study. However, our estimate appears to be typical of small to medium-sized passerines (Table 4). Excluding three studies with especially low fledgling survival rates, our postfledging survival estimate (64.3%) fell close to the average of other passerines (60.4%; average values used for species with multiple points) and within the 95% confidence interval of this sample (53.1–67.7%). Clearly, many young die soon after leaving the nest (Table 3), highlighting the importance of studying survival during this critical period.

Many native predators kill fledgling birds, as do Domestic Cats (Haskell et al. 2001, Balogh et al. 2011). Baker et al. (2005) found that cat predation on birds was highest in the spring and summer, which probably reflects predation of fledgling and juvenile birds. The high proportion of fledgling deaths attributable to cats (38%; $n = 16$) suggests that they are important predators. However, Western Screech-Owls were also important predators of fledgling towhees, which is consistent with VanCamp and Henny's (1975) report that the proportion of birds in the diet of Eastern Screech-Owls (*M. asio*) increased from 30% in fall and winter to 68% in the nesting season. Three transmittered fledglings in 2009 were killed by the same pair of owls within a 2-day period, and a fourth was killed by another pair. Screech-owls may commonly prey upon fledgling birds, particularly when they must feed their own young, but their effects are likely to be localized because of territorial spacing.

Edges.—The probability that a fledgling would die within the first month of leaving the nest was substantially greater if it was active near park edges rather than in the park interior. Surprisingly, our data suggested that young that spent time outside of the park were more likely to survive. We note, however, that time spent out of park had a relatively weak influence on survival because its parameter estimate included zero, and we suspect that the association of time outside of park with higher survival was a product of the behavior of older fledglings that were close to independence and tended to move widely with their parents. Thus, although both nests and fledglings were more likely to be found near edges, and nests near edges produced more and heavier young, the probability of surviving the postfledging period was lower for fledglings near edges. We suggest that the reversal of fates arose because the cause of offspring death changed from a combination of food limitation and predation when young were in the nest to entirely predation when nestlings fledged.

Not surprisingly, therefore, parents of young fledged from nests ≤20 m from the edge tended to move their fledglings away from the edge and into the area occupied by young fledged from nests located intermediate distances from the edge. Young fledged from nests located at intermediate distances moved little, but young fledged from nests located the farthest from the edge (>41 m) tended to move closer to the edge, though they still remained well away from the edge. Habitats in the interior of the park tended to support less understory vegetation, and nest locations had less dense vegetation cover than fledgling locations (Shipley 2011). Hence, as found in other studies (Jones and Bock 2005, King et al. 2006, Rush and Stutchbury 2008, Ausprey and Rodewald 2011), parents with nests far from the edge may have sought locations with structurally denser vegetation for fledglings, which would have likely taken towhees from the interior closer to the edge. On the other hand, movement toward the edge may have been driven by food availability, given that the higher fledging success of successful nests and heavier and larger young from nests near the edge suggests lower food availability in the interior. Once distance from edge was accounted for, we did not find that fledgling survival was associated with vegetation density (Shipley 2011), but additional studies of food availability are needed to test whether food availability varies with distance from edge. Likewise, longer-term studies are needed to distinguish between site (i.e., edge vs. interior) and individual bird effects. Given the brevity of our study, and the general site fidelity of birds, it is possible that site and individual parental quality were conflated and that losses of fledglings were a product of a few individuals. However, we are confident that this was not the case because every parent sampled more than once that lost a fledgling in one attempt also successfully raised fledglings to independence in another period ($n = 6$).

Distance to edge did not differ for fledglings killed by cats and raptors. It is not surprising that most cat predation occurred near the edge, because ~50% of the park is bordered by residential backyards where cats live. Indeed, Crooks and Soulé (1999) found that the smallest habitat fragments had the greatest cat abundance because smaller fragments have proportionally more edge where cats enter parks. However, the activity of other predators at Springbrook also appeared to be concentrated near habitat edges. Why this is so is not clear. One possibility is that predators respond positively to prey population size and settle near edges where prey populations are most abundant. With respect to owls, it may also be that light from houses near the park edges enabled them to hunt more efficiently at night. Regardless, our findings are consistent with meta-analyses suggesting that edge effects,

Table 4. Survival rates and predators of birds during the first 30 days postfledging in different habitats. In all cases, fledglings were tracked using radiotransmitters.

