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Gary E. Williams Jr.
West Virginia University

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RELATIONS OF NESTING BEHAVIOR, NEST PREDATORS, AND NESTING
SUCCESS OF WOOD THRUSHES (*HYLOCICHLA MUSTELINA*) TO
HABITAT CHARACTERISTICS AT MULTIPLE SCALES.

Gary E. Williams, Jr.

Dissertation

Submitted to the Graduate Faculty of the
College of Agriculture, Forestry, and Consumer Sciences
West Virginia University

In Partial Fulfillment of the Requirements for
the Degree of Doctor of Philosophy
in Forest Resources Science

Petra Bohall Wood, Chair
Linda Butler
Dean Coble
John Edwards
Mary Ann Fajvan
Sue Philhower Raylman

Morgantown, West Virginia

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ABSTRACT

Relations of Nesting Behavior, Nest Predators, and Nesting Success of Wood Thrushes (*Hylocichla mustelina*) to Habitat Characteristics at Multiple Scales.

Gary E. Williams, Jr.

During 1998 – 2000, I examined the relationship between the reproductive success of a declining Neotropical migrant songbird, the wood thrush (*Hylocichla mustelina*), and surrounding habitat within the highly forested region encompassing the northwestern portion of the Monongahela National Forest, West Virginia, USA. I measured nest fate, food delivery rates, and nest attendance rates of 56 videotaped nests and then related these variables to habitat measured at three concentric scales: nest site (11.3 m radius), territory (100 m), and landscape (1000 m). Predation was the most common source of failure (23 of 26 failed nests), and southern flying squirrels (*Glaucomys volans*) were the most common predator (n = 8). Probability of fledging was positively related to territory level amount of 30 – 49 yr old forest, and at the landscape level was negatively related to open, non-forested area and positively related to mean patch fractal dimension (a measure of shape complexity) of mature (> 50 yr old) forest. I found no evidence of nestling food limitation, but, as with probability of fledging, food deliveries and nest attendance rates were positively related to measures of shape complexity of mature forest within the landscape. I also used videotapes of nests to examine the efficacy of traditional methods of predicting nest predators and nest fates. Specifically, I predicted the nest predator group (avian, mammalian, snake; all 56 nests) and nest fate (fledge/fail; n = 27 nests) of nests and compared my predictions with videotaped results. Nest predator group was incorrectly assigned for 12 of 21 depredated nests for which predator identity was known. Fates of 23 of 27 nests were correctly classified. Thus, traditional methods appear to be effective at assigning nest fate, but ineffective at classifying nest predator. In another study, I compared four years (1996 – 1999) of off-road point counts of forest dwelling songbirds with counts from the North American Breeding Bird Survey (BBS) routes in the region. I generally found low agreement between BBS counts and point counts. I discuss possible reasons for this lack of agreement.

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CHAPTER 1

ARE TRADITIONAL METHODS OF DETERMINING NEST PREDATORS AND NEST FATES RELIABLE? AN EXPERIMENT WITH WOOD THRUSHES USING MINIATURE VIDEO CAMERAS

ABSTRACT

I used miniature, infrared video cameras to monitor Wood Thrush (*Hylocichla mustelina*) nests during 1998 – 2000. I documented nest predators and examined whether evidence at nests can be used to predict predator identities and nest fates. Fifty-six nests were monitored; 26 failed, with 3 abandoned and 23 depredated. I predicted predator class (avian, mammalian, snake) prior to review of video footage; predictions were incorrect 57 % of the time. Birds and mammals were underrepresented while snakes were overrepresented in my predictions. At least three factors contributed to incorrect predictions: overlap in predation patterns among predator groups, variation in predation patterns within groups, and alteration of the appearance of depredated nests by adult wood thrushes. I documented ≥ 9 nest predator species, with the southern flying squirrel (*Glaucomys volans*) taking the most nests ($n = 8$). During 2000, I predicted fate (fledge/fail) of 27 nests; 23 were classified correctly. Traditional methods of monitoring nests appear to be effective for classifying success/failure of nests, but ineffective at classifying nest predators.

INTRODUCTION

As species of Nearctic-Neotropical (Levey 1994) migrant songbirds experience population declines (Sauer et al. 1999), the identification and management of limitations upon their populations becomes critical. Predation on eggs and nestlings of songbirds is generally accepted as the primary cause of nest failure (Ricklefs 1969; Martin 1992) and may under some circumstances limit annual fecundity (Robinson 1992; Trine 1998; Schmidt and Whelan 1999), contributing to population declines (Sherry and Holmes 1992). Therefore, determining the suite of nest predators, especially common ones, of a songbird species is an essential step in formulating effective prescriptions for management of its breeding habitat. A variety of methods have been used to identify predators of songbird nests, with varying success (Major 1991; Thompson et al. 1999; Farnsworth and Simons 2000). Funds for management of breeding habitat could be allocated more efficiently if accurate and cost-efficient methods for identifying nest predators were developed.

The majority of studies of nesting success and nest predators have been conducted using periodic visual inspections of the nest and surrounding area to assess fates of nesting attempts (methodology described in Martin and Geupel 1993). These same methods are also used to classify causes of nest failure (predation, abandonment, weather, etc.) as well as specific predators or classes of predators (Best 1978; Wray et al. 1982; Christman and Dhondt 1997; Johnson 1997). Although it has often been suggested that interpretation of evidence at

nests is an ineffective method for identifying predators (Marini and Melo 1998; reviewed in Larivière 1999), evaluations of the technique using active nests are rare (but see Thompson et al. 1999 and Pietz and Granfors 2000).

Artificial nests have been used to identify predators through interpretation of bite marks on plasticine eggs, breakage of Japanese Quail (*Coturnix coturnix*) or Zebra Finch (*Taeniopygia guttata*) eggs, or disturbance to the artificial nest (Yahner and Scott 1988; Major 1991; Hannon and Cotterill 1998; King et al. 1998). Problems with artificial nest studies may limit their utility for documenting nest predator communities, however (Willebrand and Marcström 1988; Wilson et al. 1998; Heske et al. 2001; Maier and Degraaf 2001). For example, nest site selection by the researcher and the appearance of artificial nests and eggs may not truly mimic those of the target species/guild (i.e., does the predator recognize the artificial nest/eggs as a “real” nest and, if so, is it a predator that would normally depredate nests of the species/guild of interest) (discussed in Haskell 1995). Further, artificial nests lack odors and behaviors that might attract predators as well as parental presence/defense that might repel predators (Wilson et al. 1998; Thompson et al. 1999).

Still cameras employing motion sensors or some other triggering mechanism also have been used to document predators of real and artificial nests (Laurance and Grant 1994; Hernandez et al. 1997; Farnsworth and Simons 2000). Although still cameras may be effective at identifying predators of artificial nests (Hernandez et al. 1997), logistical problems can limit their

usefulness in studies of real nests. For example, Thompson et al. (1999) reported that parental triggering of motion sensors often consumed all the film in a camera before predation events occurred. Another study reported frequent failures of a mechanical triggering system (Farnsworth and Simons 2000). If still cameras randomly miss predation events and thus, predator species, it is still possible to document the species composition and relative importance of individual species of the predator community under study. If, however, missed predation events are nonrandom, then conclusions concerning predator communities and the importance of individual predator species are suspect. Still cameras may also miss important post-predation events that alter the appearance of the nest such as parental behaviors or scavenging (see below). Consequently, still cameras may be ineffective at linking predation patterns of individual species/guilds with post-predation appearance of nests.

Video cameras, especially those with infrared illuminators and time-lapse capabilities, have the potential to lessen or eliminate many of the problems described above (Thompson et al. 1999; Pietz and Granfors 2000). They also offer the possibility, in certain cases, of documenting typical predation patterns of individual predator species/guilds, which can later be used in less costly nest success studies employing traditional methods to interpret predator sign at depredated nests. Here, I present the results of a study that used videotapes of nests of Wood Thrushes (*Hylocichla mustelina*) to address two primary questions: 1.) Which species commonly depredate Wood Thrush nests in my

study area? 2.) Can evidence at nests be used to predict predator identities and nest fates? Additionally, I describe patterns of nest disturbance by specific nest predators and scavengers of Wood Thrushes, as well as post-predation behaviors of parents.

STUDY AREA AND METHODS

My study area, located in the northwestern Monongahela National Forest in Tucker County, West Virginia, USA, falls within the Allegheny Mountains and was characterized by mature forest, steep slopes, diverse plant assemblages, and 115 - 150 cm of precipitation annually (Strausbaugh and Core 1978; DeMeo 1999). Wood Thrush nests were located through behavioral cues and systematic searches (Martin and Geupel 1993) of likely nesting habitat (Buckelew and Hall 1994).

During the nesting seasons (May – August) of 1998-2000, I used miniature infrared video camera/time-lapse video recorder systems (Fuhrman Microcam2™ camera + Fieldcam LCTLV™ time-lapse VCR) to monitor the nests of Wood Thrushes until they fledged young or failed. I used four camera/recorder systems in 1998 and nine in 1999 and 2000. Each system continuously recorded for 24 h using standard T-160 videocassettes, capturing 4 images/s (one-third the speed of standard VCRs). The cameras record black-and-white images and emit infrared light at 950 nm, a wavelength not visible to vertebrate species (Aidley 1971). In complete darkness, the infrared emitters

illuminate objects up to 1 m from the camera. Cameras were attached to substrate near the nest using a clamp arm. The factory-camouflaged camera and clamp arm were modified to incorporate vegetation that matched the plant species of individual nests. Video cameras were connected to the time-lapse VCR and 12-volt battery via a 20-m cable.

Initial camera setup took 2 – 7 min., with cameras oriented so that the lens was ca 30–100 cm from the nest cup, depending upon the configuration of nest vegetation. VCRs and batteries were placed 10 – 20 m away from the nest behind a tree or other camouflage. VCRs were visited daily to exchange batteries and videocassettes, and nest contents were checked from the VCR site using a remote video monitor. Nests were not directly approached after initial camera setup except when camera views became obstructed. Approaches to recording systems were varied to minimize scent trails.

I predicted identities of nest predators based upon evidence in and around the nest during all three years (1998-2000). During 2000, I also predicted nest fates (fledge/fail) using the same methods. After I predicted nest fates and/or predator identities, I reviewed videotapes to check predictions. A nest was considered finished when daily checks revealed it was empty, when it contained egg/nestling remains, or when it became obvious that it had been abandoned. Finished nests were immediately inspected for evidence of fledging or failure. Signs of fledging included compaction of the nest rim, feces on or below the nest, or parents calling in the vicinity (Martin and Geupel 1993). I did

not actively search for fledglings in the vicinity of nests except for one instance in 1999 when a predation event on older (ca 11 d) nestlings was not recorded due to equipment failure.

Various cues were used as signs of nest failure. Cold eggs (after incubation had commenced) and no sign of parental attendance were considered signs of abandonment. Portions of nestlings or eggs in or around the nest were considered signs of predation, as was obvious nest disturbance. Disappearance of individuals or broods ≤ 11 d old was considered indicative of predation (Roth et al. 1996). Rather than predict predator species, I predicted predator class (mammalian, avian, snake). Remains of eggs/nestlings at the nest and highly disturbed nests (i.e., torn nesting materials, nest partially or fully detached from substrate) were considered indicative of mammalian predators (Best 1978; Moors 1983; Westmoreland and Best 1985; Johnson 1997). Absence of egg/nestling remains at nests was considered indicative of a bird or snake predation (Best and Stauffer 1980). Nests with no disturbance of nesting material or nest attachment were assigned as depredated by snakes or birds, depending on nest location (Best 1978; Gottfried and Thompson 1978; Westmoreland and Best 1985). Nests higher in the substrate and with sparse vegetation surrounding them were assigned as depredated by birds, while lower nests in denser vegetation were assigned to snakes. The criteria used to separate bird and snake predators were based primarily on preferences of black rat snakes (*Elaphe*

obsoleta) for habitat structure that is consistent with forest edges (Durner and Gates 1993; Blouin-Demers and Weatherhead 2001).

I also used traditional methods to monitor a sample of Wood Thrush nests. Nests were visited every 2 – 4 d until completion. Nest chronology data were used to plan additional visits on likely hatching and fledging days. Nest contents were verified from a distance whenever possible. I used nest appearance, parental behaviors, and sightings of fledglings near the nest to confirm fledging (Martin and Geupel 1993).

I compared daily failure rates of nests monitored with and without cameras to examine potential biases associated with camera-monitored nests. Additionally, I compared daily predation rates of camera nests among incubation, early nestling (0 – 6 d) and late nestling (> 6 d) stages. I calculated estimates of daily failure/predation rates using the Mayfield (1961, 1975) method, estimated variance after Hensler and Nichols (1981), and used the program CONTRAST to compare failure rates among groups (Sauer and Williams 1989).

RESULTS AND DISCUSSION

Fifty-six nests were monitored with cameras during 1998 ($n = 4$), 1999 ($n = 24$), and 2000 ($n = 28$). Nests were monitored an average of 11 d before fledging or failing (range 1 – 23 d). Twenty-six nests failed (46.4 %), including three abandoned. Abandonment occurred after one nest was incubated at least 22 d (average incubation period is 13 d); after nesting substrate shifted, causing

another nest to spill its eggs; and after a territorial conflict among three adults resulted in abandonment of a nestling. All other failures ($n = 23$) resulted from predation on nestlings ($n = 22$) or eggs ($n = 1$), with predation events occurring 0 – 16 d (mean = 7.8 ± 4.3 d) after cameras were placed at the nests. I also monitored 79 non-camera nests during 1998 ($n = 22$), 1999 ($n = 37$), and 2000 ($n = 20$). Daily failure rates of camera and non-camera nests did not differ during any nest stage (Table 1). Because nest abandonment (immediately following camera setup; $n = 29$ nests; these nests were excluded from analyses) was higher for nests early in incubation than for nests in later stages, I often deployed cameras shortly before or after hatching. This reduced camera-associated abandonment, but may have resulted in fewer documented predations of nests with eggs. Mean daily predation rate of nests did increase from incubation through the early and late-nestling stages, however ($\chi^2 = 10.93$, $P = 0.004$).

I documented ≥ 9 species of Wood Thrush nest predators (Table 2). Southern flying squirrels (*Glaucomys volans*) were the most frequent, taking 8 nests, including 7 with nestlings and 1 with eggs. The southern flying squirrel was the only predator that took nests during all 3 years of the study. Various raptor species formed the next most common group, depredating 7 nests, all with nestlings. Mice (*Peromyscus* sp.) were observed taking nestlings on 3 occasions, but are perhaps more commonly nest scavengers rather than predators (see Table 2). Black rat snakes depredated 2 nests in 2000. Other

predators included a black bear (*Ursus americanus*) and what appeared to be ants or some other arthropod species (see Table 2). Two predators were not identified due to equipment failure. Of the 23 predations, 15 were nocturnal, 7 were diurnal, and 1 could not be determined due to equipment failure. While I likely recorded many of the common Wood Thrush nest predators in my study area, I documented new predators each year, suggesting my predator list is incomplete. Presence of video cameras may have attracted some predators and repelled others (Major and Gowing 1994; Pietz and Granfors 2000), which could produce a biased list of nest predators. Although testing for this bias was beyond the scope of my study, the lack of significant differences in daily failure rates between nests monitored with cameras and nests monitored using traditional methods (Table 1) suggests that a similar suite of predators was taking both types of nests at similar rates.

Predator class (avian, mammalian, snake) was predicted from sign for the 21 depredated nests for which videotaped evidence was available (Table 2). I incorrectly assigned predator class to 12 nests. Bird and mammal predations were underestimated, while snake predations were overestimated in predictions. Although raptors took 7 nests, only 1 was correctly classified as an avian predator, with most attributed to mammals ($n = 4$). Both instances of predation by black rat snakes were correctly classified as snakes. However, snakes were incorrectly implicated in predations by a mouse, Sharp-shinned Hawk (*Accipiter striatus*), southern flying squirrel, an unidentified predator(s) that appeared to be

ants, and a case of nest abandonment. Of 11 nests depredated by mammals, only 6 were correctly assigned.

During 2000, nest fates were predicted for 27 nests using traditional methods. Predicted fates were then compared with outcomes recorded on videotapes. I correctly classified fate for 23 of 27 nests. I incorrectly classified 2 depredated nests as fledged, 1 fledged nest as depredated, and 1 abandoned nest as depredated. Nestlings were ≥ 10 d old in both depredated nests that were misclassified as fledged. Overall success/fail ratio and daily survival rates were similar for predicted fates (16 fledged/11 failed; daily survival rate = 0.9650) and actual fates (15 fledged/12 failed; daily survival rate = 0.9618) of nests.

Overlap of predation patterns of individual predator species as well as intraspecific variation in predation patterns both contributed to poor results in predicting predator groups (avian, mammalian, snake). A lack of knowledge of the suite of potential predators would have further reduced my success had I been predicting individual predator species. The predation patterns of the most common predator, the southern flying squirrel, were highly variable. At two nests, there were no obvious signs of predation, leading to a conclusion of predation by a snake at one nest and a predicted fledge at another. At the other 6 nests depredated by southern flying squirrels, there were signs of predation. Each of the 6 nests sustained damage to either the outer portion of the nest ($n = 3$), the rootlet lining of the nest cups ($n = 2$), or both ($n = 1$). At one nest

there also was damage to its points of attachment on the support branches. Five nests had some form of Wood Thrush remains in or on the nest or on the ground below. Most commonly, feathers were found inside the nest cup or on the outer portion of the nest ($n = 4$). Although southern flying squirrels killed no adult Wood Thrushes, at least some of the feathers found at depredated nests belonged to incubating/brooding females, which were attacked in 5 of 8 depredation events. At the single nest that was depredated during incubation, feathers of the adult female were found on the outer portion of the nest cup, while fragments of eggshells were found on the forest floor below the nest. Hence, feathers appear to be a good indicator of predation on eggs or nestlings, but are not necessarily indicative of adult mortality. In only one case following depredation by a southern flying squirrel did I find remains of whole or partially eaten nestlings and it was a nest that was secondarily attacked by a mouse (*Peromyscus* sp.) following the initial assault by the southern flying squirrel. It should also be noted that Wood Thrushes returned in the early morning to nests depredated by southern flying squirrels in at least 6 of 8 cases, possibly in every case; there was battery failure prior to daylight at one nest and a tape ended shortly after daylight at the other. When returning to nests, parents frequently made adjustments to nests and nest contents, possibly eating or removing fragments of nestlings or eggs. In one case, a parent removed a dead nestling from the nest.

There were no signs of disturbance to the nest or nestling remains at two of the three instances of depredation by mice (*Peromyscus* sp.). At the third nest, which was first attacked by a southern flying squirrel, there was slight disturbance to the lining of the nest cup and a partially eaten nestling below the nest. In that instance, the damage to the nest lining appeared to result from the attack of the southern flying squirrel, not the mouse. The two undisturbed nests were classified as predation by a snake and fledge, while the slightly disturbed nest was classified as depredated by a mammal. In two of three depredations involving mice, the attacks were made long after the female Wood Thrush had flushed from the nest. In one, a southern flying squirrel initially flushed the female, with the mouse taking the single remaining nestling approximately 1.7 h after the squirrel had left the nest. In the other, an unknown event caused the female to flush at 21:18 EST, with the mouse appearing nearly 6 h later. The mouse appeared to eat parts of both nestlings, but left them mostly intact and did not eat an addled egg that remained in the nest. The adult Wood Thrushes removed all nestling remains the next morning. In only one instance did a mouse attack a nest that was attended by an adult Wood Thrush, successfully capturing a nestling as the female attempted to defend the nest.

Mammals were implicated as predators for both depredations by Barred Owls. In both cases, nests were highly disturbed. Female Wood Thrushes flushed just prior to owl arrivals at each nest. In neither case did the owl immediately attack the nest. In one nest, which had three 2 – 3 d old nestlings,

the owl took each of the first two nestlings it subdued away from the nest. The owl ate the third nestling while standing in the nest cup and remained at the nest for nearly 20 min afterward, spending part of the time tearing at the nest lining. The rim of the nest had a deep depression on one side and the grooves were visible on the outside of the nest where it had been partially separated from its points of attachment to branches. At the second nest, the owl lit in the nest tree before moving to the nest and pinning one of the two 9 – 10 d old nestlings to the bottom of the nest cup with its feet. The other nestling appeared to jump from the nest just before the owl's arrival. The owl ate the nestling it caught while standing in the nest cup. Afterward, the owl picked at the nest lining with its beak, before leaving and returning to the nest several more times. It is possible that the owl was able to subdue and eat the nestling that flushed from the nest; a feather with some flesh attached was found on the ground below the nest. The nest itself was obviously damaged, with parts of both the mud lining and outer portion of the nest torn away.

The appearance of nests following predation by Accipiters ($n = 3$; at least one was *Accipiter striatus*) was variable. None of the 3 nests were attributed to avian predators; one was credited to a snake, another was credited to a mammal, while the third was judged to have fledged. In one case, the nest was obviously disturbed, with materials from one side of the outer portion of the nest dangling alongside and below the nest. There was no obvious damage to the inner or outer portions of either of the other two nests. No remains of nestlings

were found at any of the three nests. Parents returned to nests following predation in all three cases. At one nest with young (ca 4 d) nestlings, the parents carried away what appeared to be a piece of eggshell and also appeared to eat pieces of nestling remains. In all three cases, parents adjusted nesting materials following predation. There were 2 depredations by *Buteo* sp., one by a Broad-winged Hawk (*Buteo platypterus*) and the other by either a Red-shouldered Hawk (*Buteo lineatus*) or Red-tailed Hawk (*Buteo jamaicensis*). The Broad-winged Hawk did not alter the nest appearance in any way; it simply made three trips to the nest, perching beside it and removing nestlings with its beak. No nestling remains were found in or around the nest. The parents made food deliveries to the remaining nestling(s) between trips made by the hawk and also returned to inspect and brood the empty nest following predation of the third and final nestling. The parents did not appear to alter the nest appearance following predation. Based on evidence at the nest, the predator was correctly judged to be avian. In the other *Buteo* sp. predation event, the hawk attempted to attack a parent at the nest, but the parent flushed just prior to its arrival. In the process of missing the parent, the hawk grasped the nest with its talons and pulled it to the ground, presumably eating the nestlings afterward. The nest was found on the ground below the nesting substrate, but there were no nestling remains in the area. The parents returned to the site where the nest was attached to the substrate on six occasions between 1 – 2 hr post-predation. I credited this predation event to a mammalian predator.

Black rat snakes took two nests with nestlings. Both nests were attacked nocturnally. In one case the female flushed 14 min prior to the snake taking a nestling, while in the other instance, the female remained at the nest for nearly an hour after the snake appeared at the nest, pecked it as it was pushing its head under her and into the nest cup, and did not flush until the snake struck at her. There was no noticeable damage to either nest and no nestling remains were found in or around the nests. Parents returned to both nests the following morning, but did not appear to change the appearance of nests in any significant way. Snakes were frequently misidentified as causes of nest failure when nests appeared undisturbed, being implicated in four predations by other predators and one abandoned nest.

Several factors confound attempts to link evidence at depredated nests to specific nest predators or classes of predators. First, there was high intraspecific variation in the evidence that individual predator species left at nests. Second, there was overlap in depredation evidence left by different predator species. Third, my knowledge of the suite of potential predators of Wood Thrush nests was incomplete. Finally, Wood Thrush adults commonly altered depredated nests, a factor that made evidence at depredated nests hard to interpret. Based upon my predicted nest predators, it appears that parents tended to alter nests in ways that made their appearance more consistent with "clean" predators such as snakes or birds. For example, in one nest I judged the predator to be avian when the predator was a southern flying squirrel. The southern flying squirrel

left a partially-eaten nestling at the nest. Early the next morning, one of the adult Wood Thrushes carried the nestling away. Had they not done so, I would have surmised the predator to be a mammal. Additionally, the appearance of nests can rapidly change post-predation. For example, another nest that was depredated by a southern flying squirrel was correctly diagnosed as a mammal predation the morning following the event. By happenstance, another researcher re-inspected the nest the following day and concluded that the nest (which contained 10 d old nestlings at the time of depredation) had fledged.

Southern flying squirrels, while known to take Wood Thrush nests with eggs or scavenge their nests (Roth et. al 1996; Farnsworth and Simons 2000), have not been previously documented taking nestlings. In my study they were by far the most common nest predator. No other species (or genus) of predator took more than three nests, while southern flying squirrels took eight. Nearly all of the breeding range of the Wood Thrush, which includes the eastern United States and southeastern portions of Canada, falls within the geographic range of the southern flying squirrel (Linzey 1998; Roth et al. 1996). Like the Wood Thrush, the southern flying squirrel is most commonly found in deciduous forests (Sollberger 1940; Bendel and Gates 1987; Linzey 1998; Bertin 1977; Roth et al. 1996). Further, a study of microhabitat preferences of southern flying squirrels found that, within forests, they tended to concentrate activities in areas with more saplings in the understory (Bendel and Gates 1987); saplings are a preferred nesting substrate of wood thrushes (Roth et al. 1996). This begs a

number of questions. Are commonly implicated nest predators such as raccoons and corvids unimportant nest predators in areas dominated by mature, mostly contiguous forest, such as the Monongahela National Forest? Do southern flying squirrels frequently depredate the nests of Wood Thrushes and other forest-dwelling Nearctic-Neotropical migrant songbirds in other areas? Do mast-producing forests that are heavily dissected with roads and logging trails (potential glideways) provide ideal habitat for southern flying squirrels?

A number of nests were depredated shortly before nestlings were ready to fledge. In fact, 9 of 23 depredated nests contained nestlings that were at or beyond ages (10 d) considered indicative of nest success in other studies of Wood Thrushes (Fauth 2001). It is quite possible, even likely, that some studies misclassify fates of nests that are depredated late in the nestling stage, leading to overestimates of nest success rates. Although I used traditional methods to assess nest fates, it is worth noting that nests were visited (from a distance of 10 – 20 m) daily as opposed to once every 3 – 4 d as is typical of most traditional studies of nesting success. Further, I used video monitors to visually confirm nest contents. Thus, I was presumably better able to evaluate nestling ages and likely fledge dates than most traditional studies of nesting success. Even so, 3 depredated nests with older nestlings (age of oldest nestling = 13 d, 13 d, 10 d) were classified as fledged prior to review of videotapes. Such events reinforce the importance of carefully monitoring nest chronology and planning visits around likely fledge dates (Martin and Geupel 1993). My study also underscores

the necessity of locating fledged young in the vicinity of the nest site to confirm nesting success. While alarm calls by parents in the vicinity of nests have been suggested as a possible indication of fledging (Martin and Geupel 1993), I found this to be undependable and was frequently scolded by the owners of nests during nest inspections on the day following depredation.

Finally, while it is advisable to minimize disturbance to nests during checks, it is also important to verify contents (preferably from a distance) whenever possible because parents may continue typical patterns of behavior around nests following predation. Parents returned to depredated nests in 19 of 20 cases for which these data are available, generally visiting nests minutes or hours after diurnal predation events or the morning following nocturnal predation events. Multiple visits were made to most nests. Common activities included food deliveries, inspection and adjustment of nest materials, removal of remains of eggs and nestlings, and brooding of dead nestlings or the empty nest cup. A researcher using behavioral cues to determine the status of recently depredated nests is likely to judge them as active. Such a mistake would, at the least, skew daily survival estimates upward (i.e., failure to discover predation until the next visit) and could lead to an incorrect assessment of nest fate.

Traditional methods for monitoring nests appear to be effective for classifying success/failure of nests, provided that close attention is paid to nest chronology and determining nest contents. However, interpretation of sign at nests to classify nest predators was almost wholly ineffective. Videotaping nests

using cameras with infrared capabilities generally provides unambiguous data regarding nest predators and nest fates. Although this technique is quite labor intensive and expensive (one camera/vcr system currently costs approximately \$5,000, but see King et al. 2001 for a less costly alternative), there presently appear to be no equally effective, less expensive methods for documenting nest predator communities.

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Table 1. Comparisons of daily failure rates (\pm SD) during incubation stage, early nestling stage (age of brood = 0 – 6 d), late nestling stage (age of brood > 6 d), and for combined stages of Wood Thrush nests monitored with cameras (n = 56) and monitored using traditional methods (n = 79) in the Monongahela National Forest, West Virginia during 1998 - 2000.

Comparison	Daily Failure Rate	Obs. Days	χ^2	P
Camera Combined	0.043 \pm 0.008	607	0.41	0.52
Non-camera Combined	0.037 \pm 0.006	990		
Camera Incubation	0.022 \pm 0.013	134	0.80	0.37
Non-camera Incubation	0.036 \pm 0.009	441		
Camera Early Nestling	0.035 \pm 0.012	228	0.21	0.64
Non-camera Early Nestling	0.028 \pm 0.010	287		
Camera Late Nestling	0.061 \pm 0.015	245	0.59	0.44
Non-camera Late Nestling	0.046 \pm 0.013	262		

Table 2. Actual predators, predicted predator class, and timing of predation of Wood Thrush nests monitored with video cameras in the Monongahela National Forest, West Virginia during 1998 - 2000.. Class of nest predator (avian, mammalian, snake) was predicted via interpretation of evidence in and around failed nests. Video footage was reviewed afterward to verify predator identity.

Predator Species	Total	Inc.	Timing of Predation		Incorrect Predictions (n)
			Nestlings 0 – 6 d	Nestlings > 6 d	
<i>Glaucomys volans</i> (Southern Flying squirrel) ^a	8	1	1	6	avian (1), snake (1), fledge (1)
<i>Peromyscus</i> sp. (Mouse) ^{ab}	3	0	1	2	snake (1), fledge (1)
<i>Accipiter</i> sp. ^c	2	0	0	2	mammalian (1), fledge (1)
<i>Accipiter striatus</i> (Sharp-shinned Hawk)	1	0	1	0	snake (1)
<i>Strix varia</i> (Barred Owl)	2	0	1	1	mammalian (2)
<i>Elaphe obsoleta</i> (Black Rat Snake)	2	0	1	1	none
<i>Buteo platypterus</i> (Broad-winged Hawk)	1	0	0	1	none
<i>Buteo</i> sp. ^d	1	0	1	0	mammalian (1)
<i>Ursus americanus</i> (Black Bear)	1	0	0	1	none
Ants or other arthropods ^e	1	0	1	0	snake (1)

^aIncludes one predation event where both a southern flying squirrel and a mouse took nestlings. A southern flying squirrel made the initial attack on the nest and was the cause of damage to the cup, which led us to predict a mammalian predator. The mouse removed a nestling from the nest approximately 1.1 h after the southern flying squirrel had left the nest (1.7 h after the initial attack).

^bIncludes a predation event where, for unknown reasons, the brooding female flushed from the nest shortly after dusk. The mouse attacked the unattended nest containing the 4 d old brood approximately 6 hours later. Neither parent returned until the following morning, when all the nestlings were dead.

^cPredator was either *A. striatus* (Sharp-shinned Hawk) or *A. cooperii* (Cooper's Hawk).

^dPredator was either *B. jamaicensis* (Red-tailed Hawk) or *B. lineatus* (Red-shouldered Hawk).

^eAnts or other arthropods were not seen. I based my conclusion on the behaviors of the adult female, who constantly pecked at unseen objects in the nest over the course of 16+ hours, and the 6 d old brood, who writhed as though they were trying to shake something from their bodies and ultimately jumped from the nest during the night.

CHAPTER 2

RELATIONS OF WOOD THRUSH NEST SUCCESS, NEST ATTENDANCE RATES, AND FOOD DELIVERY RATES TO NEST SITE, TERRITORY, AND LANDSCAPE LEVEL MEASURES OF HABITAT

ABSTRACT

Here I describe the results of a study of constraints upon Wood Thrush (*Hylocichla mustelina*) fledging success within a primarily forested region. I used infrared miniature video cameras to document attendance, food delivery rates, and causes of nest failure. I measured habitat at three scales: nest site, territory, and landscape. I examined relationships among nesting behaviors, outcomes, and habitat. Fifty-six nests were monitored during 1998 – 2000. Attendance and food delivery rates were measured for 8,241 15-min intervals. Predation was the most common source of failure (23 of 26 failures) and southern flying squirrels (*Glaucomys volans*) were the most common predator (n = 8). Probability of fledging was positively related to the territory level amount of 30 – 49 yr old forest, and at the landscape level, negatively related to amount of open, non-forested area and positively related to mean patch fractal dimension (a measure of shape complexity) of mature (> 50 yr old) forest patches in the landscape. Models of attendance and food deliveries also were positively related to landscape level shape complexity of mature forest patches, but there was inconsistency among important nest site and territory level habitat

variables in the models. Food delivery rates increased with brood size and nestling age, suggesting food may not limit fledging success. Changes that simplify shapes of mature forest patches in the landscape may reduce the ability of Wood Thrushes to fledge young via higher predation rates and lower food availability. Investigation of landscape-related determinants of population levels of important nest predators of Wood Thrushes, such as the southern flying squirrel, deserve further study. A landscape level perspective is needed to effectively manage Wood Thrush breeding habitat in this region.

INTRODUCTION

Concern over potential declines in populations of Nearctic-Neotropical (Levey 1994) migratory songbirds has stimulated investigations of potential factors that may either cause species to decline or limit their ability to recover (Hagan and Johnston 1992; Finch and Stangel 1993; Martin and Finch 1995). The Wood Thrush (*Hylocichla mustelina*) is a species of particular concern because, while still common and widespread, data from the North American Breeding Bird Survey (BBS) suggest that it has experienced significant range-wide population declines during the period 1980 – 2000 (mean annual decline = - 1.3 %, $P < 0.01$; Sauer et al. 2001). Although only marginally significant, the BBS trend for West Virginia is similar (mean annual decline = - 0.9 %, $P = 0.07$; Sauer et al. 2001).

Various factors can limit populations of migratory birds. Limitation may occur during over-wintering, along migratory routes, during the breeding season, or through a combination of these factors (Sherry and Holmes 1995; Moore et al. 1995). Within the breeding season, juvenile survival, number of nesting attempts, and nesting success, among other demographic parameters, may all serve to constrain population levels of a species (Donovan and Thompson 2001). Breeding Wood Thrushes prefer deciduous or mixed forests with a closed canopy, moderately developed understory, and a somewhat open forest floor with moist leaf litter (Bertin 1977; Roth et al. 1996). Variability in nesting success has been tied to a number of habitat-related factors. While there appear

to be regional differences in patch sizes required to maintain source populations (Trine 1998), studies conducted in both the East (Hoover et al. 1995; Weinberg and Roth 1998) and Midwest (Donovan et al. 1995) have noted a positive relation between nesting success and forest patch size. In the Midwest, high rates of brood parasitism by brown-headed cowbirds (*Molothrus ater*) combined with high nest predation rates may limit annual productivity of Wood Thrushes, producing population sinks (Robinson 1992; Trine 1998). For example, a multiyear study of Wood Thrushes in Illinois found both high rates of parasitism (75 – 95 %) and high rates of nest predation (50 – 80 %), noting that predation rates alone would be sufficient to produce population sinks at some sites (Trine 1998). Brood parasitism is less common in the eastern portion of the breeding range of the Wood Thrush (Hoover and Brittingham 1993) and nest predation is generally the most common cause of nest failure (Hoover et al. 1995; Weinberg and Roth 1998; Farnsworth and Simons 1999; Chapter 1). In a Pennsylvania study, 95 % of all known nest failures were attributed to predation (Hoover et al. 1995). Similarly, a study of Wood Thrushes nesting in contiguous forest in Great Smoky Mountains National Park noted that only 7 of 416 nests were parasitized (5 of 7 fledged host young), while 225 (54 %) of nests were depredated (Farnsworth and Simons 1999). Weinberg and Roth (1998) concluded that effects of cowbird parasitism on Wood Thrush nesting success in small forest fragments in Delaware were negligible when compared to the effects of predation, which ranged from 41 – 65 %.

Although nest predation and brood parasitism are well-documented constraints of songbird nesting success, there also is evidence that food availability can limit reproductive output of some species. Numerous manipulative experiments and observational studies have noted positive associations between increased food supply and reproductive success (reviewed in Martin 1987). Recently, investigators have linked forest fragmentation and habitat structure to food availability and provisioning rates. In a study of Ovenbirds breeding in forest fragments, Burke and Nol (1998) found that (1) within fragments, male Ovenbirds chose territories that contained higher biomasses of invertebrates than random sites and (2) invertebrate biomass decreased with decreasing fragment size, which suggests Ovenbirds in small fragments may be food limited. However, as noted by Zanette et al. (2000), measures of overall invertebrate biomass, while suggestive, are not necessarily indicative of food availability for a particular songbird species. A study in West Virginia compared invertebrate biomass among unharvested controls and forest stands harvested with clearcutting and two-age methods 15 years previously, finding that controls had significantly higher invertebrate biomass (Duguay et al. 2000). The study also found a positive association between invertebrate biomass and growth of Wood Thrush nestlings. In a study of Eastern Yellow Robins (*Eopsaltria australis*) nesting in large and small forest fragments in Australia, small fragments had lower invertebrate biomass. Further, nestlings in small fragments experienced lower provisioning rates and had shorter bill lengths

than their counterparts in large fragments, providing evidence of direct consequences of reduced food availability (Zanette et al. 2000).

Though many studies have examined either nest predation or food limitation, few have simultaneously examined both (Rodenhouse and Holmes 1992), and I know of none that have directly documented specific causes of nest failure and measured food delivery rates. When multiple hypothesized limiting factors are measured in concert, investigations can begin to tease apart proximate and ultimate factors controlling nesting success of a species in question. I began my three year study with the working hypothesis that even in a primarily forested region such the Monongahela National Forest, West Virginia, differences in the composition and configuration of land cover surrounding nests could constrain nesting success of Wood Thrushes. I further hypothesized that these constraints would result from differences in rates of nest predation, food provisioning, and nest attendance, all of which could be interrelated. To investigate this possibility, I used miniature infrared video camera systems placed at Wood Thrush nests to monitor nesting behaviors, outcomes, and causes of failure. I then used a combination of on-the-ground measurements and interpretation of aerial photographs to develop a multi-scale approach of measuring nesting habitat, including nest site, territory-level, and landscape-level measurements.

STUDY AREA AND METHODS

My study was conducted during the breeding seasons (May – August) of 1998 – 2000 and my study area included much of the northwestern Monongahela National Forest, West Virginia, USA, including portions of the Colebank, St. George, Parsons, Montrose, and Mozark Mountain quadrangles. The area falls within the Allegheny Mountains and was characterized by steep slopes, diverse plant assemblages (Strausbaugh and Core 1978), and 115 - 150 cm of precipitation annually (DeMeo 1999). Common forest associations include red spruce (*Picea rubens*), northern hardwoods, and mixed mesophytic types (DeMeo 1999). Within my study area, Wood Thrushes are most common in mixed mesophytic forest (DeMeo 1999; Williams and Wood unpublished data), and I focused my searches in this forest type.

Between 1870 and 1920, nearly all of the forested land within my study area and in the surrounding region was clearcut (Hicks 1998; Schuler and Gillespie 2000). Most of the harvested areas were allowed to naturally regenerate and at the time of my study, canopy heights of 25 m or more were typical, with heights of trees in many areas exceeding 30 m. While some harvesting has occurred in the interim between 1920 and the time of my study, primarily via even-aged management, most of the forest in my study area was in age classes that approximate the understory re-initiation phase of even-aged (single cohort) stand development as described by Oliver and Larson (1996). Briefly, understory re-initiation occurs after dominance has been established

among canopy trees, a large proportion of competing stems have died, and live trees whose crowns form the forest canopy are more widely spaced than in earlier stages of development (Oliver and Larson 1996). This change in structure from earlier, denser growth of tree stems and crowns, allows more light to reach the forest floor. The increased available light on the forest floor stimulates the growth and development of herbaceous plants and shrubs, as well as saplings and small trees (Oliver and Larson 1996), which are a preferred nesting substrate for Wood Thrushes (Roth et al. 1996). In summary, the landscape matrix of my study area is dominated by forest at ages preferred by Wood Thrushes and both regenerating forest and non-forest habitats are minor, but increasing, components within the landscape.

Common canopy species in my study area included sugar maple (*Acer saccharum*), red oak (*Quercus rubra*), beech (*Fagus grandifolia*), tulip tree (*Liriodendron tulipifera*), basswood (*Tilia americana*), black cherry (*Prunus serotina*), eastern hemlock (*Tsuga canadensis*), and chestnut oak (*Quercus prinus*). Common woody species in the understory and midstory include beech, sugar maple, striped maple (*Acer pensylvanicum*), spice bush (*Lindera benzoin*), mountain laurel (*Kalmia latifolia*), and great rhododendron (*Rhododendron maximum*). Common herbaceous plants and woody vines include wood nettle (*Laportea canadensis*), black cohosh (*Cimicifuga racemosa*), blue cohosh (*Caulophyllum thalictroides*), greenbrier (*Smilax* sp.), and various species of

fern. The forest floor generally had a well-developed litter layer and windthrow logs and other coarse woody debris were common.

Nest Searching and Nest Monitoring. No defined survey plots were used for nest searches; Wood Thrush nests were located through behavioral cues and systematic searches (Martin and Geupel 1993) of likely nesting habitat. Once a nest was located, a flag marked with distance and compass bearing to the nest was placed 10 – 20 m away. Nest contents were ascertained either through direct observation or behavioral cues every 2 – 4 d until fledging, failure, or until a camera was placed at the nest.

Camera Setup and Monitoring. I used miniature infrared video camera/time-lapse video recorder systems (Fuhrman Microcam2™ camera + Fieldcam LCTLV™ time-lapse video recorder) to monitor the nests of Wood Thrushes until they fledged young or failed. I used four camera/recorder systems in 1998 and nine systems in 1999 and 2000. Each system was configured to continuously record for 24 h using standard T-160 videocassettes, capturing 4 images/s (one-third of the speed of standard videocassette recorders). The cameras record black-and-white images and emit infrared light at 950 nm, a wavelength not visible to vertebrate species (Aidley 1971). In complete darkness, the infrared emitters illuminate objects up to 1 m from the camera, although better results are obtained at distances of 30 – 70 cm. Video cameras are attached to an articulating clamp arm, which is used to secure the camera to substrate near the nest. The camera housing and articulating clamp

arm came equipped with a cloth camouflage sleeve, but were modified to incorporate vegetation that matched the plant species of individual nests. Video cameras connect to the time-lapse recording system and a 12-volt battery via a 20 m cable.

Initial setup of a video camera at a nest took 2 – 7 min. I oriented the cameras so that the lens was ca 30–100 cm from the nest cup, depending upon the configuration of vegetation surrounding the nest. Time-lapse recorders and batteries were placed 10–20 m away from the nest behind a tree, rock, or other form of camouflage. During daily visits to nests, batteries and videocassettes were exchanged and nest contents were checked using a portable monitor. Nest visits typically took 2 – 5 min. Nests were not directly approached after initial camera setup except in cases where camera views had become obstructed. Approaches to recording systems were varied to minimize human scent trails.

Habitat Measurements. Because I was interested in discovering relationships between habitat and events and outcomes at nests and because my study was exploratory in nature, I took a multi-scale approach to habitat sampling. The object of such a strategy is to identify scales at which important predictor variables exhibit the maximum degree of variability (Turner et al. 2001). I chose three concentric circular scales at which to measure the habitat surrounding nests: nest site (microhabitat) scale (11.3 m radius), territory scale (100 m radius; corresponds approximately to the largest reported Wood Thrush territory sizes; Roth et al. 1996), and landscape scale (1000 m radius). Habitat

at the nest site scale was measured in the field while habitat at the territory and landscape scales was measured using a GIS (see below). These scales were chosen because the processes that can affect nest outcomes may occur at differing scales. For example, the primary factors that control nest predator populations may be related to landscape-scale disturbance, while the primary factors that control food availability may be related to territory-scale factors such as the amount of mature forest with well-developed leaf litter. Further, different habitat variables might interact across scales.

Nest scale measurements. Vegetation and other habitat characteristics were sampled in an 11.3 m radius (0.04 ha) circular plot centered around each nest using methods modified from James and Shugart (1970) and BBIRD (1997) protocols. The height of a representative canopy tree within the plot was measured using a clinometer. Nest height was measured using a meter tape. All live trees and snags within the 11.3 m plot were measured and placed in the following diameter classes: >7.5 – 15 cm, >15 – 30 cm, and >30 – 37.5 cm and > 37.5 cm. Additionally, all saplings and woody shrubs (diameter < 7.5 cm and height >50 cm) were counted within a 5-m diameter circular subplot centered upon the nest. Species of all live trees, saplings, and wood shrubs was recorded. Canopy cover and ground cover were assessed using a sighting tube. Sighting tube measurements were taken at 5 evenly spaced points in each cardinal direction (n = 20) within the 11.3 m plot. Ground cover class (herbaceous vegetation, leaf litter) and canopy cover (0.5 – 3 m, 3 – 6 m, 6 – 12 m, 12 – 18

m, 18 – 24 m, > 24 m) were assessed at each of the 20 sample points. Thus, each sampling point represented 5 % (1/20) of the possible number of sighting tube “hits”. Canopy cover was summarized using two measures: total number of sighting tube hits and Simpson’s measure of evenness (Krebs 1999). Total number of sighting tube hits give a general index of overall canopy cover throughout all vertical strata. Simpson’s measure of evenness, which varies from 0 – 1, is typically used to describe species diversity, but, more generally, it describes the evenness of distribution of categorized measurements (Krebs 1999). Using individual canopy layers as categories, I used Simpson’s measure of evenness to describe vertical distribution of foliage. A canopy whose vertical distribution was perfectly even (equal hits for each layer) would have an index of 1, while highly uneven distributions approach an index of 0.

Territory and landscape measurements. Land cover maps were created by digitizing aerial photos into a GIS using Arcview 3.2. I used Digital Ortho Quarterquad (DOQQ) photographs taken by the National Aerial Photography Program (NAPP) as my primary data source. The photographs were taken from 1997-1999, which reflects land cover at the time my study was conducted. The photographs had 1 m resolution and were taken at times of the year when deciduous trees were leafless, making most roads, streams, and logging trails clearly visible. In addition to NAPP photos, I also used GIS coverages of forest stands, roads, and streams produced by the USDA Monongahela National Forest (MNF) to aid in interpretation of photographs. Year of last harvest data were

available for most stands from MNF and were used as an aid to image interpretation. Using all of these data, I digitized land cover into four forest age categories, three road categories, one water category (streams were the only common type of water body), and two non-forest categories, open and developed (Table 1). Ground-truthing was employed to verify accuracy of digitized land cover categories. Nest site coordinates were obtained using a military GPS unit that provided instantaneous error estimates. Coordinates with an error of 12 m or less were obtained for all nests. After overlaying nest sites on NAPP photographs, adjustments to coordinates were made, if necessary, to reflect the nest's position in relation to landmarks noted in the field.

All land coverages were digitized into shapefiles. Shapefiles of the various cover types were integrated into a single master shapefile. The master coverage shapefile was then converted to raster format with 1 m cell size, the same as the pixel size of the NAPP photographs. Nest sites were buffered with concentric circles with 100 m (territory) and 1000 m (landscape) radii. Thus, I set territory level measurements at 3.14 ha, an area slightly larger than the largest breeding territory size reported in the literature (2.8 ha; Roth et al. 1996), while landscape level measurements were made on an area of 314 ha, an area theoretically large enough to contain at least 100 Wood Thrush breeding territories.

Habitat coverages and landscape metrics were quantified at both buffer sizes for each nest using the Patch Analyst Grid extension (Elkie et al. 1999) for ArcView. Except where noted, metrics were computed upon the Mature (forest >

50 yr old) cover type. Total core area (TCA) was computed at the landscape scale only and was calculated assuming a 100 m edge effect. The amount of core area for a particular buffer is equal to the total area of mature forest that is > 100 m from the nearest non-mature-forest cover type. The following metrics were measured at both territory and landscape scales: Class area (total area of a particular cover type; computed for all cover types), mean patch size (MPS; mean size of mature forest patch), edge density (m edge/ha), contrast weighted edge density (McGarigal and Marks 1994; see Table 2 for weights), mean shape index (MSI; a measure of mean patch shape complexity), area weighted mean shape index (AWMSI; similar to MSI, but weighted by size of patches), mean patch fractal dimension (MPFD; another measure of mean patch shape complexity), area weighted mean patch fractal dimension (AWMPFD; similar to MPFD, but weighted by patch size), and interspersion-juxtaposition index (IJI; a measure of the distribution of patches).

Transcription of Videotapes. Videotapes provided continuous information concerning activity at nests. Overall, I obtained 602 nest days (approximately 14,500 hr) of video footage. I initially attempted to transcribe all behavior on all tapes, but found this approach too time-consuming. To streamline transcription, I first eliminated quantification of nighttime (21:00:00 – 06:00:00 EST) behaviors except in cases of nocturnal predation. I did this after noting that females continuously incubate or brood from dusk until early the following morning except in cases of nocturnal predation. To further streamline transcription, I also

chose to systematically sample daytime nest activities by transcribing 15 min of each daytime hour (06:00:00 – 21:00:00 EST). I divided hours into the following 15 min intervals: 0:00 – 15:00, 15:00 – 30:00, 30:00 – 45:00, and 45:00 – 60:00 and randomly selected one of the four intervals from each daylight hour for transcription. Thus, 225 min of footage (15 intervals x 15 min) were transcribed for each full day of observation.

Three behavioral states were quantified during transcription: nest attendance (AT), food deliveries to nestlings (DEL), and unattended eggs/nestlings (YA). Nest attendance included any time a parent was within the field of view. Occasionally, nest attendance was inferred when nestlings suddenly began begging for food, but a parent was not in view. In such situations, the parent typically appeared in view seconds after begging behaviors had commenced. My initial goal with respect to food deliveries was to quantify both taxa and quantities of prey items delivered to nestlings. This proved impossible, however, as camera angle, position of parent with respect to the camera, size of prey items, and other factors prevented consistent identification and quantification of prey during individual deliveries. Therefore, I settled upon quantifying individual deliveries of food to nestlings as an index of quantity of food provided to a nest. While there was variability in the taxa and quantities of prey items among deliveries, I assumed that, overall, counts of deliveries would provide a reliable index of the amount of food a brood received (McCarty 2002). Any trip to the nest by a parent where at least one nestling was fed at least one

food item was counted as a delivery. I made no attempt to count prey items or determine the number of nestlings fed during an individual food delivery; even if multiple items were delivered and/or multiple nestlings were fed during a provisioning visit, it was still counted as a single delivery. Provisioning of food by the male to the adult female was not counted as a delivery unless she, in turn, fed the item to nestlings. The last behavioral state, unattended eggs/nestlings, was recorded at any time that neither parent was within the field of view. The only exception to this rule occurred in cases where parental attendance could be inferred via nestling begging behaviors as described above.

Statistical Analyses. Since individual nests were considered the sampling units, all response and explanatory variables were summarized by nest. Differences among all measured variables were considered significant at $\alpha \leq 0.10$. Since attendance and food delivery rates vary with the chronology of the nest (i. e. increase/decrease with nest stage; see below), they were segregated into discrete categories to eliminate biases. Nest attendance rates were divided into three categories: incubation, early nestling (hatch – 6 d), and late nestling (> 6 d). No nests were monitored with cameras during the laying period. Prey delivery rates to nestlings were divided into the early and late nestling periods described above. Nest attendance is reported as a proportion of daylight hours, while prey delivery rates are reported as deliveries/d. Relationships among attendance and food delivery rates were examined using Pearson Product Moment correlation analyses.

I used multiple logistic regression to investigate relationships of habitat variables and year with nest outcomes (fledge/fail), brood sizes, and probability of predation by the most commonly documented predator. Multiple logistic regression models also were used to examine relationships between nest outcomes and nest attendance and prey delivery rates. All explanatory variables were tested for normality using Shapiro-Wilk tests. I eliminated some highly correlated variables by performing univariate tests on each variable using nest outcome as the class and retaining only those variables that had $P \leq 0.35$ for development of regression models. Two-tailed t-tests were used for normally distributed variables, while two-tailed Wilcoxon Rank Sum tests were used for non-normally distributed variables. I also used univariate tests to examine scale-related (territory versus landscape) differences in percent coverage of each land cover type.

Variance inflation factors (VIF) were used to identify potential collinearity problems in logistic regression models (Neter et al. 1996). Because VIF can occasionally fail to detect serious collinearity in logistic models, I used the weight matrix that is produced with the maximum likelihood algorithm to adjust linear combinations of variables before examining VIF (Allison 2001). Variance inflation factors > 10 were considered indicative of potential collinearity problems (Neter et al. 1996). Variables causing collinearity problems generally had similar variance inflation factors. Removing one of the correlated variables at a time until variance inflation factors were < 10 for all variables ameliorated collinearity

problems. Choosing variables for elimination is a subjective process, but in the case of land cover variables, which were often responsible for collinearity problems in individual models, I chose to remove the variable that was smallest in area.

Candidate models were developed from the reduced set of variables using the all-possible-subsets (APS) algorithm within the SAS logistic regression procedure (SAS Institute 1995; Budnik et al. 2002). The APS method ranks candidate models based upon a likelihood ratio χ^2 score that compares the model in question with a model where all explanatory variables have coefficients of zero (Allison 2001). A number of factors were used to assess overall model quality. These included Akaike's Information Criterion (AIC; a measure of model fit which penalizes the addition of new parameters), likelihood ratio χ^2 (explained above), percent model concordance (concordance hereafter), and Somer's D statistic (Neter et al. 1996; Hilborn and Mangel 1997; Allison 2001). Concordance is produced using the estimated probability of success generated for each nest by the SAS logistic regression algorithm. Each nest either fledged or failed. Percent concordance compares estimated probabilities of success for all possible pairings of fledged and failed nests. In a pairing of fledged and failed nests, the estimated success probability of a fledged nest can either be higher than the failed nest (concordant), lower than the failed nest (discordant), or equal to the failed nest (tied). Concordance is simply the percentage of fledge/fail pairings whose success probabilities are concordant. Somer's D statistic is closely related

to concordance, the difference being that it penalizes the model for incorrect predictions. D varies between -1 and 1 and is calculated:

$$D = (C - D)/(C + D + T)$$

where C = number concordant pairs, D = number of discordant pairs, and T = number of tied pairs (Allison 2001).

Multiple linear regressions were used to examine relationships among behavioral measures (attendance, food deliveries) and habitat variables. Regression models were developed using APS as described above except that models were ranked by adjusted- R^2 values, a method that penalizes the addition of parameters to a model. Collinearity was assessed using variance inflation factors. Multiple linear regression models were evaluated based upon significance level of the overall model, adjusted- R^2 , R^2 , and Mallows's C_p (hereafter C_p) values. I attempted to maximize adjusted- R^2 and R^2 , and select models with C_p values that were both small and \leq the number of estimated parameters in the model (Neter et al. 1996). The relative importance of individual variables within regression models were assessed using standardized beta coefficients. By standardizing beta coefficients, it is possible to use coefficient values as a measure of the relative strength of the contribution of an individual explanatory variable within a model on the response (Neter et al. 1996).