Species	n	Habitat	Survival rate (%) [a]	Predators [b]	Reference
Acadian Flycatcher (*Empidonax virescens*)	31	Rural to urban gradient	63.9	Red Fox, Coyote, American Red Squirrel	Ausprey and Rodewald 2011
Great Tit (*Parus major*) and Coal Tit (*P. ater*)	342	Mature forest	38.9	Eurasian Jay, Great Spotted Woodpecker, Sparrowhawk, Marten	Naef-Daenzer et al. 2001
Gray Catbird (*Dumetella carolinensis*)	47	Urban landscape	52.9	Domestic Cat, Black Rat Snake, Red-shouldered Hawk	Balogh et al. 2011
Western Bluebird (*Sialia mexicana*)	26	Restoration-treated forest	51.2	Unknown	Wightman 2009
Wood Thrush (*Hylocichla mustelina*)	45	Mature forest	63.5	Cooper's Hawk, Timber Rattlesnake, Broad-winged Hawk	Anders et al. 1997
American Robin (*Turdus migratorius*)	15	Urban landscape	59.8	Mammals and birds	Whittaker and Marzluff 2009
White-throated Thrush (*T. assimilis*)	53	Coffee and pasture	56.2	Swallow-tailed Kite, snakes	Cohen and Lindell 2004
Ring Ouzel (*T. torquatus*)	110	Upland grassland	0.5-22.9	Raptors and mammals	Sim et al. 2013
Worm-eating Warbler (*Helmitheros vermivorum*)	60	Mature forest	67.9	Sciurids and hawks	Vitz and Rodewald 2011
Ovenbird (*Seiurus aurocapilla*)	41	Mature forest	69.6	Eastern Chipmunk, *Accipiter* spp.	King et al. 2006
Ovenbird	51	Mature forest	77.6	Eastern Chipmunk, snakes, Domestic Cat, hawks	Vitz and Rodewald 2011
Ovenbird	74	Managed forests near clearcuts	27.1	Raptors and small mammals	Streby and Andersen 2011
Eastern Meadowlark (*Sturnella magna*)	50	Grassland	83.5-88.7	Eastern Garter Snake	Kershner et al. 2004
Eastern Meadowlark	107	Grassland	83.5	Northern Watersnake, Bullsnake	Suedkamp Wells et al. 2007
Lark Bunting (*Calamospiza melanocorys*)	23	Grassland	22.2	Raptors	Yackel Adams et al. 2001
Spotted Towhee (*Pipilo maculatus*)	15	Urban landscape	83.5	Mammals and birds	Whittaker and Marzluff 2009
Dickcissel (*Spiza americana*)	60	Grassland	52.2	Unknown	Berkeley et al. 2007
Northern Cardinal (*Cardinalis cardinalis*)	45	Rural to urban gradient	70.7	Red Fox, Coyote, American Red Squirrel	Ausprey and Rodewald 2011
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	42	Forest fragments surrounded by agriculture	49.8	Eastern Chipmunk, Common Grackle, Eastern Garter Snake, raptors	Moore et al. 2010

[a] Survival rates were calculated by extrapolating the daily survival rate from the literature to 30 days postfledging to enable direct comparison among studies.
[b] Timber Rattlesnake (*Crotalus horridus*), Eastern Garter Snake (*Thamnophis sirtalis*), Black Rat Snake (*Pantherophis obsoletus*), Bullsnake (*Pituophis catenifer*), Northern Watersnake (*Nerodia sipedon*), Broad-winged Hawk (*Buteo platypterus*), Cooper's Hawk (*Accipiter cooperii*), Red-shouldered Hawk (*B. lineatus*), Sparrowhawk (*A. nisus*), Swallow-tailed Kite (*Elanoides forficatus*), Eurasian Jay (*Garrulus glandarius*), Great Spotted Woodpecker (*Dendrocopos major*), Common Grackle (*Quiscalus quiscula*), Eastern Chipmunk (*Tamias striatus*), American Red Squirrel (*Tamiascurus hudsonicus*), Coyote (*Canis latrans*), Red Fox (*Vulpes vulpes*), and Marten (*Martes* sp.).

when they exist, are most often expressed within the first 50 m of the edge (Paton 1994, Batáry and Báldi 2004), because none of the fledglings located far from the edge died (i.e., >41 m, mean = 58.7 ± 2.30 m, *n* = 12).

Residential edges as ecological traps.—All evidence suggests that edges are attractive to female towhees: towhee nests were located significantly closer to edge than were random points (present study), the earliest-breeding females nest near edges (Bartos Smith et al. 2012), and more and heavier young fledge from edge nests (Bartos Smith et al. 2012, present study). Edges receive abundant solar radiation that

may enhance primary productivity and yield more natural food (Murcia 1995, Jokimäki et al. 1998). Edges may thus be naturally attractive to towhees, but anthropogenic sources of food (i.e., bird feeders) in the backyards that border the park may augment the attractiveness of edges because adult towhees regularly used bird feeders during the nesting season (S. Bartos Smith and A. A. Shipley pers. obs.).