Regression diagnostics were used to examine the fit of both multiple linear and multiple logistic regression models. Residuals, residual plots,

studentized deleted residuals, and standardized deviance residuals (logistic only) were used to detect outlying observations and examine appropriateness of models. An observation was considered an outlier if it had a standardized residual > 3 (i.e., > 3 standard deviations from expected). Cook's Distance, DFFITS, and DFBETAS were examined to determine whether any outlying observation was also influential (Neter et al. 1996). Observations that produced influential outliers were examined for possible measurement or data entry errors, but none were found. No observations were deleted from any analysis; outlying values were considered to be both correctly measured and biologically meaningful.

I also examined differences in stage-specific food delivery rates among broods of differing sizes. First, I tested for differences in *overall* delivery rates to nests with 1, 2, 3, and 4 nestlings. I also compared *per nestling* delivery rates to nests with 1, 2, 3, and 4 nestlings. I used one-way analysis of variance (ANOVA) to test for overall differences and used Fisher's Least Significant Difference tests to examine pairwise differences.

RESULTS

Nest Attendance and Food Delivery Rates. I measured daytime (06:00:00 – 21:00:00 EST) nesting behaviors of 8,241 15-min intervals from 56 individual nests. During the early nestling stage (hatch – 6 d), daytime attendance rates averaged 73 % and did not differ between successful and

unsuccessful nests ($t = 0.01$, $P = 0.99$). Attendance decreased sharply during the late nestling stage (day 7 – fledge/fail), averaging 45 % and did not differ between successful and unsuccessful nests ($t = 1.31$, $P = 0.20$).

Prey deliveries to nests varied between the early (73.3/d) and late (115.9/d) nestling stages ($t = 8.49$, $P < 0.001$). Common prey items included lepidopteran and other caterpillar-like larvae, earthworms, and small insects. Small salamanders also were occasionally fed to nestlings. I did not observe any instances of nestlings being fed fruit or other plant materials. I found no evidence of differences in food delivery rates between unsuccessful and successful nests during the early ($t = 0.68$, $P = 0.50$) or late nestling stages ($t = 1.05$, $P = 0.30$).

I also examined relationships between attendance at nests and food delivery rates. All variables met normality assumptions, so Pearson product moment correlations are reported (Zar 1999). There were weak, but significant, negative within-stage correlations between nest attendance and food delivery rates during both nestling stages (Figures 1 and 2). There was a strong, significant, positive correlation between early nestling and late nestling food delivery rates (Figure 3), which suggests that food availability was consistent throughout the nestling stage. I also found significant positive relationships between nest attendance of adjacent nest stages (incubation vs. early nestling; early nestling vs. late nestling), but no significant relationship between

attendance during incubation and attendance during the late nestling stage (Figures 4, 5, and 6).

Finally, I compared food delivery rates among broods of different sizes. In a comparison of overall delivery rates to nests, there were significant differences in total daily deliveries to nests that were attributable to brood size during both the early ($F = 4.04$, $P = 0.01$) and late nestling stages ($F = 3.24$, $P = 0.03$). Mean daily delivery rates to nests tended to increase with increasing brood size during both the early and late nestling stages, but not all differences were significant (Figure 7). I also compared daily food delivery rates to broods of different sizes on a per nestling basis. Unlike overall delivery rates, per nestling delivery rates tended to decrease with increasing brood size (Figure 8) during both the early ($F = 8.00$, $P < 0.001$) and late ($F = 5.60$, $P = 0.003$) nestling stages. Pairwise comparisons revealed differences among broods with one nestling and all other brood sizes during both nestling stages (Figure 8).

Sources of Nest Failure. Fifty-six nests were monitored with cameras during 1998 ($n = 4$), 1999 ($n = 24$), and 2000 ($n = 28$). Twenty-six nests failed (46.4 %), including three that were abandoned. All other failures ($n = 23$) resulted from predation on nestlings ($n = 22$) or eggs ($n = 1$). Daily failure rates of nests monitored with cameras did not differ from nests monitored without cameras (see Chapter 1). One nest was parasitized, containing one Wood Thrush nestling and one Brown-headed Cowbird nestling; both host and cowbird young fledged.

I documented ≥ 9 species of Wood Thrush nest predators, adding new predators each year (see Chapter 1). Southern flying squirrels (*Glaucomys volans*) were the most frequent, taking 8 nests, including 7 with nestlings and 1 with eggs. The southern flying squirrel was the only predator that depredated nests during all 3 years of the study.

Habitat Measures. Fifty habitat variables were measured for each nest, including 14 nest site variables, 17 territory-level variables, and 19 landscape variables. With the exception of measures of total core area, the same variables were measured at both the territory-level and landscape-level.

Microhabitat variables measured at sites of successful and unsuccessful nests were largely similar (Table 3). The only variable that differed significantly was percentage of leaf litter ground cover (litter hereafter), which was lower for nests that fledged young ($t = 2.08$, $P = 0.04$). At the territory level, four measures of land cover and one measure of shape complexity differed among successful and unsuccessful nests. Successful nests tended to have less mature forest and logging trails and more water and forest in the 30 – 49 yr old category (Table 3; Figure 9). Successful nests also had higher Area-weighted Mean Shape Indices (higher values indicate mature forest patches with more complex shapes) than unsuccessful nests. At the landscape level, successful and unsuccessful nests differed in three land cover measures, two indices of shape, and one index of contagion. Successful nests had less open, non-forested habitat (Open hereafter), less logging trails, and more maintained roads (Figure 10).

Successful nests also had higher Mean Patch Fractal Dimensions (MPFD) and Mean Shape Indices (MSI) than unsuccessful nests, both of which are indicative of higher complexity of mature forest patch shapes. Interspersion-juxtaposition Index, a measure of the relative interspersion of mature forest patches was lower for successful nests than unsuccessful ones ($t = 1.74$, $P = 0.09$). Amount of logging trails was the only variable that was significantly different according to nest outcome at both the territory- and landscape-level scales; failed nests had larger amounts of logging trails.

Wilcoxon Rank Sum tests revealed that the proportion of every land cover class differed significantly between territory-level and landscape-level measures (Figure 11). Territories contained proportionally more mature forest and less of each of the other younger forest categories than was available in the surrounding landscape. Territories also contained proportionally more Water than was available in the landscape. Of the human-related land covers (paved roads; maintained roads; logging trails; open; developed) territory-level measures had proportionally less of all but maintained roads.

Nest Outcome and Habitat. A variety of measures were used to select the five best models relating probability of fledging to habitat (Table 4). Akaike's Information Criterion ranged from 63.37 – 64.70 and all five models had high concordance values (range: 81 – 86 %) and high values of the Somer's D statistic (range: 62 – 71). None of the models had serious collinearity problems. Variance inflation factors for all models ranged from 1.01 to 1.19, far below the

cutoff value of 10 considered indicative of potential collinearity problems (Neter et al. 1996). The number of variables in the models ranged from three to five, with variables from all three spatial scales (nest site, territory, landscape) represented in all but one model. Three variables were common to all models and each one had stable coefficients across models. At the territory level, the amount of forested habitat 30 – 49 years old was positively related to the probability of fledging in all models. At the landscape scale, the amount of Open habitat was negatively related and MPFD positively related to probability of fledging in all models. The amount of Water at the territory scale (positive relationship) was present in two models, while Litter (negative) and % herbaceous ground cover (positive) were found in two models and one model, respectively.

Nest Attendance, Food Delivery Rates, and Habitat. Models relating attendance and food delivery rates to surrounding habitat are summarized in Table 5. The models presented for each behavior/nest stage are ranked by adjusted R^2 values. All models have Mallows's C_p values that are less than the number of parameters, which is indicative of a lack of bias in the models (Neter et al. 1996). Prior to ranking, one model of nest attendance during incubation was eliminated from consideration due to collinearity problems as evidenced by variance inflation factors. All behavior-habitat models presented have variables with variance inflation factors ranging from 1.05 – 4.23, with the vast majority having values less than 2.

All models of attendance contain at least one variable from each habitat scale (nest site, territory, landscape). Four variables are found in all models of attendance at all nest stages: large saplings at the nest site, amount of logging trails and Open habitat in the landscape, and MPFD of the landscape. Additionally, herbaceous ground cover and Litter at the nest site, and MSI of the landscape are found in ≥ 12 models. Territory level amount of Mature forest (all incubation) or forest 30 – 49 yrs old (all early and late nestling) are found in all models of attendance. The explanatory capabilities of attendance models were highest during the incubation stage (R^2 range = 0.52 – 0.57), lowest during the early nestling stage (R^2 range = 0.37 – 0.39), and intermediate during the late nestling stage (R^2 range = 0.49 – 0.51). An examination of standardized regression coefficients revealed that the relative importance of particular variables changed during the nest cycle. During incubation, the territory level amount Mature forest exhibited a strong positive relationship with nest attendance and was the most influential variable in all regression models. During the early nestling stage, however, a strong positive relationship with Litter emerges, with landscape level MPFD also showing a significant positive relationship in 4 of 5 models. During the late nestling stage, Litter is once again the most influential variable in all models. In these models a strong negative association between late nestling attendance rates and both amount of maintained roads and Open habitat in the landscape also emerges, with coefficients similar to, but slightly smaller than, Litter.

The relationships between measures of habitat and food delivery rates were not as strong as those of nest attendance rates, as evidenced by lower R^2 values, which ranged from 0.26 – 0.33 (Table 5). As with attendance in the late nestling stage, food delivery rates in both the early and late nestling stages exhibited a negative relationship with amount of maintained roads in the landscape. Maintained roads were the most important predictor of food delivery rates in all late nestling stage models and 4 of 5 early nestling stage models. Other important predictor variables included nest site tree species diversity (positive relationship) and territory level amount of 30 – 49 yr old forest (negative) and MSI at both the territory (positive) and landscape (positive) scales.

Nest Outcome, Nest Attendance, and Food Delivery Rates. Relationships between nest outcome and nest attendance and food delivery rates were examined using multiple logistic regression. Nest outcome was significantly related to behavioral variables (likelihood ratio $\chi^2 = 10.5$, $P = 0.07$). Within the model, the coefficients of both nest attendance and food deliveries within the late nestling stage were significant ($P = 0.03$, $P = 0.10$) and were negatively related to probability of fledging, while the coefficient of food delivery rate during early nestling stage was approaching significance ($P = 0.11$) and was positively related to fledging. The overall model had 91.7 % concordance and a Somer's D statistic of 0.83, both of which are indicative of strong agreement between predicted probability of fledging and actual nest outcome. Variance inflation

factors were within allowable limits (range = 1.82 – 8.47) but approaching levels indicative of collinearity problems, indicating caution is warranted in interpreting the results of this model.

Southern Flying Squirrel Predation and Habitat. Since southern flying squirrels were the most common predator of Wood Thrush nests ($n = 8$), I explored the relationship between the probability of predation by this species and surrounding habitat. For these analyses, I eliminated nests that were taken by other predator species from the dataset, the reasoning being that predation by another predator removed that nest from the potential pool of nests available to southern flying squirrels. Nests depredated by southern flying squirrels had significantly more territory-level logging trails and forest < 10 yr old (Wilcoxon Rank Sum = 308.5, $P = 0.05$; Wilcoxon Rank Sum = 288.5, $P = 0.009$, respectively) and shorter canopy heights at nest sites (Wilcoxon Rank Sum = 153, $P = 0.08$).

The five best logistic regression models exhibited high Concordance (Range = 83 – 90) and Somer's D statistics (Range = 0.66 – 0.78), indicating consistent agreement between model predictions and predation/non-predation by southern flying squirrels (Table 4). Three variables, herbaceous cover at the nest site and Water and MPFD at the landscape level, were present in all models, with all three exhibiting a negative relationship with probability of southern flying squirrel predation. Territory level amount of forest < 10 yr old was present in 3 of 5 models and was positively associated with probability of southern flying

squirrel predation. Thus, it appears that southern flying squirrels are more likely to depredate nests in landscapes that are drier, have mature forest patches with simpler shapes, and have a larger proportion of recently harvested forest within the nesting territory.

DISCUSSION

Models that used habitat variables to predict probability of fledgling were quite consistent, with three variables, landscape level MPFD and Open habitat, and territory level amount of forest 30 – 49 yr old, found in all five models (Table 6). Open land cover, as I defined it, was comprised primarily of pastures and other grasslands, cropland, and artificial wildlife openings and was a small component in both territory level and landscape level measures of habitat (Figures 9 and 10). However, when comparing territory-level Wood Thrush habitat to available habitat in the surrounding landscape, territories contained significantly lower proportions of open habitat than was available in the landscape (Figure 11). Given that (1) Wood Thrushes are selecting territories with less landscape level Open land cover, (2) failed nests occur in landscapes with more Open habitat, (3) predation is the overwhelmingly most common source of nest failure, it seems reasonable to hypothesize that open land cover, either alone or in interaction with other factors, tends to produce conditions favorable to predation of nests.

The interface of Open land cover with forested habitat tends to produce distinct (hard) edges. Although edge density was not retained in any of the nest outcome – habitat models in my study, other studies have noted a positive relationship between nest predation rates and edge habitat (Gates and Gysel 1978; reviewed in Paton 1994). The fact that Wood Thrushes select territories with less open land cover than is generally available suggests that, unless they increase nesting densities within forest patches that occur in more open landscapes they are not nesting in greater densities in landscapes with higher proportions of open land cover. On the other hand, it is quite possible that at least some of the predator species (see Chapter 1), such as *Peromyscus* sp., black rat snakes, and accipiters might respond favorably to increases in open habitat and the forest-Open interface (Dijak and Thompson 2000).

Mean patch fractal dimension (MPFD) was the other landscape level variable that was significantly associated with nest outcome (Table 6). Nests were more likely to fledge in landscapes where mature forest patches had higher MPFD values. Perhaps not surprisingly, the most common source of nest failure, southern flying squirrel predation, was negatively associated with MPFD. MPFD is derived from area-perimeter ratios, and is scaled in a way that a landscape composed of very simple shapes, such as squares, would have an MPFD approaching one, whereas a landscape composed of patches with highly convoluted borders would have an MPFD approaching two (McGarigal and Marks 1994). A study of old growth and second growth forests in the Great Lakes

region noted that the fractal dimension of old growth forest patches was higher and suggested that human disturbance produced forest patches with simpler shapes (Mladenoff et al. 1993). In a simulation study, Palmer (1992) found that increasing fractal dimension generally allowed more species to coexist both at the microsite and landscape level. The MPFD of mature forest patches within landscapes of my study varied between 1.14 and 1.26, and nests with lower MPFD values were more likely to fail. In other words, successful nests tended to be found in landscapes where mature forest patches had more complex shapes, on average, than did unsuccessful nests. These findings are consistent with the results of a theoretical study of the effect of spatial pattern on avian demography (With and King 2001). Simulations from that study compared lifetime reproductive output of species in random (more fragmented) versus fractal (more clumped) landscapes, with results indicating that lifetime reproductive output was highest in fractal landscapes with higher degrees of clumping. The relationship of MPFD of mature forest patches and other habitat measures to populations of important nest predator species in the landscape merits future study (Heske et al. 2001). In my study areas, it would be especially important to investigate interrelationships among current forest harvesting levels and methods, MPFD, and southern flying squirrel populations.

Models relating nest attendance and food delivery rates to habitat were complex and exhibited a moderate degree of variability according to the behavior being measured (Table 5; Table 9). Nest attendance rate, for example, was

positively related to the amount of leaf litter and herbaceous ground cover during both nestling stages, but negatively related to these two variables during incubation. The reverse is true of number of large saplings (a primary nesting substrate) at the nest site, with a positive relation during incubation and a negative relation during both nestling stages. No territory level habitat measures were found in all models of nest attendance.

At least part of the variability in behavior-habitat models could be due to changes in parental priorities over the course of the nest cycle. During incubation, the necessity of maintaining egg temperatures for developing embryos likely overwhelms other considerations (Gill 1990). The adults have no food provisioning responsibilities other than to themselves, so various habitat factors such as those that may indicate the quality of foraging habitat (litter ground cover, for example) may not be closely linked with attendance. During the early nestling stage, parental priorities would be expected to change. The female must balance thermoregulatory responsibilities to the young with the need to deliver food to them (Lanyon 1979). The male, who generally spends little time at the nest during incubation must now make frequent food deliveries. During the latter part of the nestling stage, when nestlings are larger and require more food, parents would be expected to focus even more attention on gathering food. Therefore, one would expect progressively tighter linkages between parental attendance and nest site and territory level indicators of food availability. Additionally, one would expect consistency between factors that

allow for higher attendance and higher food delivery rates. Indicators of better foraging habitat (leaf litter coverage, high proportion of mature forest) would therefore be expected to exhibit positive relationships with attendance rates since less time would have to be spent finding food items. Within nest site and territory measures, I found no such indicators.

At the landscape level, one or both of two indices of shape complexity, Mean Shape Index or Mean Patch Fractal Dimension, were positively associated with both nest attendance rates and food delivery rates throughout the incubation-early nestling-late nestling continuum. This is an interesting result, given that there are weak, inverse relationships between food delivery rates and attendance. Still, it appears that the degree of complexity of shape of mature forest patches within the landscape has a positive effect, not only on likelihood of fledging, but also on two behavioral components that are potentially related to success.

If fledging success, nest attendance, and food delivery rates all increase relative to landscape-level shape complexity of mature forest patches, why is there a negative relationship between fledging success and late nestling stage food delivery and nest attendance? The relationship is quite likely an artifact of the way food delivery rates and nest attendance were measured. Since Wood Thrushes tend to sharply reduce attendance and food deliveries just prior to fledging, and because many unsuccessful nests failed before reaching this stage, the output of the model could be an artifact of my combining food deliveries and

attendance rates during the late nestling stage. This would explain the non-intuitive negative relationship between late nestling food delivery and attendance rates with fledging probability. In other words, it is possible that the model is simply being influenced by the lack of a sharp decrease in prey deliveries and attendance at nests that failed a few days before fledging. A simple solution to this problem would be to use a truncated late nestling stage for comparisons, stopping at day 10 or 11, post-hatch. Unfortunately, such an approach requires knowledge of precise hatch dates and these data are not available for all nests because many were found after hatching. Given this explanation, it seems plausible that the consistency among fledging success, nest attendance, and food delivery rates with respect to landscape level shape complexity of mature forest patches indicates a more general pattern of overall habitat quality that is tied to the distribution of mature forest within the landscape.

As mentioned, I found no strong evidence of a relationship between food delivery rates and fledging. Three additional lines of evidence suggest that food was not a limiting factor on the nests that I studied. First, parents demonstrated the ability to adjust food delivery rates upward as nestlings got older. If food were a limiting resource, parents would not be expected to substantially increase deliveries in response to increasing food requirements of older broods. In this study, food deliveries increased an average of 58 % between the early and late nestling stages. Second, parents of larger broods made more daily deliveries to nests than parents of smaller broods. Deliveries per nest would presumably level

off, not increase, with increasing brood size if food were limiting. However, it is possible that parents with larger broods might have occupied better foraging habitat, which would also produce such a pattern. Finally, while per nestling delivery rates (PNDR) were greater for broods with single nestlings, no differences in PNDR were found among two, three, and four nestling broods in the early nestling stage. Further, PNDR did not differ between three or four nestling broods during the late nestling stage. This plasticity in food delivery rates suggests that parents have the ability to adjust their deliveries upward or downward, depending on nest stage or brood size. Considered together, this information suggests that food availability did not influence the outcomes of these nests. This does not mean that food deliveries to nestlings are having no effects on survival; it simply means that effects, if present, are expressed after fledging. Other studies have noted evidence of food limitation in more fragmented areas (Burke and Nol 1998; Zarette et al. 2000). It would be interesting to investigate the manner in which insect availability varies with degree of alteration of landscape. It may be that available prey decreases linearly with some measure of forest fragmentation or perhaps prey are somewhat consistently available across a wide degree of forest fragmentation before reaching some critical threshold beyond which availability sharply decreases.

Based upon the results of this study, it appears that changes that simplify shapes of mature forest patches in the landscape may reduce the ability of Wood

Thrushes to fledge young via higher predation rates and lower food availability. These results underscore the need for landscape level planning and management of forest resources. If the Wood Thrush continues to decline in West Virginia and other parts of its range (Sauer et al. 2001), greater emphasis must be placed on identifying large parcels of land as management units. Given that West Virginia and other eastern states contain the highest densities of breeding Wood Thrushes (Sauer et al. 2001) and the level of private land ownership in these states is high (DiGiovanni 1990; Hicks Jr. 1998), areas of public land such as the Monongahela National Forest would seem the most feasible candidates for landscape scale management.

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Table 1. Classification scheme for land cover types that were present within the study area in the Monongahela National Forest, West Virginia from 1998 - 2000. Land covers were digitized from Digital Ortho Quarterquad photos taken between 1997 – 1999 using ArcView. Linear features were digitized as lines and buffered to standardized widths. All other features were digitized as non-overlapping polygons.

Habitat Type	Description
Mature	Forested habitat at the understory re-initiation stage of development. Stand origin of 1947 or earlier.
Forest 30 – 49 yr old	Forested habitat in the latter stem exclusion stage of development. Stand origin from 1948 – 1967.
Forest 10 – 29 yr old	Forested habitat in the early stem exclusion stage of development. Stand origin from 1968 – 1987.
Forest < 10 yr old	Forested habitat in the stand initiation stage of development. Stand origin from 1988 – 2000.
Paved Road	Paved roads or highways. Digitized width was standardized to 14 m.
Maintained Road	Unimproved or surfaced with rock. Mostly open canopy. Usually open to vehicular traffic for at least part of the year. Digitized width was standardized to 10 m.
Logging Trail	Unimproved trails used primarily for removal of timber. Usually closed canopy. Usually closed to/unsuitable for vehicular traffic. Digitized width was standardized to 6 m.
Water	Includes streams, rivers, and areas of open water. Streams were standardized to a width of 5 m. Open water and rivers were digitized as polygons.
Developed	Areas of human residence and/or commerce. Developed areas were generally individual homesteads or low to moderate density residential areas.
Open, Non-forested	Any permanently or semi-permanently non-forested area that was not classified as developed. Open areas were usually pasture, cropland, human-constructed wildlife openings, or open areas used for maneuvering forest-harvesting equipment.

Table 2. Weights assigned to habitat interfaces for the calculation of contrast weighted edge density (CWED). For the purposes of this study, only the interface between Mature and other coverage types was considered an edge. All other interfaces (e.g., Paved Road – Open) were assigned weights of zero.

Habitat	Habitat	Edge Weight
Mature	Forest 30 – 49 yr old	0.00
Mature	Forest 10 – 29 yr old	0.50
Mature	Forest < 10 yr old	1.00
Mature	Paved Road	1.00
Mature	Maintained Road	0.80
Mature	Logging Trail	0.50
Mature	Water	0.25
Mature	Developed	1.00
Mature	Open	1.00

Table 3. Means and standard deviations (STD) of habitat variables measured at three scales (nest site, territory, and landscape) for successful and unsuccessful Wood Thrush nests monitored on the Monongahela National Forest, West Virginia during 1998 – 2000.

Variable	<u>Overall</u>		<u>Fail</u>		<u>Fledge</u>		t ^a	Wilc. ^{ab}	P ^c
	Mean	STD	Mean	STD	Mean	STD			
<i>Nest Site</i>									
Canopy Height (m)	28.24 ± 5.74		27.49 ± 5.83		28.89 ± 5.67			688.5	0.40
Nest Height (m)	2.48 ± 0.84		2.47 ± 0.92		2.49 ± 0.77			725.0	0.80
Herbaceous Ground Cover (%)	22.41 ± 15.26		19.62 ± 15.87		24.83 ± 14.53			663.0	0.21
Leaf Litter Ground Cover (%)	61.34 ± 18.60		66.73 ± 20.39		56.67 ± 15.77		2.08		0.04
Foliage (# hits/120)	47.34 ± 10.74		47.35 ± 11.49		47.33 ± 10.24			745.0	0.95
Simpsons Index of Foliage Evenness	0.82 ± 0.10		0.82 ± 0.11		0.82 ± 0.10			747.0	0.93
# Saplings < 2.5 cm diameter	103.91 ± 304.42		139.42 ± 437.33		73.13 ± 93.62			665.5	0.22
# Saplings > 2.5 cm diameter	12.20 ± 10.81		10.54 ± 9.32		13.63 ± 11.92			667.5	0.23
# Saplings of all sizes	75.90 ± 85.00		63.42 ± 64.79		86.77 ± 99.04			660.5	0.19
Sapling Species Richness	7.84 ± 3.65		7.31 ± 3.03		8.30 ± 4.11		1.01		0.31
# Trees 7.5 - 15 cm dbh	8.18 ± 5.91		7.81 ± 6.50		8.50 ± 5.44			695.5	0.46
# Trees 15 - 30 cm dbh	4.41 ± 2.42		4.38 ± 2.02		4.43 ± 2.75			752.5	0.86
# Trees 30 - 37.5 cm dbh	1.63 ± 1.79		1.73 ± 1.99		1.53 ± 1.63			756.0	0.81
# Trees > 37.5 cm dbh	2.30 ± 1.87		2.00 ± 1.60		2.57 ± 2.06			679.0	0.31
Tree Species Richness	6.07 ± 1.91		5.69 ± 1.38		6.40 ± 2.24			678.5	0.31
<i>Territory</i>									
Mature (Forest > 50 yrs) (ha)	2.49 ± 0.55		2.64 ± 0.46		2.36 ± 0.60			852.5	0.07
Forest 30 - 49 yrs (ha)	0.09 ± 0.30		0.01 ± 0.03		0.17 ± 0.39			636.5	0.01
Forest 10 - 29 yrs (ha)	0.21 ± 0.42		0.17 ± 0.36		0.25 ± 0.46			732.0	0.87
Forest < 10 yrs	0.05 ± 0.17		0.05 ± 0.19		0.04 ± 0.15			773.0	0.96
Logging Trails (ha)	0.07 ± 0.09		0.09 ± 0.07		0.06 ± 0.11			851.0	0.06
Unpaved Maintained Roads (ha)	0.15 ± 0.12		0.14 ± 0.14		0.16 ± 0.10			698.5	0.49
Paved Roads (ha)	0.00 ± 0.00		0.00 ± 0.00		0.00 ± 0.00		na	na	na
Streams, Rivers, Ponds (ha)	0.04 ± 0.05		0.02 ± 0.03		0.05 ± 0.05			622.5	0.04

Table 3 continued.