At the same time, it seems likely that the suitability of edge as nesting habitat has declined at Springbrook and other parks surrounded by residential neighborhoods because of the combined losses of fledglings to native predators and Domestic Cats. Unlike

the density of native predators, Domestic Cat density is not limited by territorial behavior, and at parks large enough to support raptors, predation of fledgling birds by cats will probably be additive to that of native predators. If numbers of cats are large, they may have disproportionate negative effects on towhee fledgling survival. Experimental work is thus needed to test our hypothesis that urban park edges create severe traps because of the simultaneous increase in attractiveness arising from the presence of feeders in backyards abutting the park, and an increase in the loss of fledglings to predators, including cats supported by neighborhood residents.

To date, most avian studies of habitat edges indicate that nest success or number of young fledged was lower near the edges of forests bordering rural fields, grasslands, corridors, or clearcuts (Gates and Gysel 1978, Chasko and Gates 1982, Johnson and Temple 1990, Flaspohler et al. 2001, Weldon and Haddad 2005). We found the opposite, but after accounting for losses during the postfledging period, the higher production of fledglings near edges was negated by their higher mortality in the 3- to 4-week period after fledging. Our results are thus consistent with those of other studies in suggesting that edges often function as ecological traps, but we caution that this was apparent only after including the last stage of parental care, and we urge others to incorporate the postfledging period in studies of reproductive success.

Literature Cited

Anders, A. D., D. C. Dearborn, J. Faaborg, and F. R. Thompson III. 1997. Juvenile survival in a population of Neotropical migrant birds. Conservation Biology 11:698–707.

Andrén, H. 1992. Corvid density and nest predation in relation to forest fragmentation: A landscape perspective. Ecology 73:794–804.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. Journal of Wildlife Management 74:1175–1178.

Ausprey, I. J., and A. D. Rodewald. 2011. Postfledging survivorship and habitat selection across a rural-to-urban landscape gradient. Auk 128:293–302.

Baker, P. J., A. J. Bentley, R. J. Ansell, and S. Harris. 2005. Impact of predation by domestic cats *Felis catus* in an urban area. Mammal Review 35:302–312.

Balogh, A. L., T. B. Ryder, and P. P. Marra. 2011. Population demography of Gray Catbirds in the suburban matrix: Sources, sinks, and domestic cats. Journal of Ornithology 152:717–726.

Bartos Smith, S., J. E. McKay, J. K. Richardson, and M. T. Murphy. 2012. Edges, trails and reproductive performance of Spotted Towhees in urban greenspaces. Pages 167–181 *in* Urban Bird Ecology and Conservation (C. A. Lepczyk and P. S. Warren, Eds.). Studies in Avian Biology, no. 45.

Batáry, P., and A. Báldi. 2004. Evidence of an edge effect on avian nest success. Conservation Biology 18:389–400.

Berkeley, L. I., J. P. McCarty, and L. L. Wolfenbarger. 2007. Postfledging survival and movement in Dickcissels (*Spiza americana*): Implications for habitat management and conservation. Auk 124:396–409.

Blouin-Demers, G., and P. J. Weatherhead. 2001. Habitat use by black rat snakes (*Elaphe obsoleta obsoleta*) in fragmented forests. Ecology 82:2882–2896.

Bollinger, E. K., P. B. Bollinger, and T. A. Gavin. 1990. Effects of hay-cropping on eastern populations of the Bobolink. Wildlife Society Bulletin 18:142–150.

Chalfoun, A. D., M. J. Ratnaswamy, and F. R. Thompson III. 2002. Songbird nest predators in forest–pasture edge and forest interior in a fragmented landscape. Ecological Applications 12:858–867.

Chasko, G. C., and J. E. Gates. 1982. Avian habitat suitability along a transmission-line corridor in an oak–hickory forest region. Wildlife Monographs, no. 82.

Cohen, E. B., and C. A. Lindell. 2004. Survival, habitat use, and movements of fledgling White-throated Robins (*Turdus assimilis*) in a Costa Rican agricultural landscape. Auk 121:404–414.

Cox, D. R. 1972. Regression models and life-tables. Journal of the Royal Statistical Society, Series B 34:187–220.

Crooks, K. R., and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563–566.

Fair, J. M., E. Paul, and J. Jones, Eds. 2010. Guidelines to the Use of Wild Birds in Research, 3rd ed. Ornithological Council, Washington, D.C.