Variable	<u>Overall</u>		<u>Fail</u>		<u>Fledge</u>		t	Wilc.	P
	Mean	STD	Mean	STD	Mean	STD			
<i>Territory</i>									
Open Non-forested (ha)	0.02	± 0.06	0.02	± 0.04	0.03	± 0.07		734.0	0.87
Human Habitation or Commerce (ha)	0.00	± 0.00	0.00	± 0.00	0.00	± 0.00	na	na	na
Mean Patch Size (ha)	0.94	± 0.66	1.00	± 0.72	0.88	± 0.61		774.0	0.60
Mean Patch Fractal Dimension	1.13	± 0.06	1.13	± 0.05	1.14	± 0.07		732.5	0.90
Area Weighted Mean Patch Fractal Dimension	1.08	± 0.03	1.08	± 0.03	1.09	± 0.04	1.50		0.14
Mean Shape Index	1.59	± 0.32	1.52	± 0.37	1.65	± 0.25		677.5	0.31
Area Weighted Mean Shape Index	1.49	± 0.22	1.44	± 0.18	1.54	± 0.24	1.72		0.09
Contrast Weighted Edge Density (m/ha)	164.53	± 86.74	166.65	± 85.23	162.69	± 89.44	0.17		0.87
Interspersion-Juxtaposition Index	62.25	± 36.31	54.28	± 39.05	69.16	± 32.85		662.0	0.20
<i>Landscape</i>									
Mature (Forest > 50 yrs) (ha)	231.84	± 21.22	234.46	± 13.10	229.57	± 26.36	0.90		0.38
Forest 30 - 49 yrs (ha)	14.70	± 14.95	13.12	± 13.24	16.07	± 16.39		678.5	0.31
Forest 10 - 29 yrs (ha)	25.50	± 20.01	23.07	± 18.08	27.60	± 21.63		695.0	0.46
Forest < 10 yrs	13.59	± 9.30	15.29	± 9.48	12.12	± 9.05		823.0	0.19
Logging Trails (ha)	8.12	± 2.74	8.79	± 2.81	7.53	± 2.59	1.74		0.09
Unpaved Maintained Roads (ha)	5.88	± 2.09	5.37	± 1.84	6.33	± 2.21	1.75		0.09
Paved Roads (ha)	0.98	± 1.29	1.15	± 1.40	0.83	± 1.19		776.0	0.54
Streams, Rivers, Ponds (ha)	2.29	± 1.73	2.22	± 2.22	2.34	± 1.18		663.5	0.21
Open Non-forested (ha)	6.79	± 6.54	8.50	± 7.21	5.31	± 5.62		845.5	0.09
Human Habitation or Commerce (ha)	0.65	± 1.47	0.59	± 0.98	0.70	± 1.81		781.5	0.44
Mean Patch Size (ha)	6.39	± 2.40	6.18	± 2.20	6.56	± 2.59		735.5	0.93
Mean Patch Fractal Dimension	1.19	± 0.03	1.18	± 0.02	1.20	± 0.03		608.5	0.03
Area Weighted Mean Patch Fractal Dimension	1.16	± 0.02	1.15	± 0.02	1.16	± 0.02		711.0	0.63
Mean Shape Index	2.04	± 0.14	1.99	± 0.09	2.08	± 0.16		610.0	0.04
Area Weighted Mean Shape Index	2.89	± 0.42	2.85	± 0.43	2.92	± 0.42		704.0	0.55
Contrast Weighted Edge Density (m/ha)	87.74	± 20.34	87.42	± 18.99	88.03	± 21.75		731.0	0.88
Interspersion-Juxtaposition Index	82.71	± 5.53	82.76	± 6.12	82.66	± 5.07	1.74		0.09

Table 3 continued.

Variable	<u>Overall</u>		<u>Fail</u>		<u>Fledge</u>		t	Wilc.	P
	Mean	STD	Mean	STD	Mean	STD			
<i>Landscape</i>									
Total Core Area 1 ^d	83.76	± 29.02	86.90	± 27.00	81.03	± 30.86		789.0	0.44
Total Core Area 2 ^d	58.10	± 30.05	59.93	± 25.53	56.52	± 33.83	0.42		0.68

^aStudent's t values are reported for normal data; Wilcoxon Rank scores are reported for data that are not normal.

^bWilc. = Wilcoxon Rank score.

^cP-values less than 0.35 (bold face) indicate variables retained for development of regression models.

^dTotal Core Area was computed two ways. Logging trails were considered edges in the computation of Total Core Area 1, while they were not considered edges in the computation of Total Core Area 2.

Table 4. Summary of characteristics of the five best multiple logistic regression models relating the probability of fledging and probability of southern flying squirrel depredation to habitat variables for Wood Thrush nests monitored in the Monongahela National Forest, West Virginia during 1998 - 2000. Models are ranked by Akaike's Information Criterion, a measure of model fit that penalizes the addition of extra parameters into the model. Asterisks indicate coefficients that are significant at $\alpha \leq 0.10$.

	AIC	C % ^a	SOMER'S D	Overall χ^2	Var ^b	Nest Site		Territory		Landscape				
						Leaf Litter	Herbaceous	Forest < 10 yr	Forest 30 – 49 yr	Logging Trail	Water	Forest < 10 yr	Forest 30 – 49 yr	Water
Fledge														
	63.37	85	69	<0.0001	4	0.18			8.26*			-0.14*	40.79*	
	63.73	84	69	<0.0001	4	-0.15			8.02*			-0.13*	33.91*	
	64.18	81	62	<0.0001	3				7.17*			-0.14*	34.79*	
	64.65	86	71	0.0002	5	-0.14			7.70*	8.03		-0.12*	32.11*	
	64.70	82	65	0.0001	4				6.82*	9.29		-0.13*	32.21*	
S. Flying Squirrel Predation														
	36.95	89	78	0.01	5	-0.38*		2.80				-0.11	-1.04	-35.21
	36.99	86	73	0.02	4	-0.34*		2.49					-1.04	-36.81*
	36.99	90	80	0.01	5	-0.30		3.88*			0.12	-0.64		-58.46*
	37.08	83	66	0.03	4	-0.36*			3.42			-0.97		-32.39
	37.08	88	75	0.02	4	-0.36*						-0.09	-0.94	-33.53

^aPercent Concordance.

^bnumber of habitat variables in the model.

^cMean Patch Fractal Dimension of Mature (> 50 yr old) forest.

Table 5. Summary of multiple linear regression models relating attendance and food delivery rates to habitat variables for Wood Thrush nests monitored in the Monongahela National Forest, West Virginia during 1998 - 2000. Standardized coefficients are presented. Models are ranked by adjusted-R² values. Asterisks denote coefficients that are significant at $\alpha \leq 0.10$.

Adj. R ²	R ²	C _p	P	Var	Nest Site				Territory Scale					Landscape Scale							
					Herbaceous	Leaf Litter	# Saplings > 2.5 cm dbh	Tree Species Richness	# Trees > 37.5 cm dbh	Mature	Forest 30 – 49 yr	Logging Trail	Water	MSI ^d	AWMSI ^e	Forest 30 – 49 yr	Forest < 10 yr	Maintained	Logging Trail	Water	Open Non-forested
Att. ^a Inc. ^b																					
0.37	0.55	0.39	0.02	8	-0.46*	-0.40	0.43*	0.24	0.97*							0.37*	-0.40*	0.34*			
0.36	0.55	0.57	0.02	8	-0.18		0.36*		0.85*	0.35					0.41*	-0.44*	0.22	0.47*			
0.36	0.57	2.07	0.03	9	-0.47*	-0.40	0.41*	0.27	0.99*						0.39*	0.39	0.13	0.29			
0.36	0.52	-0.69	0.02	7	-0.18		0.38*		0.81*	0.25					0.37*	-0.46*		0.51			
0.35	0.52	-0.66	0.02	7			0.35*		0.88*	0.36					0.45*	-0.45*	0.22	0.50*			
Att. Early Nstl. ^c																					
0.18	0.39	7.74	0.07	12	0.32	0.62*	-0.25*	-0.24		0.45*	0.37*	-0.15			0.38*	-0.21	-0.27	0.28*	0.42*		
0.18	0.37	6.63	0.06	11	0.28	0.62*	-0.24*	-0.26		0.43*	0.40*				0.37*	-0.23	-0.26	0.25	0.43*		
0.17	0.38	8.02	0.08	12	0.26	0.52*	-0.26*	-0.23		0.40*	0.36*	-0.16			-0.25	0.41*	-0.38*	0.26	0.45*		
0.17	0.38	8.04	0.08	12	0.30	0.60*	-0.26*		0.35*		-0.23	0.22			-0.32*	0.40	-0.21	-0.39	0.19	0.38	
0.17	0.38	8.04	0.08	12	0.28	0.55*	-0.22		0.38*	0.19	-0.16				-0.21	0.41*	-0.21	-0.33*	0.28*	0.38*	
Att. Late Nstl.																					
0.27	0.49	9.92	0.03	13	0.48*	0.78*	-0.24		0.44*		-0.28*	0.36*			0.50*	-0.66*	0.50*	0.40*	-0.75*	0.27	0.28
0.27	0.50	11.32	0.04	14	0.43*	0.78*	-0.22		0.41*		-0.25	-0.15	0.41*		0.45*	-0.63*	0.47*	0.39*	-0.72*	0.25	0.29
0.26	0.50	11.50	0.04	14	0.46*	0.74*	-0.22	0.12	0.43*		-0.31*	0.37*			0.51*	-0.70*	0.51*	0.39*	-0.73*	-0.29	0.28
0.26	0.49	11.65	0.04	14	0.47*	0.78*	-0.26	-0.09	0.46*		-0.29*	0.39*			0.47*	-0.62*	0.49*	0.39*	-0.73*	0.25	0.29*
0.26	0.51	12.79	0.05	15	0.40*	0.73*	-0.20	0.13	0.40*		-0.28	-0.16	0.42*		0.46*	-0.68*	0.48*	0.38*	-0.70*	0.27	0.29*

Table 5 continued.

						Nest Site			Territory Scale					Landscape Scale												
						Herbaceous	Leaf Litter	# Saplings > 2.5 cm dbh	Tree Species Richness	# Trees > 37.5 cm dbh	Mature	Forest 30 – 49 yr	Logging Trail	Water	MSI ^d	AWMSI ^e	Forest 30 – 49 yr	Forest < 10 yr	Maintained	Logging Trail	Water	Open Non-forested	MSI ^d	MPFD ^f		
Adj. R ²	R ²	C _p	P	Var																						
Food Early Nstl.																										
0.16	0.30	2.41	0.05	8	-0.18			0.36*			-0.31*		0.24				0.19	-0.37*	-0.24				0.29*			
0.15	0.31	4.01	0.07	9	-0.28	-0.13		0.36*			-0.30*		0.24				0.18	-0.37*	-0.24				0.27			
0.15	0.31	4.05	0.08	9	-0.19			0.36*			-0.33*		0.24				0.20	-0.37*	-0.29*				0.31*	-0.10		
0.15	0.33	5.24	0.09	10				0.33*		-0.22	-0.30*		0.21	0.23	-0.32		0.26	-0.36*	-0.16				0.37*			
0.15	0.27	1.81	0.06	7	-0.18			0.31*			-0.28*		0.21					-0.36*	-0.22				0.24			
Food Late Nstl.																										
0.17	0.30	-1.45	0.05	7	0.16			-0.18					-0.29*	0.43*			-0.26		-0.54*				0.32*			
0.17	0.28	-2.68	0.04	6				-0.16					-0.24	0.37*			-0.27		-0.55*				0.32*			
0.16	0.26	-3.78	0.04	5									-0.21	0.35*			-0.25		-0.56*				0.30			
0.16	0.29	-1.16	0.06	7		-0.11	-0.17						-0.25	0.40*			-0.26		-0.54*				0.31*			
0.16	0.27	-2.37	0.05	6									0.19	0.39*	-0.17		-0.27		-0.51*				0.34			

^aAttendance.

^bIncubation.

^cNestling.

^dMean Shape Index of Mature patches.

^eArea-weighted Mean Shape Index of Mature patches.

^fMean Patch Fractal Dimension of Mature patches.

Table 6. Probability of fledging, probability of southern flying squirrel predation, nest attendance rates, and food delivery rates in relation to habitat variables for Wood Thrush nests monitored in the Monongahela National Forest, West Virginia during 1998 - 2000. All habitat variables listed appeared in at least 2 of 5 best models for a particular response. Asterisks denote variables that were significant in at least two models. Positive relationships are denoted by plus sign, while negative relationships are denoted by minus sign.

Model	Nest Site					Territory Level					Landscape Level									
	Herbaceous	Leaf Litter	# Saplings > 2.5 cm dbh	Tree Species Richness	# Trees > 37.5 cm dbh	Mature	Forest 30 – 49 yr	Forest < 10 yr	Logging Trail	Water	MSI ^b	AWMIS ^c	Forest 30 – 49 yr	Forests < 10 yr	Maintained	Logging Trail	Water	Open Non-forested	MSI ^b	MPPFD ^d
Attendance																				
Incubation	-*	-	+	+		+		+							+	+		-*	+	+
Early Nestling	+	+	-*	+			+	+							+	+	-	-	+	+
Late Nestling	+	+	-		+		+		*		+		+	+	*	+	+	-*	+	+
Food Delivery Rate																				
Early Nestling	-			+			-*		+				+	+	-*	-			+	
Late Nestling			-						-	+			-	-	-*				+	
Fledge		-					-		+									-*		+
S Fl. Squirrel Pred.^a	-*							+					-				-			-*

^aProbability of predation by southern flying squirrel.
^bMean Shape Index of Mature patches.
^cArea-weighted Mean Shape Index of Mature patches.
^dMean Patch Fractal Dimension of Mature patches.

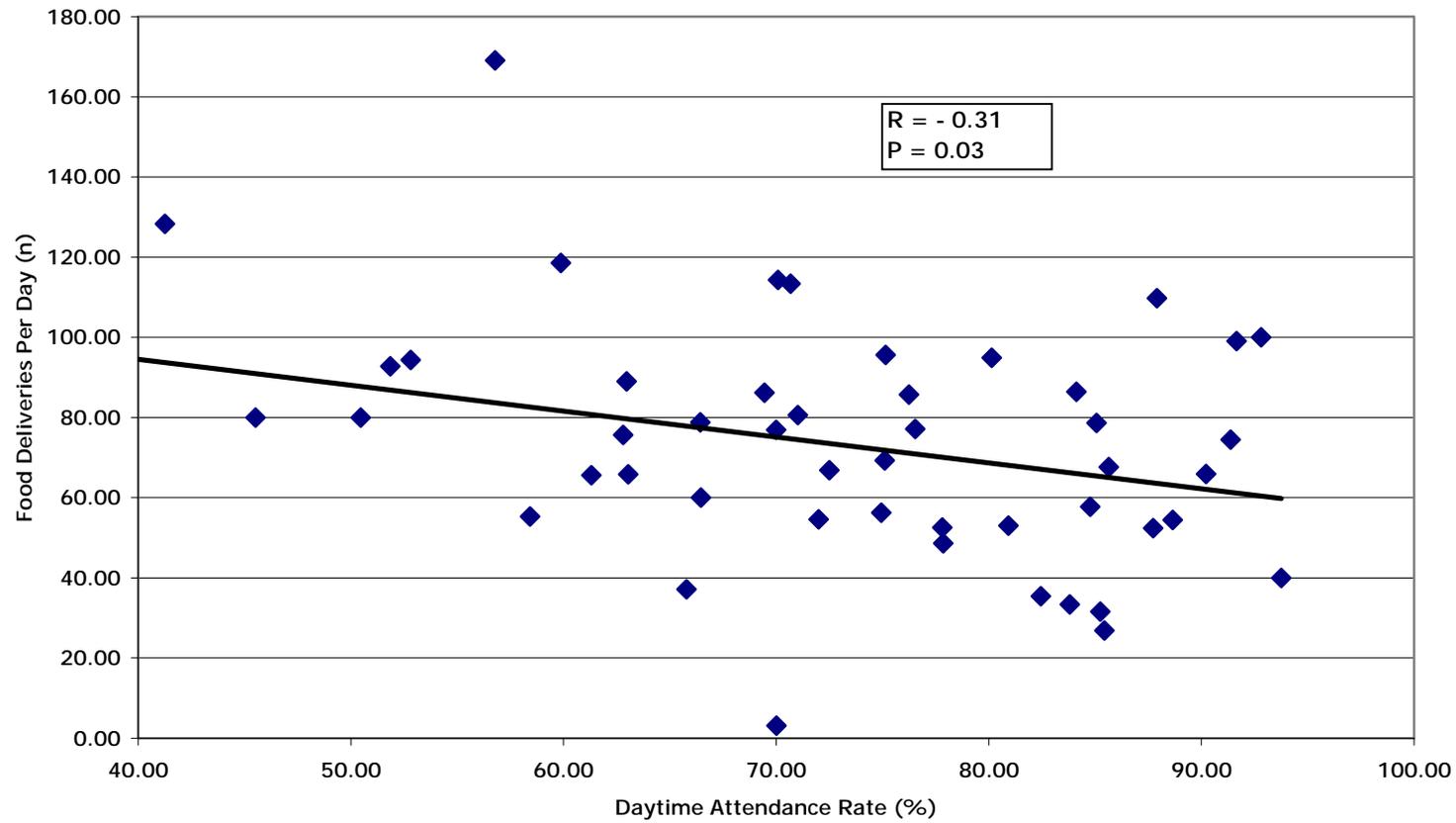


Figure 1. Pearson product moment correlations between food delivery rates (deliveries/d) and daytime attendance rates (%) during the early nestling stage for Wood Thrush nests monitored in the Monongahela National Forest, West Virginia during 1998 - 2000.

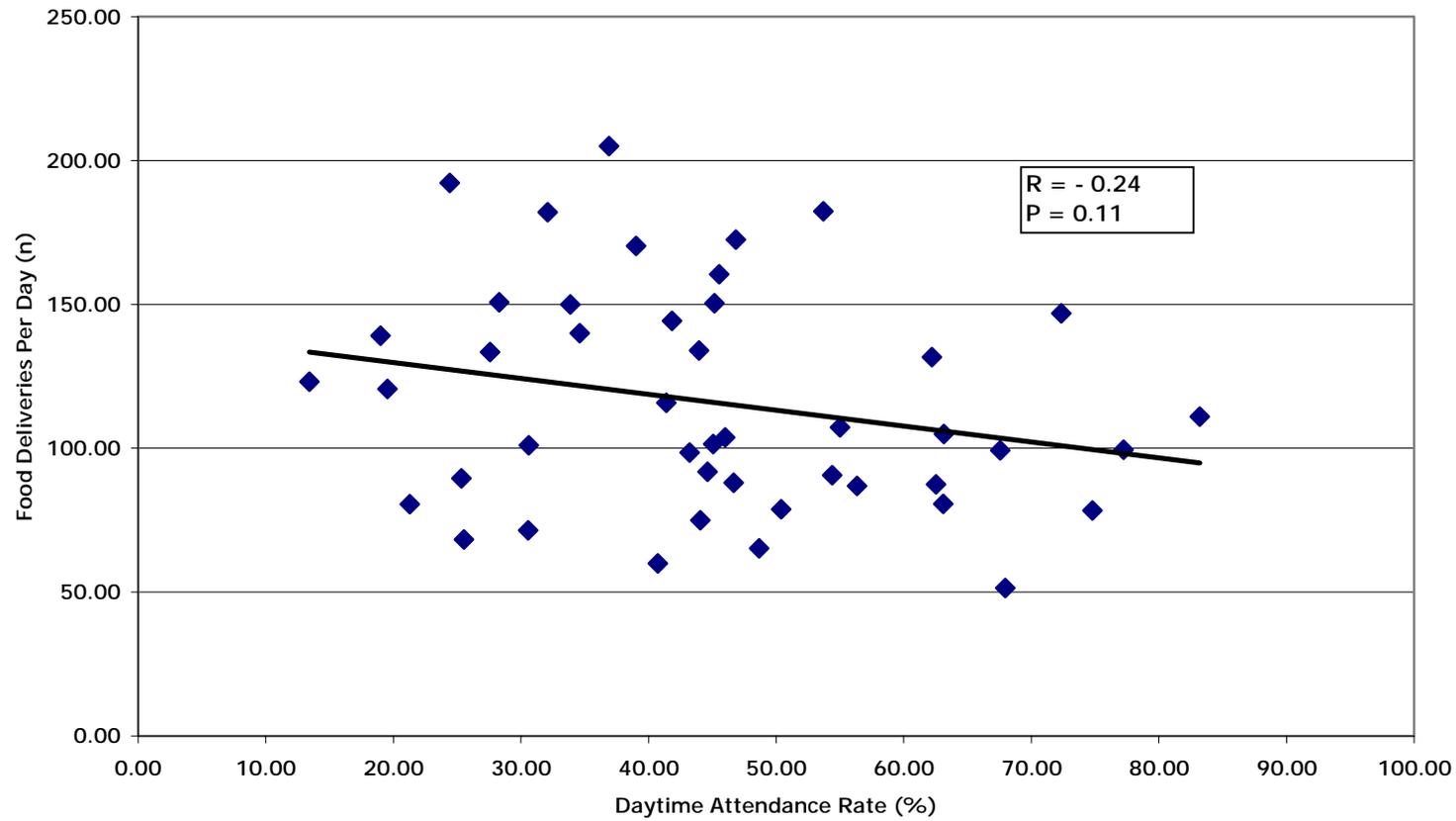


Figure 2. Pearson product moment correlations between food delivery rates (deliveries/d) and daytime attendance rates (%) during the late nestling stage for Wood Thrush nests monitored in the Monongahela National Forest, West Virginia during 1998 - 2000.

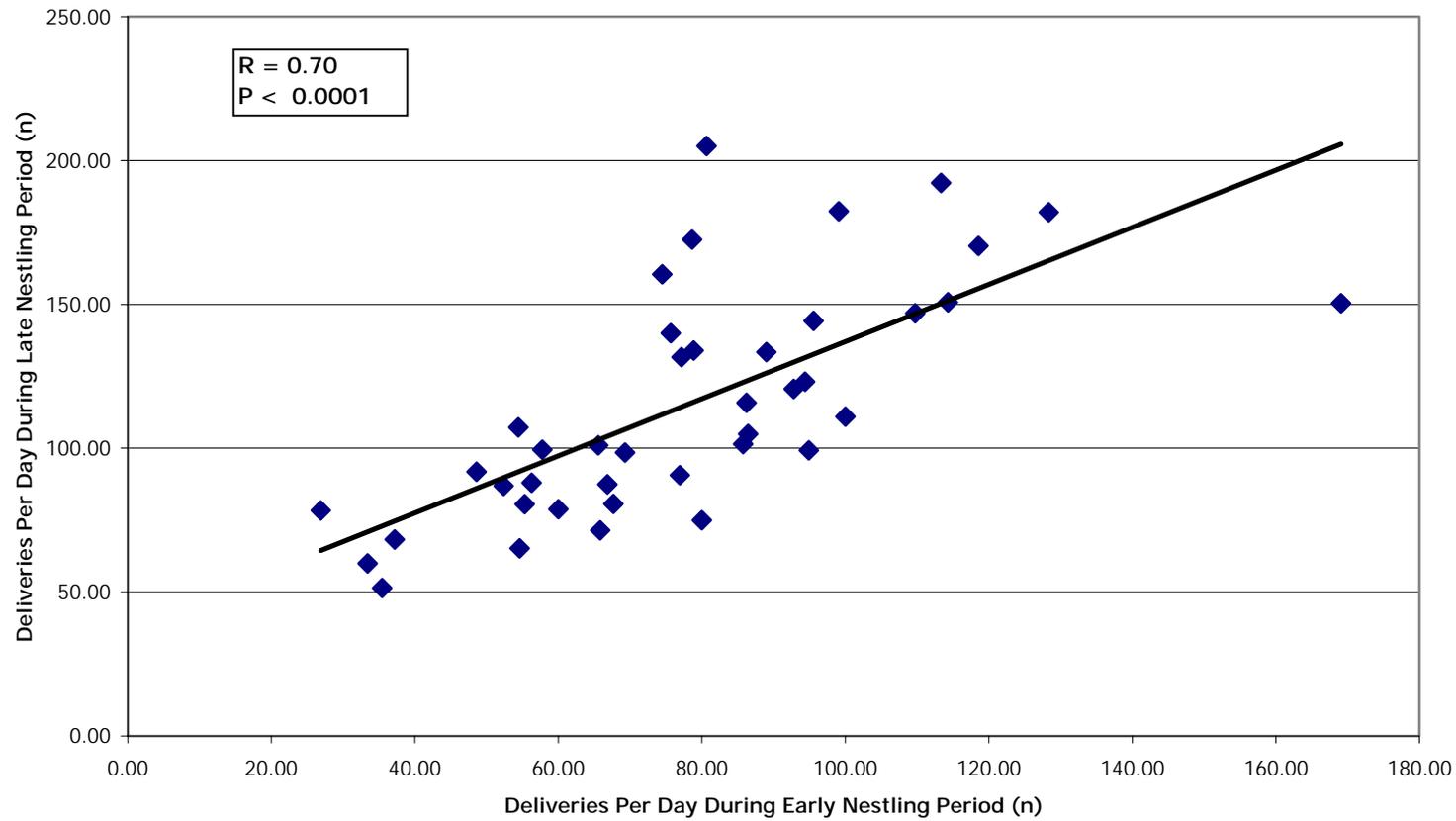


Figure 3. Pearson product moment correlations between food delivery rates (deliveries/d) between the early and late nestling stages for Wood Thrush nests monitored in the Monongahela National Forest, West Virginia during 1998 - 2000.

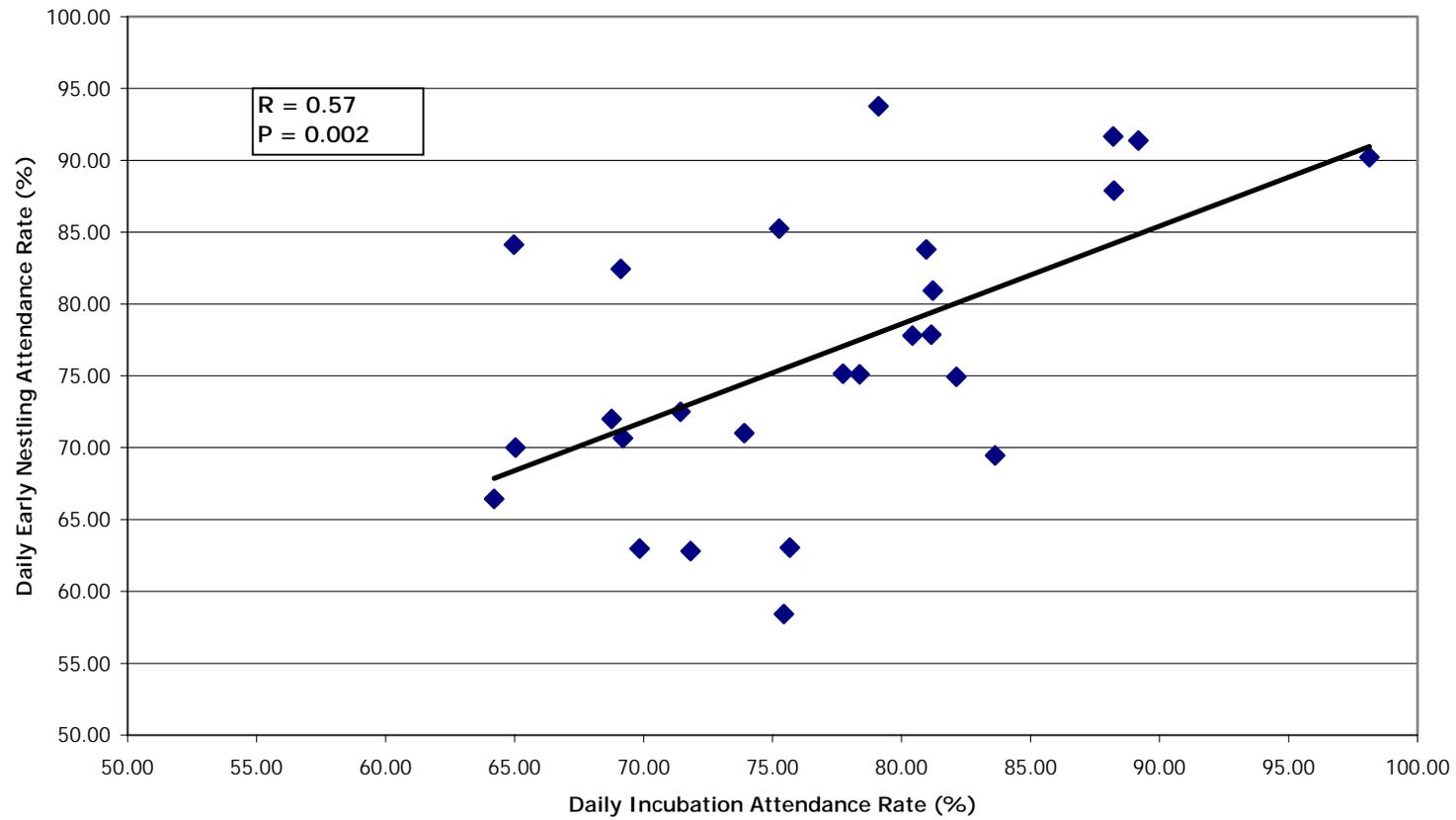


Figure 4. Pearson product moment correlations between daytime nest attendance (%) during incubation and the early nestling stage for Wood Thrush nests monitored in the Monongahela National Forest, West Virginia during 1998 - 2000.

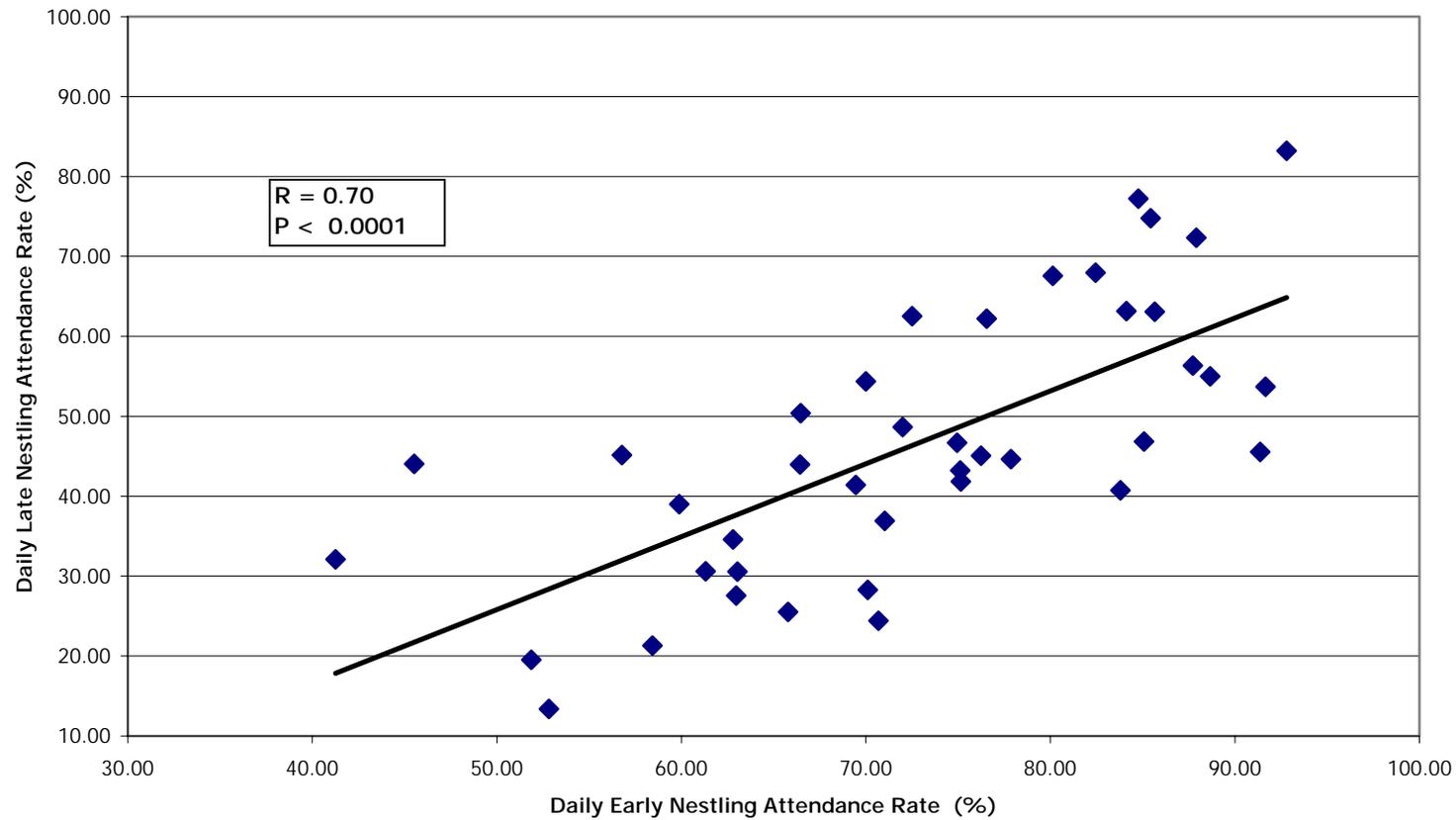


Figure 5. Pearson product moment correlations between daytime nest attendance (%) during the early and late nestling stages for Wood Thrush nests monitored in the Monongahela National Forest, West Virginia during 1998 - 2000.

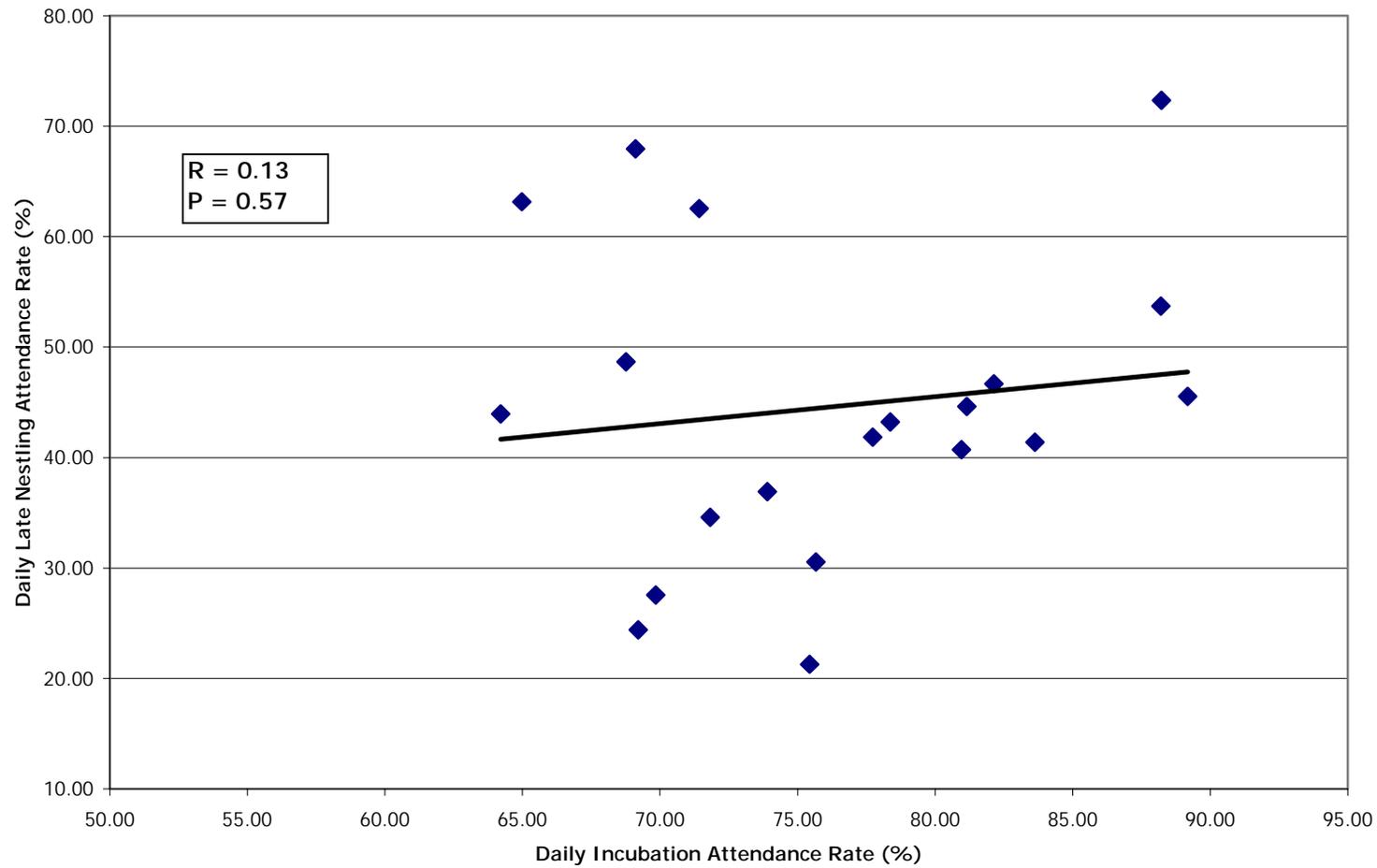


Figure 6. Pearson product moment correlations between daytime nest attendance (%) during incubation and the late nestling stage for Wood Thrush nests monitored in the Monongahela National Forest, West Virginia during 1998 - 2000.

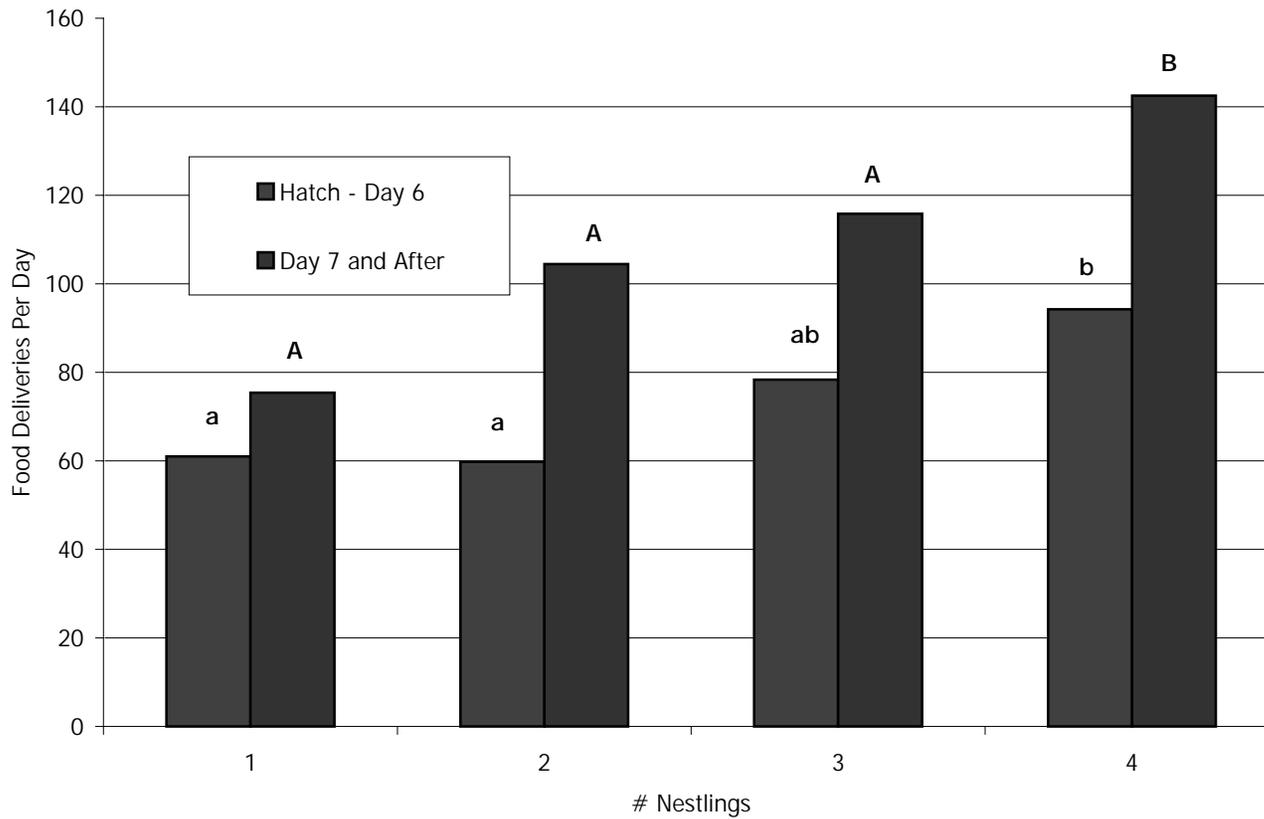


Figure 7. Average number of food deliveries to nests per day as a function of nestling stage and brood size for Wood Thrush nests monitored in the Monongahela National Forest, West Virginia during 1998 - 2000. Within a nestling stage, means of food deliveries with the same letter did not differ ($\alpha > 0.10$).

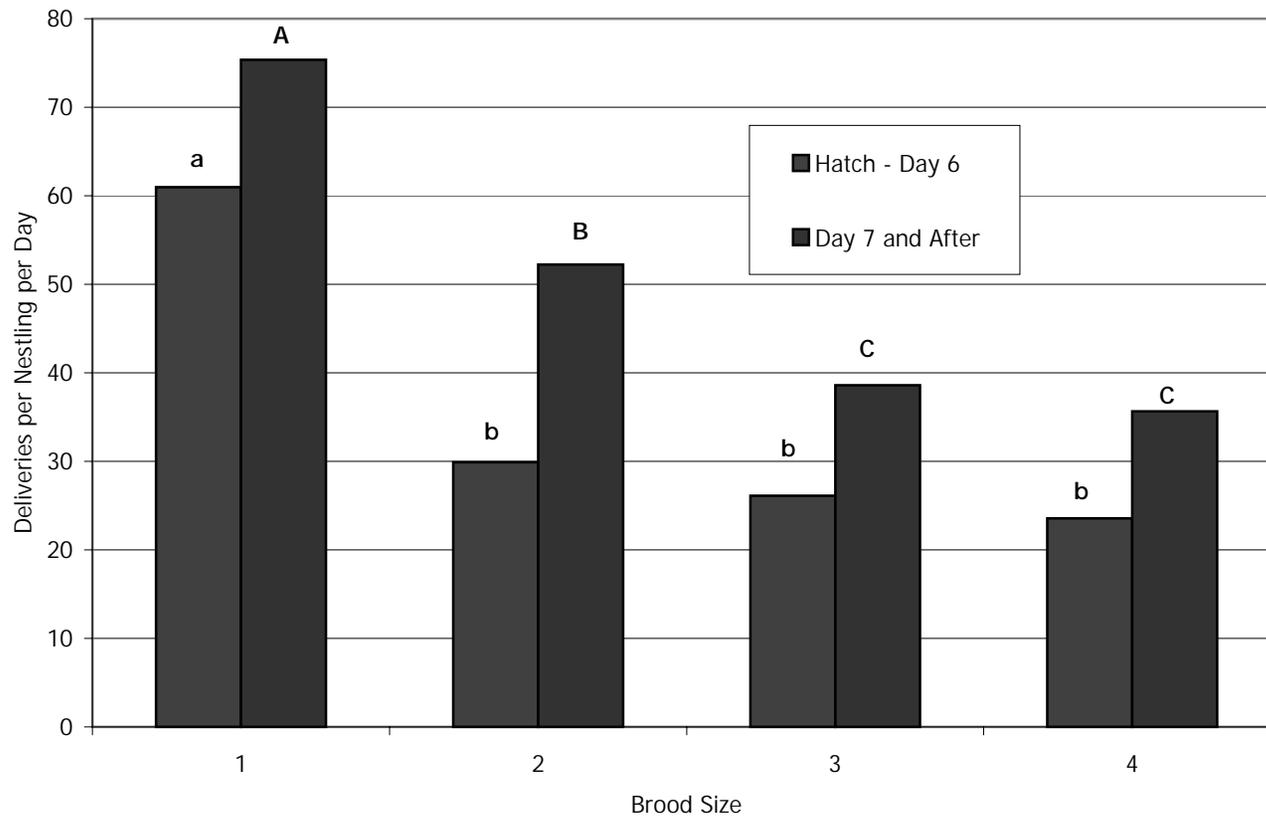


Figure 8. Average number of food deliveries to individual nestlings per day as a function of nestling stage and brood size for Wood Thrush nests monitored in the Monongahela National Forest, West Virginia during 1998 - 2000. Within a nestling stage, means of food deliveries with the same letter did not differ ($\alpha > 0.10$).

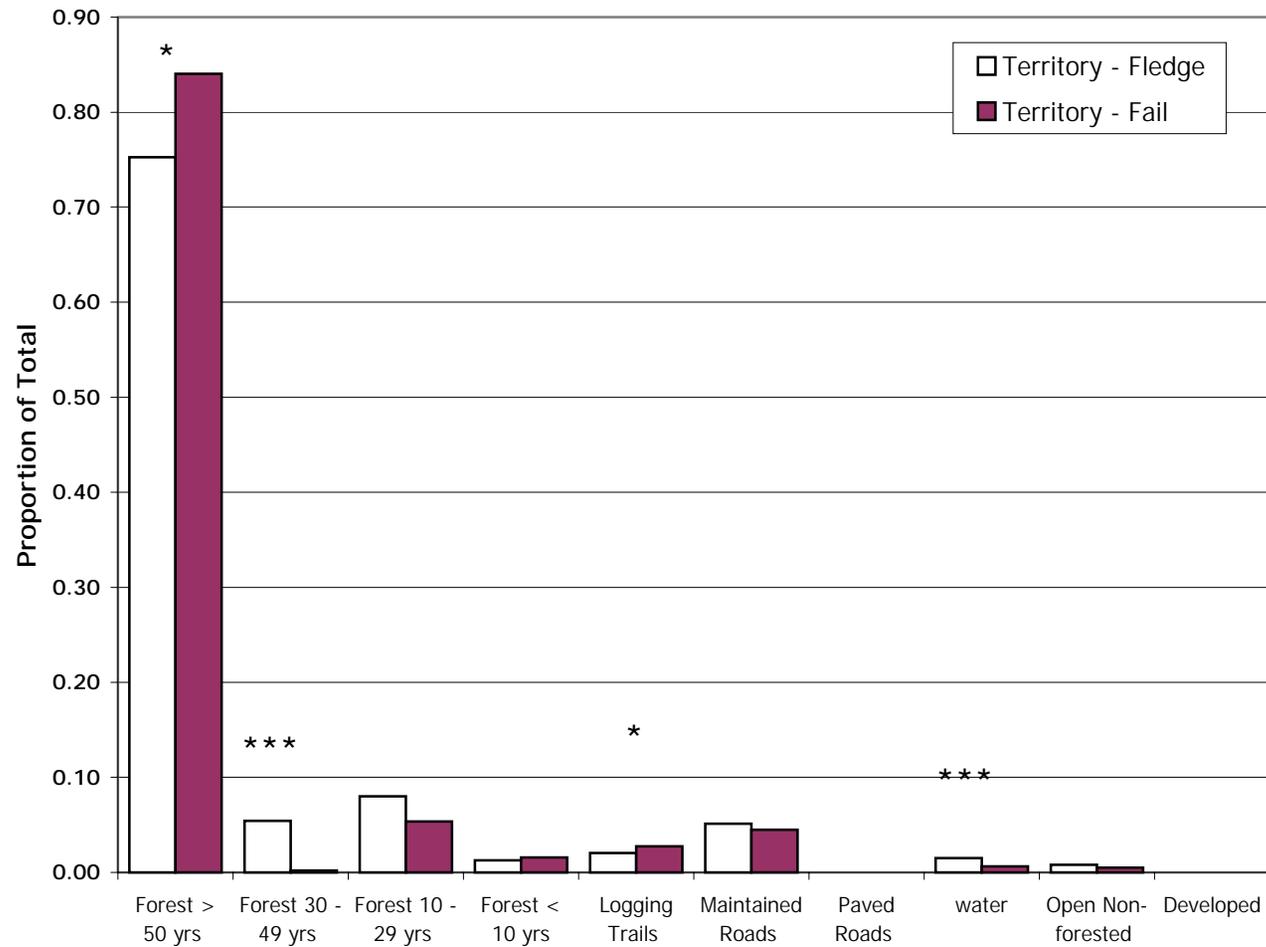


Figure 9. Proportion of land cover classes in territory level measures of successful and unsuccessful Wood Thrush nests monitored in the Monongahela National Forest, West Virginia during 1998 - 2000. Significance is denoted by asterisks: * = 0.10, *** = 0.01.

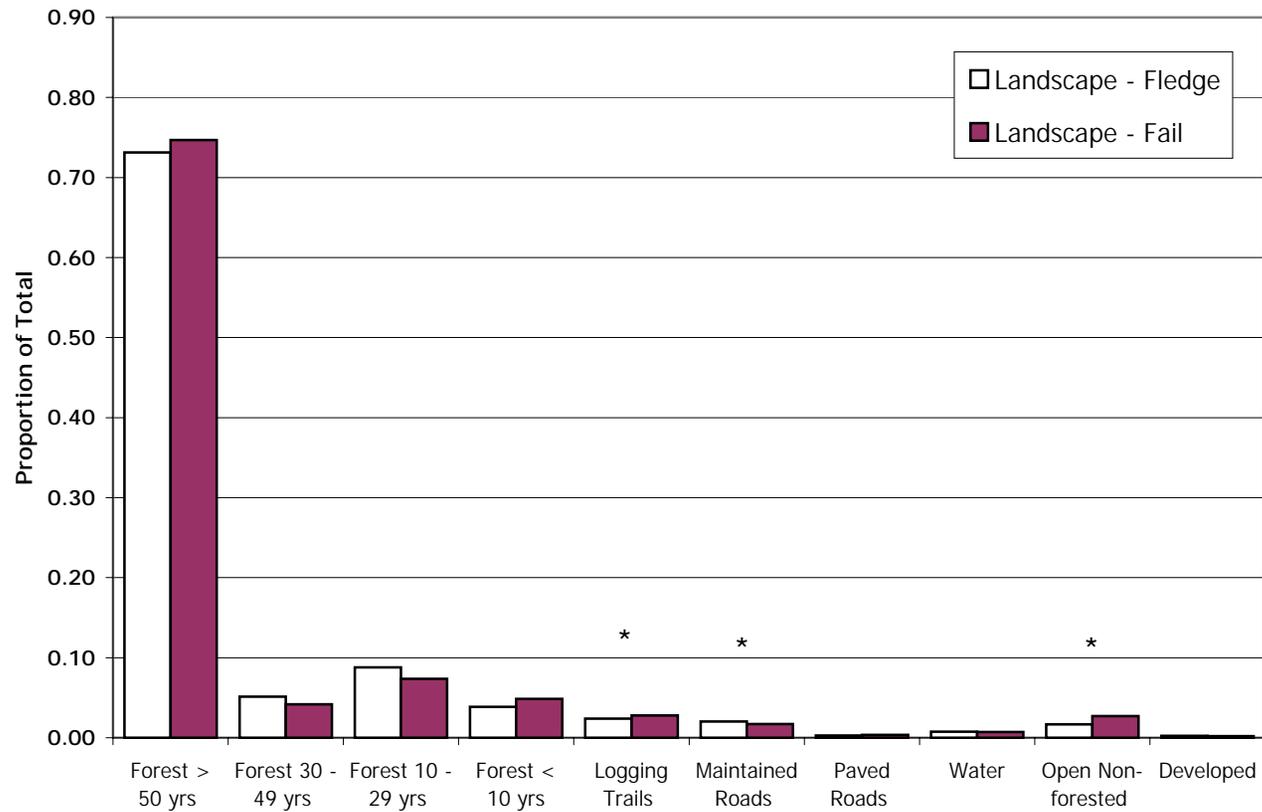


Figure 10. Proportion of land cover classes in landscape level measures of successful and unsuccessful Wood Thrush nests monitored in the Monongahela National Forest, West Virginia during 1998 - 2000. Significance is denoted by asterisks: * = 0.10.

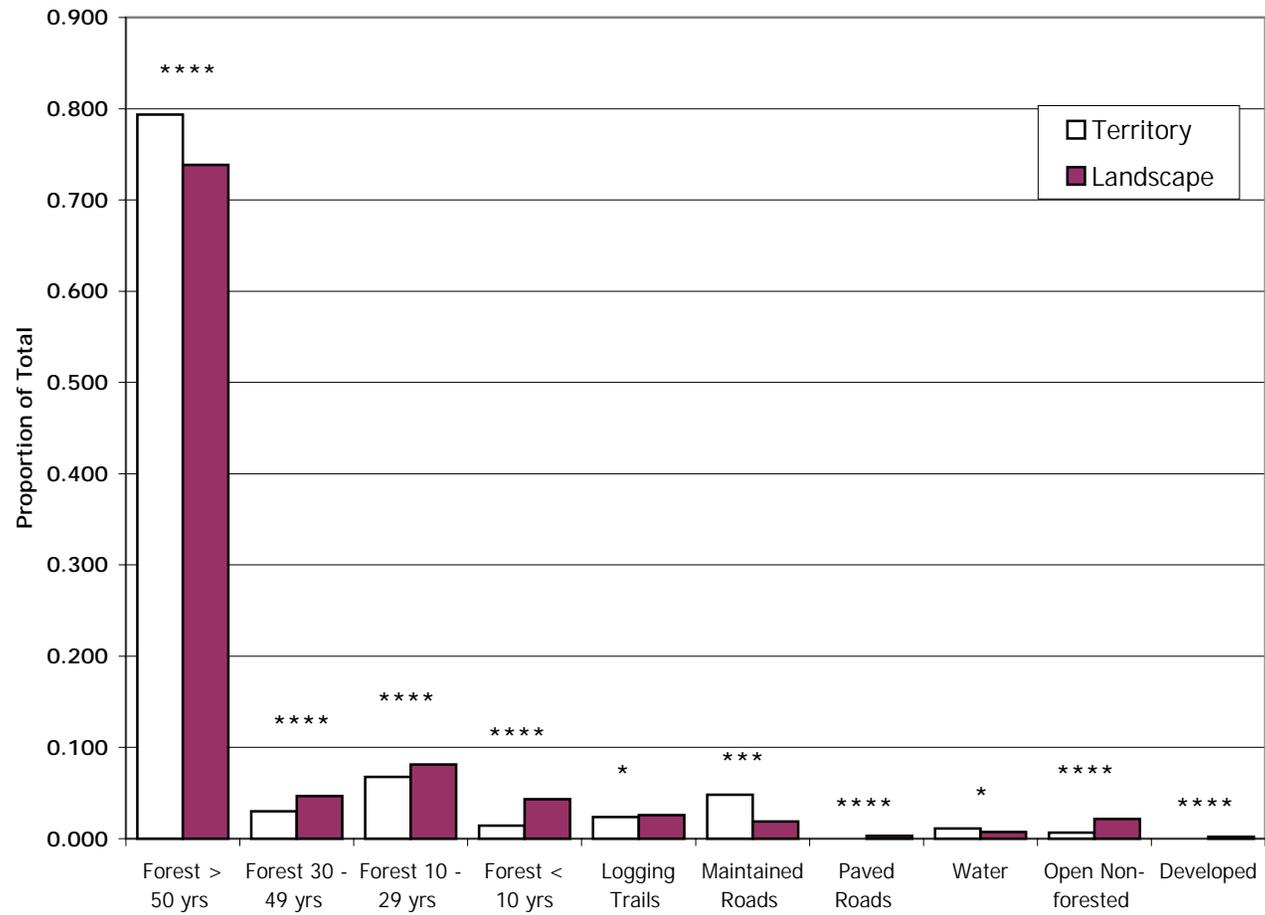


Figure 11. Landscape level versus territory level land cover of nests monitored in the Monongahela National Forest, West Virginia during 1998 - 2000. Significance is denoted by asterisks: * = 0.10, *** = 0.01, **** = 0.001.