Flaspohler, D. J., S. A. Temple, and R. N. Rosenfield. 2001. Species-specific edge effects on nest success and breeding bird density in a forested landscape. Ecological Applications 11:32–46.

Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field–forest ecotones. Ecology 59:871–883.

Greenlaw, J. S. 1996. Spotted Towhee (*Pipilo maculatus*). *In* The Birds of North America, no. 263 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Haskell, D. G., A. M. Knupp, and M. C. Schneider. 2001. Nest predator abundance and urbanization. Pages 243–258 *in* Avian Ecology and Conservation in an Urbanizing World (J. M. Marzluff, R. Bowman, and R. Donnelly, Eds.). Kluwer Academic, Norwell, Massachusetts.

Heske, E. J. 1995. Mammalian abundances on forest–farm edges versus forest interiors in southern Illinois: Is there an edge effect? Journal of Mammalogy 76:562–568.

Horváth, G., B. Bernáth, and G. Molinár. 1988. Dragonflies find crude oil visually more attractive than water: Multiple-choice experiments on dragonfly polarotaxis. Naturwissenschaften 85:292–297.

Howell, C. A., W. D. Dijak, and F. R. Thompson III. 2007. Landscape context and selection for forest edge by breeding Brown-headed Cowbirds. Landscape Ecology 22:273–284.

Johnson, R. G., and S. A. Temple. 1990. Nest predation and brood parasitism of tallgrass prairie birds. Journal of Wildlife Management 54:106–111.

Jokimäki, J., E. Huhta, J. Itämies, and P. Rahko. 1998. Distribution of arthropods in relation to forest patch size, edge, and stand characteristics. Canadian Journal of Forest Research 28:1068–1072.

JONES, Z. F., AND C. E. BOCK. 2005. The Boterri's Sparrow and exotic Arizona grasslands: An ecological trap or habitat regained? Condor 107:731–741.

KAISER, S. A., AND C. A. LINDELL. 2007. Effects of distance to edge and edge type on nestling growth and nest survival in the Wood Thrush. Condor 109:288–303.

KERSHNER, E. L., AND E. K. BOLLINGER. 1996. Reproductive success of grassland birds at east-central Illinois airports. American Midland Naturalist 136:358–366.

KERSHNER, E. L., J. W. WALK, AND R. E. WARNER. 2004. Postfledging movements and survival of juvenile Eastern Meadowlarks (*Sturnella magna*) in Illinois. Auk 121:1146–1154.

KING, D. I., R. M. DEGRAAF, M. L. SMITH, AND J. P. BUONACCORSI. 2006. Habitat selection and habitat-specific survival of fledgling Ovenbirds (*Seiurus aurocapilla*). Journal of Zoology (London) 269:414–421.

KOLBE, J. J., AND F. J. JANZEN. 2002. Impact of nest-site selection on nest success and nest temperature in natural and disturbed habitats. Ecology 83:269–281.

KRISKA, G., G. HORVÁTH, AND S. ANDRIKOVICS. 1998. Why do mayflies lay their eggs en masse on dry asphalt roads? Water-imitating polarized light reflected from asphalt attracts Ephemeroptera. Journal of Experimental Biology 201:2273–2286.

LICHTI, N. I. 2004. Biogeography of vascular plants and small mammals in forest fragments in Portland, Oregon: Effects of local habitat, landscape composition and patch size. M.S. thesis, Portland State University, Oregon.

MANOLIS, J. C., D. E. ANDERSEN, AND F. J. CUTHBERT. 2002. Edge effect on nesting success of ground nesting birds near regenerating clearcuts in a forest-dominated landscape. Auk 119:955–970.

MARZLUFF, J. M., J. J. MILLSPAUGH, P. HURVITZ, AND M. S. HANDCOCK. 2004. Relating resources to a probabilistic measure of space use: Forest fragments and Steller's Jays. Ecology 85:1411–1427.

METRO. 2004. Regional land information system. Metro Data Resource Center, Portland, Oregon. [Online.] Available at www.oregonmetro.gov.

MOORE, L. C., B. J. M. STUTCHBURY, D. M. BURKE, AND K. A. ELLIOTT. 2010. Effects of forest management on postfledging survival of Rose-breasted Grosbeaks (*Pheucticus ludovicianus*). Auk 127:185–194.

MURCIA, C. 1995. Edge effects in fragmented forests: Implications for conservation. Trends in Ecology & Evolution 10:58–62.