CHAPTER 3

RELATIONS AMONG OFF-ROAD POINT COUNTS OF FOREST-DWELLING BIRDS AND MULTI-SCALE SUMMARIES OF NORTH AMERICAN BREEDING BIRD SURVEY DATA

ABSTRACT

The North American Breeding Bird Survey (BBS) is the most commonly cited source of data for inferences regarding population trends of forest-dwelling songbirds. Because the BBS is a roadside survey, it may not truly reflect trends in populations of species that specialize in forest interior habitat or actively avoid roadsides. To assess this possibility, I compared counts of bird species from BBS routes within 25, 50, and 100 km of point count surveys of forest interior habitat. Non-parametric Spearman Rank correlations were used to examine BBS-point count relationships for individual species and for groupings of species based on habitat preferences [forest interior (IN), interior-edge (IE), edge (ED)] and area sensitivity [sensitive (SEN), insensitive (INS)]. Both IN and IE species groupings exhibited significant weak to moderate correlations (correlation range = 0.34 – 0.42; $P < 0.05$ for all pairings), while no significant correlations were detected for the ED grouping. Weak, significant correlations existed between BBS surveys and point counts of SEN species (correlation range 0.29 – 0.35; $P < 0.05$ for all pairings); no significant correlations were found for INS species. For 25 individual species examined, only 12 of 75 point count-BBS pairings were significantly correlated, including 6 significant negative correlations. A number of

factors are discussed that could have produced the general lack of agreement between point counts and the BBS, including the effectiveness of roadside surveys for sampling forest-dwelling species, sample size, detectability problems, and habitat-related biases. More comparisons across broader temporal and geographic scales are needed to determine whether BBS routes are reliable indicators of population trends of forest-dwelling species.

INTRODUCTION

Forest-dwelling songbirds, especially Nearctic-Neotropical migrants, have been the subjects of much research over the last twenty years, owing to concerns over population declines (Hagan and Johnston 1992; Finch and Stangel 1993; Martin and Finch 1995). While there have been numerous individual studies that have indicated localized population declines (e.g. Sherry and Holmes 1992; Roth and Johnson 1993), the primary source of data for inferences regarding population trends has been the North American Breeding Bird Survey (BBS), the most extensive annual survey of breeding birds in North America (Peterjohn et al. 1995).

The BBS is conducted by counting birds along permanent, 24.5 mi (39.4 km) roadside survey routes. The relationship between habitat along roadside survey routes and surrounding regions has the potential in certain situations to obscure interpretation of trends in species' populations (Peterjohn et al. 1995; Bart et al. 1995). For example, if the habitat composition along a survey route is not representative of the habitat composition in the region, then some bird species may not be sampled in proportion to actual population sizes within the region (Bart et al. 1995). In theory, this is not a problem as long as population trends along BBS routes are similar to population trends away from routes (Butcher et al. 1993). If, however, population trends along BBS routes differ from the surrounding region, then bias is present and conclusions concerning population trends are suspect (Butcher et al. 1993). Another problem with BBS

and other surveys limited to roadsides involves habitat preferences of some species for areas away from roads (Peterjohn et al. 1995). If a species actively avoids roads, then the BBS may be an inappropriate source of data from which to assess its population trend. Forest-dwelling birds classified as area sensitive interior specialists (Freemark and Collins 1992) are species whose BBS count trends could potentially be biased due to avoidance of roadside edges and differences in habitat composition between roadsides and surrounding forest. To shed light on this possibility, I examined relationships among groupings of bird species surveyed via off-road point count surveys of forest interior habitat and concurrent BBS counts in the surrounding area. I used a multi-scale approach to determine whether inclusion of broader/narrower geographic BBS coverage best agreed with point count results. I predicted that point counts of area sensitive forest interior specialists would exhibit poor agreement with Breeding Bird Survey results.

STUDY AREA AND METHODS

All point count data were collected within the Monongahela National Forest (MNF), in northeastern West Virginia (Figure 1) during 1996 – 1999. The study area falls within the Allegheny Plateau and is characterized by steep slopes, diverse plant assemblages (Strausbaugh and Core 1978), and 115 - 150 cm of precipitation annually (DeMeo 1999). Between 1870 and 1920, nearly all of the forested land within this area was clearcut (Hicks 1998; Schuler and Gillespie 2000). Most of the harvested areas were allowed to naturally regenerate,

however, and at the time of this study much of the forest was in mature age classes.

Eight off-road transects were established within mixed mesophytic forest as part of a study of the effects of landscape level habitat fragmentation on forest songbirds (DeMeo 1999). Each transect contained 9 - 17 points ($n = 99$ points), depending on length, with 250 m intervals between points (Ralph et al. 1993). Starting points of transects were randomly established, but transects were oriented approximately perpendicularly to mountain slopes to capture as much environmental variation as possible within the heavily forested habitat (DeMeo 1999).

Individual point counts lasted for 10 min, with observers recording all birds detected within a 50 m radius. Point counts commenced no earlier than 30 min before sunrise and ended no later than 10:00:00 EST. All transects were surveyed between 23 May and 30 June during all years. Each point was sampled twice during each breeding season, with surveys approximately two weeks apart. Species-specific totals were tallied annually by point, using the higher of that year's survey counts as the total. Species totals were summed across points and transect to produce a total count per species per year.

I used 1996 – 1999 BBS data for all routes within 25 km, 50 km, and 100 km radii of the centroid of the point counts, which included routes in West Virginia, Virginia, Maryland, and Pennsylvania (Figure 1). If at least one-third of a route fell within a buffer, it was included. Three routes were within a 25 km

radius, 10 within 50 km, and 31 within 100 km (see Appendix 1 for buffer-specific lists of BBS routes). Not all routes were surveyed in all years, however, so I standardized counts by summing annual species totals within each buffer distance (25, 50, 100 km) across routes, then dividing by the number of routes surveyed that year. The standardized data for each buffer size are thus the average count of each species per route per year.

I used correlation analyses to examine relationships between annual species totals from point counts and BBS routes. Correlations were considered significant at $\alpha = 0.05$. I focused analyses on species that were commonly detected (hereafter COMMON) during point count surveys. Specifically, I only analyzed species that were both (1) observed in at least 3 of 4 years and (2) ranked among the 20 most commonly detected species in at least 2 of 4 years. Since count data typically are not normally distributed, I used non-parametric Spearman Rank correlations (r_s ; Zar 1999). In addition to analyzing point count – BBS correlations of individual species, I also examined correlations among categories consisting of pooled groups of COMMON species. COMMON species were grouped by habitat preference [Forest Interior (INT), Interior and Edge (IE), or Edge (ED)] and area sensitivity [Sensitive (SEN), Insensitive (INS)] after the classification scheme of Freemark and Collins (1992) for these analyses.

Finally, I examined differences in overall relative abundances of COMMON species between BBS counts and point counts. For these analyses, I simply ranked the average abundance of each species within each year for each

sampling method (point counts, 25 km , 50 km, and 100 km BBS buffers). I then calculated an average ranking for each species-sampling method across the four years of the study to use as the basis for comparisons.

RESULTS

A total of 59 species were detected with point count surveys during 1996 – 1999, including 24 INT species, 22 IE species, and 13 ED species (see Appendix 2 for species list). Thirty-two SEN and 19 INS species were detected; area requirements of 8 species are unknown. All species detected by point counts were detected through BBS counts at the 50 km and 100 km scales. The Black-billed Cuckoo (*Coccyzus erythrophthalmus*) was the only species detected through point counts (one detection in 4 yr) that was not detected during any year at the 25 km scale on BBS routes.

Twenty-five species were classified as COMMON using the criteria described above. COMMON species included 12 INT, 9 IE, and 4 ED specialists. Sixteen of the species were considered SEN, 7 were INS, and 2 had unknown area requirements. Relative abundance rankings, while generally consistent among BBS routes within different buffer sizes, were quite different between point counts and BBS routes, with ED species tending to have higher ranks on BBS routes and certain INT and IE species ranked higher on point counts (Table 1). Among the set of common species, the Black-and-white Warbler, for example, was the second most abundant point count species, but was the 15th,

20th, and 21st most common species among the 25, 50, and 100 km buffers. American Robins were the 14th most common point count species, but were the 1st or 2nd most common species detected on BBS routes within each buffer size. Red-eyed Vireos and Wood Thrushes, two of the most commonly detected species, were an exception to this pattern. Relative abundance rankings of both species exhibited close agreement between point counts and BBS counts.

Counts of INT species were significantly correlated among point count surveys and buffers of BBS routes, but correlation coefficients of point count-buffer pairs indicated a weak to moderate positive relationship, ranging from 0.37 – 0.42 (Table 2). A similar pattern was exhibited by IE species with significant positive correlations ranging from 0.34 – 0.40. No significant correlations existed between point count-buffer pairings of ED species. Counts of SEN species detected via point counts were significantly correlated with BBS counts within each buffer (Table 2), but the relationship was weak (correlation range = 0.29 – 0.35). No significant correlations were found between point count-buffer pairings of INS species. Buffer-buffer pairs of BBS counts for the various habitat and area sensitivity groups were highly correlated, with all correlations significant and 11 of 16 correlation coefficients > 0.85.

Correlations among point counts and BBS buffers were also examined for individual COMMON species. Of the 75 possible point count-buffer pairings, there were 12 significant correlations (Table 2; Appendix 3). Interestingly, 6 of 12 significant correlations were negative (Figs. 2 – 6).

DISCUSSION

Species-specific point count – BBS comparisons generally indicated that correlations between the two survey methods were weak, with only 6 significant positive correlations out of 75 possible pairings. Additionally, none of the correlations among habitat and area sensitivity groupings were highly correlated. A number of factors could explain the absence of a strong relationship between point counts and the BBS. One simple explanation for the lack of agreement between survey methods is that the sample size was too small to have a reasonable possibility of detecting strong relationships. That is, a longer time series would have demonstrated that a strong relationship did exist. While there is some merit to this argument, it should be noted that I did detect strong correlation among BBS counts in different buffer sizes. If sample size were strongly limiting my ability to detect correlations in the data, I would not expect such tight agreement among BBS routes in the different buffers. Observer bias (Sauer et al. 1994) is another possible source of variation for both BBS and off-road point counts. I made no attempt to assess this possibility in my analyses. A local expert verified species identification and distance estimation skills of all point count observers in all years, however (DeMeo 1999; G. Williams, unpubl. data).

The maximum detection distance of songs varies by species (Emlen 1984) and could be another source of variability between point count and BBS abundance measures. Species with loud, easily detected songs (e.g. Wood

Thrush, Red-eyed Vireo, Acadian Flycatcher, Ovenbird) had relatively similar ranks between methods, while others with quieter songs, such as the Black-and-white Warbler, did not (Table 1). A study of forest birds in Wisconsin found that some species such as American Crows (*Corvus brachyrhynchos*) were audible at distances greater than 700 m while others became inaudible at distances as small as 72 m (Wolf et al. 1993). The study also found that even within the audible range of a species, conspecifics often became less distinguishable from one another as observer distance increased, noting that this phenomenon would likely cause undercounts of species in studies where large or unlimited radii points are used. Thus, BBS counts, with radii of 402 m (0.25 mi), have the potential to undercount species in two ways: failure to detect individuals of species with short detection distances and confusion of conspecifics detected at large distances.

Differences in habitat between off-road point counts and BBS routes were almost certainly a source of variation in counts among survey methods and could have decreased agreement in counts in a number of ways. First, habitat composition varied between point counts and BBS surveys. Point count surveys were conducted off-road in areas dominated by mature, mixed mesophytic forest. Further, transects were located entirely within the publicly owned Monongahela National Forest, in an area where agriculture, residential, or other non-forest land uses are uncommon. While roadside BBS routes were drawn from the same region, they also passed through some private, non-forested land,

which was not the case with point count transects. Further, roads themselves are sources of habitat edges and road maintenance may introduce small bands of early successional habitat, even in areas dominated by forest. Finally, BBS routes used in analyses covered a greater range in elevation, which itself is an important determinant of forest type (i.e., mixed mesophytic vs. northern hardwoods vs. red spruce; Strausbaugh and Core 1978).

As a group, ED species exhibited no significant correlations among point counts and BBS routes. Given that point count transects were placed in mature forest with only small amounts of early successional habitat, it is likely that they would be an inadequate indicator of early successional (ED) species. On the other hand, BBS routes may tend to have a greater proportion of early successional habitat as indicated by the relatively high rankings of abundances of species that prefer this type of habitat (Table 1). Thus, poor agreement in counts of these species is not surprising.

In a similar way, BBS routes employed in this study may not adequately survey the mature, forest interior habitat that is preferred by many of the species documented in off-road point counts. Although BBS surveys documented nearly all of the INT and IE species found through point count surveys, agreement among counts was low (Tables 1 and 2; Figs. 2 – 6). If BBS routes are not providing a thorough survey of this habitat type, then it is possible that they would not prove to be reliable indicators of population trends of breeding birds in these habitats. In such a situation, it would be expected that off-road point

counts would provide a better index of populations of forest interior species and, possibly, interior-edge species than would BBS routes. A study in Montana that compared species lists and abundances of paired roadside and off-road point count surveys produced conclusions similar to mine (Hutto et al 1993). They noted that while both methods produced similar species lists, abundances of many species varied between roadside and off-road point counts. Furthermore, they suggested that the differences in abundances might have been a result of habitat changes associated with roads. Another study conducted in Maine and New Hampshire found a general lack of agreement between population indices of BBS routes and surveys of a tract of mature forest, noting that there were fewer significant correlations between population indices than would be expected by chance (Witham and Hunter 1992).

While this study and others suggest that BBS routes may not adequately survey some species or groups of species (Witham and Hunter 1992; Hutto et al. 1993), there is another possibility that could account for the lack of agreement between point counts and BBS counts in this study. Because abundances of species in the region vary among habitat types (DeMeo 1999), it is possible that BBS routes, which survey a broad spectrum of habitats, may more truly reflect species' population trends than off-road point counts that were specific to intact, mixed mesophytic habitat. Consider the case of a species for which intact, mixed mesophytic forest is optimal, preferred habitat. When mixed mesophytic habitat is saturated, excess individuals would have to shift into less optimal habitats. In

such a scenario, the off-road point count surveys in this study may have accurately assessed abundances in optimal habitat, while completely neglecting to document abundances on more marginal habitats, whereas BBS surveys, with their coverage of multiple habitats, could have more accurately captured the trend in counts of the species. This and all the other aforementioned factors could have contributed to the general lack of agreement between point count and BBS surveys. More comparisons are needed across larger geographical and temporal scales to tease apart the relative importance of individual sources of variation and to evaluate the comparative effectiveness of the two survey methods.

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Table 1. Relative abundance rankings of COMMON species (see Methods for definition) observed through point counts of forest interior habitat in the Monongahela National Forest, West Virginia from May – June, 1996 - 1999. Species rankings were calculated for point counts of off-road, forested habitat and for all BBS routes within 25, 50, and 100 km of the centroid of the point count transects. Rankings are the average abundance rank across the four years of the study.

Species	Habitat	Area Sensitivity	Ranks			
			Pt. Count	25km	50 km	100 km
Acadian Flycatcher	INT	SEN	9	4	12	11
American Redstart	INT	SEN	5.5	8	13	13
Black-and-white Warbler	INT	SEN	2	15	20	21
Black-throated Blue Warbler	INT	SEN	11	12	21	25
Black-throated Green Warbler	INT	SEN	5.5	16	10	17
Blue-headed Vireo	INT	unknown	12	23	24	23
Cerulean Warbler	INT	SEN	24	25	25	24
Hooded Warbler	INT	SEN	7	17	23	19
Ovenbird	INT	SEN	10	11	8.5	9
Scarlet Tanager	INT	SEN	3	10	7	7
Veery	INT	SEN	15	21	18	18
White-breasted Nuthatch	INT	SEN	13	24	19	16
Black-capped Chickadee	IE	INS	19	14	15	14
Blue Jay	IE	INS	22.5	13	17	10
Dark-eyed Junco	IE	unknown	22.5	20	16	20
Eastern Towhee	IE	INS	17	9	4	4
Eastern Wood-pewee	IE	INS	18	18	11	12
Red-eyed Vireo	IE	SEN	1	1	2	1
Rose-breasted Grosbeak	IE	SEN	8	22	22	22
Tufted Titmouse	IE	SEN	25	6	6	5
Wood Thrush	IE	SEN	4	5	5	6
American Robin	ED	INS	14	2	1	2
Cedar Waxwing	ED	INS	21	7	8.5	8
Chestnut-sided Warbler	ED	SEN	16	19	14	15
Indigo Bunting	ED	INS	20	3	3	3

^aINT = forest interior, IE = interior-edge, ED = edge

^bSEN = area sensitive, INS = not area sensitive

Table 2. Spearman Rank correlations (r_s) of off-road point counts with 25, 50, and 100 km buffers of BBS routes for species detected through point counts conducted in the Monongahela National Forest, West Virginia during May – June, 1996 – 1999. Included are correlations of individual species, habitat groupings, and area sensitivity groupings. Individual species are listed alphabetically by habitat preference.

Grouping/Species	25 km		50 km		100 km	
	r_s	P	r_s	P	r_s	P
All Interior Species	0.37	0.009	0.40	0.005	0.42	0.003
All Interior-Edge Species	0.40	0.02	0.34	0.05	0.34	0.04
All Edge Species	0.21	0.43	0.07	0.79	0.11	0.69
All Area Sensitive Species	0.35	0.005	0.31	0.01	0.29	0.02
All Area Insensitive Species	0.23	0.25	0.19	0.34	0.17	0.39
<i>Individual Interior Species</i>						
Acadian Flycatcher	0.20	0.80	0.00	1.00	1.00	< 0.001
American Redstart	-0.32	0.68	-0.40	0.60	1.00	< 0.001
Black-and-white Warbler	-0.63	0.37	0.80	0.20	0.00	1.00
Black-throated Blue Warbler	-0.63	0.37	-0.80	0.20	-1.00	< 0.001
Black-throated Green Warbler	-0.74	0.26	0.26	0.74	-0.40	0.60
Blue-headed Vireo	-0.74	0.26	0.80	0.20	-0.20	0.80
Cerulean Warbler	0.11	0.89	0.40	0.60	0.80	0.20
Hooded Warbler	-0.80	0.20	-0.80	0.20	0.80	0.20
Ovenbird	-0.39	0.61	-0.21	0.79	0.95	0.05
Scarlet Tanager	-0.40	0.60	-1.00	< 0.001	0.40	0.60
Veery	-1.00	< 0.001	-0.80	0.20	-0.40	0.60
White-breasted Nuthatch	0.80	0.20	0.80	0.20	1.00	< 0.001
<i>Individual Interior-Edge Species</i>						
Black-capped Chickadee	1.00	< 0.001	-0.32	0.68	0.40	0.60
Blue Jay	0.20	0.80	0.40	0.60	0.40	0.60
Dark-eyed Junco	0.77	0.23	0.40	0.60	0.40	0.60
Eastern Towhee	0.40	0.60	-0.80	0.20	0.00	1.00
Eastern Wood-pewee	0.40	0.60	0.40	0.60	0.60	0.40
Red-eyed Vireo	-1.00	< 0.001	-1.00	< 0.001	-0.40	0.60
Rose-breasted Grosbeak	-0.20	0.80	-0.40	0.60	-0.60	0.40
Tufted Titmouse	0.40	0.60	0.40	0.60	0.60	0.40
Wood Thrush	0.20	0.80	-0.40	0.60	-0.20	0.80
<i>Individual Edge Species</i>						
American Robin	-0.32	0.68	-0.80	0.20	-0.40	0.60
Cedar Waxwing	1.00	< 0.001	0.80	0.20	0.40	0.60
Chestnut-sided Warbler	0.40	0.60	-0.40	0.60	0.40	0.60
Indigo Bunting	-0.80	0.20	-1.00	< 0.001	-0.20	0.80

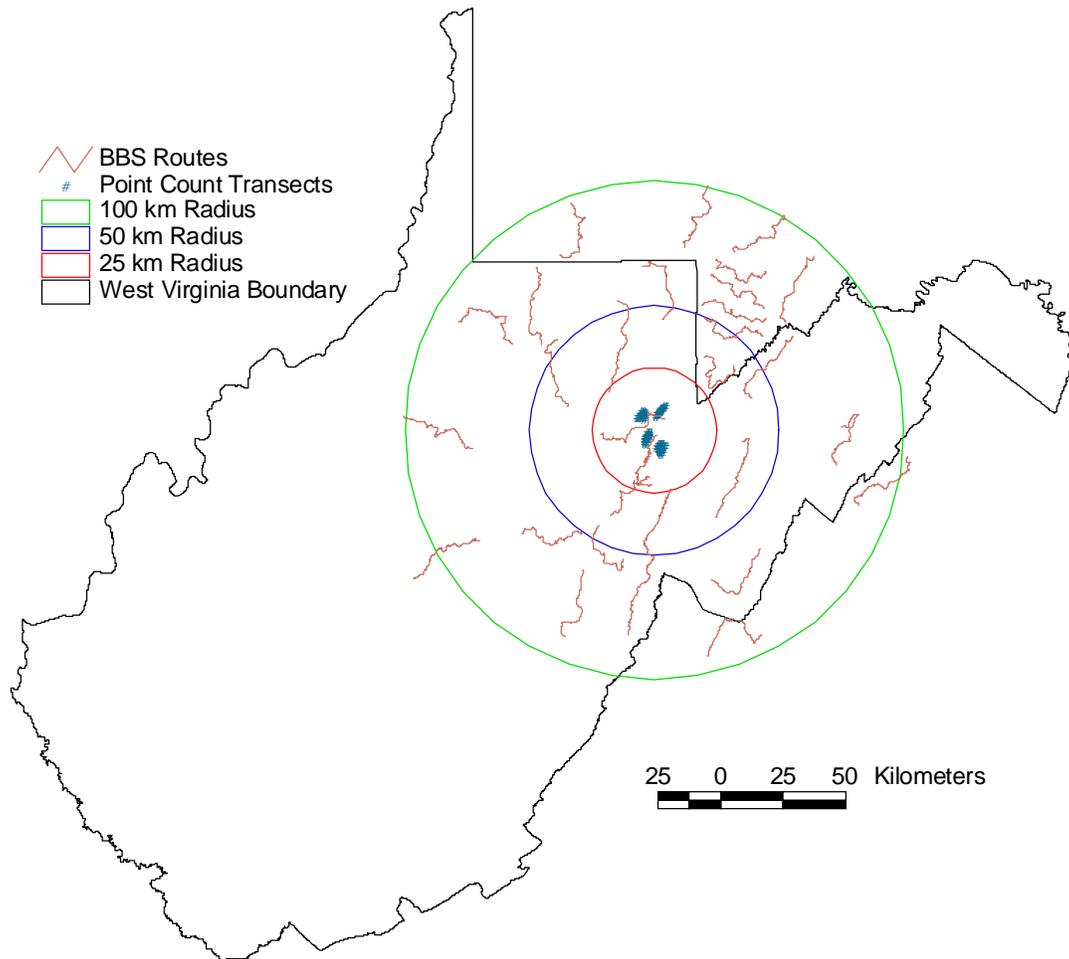


Figure 1. Map of study area including point count transects and Breeding Bird Survey routes. Circles on map correspond to 25 km, 50 km, and 100 km radius buffers around the centroid of the point count transects. For inclusion in analyses, at least one-third of a route had to fall within the buffer distance in question.

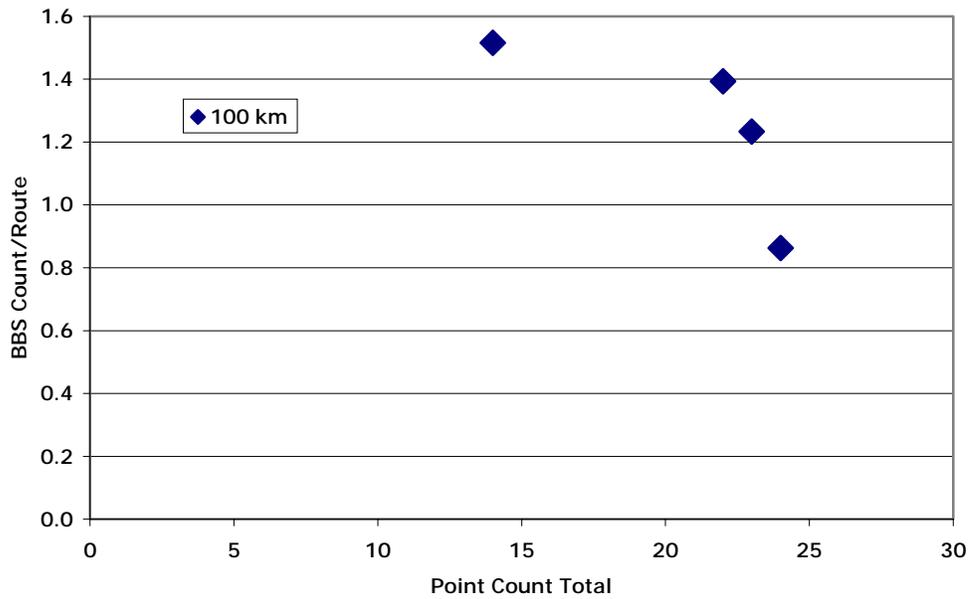


Figure 2. Comparison of point count and BBS surveys of Black-throated Blue Warblers. This species exhibited a significant, negative Spearman Rank correlation between point counts and BBS surveys within 100 km.

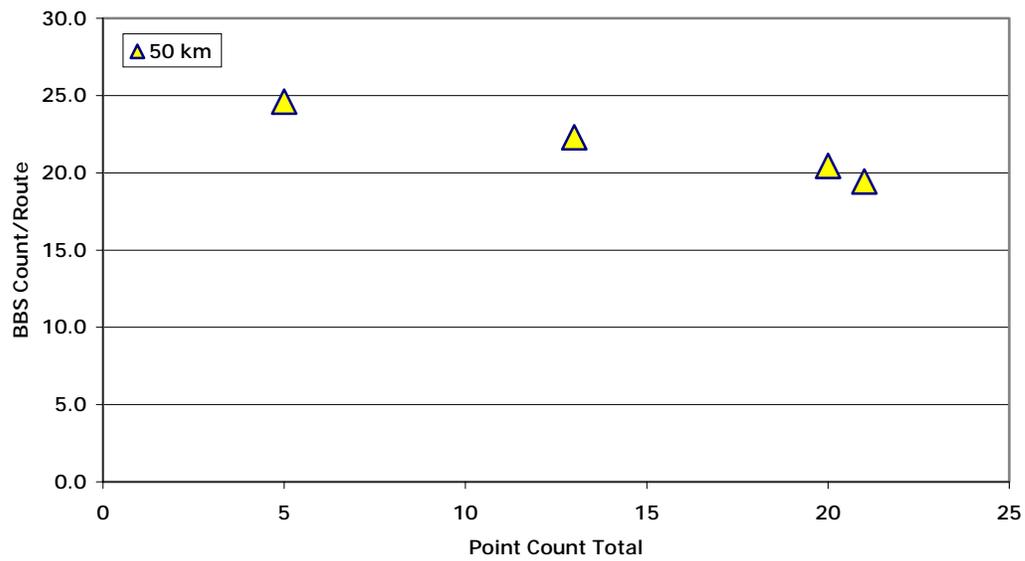


Figure 3. Comparison of point count and BBS surveys of Indigo Buntings. This species exhibited a significant, negative Spearman Rank correlation between point counts and BBS surveys within 50 km.