NAEF-DAENZER, B., F. WIDMER, AND M. NUBER. 2001. Differential post-fledging survival of Great and Coal tits in relation to their condition and fledging date. Journal of Animal Ecology 70:730–738.

NIEMUTH, N. D., AND M. S. BOYCE. 1997. Edge-related nest losses in Wisconsin pine barrens. Journal of Wildlife Management 61:1234–1239.

NUSSBAUM, R. A., E. D. BRODIE, JR., AND R. M. STORM. 1983. Amphibians and Reptiles of the Pacific Northwest. University Press of Idaho, Moscow.

PACKARD, J. M., R. K. FROHLICH, J. E. REYNOLDS III, AND J. R. WILCOX. 1989. Manatee response to interruption of a thermal effluent. Journal of Wildlife Management 53:692–700.

PATON, P. W. C. 1994. The effect of edge on avian nest success: How strong is the evidence? Conservation Biology 8:17–26.

PATTEN, M. A., AND D. T. BOLGER. 2003. Variation in top-down control of avian reproductive success across a fragmentation gradient. Oikos 101:479–488.

RAPPOLE, J. H., AND A. R. TIPTON. 1991. New harness design for attachment of radio transmitters to small passerines. Journal of Field Ornithology 62:335–337.

REMEŠ, V. 2003. Effects of exotic habitat on nesting success, territory density, and settlement patterns in the Blackcap (*Sylvia atricapilla*). Conservation Biology 17:1127–1133.

RIES, L., AND W. F. FAGAN. 2003. Habitat edges as a potential ecological trap for an insect predator. Ecological Entomology 28:567–572.

ROBERTSON, B. A., AND R. L. HUTTO. 2006. A framework for understanding ecological traps and an evaluation of existing evidence. Ecology 87:1075–1085.

RODEWALD, A. D., D. P. SHUSTACK, AND L. E. HITCHCOCK. 2010. Exotic shrubs as ephemeral ecological traps for nesting birds. Biological Invasions 12:33–39.

RUSH, S. A., AND B. J. M. STUTCHBURY. 2008. Survival of fledgling Hooded Warblers (*Wilsonia citrina*) in small and large forest fragments. Auk 125:183–191.

SHAFFER, T. L. 2004. A unified approach to analyzing nest success. Auk 121:526–540.

SHIPLEY, A. A. 2011. Postfledging survival and habitat use of Spotted Towhees (*Pipilo maculatus*) in an urban park. M.S. thesis, Portland State University, Portland, Oregon.

SIM, I. M. W., S. C. LUDWIG, M. C. GRANT, J. L. LOUGHREY, G. W. REBECCA, AND J. M. REID. 2013. Postfledging survival, movements, and dispersal of Ring Ouzels (*Turdus torquatus*). Auk 130:69–77.

SMALL, S. L. 2005. Mortality factors and predators of Spotted Towhee nests in the Sacramento Valley, California. Journal of Field Ornithology 76:252–258.

ST. JOHN, A. 2002. Reptiles of the Northwest. Lone Pine, Edmonton, Alberta.

STREBY, H. M., AND D. E. ANDERSEN. 2011. Seasonal productivity in a population of migratory songbirds: Why nest data are not enough. Ecosphere 2:article 78.

SUEDKAMP WELLS, K. M., M. R. RYAN, J. J. MILLSPAUGH, F. R. THOMPSON III, AND M. W. HUBBARD. 2007. Survival of post-fledging grassland birds in Missouri. Condor 109:781–794.

VANCAMP, L. F., AND C. J. HENNY. 1975. The screech owl: Its life history and population ecology in northern Ohio. North American Fauna no. 71.

VITZ, A. C., AND A. D. RODEWALD. 2011. Influence of condition and habitat use on survival of post-fledging songbirds. Condor 113:400–411.

WELDON, A. J., AND N. M. HADDAD. 2005. The effects of patch shape on Indigo Buntings: Evidence for an ecological trap. Ecology 86:1422–1431.

WHITTAKER, K. A., AND J. M. MARZLUFF. 2009. Species-specific survival and relative habitat use in an urban landscape during the postfledging period. Auk 126:1257–1276.

WIGHTMAN, C. S. 2009. Survival and movements of fledgling Western Bluebirds. Southwestern Naturalist 54:248–252.

WOODWARD, A. A., A. D. FINK, AND F. R. THOMPSON III. 2001. Edge effects and ecological traps: Effects on shrubland birds in Missouri. Journal of Wildlife Management 65:668–675.

YACKEL ADAMS, A. A., S. K. SKAGEN, AND R. D. ADAMS. 2001. Movements and survival of Lark Bunting fledglings. Condor 103:643–647.

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