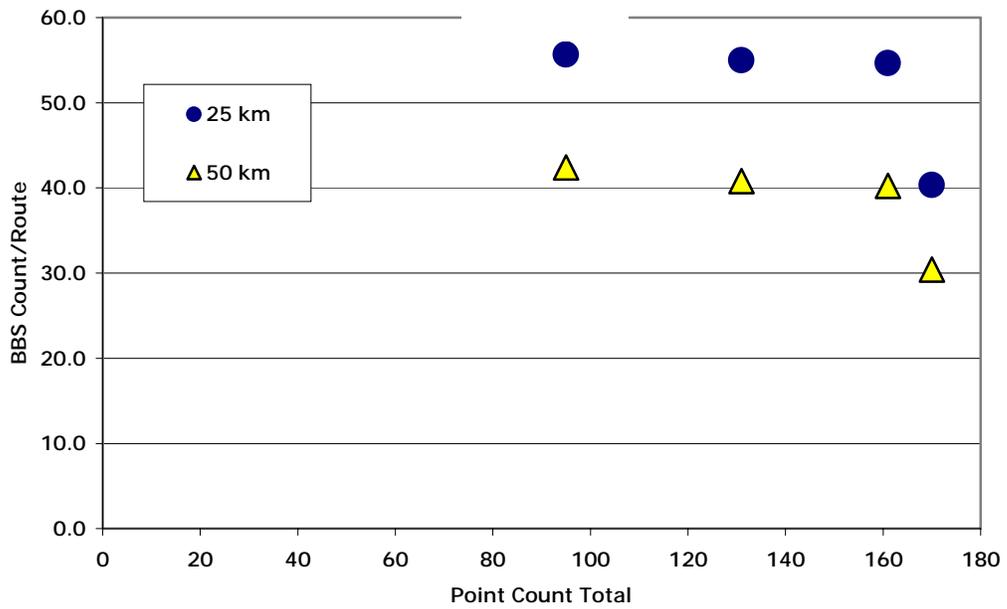


Figure 4. Comparison of point count and BBS surveys of Red-eyed Vireos. This species exhibited a significant, negative Spearman Rank correlation between point counts and BBS surveys within 25 and 50 km.

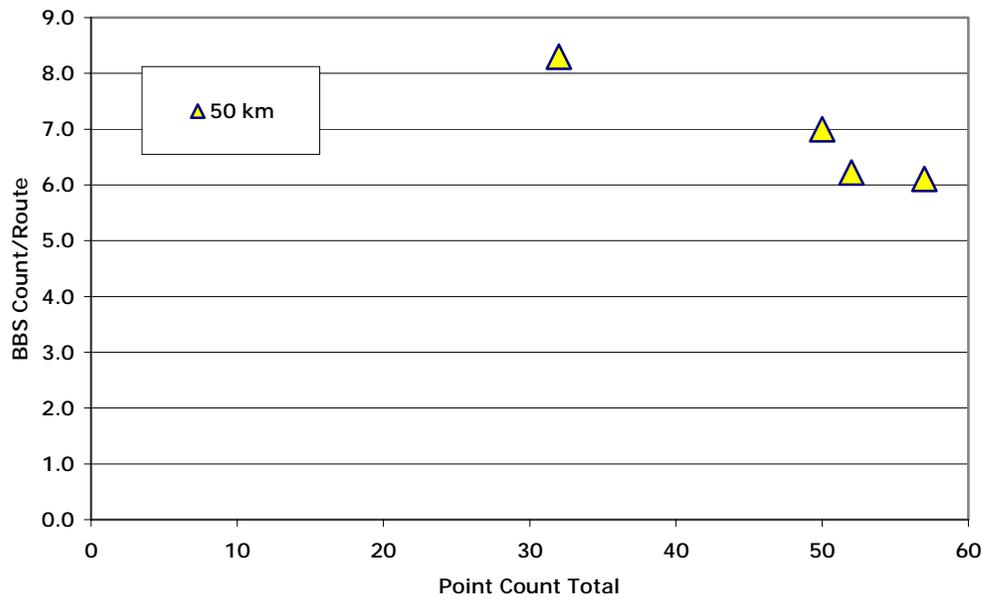


Figure 5. Comparison of point count and BBS surveys of Scarlet Tanagers. This species exhibited a significant, negative Spearman Rank correlation between point counts and BBS surveys within 50 km.

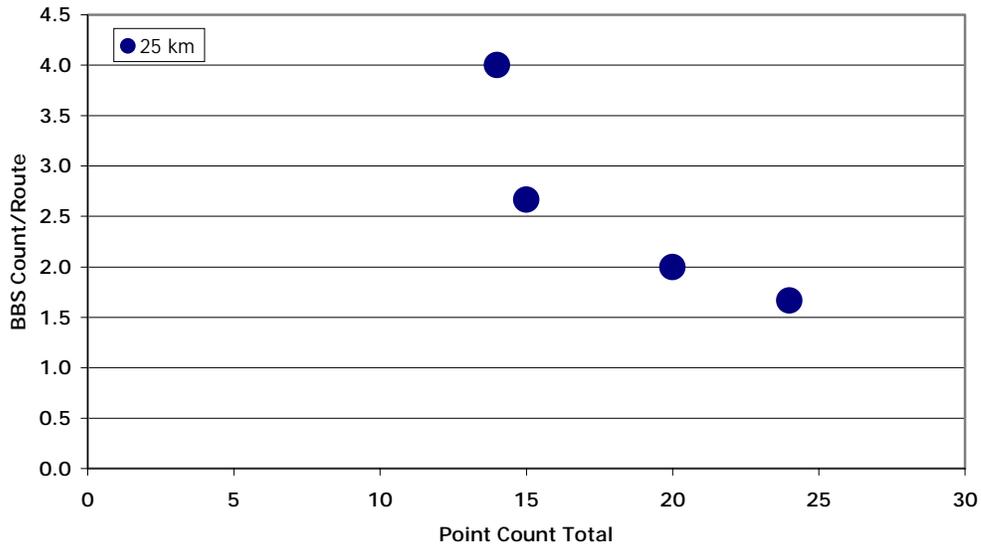


Figure 6. Comparison of point count and BBS surveys of the Veery. This species exhibited a significant, negative Spearman Rank correlation between point counts and BBS surveys within 25 km.

Appendix 1. List of North American Breeding Bird Survey routes included in analyses. Routes are classified according to distance from the centroid of off-road point counts conducted within the Monongahela National Forest, West Virginia from 1996 – 1999. Some Breeding Bird Survey routes were not surveyed during all years.

100 km	50 km	25 km
ACCIDENT	BISMARK	BOWDEN
BISMARK	BOWDEN	DAILEY
BOWDEN	DAILEY	MEADOWVILLE
CANAAN	GREER	
DAILEY	MEADLAND	
FINZEL	MEADOWVILLE	
FLOYD	MO OF SENECA	
GARRETT	STEYER	
GLADE RUN	VINDEX	
GREEN BANK	WYMER	
GREER		
JEFFERSON		
JENNINGS		
JEROME		
LOST RIVER		
MCDONALD		
MEADLAND		
MEADOWVILLE		
MILL RUN		
MO OF SENECA		
MONONGAH		
RUTHBELLE		
SMITHFIELD		
STEYER		
SUGAR GROVE		
SUTTON		
VALLEY HEAD		
VINDEX		
W AUGUSTA1		
W AUGUSTA2		
WYMER		

Appendix 2. List of Apodiformes, Cuculiformes, Passeriformes, and Piciformes species detected via point counts on Monongahela National Forest study area, 1996 – 1999. Species are categorized according to the habitat use and area sensitivity scheme of Freemark and Collins (1992).

Common Name	Scientific Name	Habitat ^a	Area Sensitivity ^b
Acadian Flycatcher	<i>Empidonax vireescens</i>	INT	SEN
American Crow	<i>Corvus brachyrhynchos</i>	ED	SEN
American Goldfinch	<i>Carduelis tristis</i>	ED	INS
American Redstart	<i>Setophaga ruticilla</i>	INT	SEN
American Robin	<i>Turdus migratorius</i>	ED	INS
Baltimore Oriole	<i>Icterus galbula</i>	ED	INS
Black-and-white Warbler	<i>Mniotilta varia</i>	INT	SEN
Black-billed Cuckoo	<i>Coccyzus erythrophthalmus</i>	IE	unk
Blackburnian Warbler	<i>Dendroica fusca</i>	INT	unk
Black-capped Chickadee	<i>Poecile atricapillus</i>	IE	INS
Black-throated Blue Warbler	<i>Dendroica caerulescens</i>	INT	SEN
Black-throated Green Warbler	<i>Dendroica virens</i>	INT	SEN
Blue Jay	<i>Cyanocitta cristata</i>	IE	INS
Blue-gray Gnatcatcher	<i>Poliopitila caerulea</i>	IE	SEN
Blue-headed Vireo	<i>Vireo solitarius</i>	INT	unk
Brown Creeper	<i>Certhia americana</i>	INT	SEN
Brown-headed Cowbird	<i>Molothrus ater</i>	ED	INS
Canada Warbler	<i>Wilsonia canadensis</i>	INT	SEN
Cedar Waxwing	<i>Bombycilla cedrorum</i>	ED	INS
Cerulean Warbler	<i>Dendroica cerulea</i>	INT	SEN
Chestnut-sided Warbler	<i>Dendroica pensylvanica</i>	ED	SEN
Chipping Sparrow	<i>Spizella passerina</i>	ED	unk
Common Yellowthroat	<i>Geothlypis trichas</i>	IE	INS
Dark-eyed Junco	<i>Junco hyemalis</i>	IE	unk
Downy Woodpecker	<i>Picoides pubescens</i>	IE	INS
Eastern Towhee	<i>Pipilo erythrophthalmus</i>	IE	INS
Eastern Wood-pewee	<i>Contopus virens</i>	IE	INS
Golden-crowned Kinglet	<i>Regulus satrapa</i>	INT	unk
Gray Catbird	<i>Dumetella carolinensis</i>	IE	INS
Great Crested Flycatcher	<i>Myiarchus crinitus</i>	IE	SEN
Hairy Woodpecker	<i>Picoides villosus</i>	INT	SEN
Hermit Thrush	<i>Catharus guttatus</i>	INT	SEN
Hooded Warbler	<i>Wilsonia citrina</i>	INT	SEN
Indigo Bunting	<i>Passerina cyanea</i>	ED	INS
Kentucky Warbler	<i>Oporornis formosus</i>	INT	SEN
Least Flycatcher	<i>Empidonax minimus</i>	ED	SEN
Louisiana Waterthrush	<i>Seiurus motacilla</i>	INT	SEN
Magnolia Warbler	<i>Dendroica magnoia</i>	INT	INS
Mourning Warbler	<i>Oporornis philadelphia</i>	ED	SEN
Northern Cardinal	<i>Cardinalis cardinalis</i>	IE	INS

Appendix 2 continued.

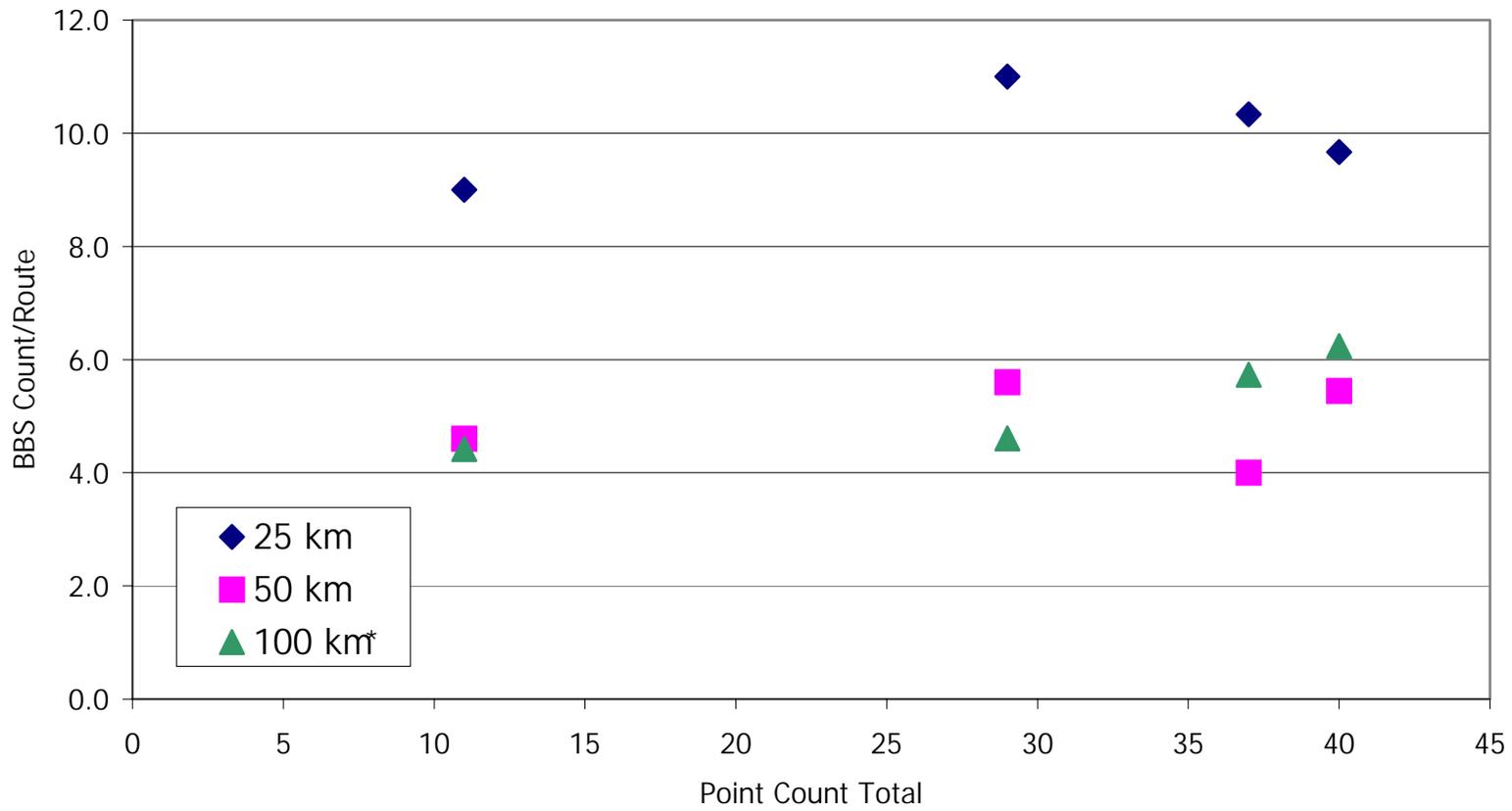
Common Name	Scientific Name	Habitat ^a	Area Sensitivity ^b
Northern Flicker	<i>Colaptes auratus</i>	IE	INS
Northern Parula	<i>Parula americana</i>	IE	SEN
Ovenbird	<i>Seiurus aurocapillus</i>	INT	SEN
Pileated Woodpecker	<i>Dryocopus pileatus</i>	INT	SEN
Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	IE	SEN
Red-eyed Vireo	<i>Vireo olivaceus</i>	IE	SEN
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	IE	SEN
Ruby-throated Hummingbird	<i>Archilochus colubris</i>	ED	INS
Scarlet Tanager	<i>Piranga olivacea</i>	INT	SEN
Song Sparrow	<i>Melospiza melodia</i>	ED	INS
Tufted Titmouse	<i>Baeolophus bicolor</i>	IE	SEN
Veery	<i>Catharus fuscescens</i>	INT	SEN
White-breasted Nuthatch	<i>Sitta carolinensis</i>	INT	SEN
White-eyed Vireo	<i>Vireo griseus</i>	IE	INS
Winter Wren	<i>Troglodytes troglodytes</i>	INT	unk
Wood Thrush	<i>Hylocichla mustelina</i>	IE	SEN
Worm-eating Warbler	<i>Helmitheros vermivorus</i>	INT	SEN
Yellow-billed Cuckoo	<i>Coccyzus americanus</i>	IE	unk
Yellow-throated Vireo	<i>Vireo flavifrons</i>	IE	SEN

^aINT = Forest Interior, I-E = Forest Interior and Edge, ED = Forest Edge.

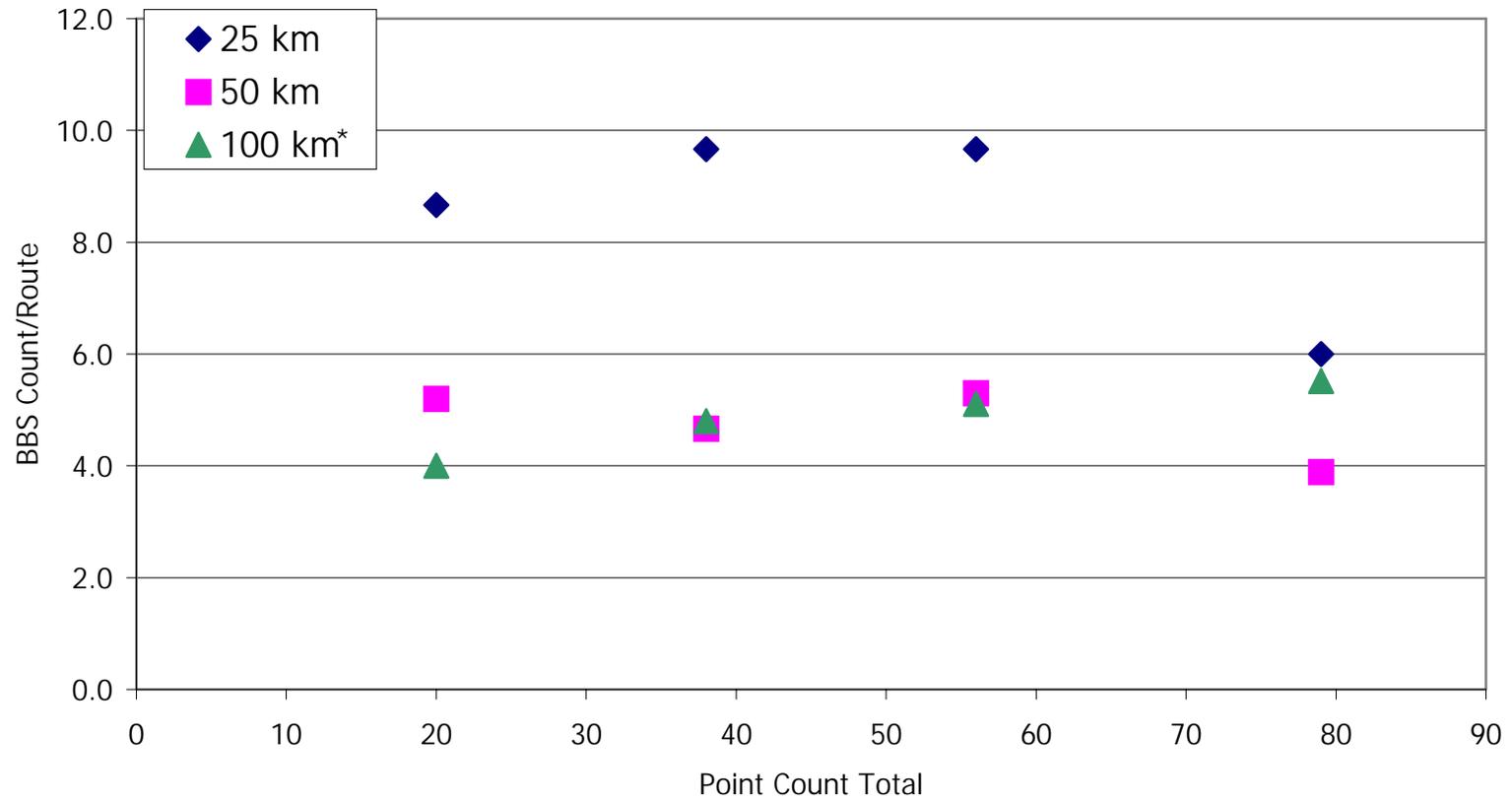
^bINS = Area Insensitive, SEN = Area Sensitive, unk = Unknown

Appendix 3. Comparisons of COMMON (see Methods for definition) species detected via off-road point counts with Breeding Bird Survey Counts within 25, 50, and 100 km buffers of point count transects. Comparisons are based upon point counts and Breeding Bird Surveys conducted from 1996 – 1999. Species are listed in alphabetical order by habitat preference. Point count – buffer pairings with significant ($\alpha = 0.05$) Spearman Rank correlations are denoted with an asterisk in the legend. Habitat preference (INT, IE, ED) and area sensitivity (SEN, INS) are noted in parentheses beside the species' name.

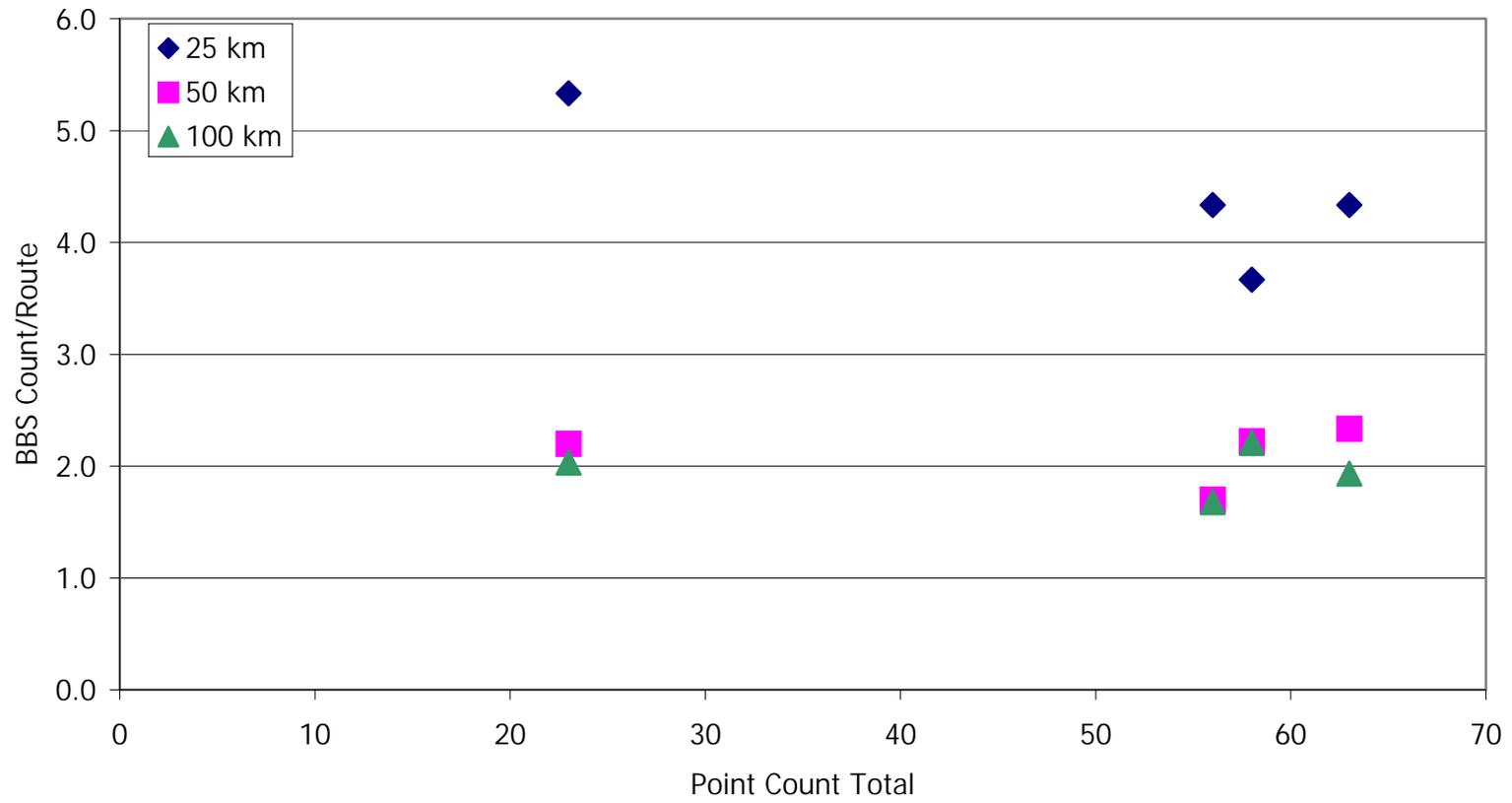
Acadian Flycatcher (INT, SEN)



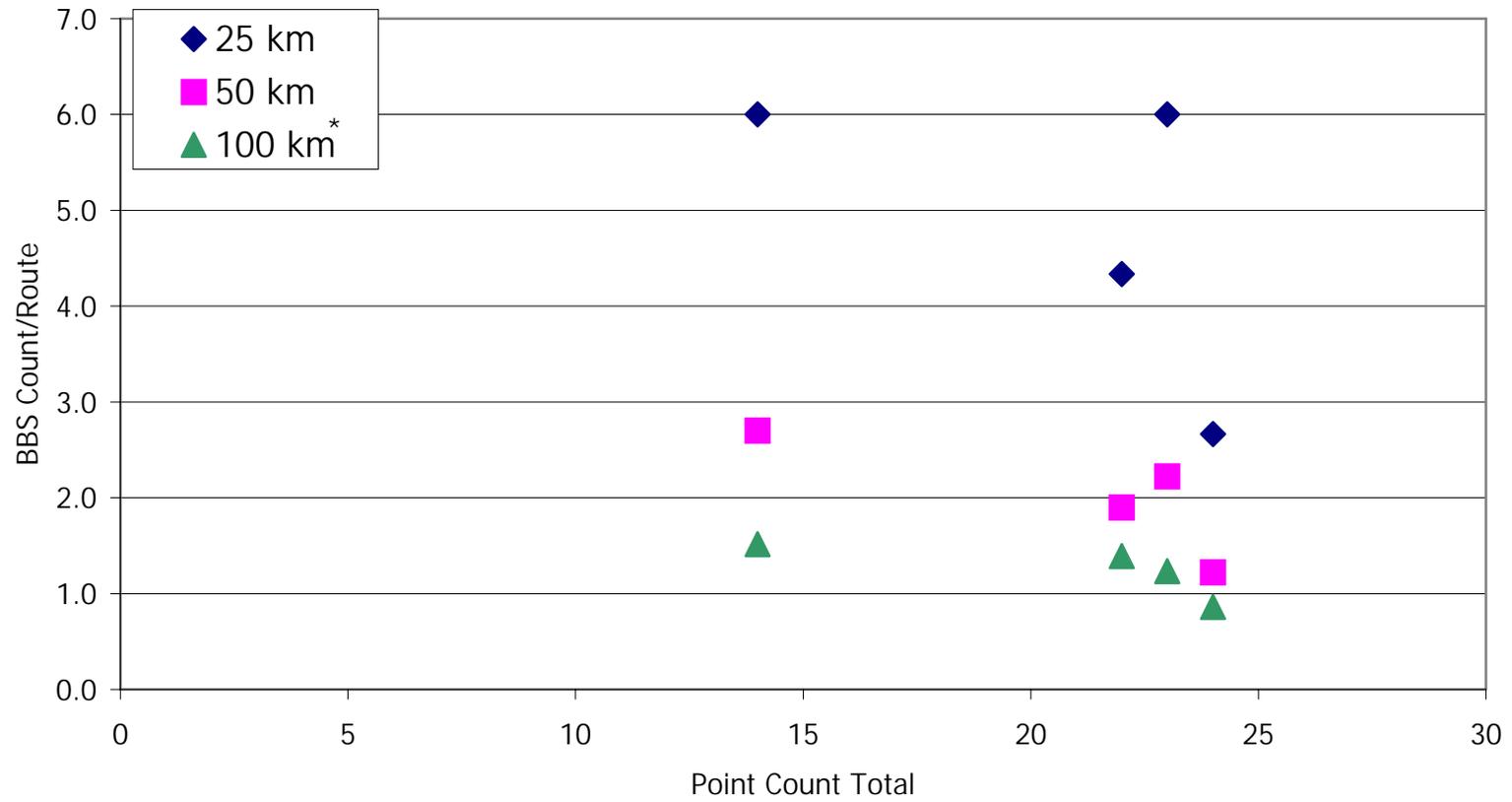
American Redstart (INT, SEN)



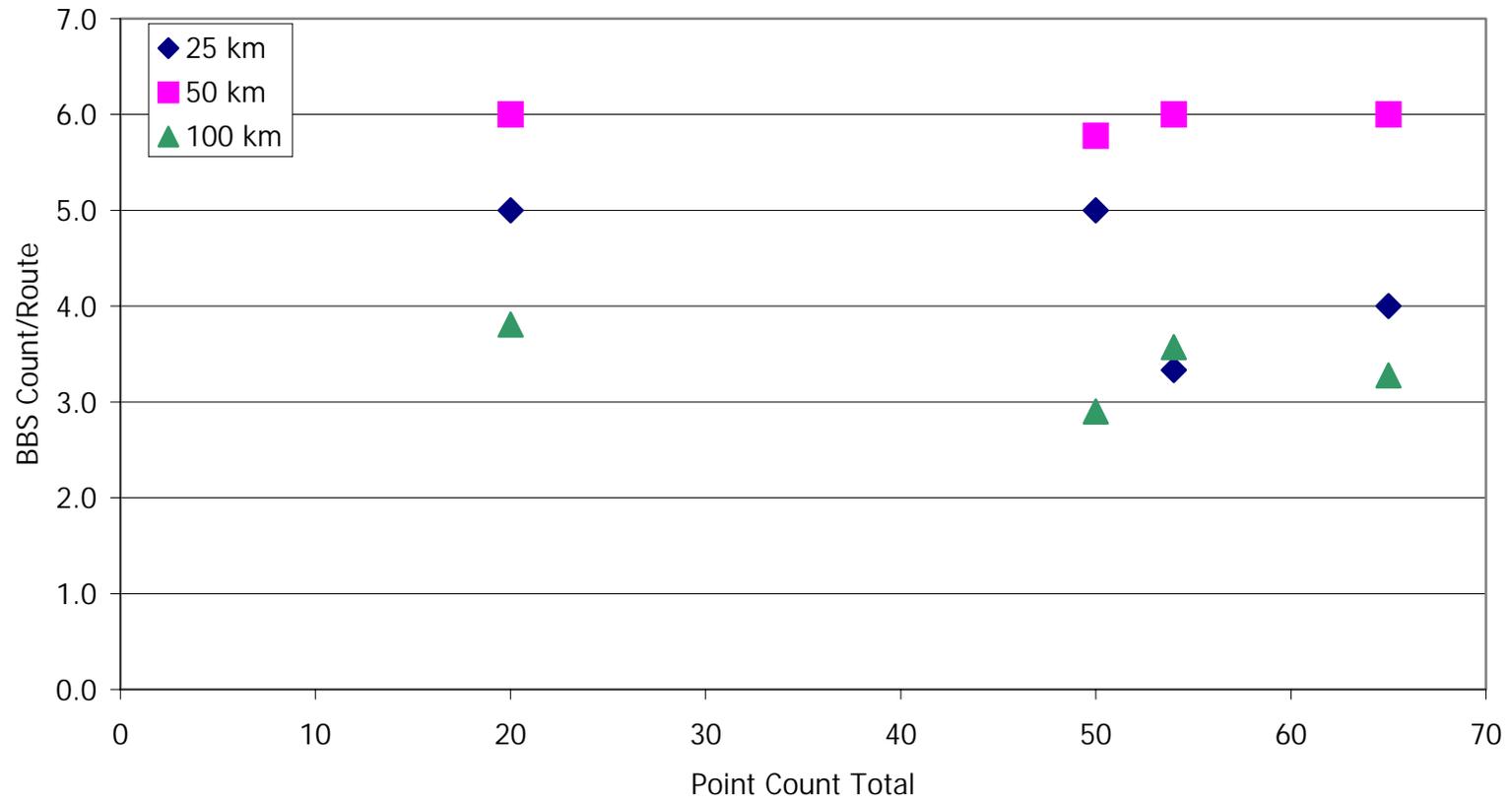
Black-and-white Warbler (INT, SEN)



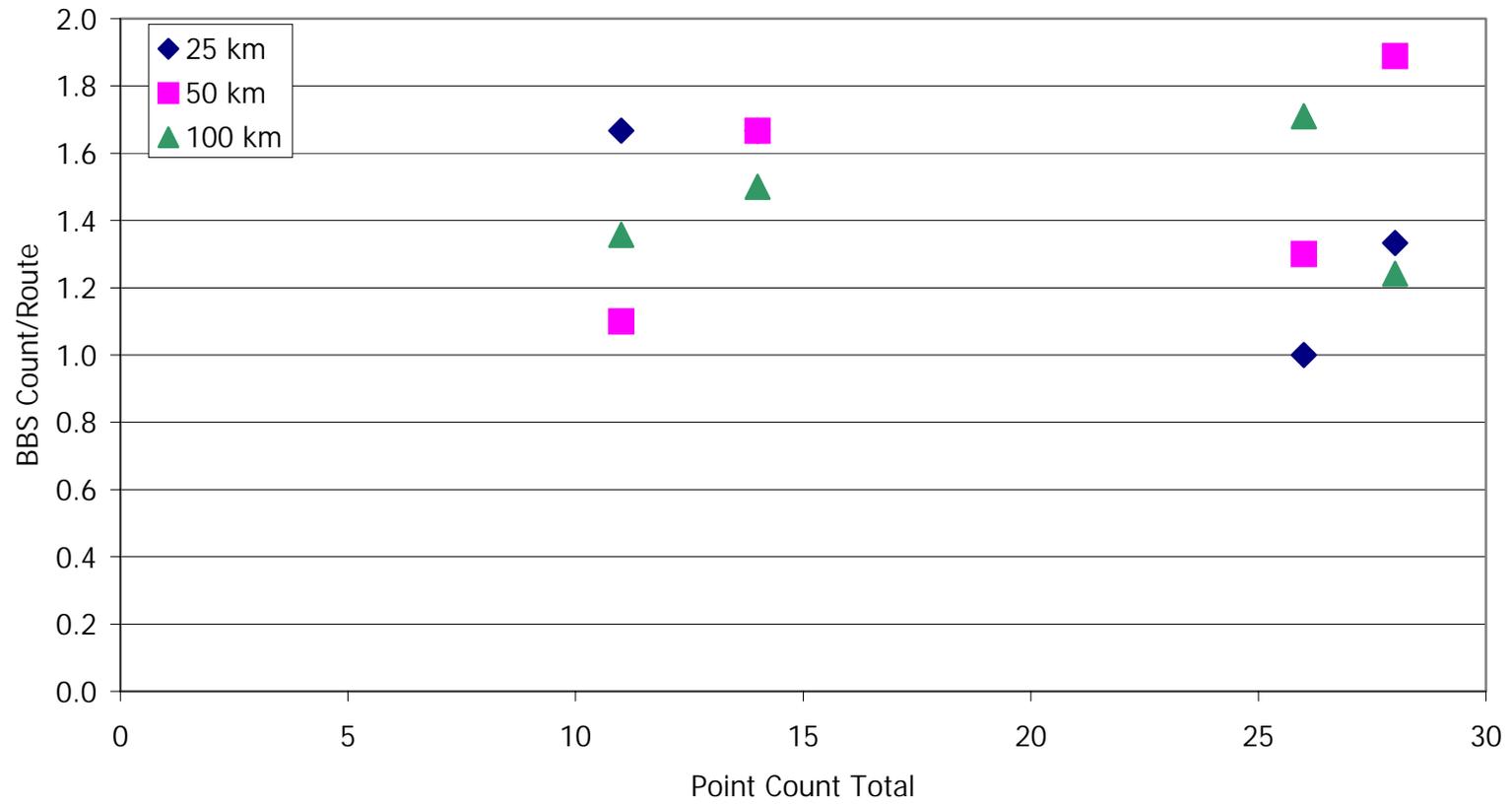
Black-throated Blue Warbler (INT, SEN)



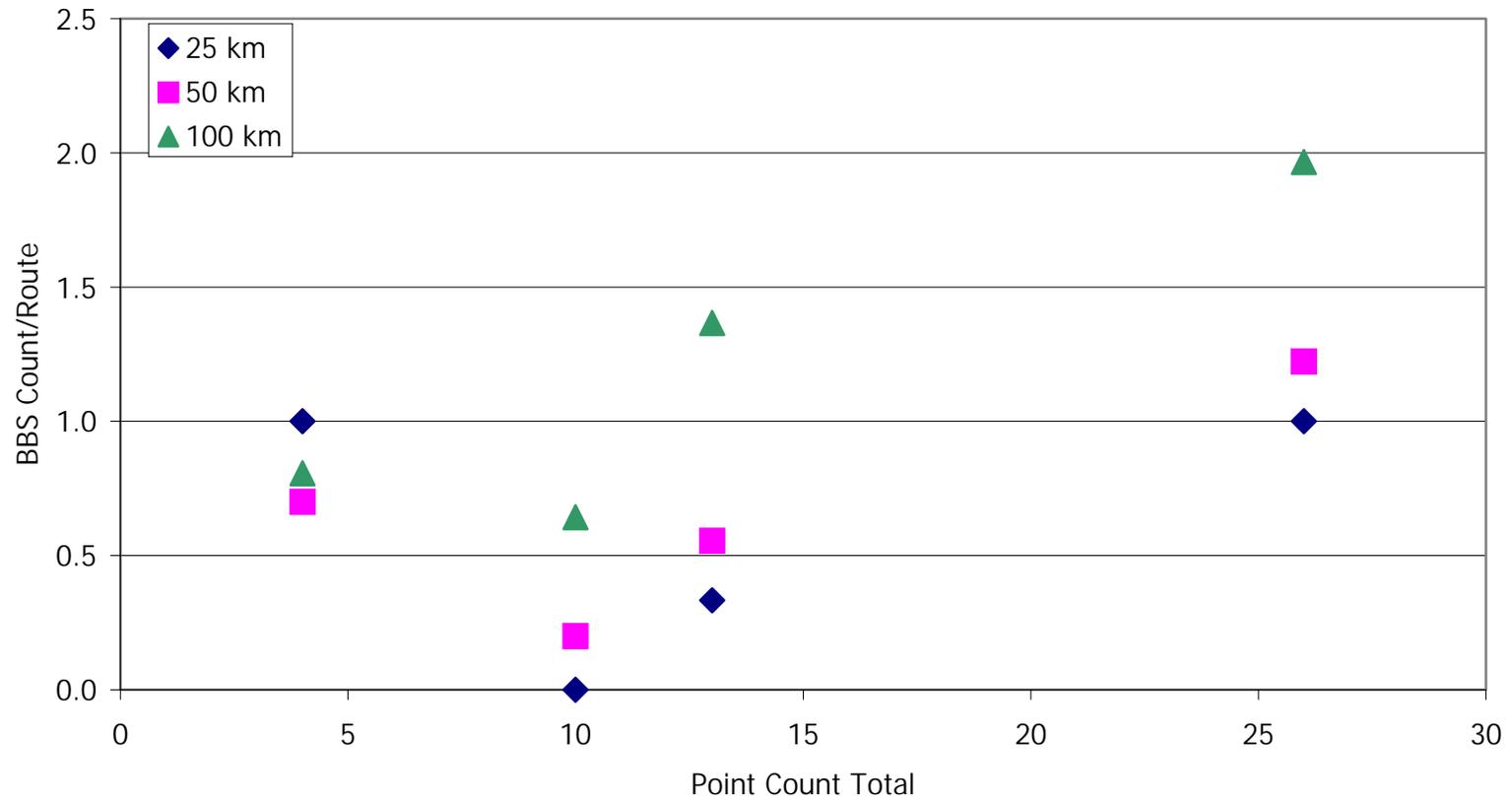
Black-throated Green Warbler (INT, SEN)



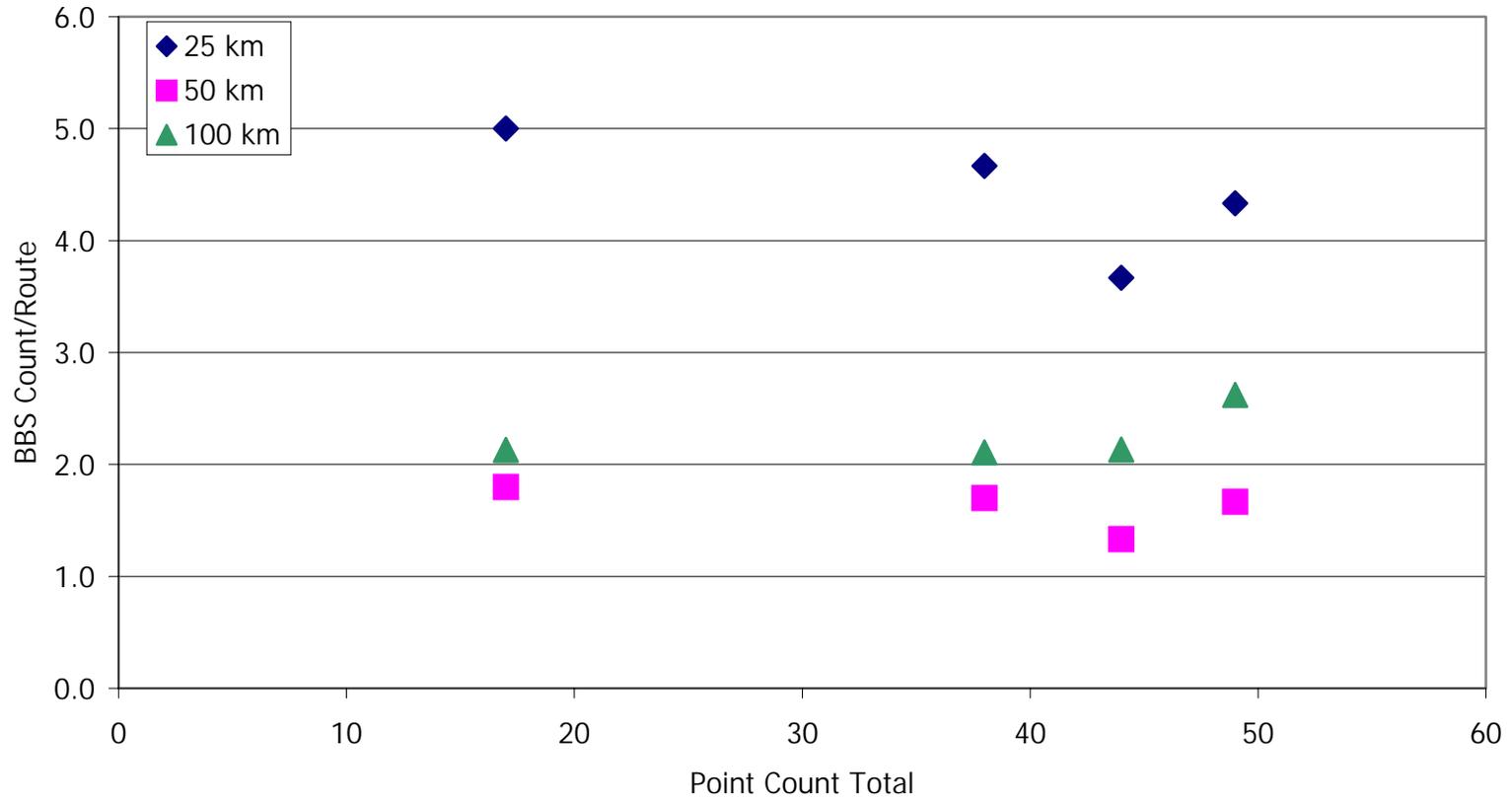
Blue-headed Vireo (INT, unknown)



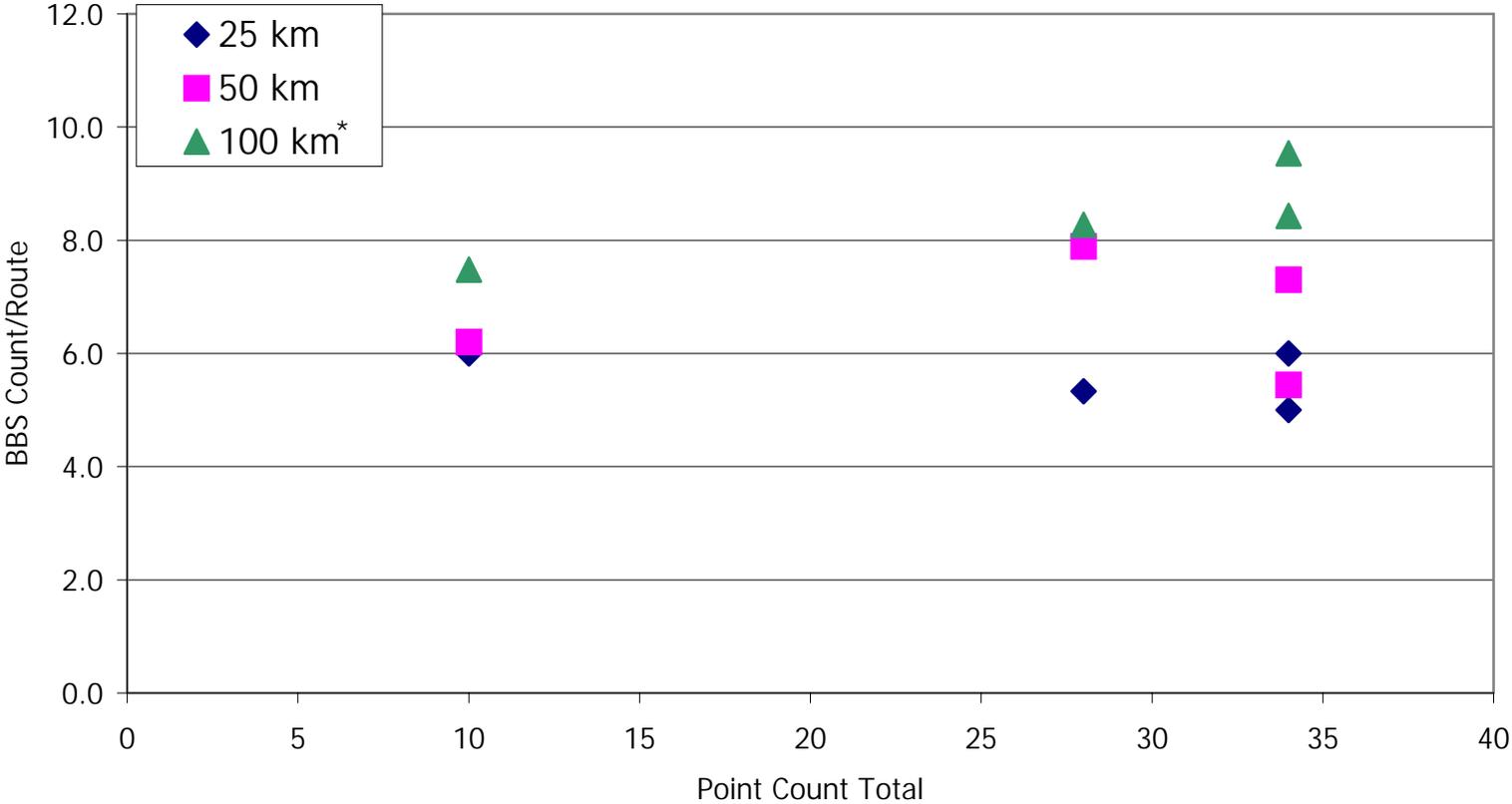
Cerulean Warbler (INT, SEN)



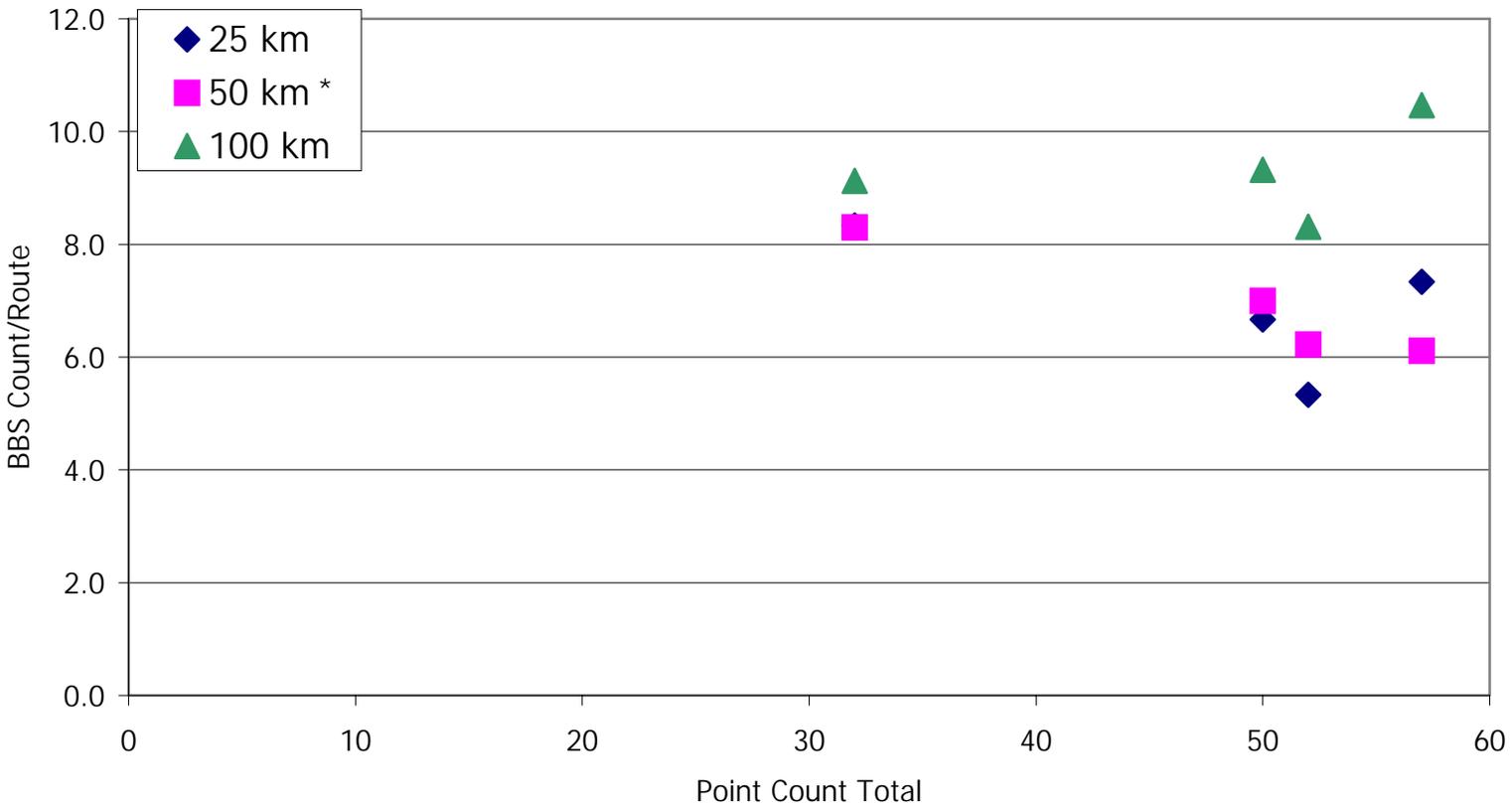
Hooded Warbler (INT, SEN)



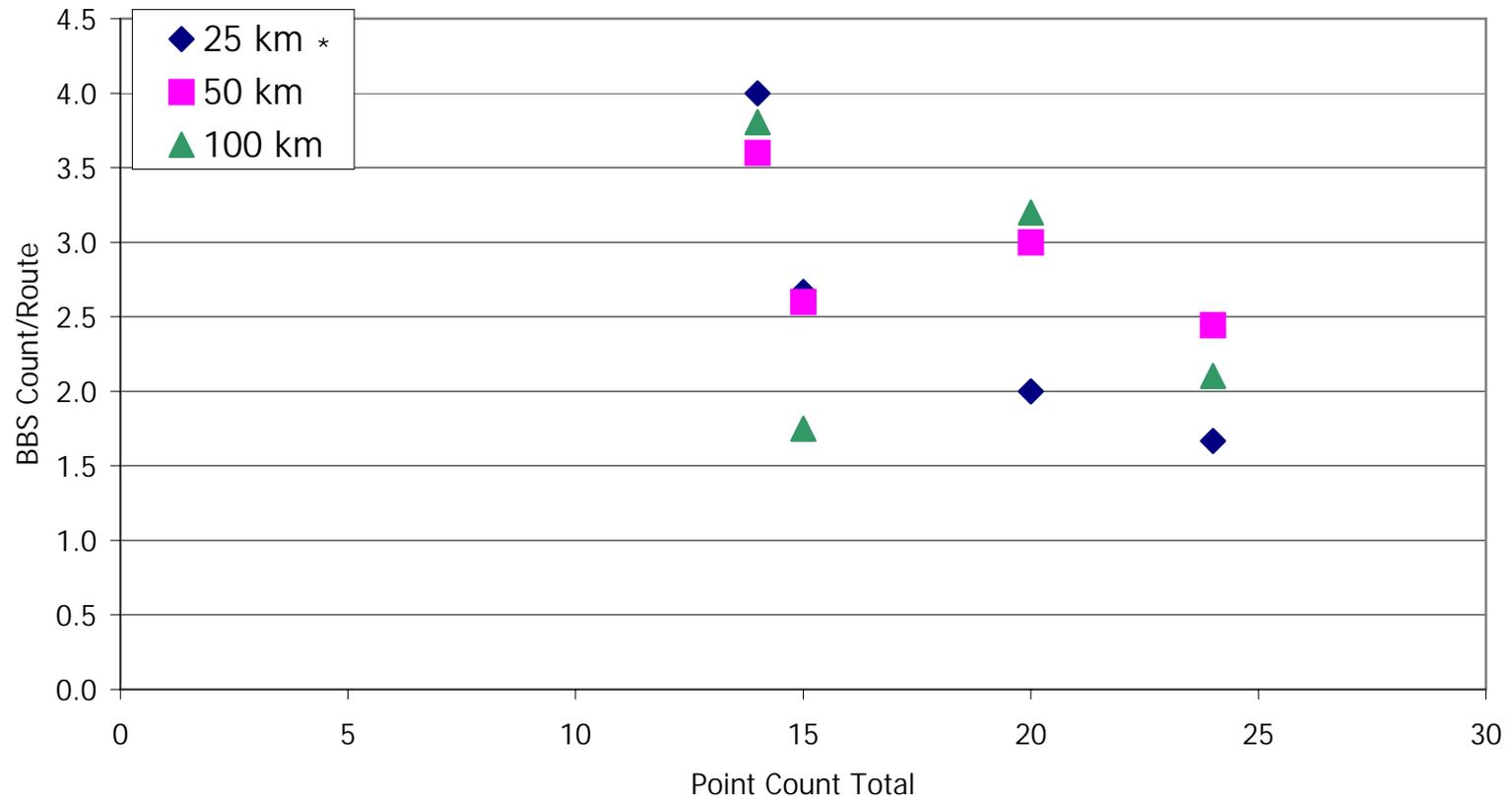
Ovenbird (INT, SEN)



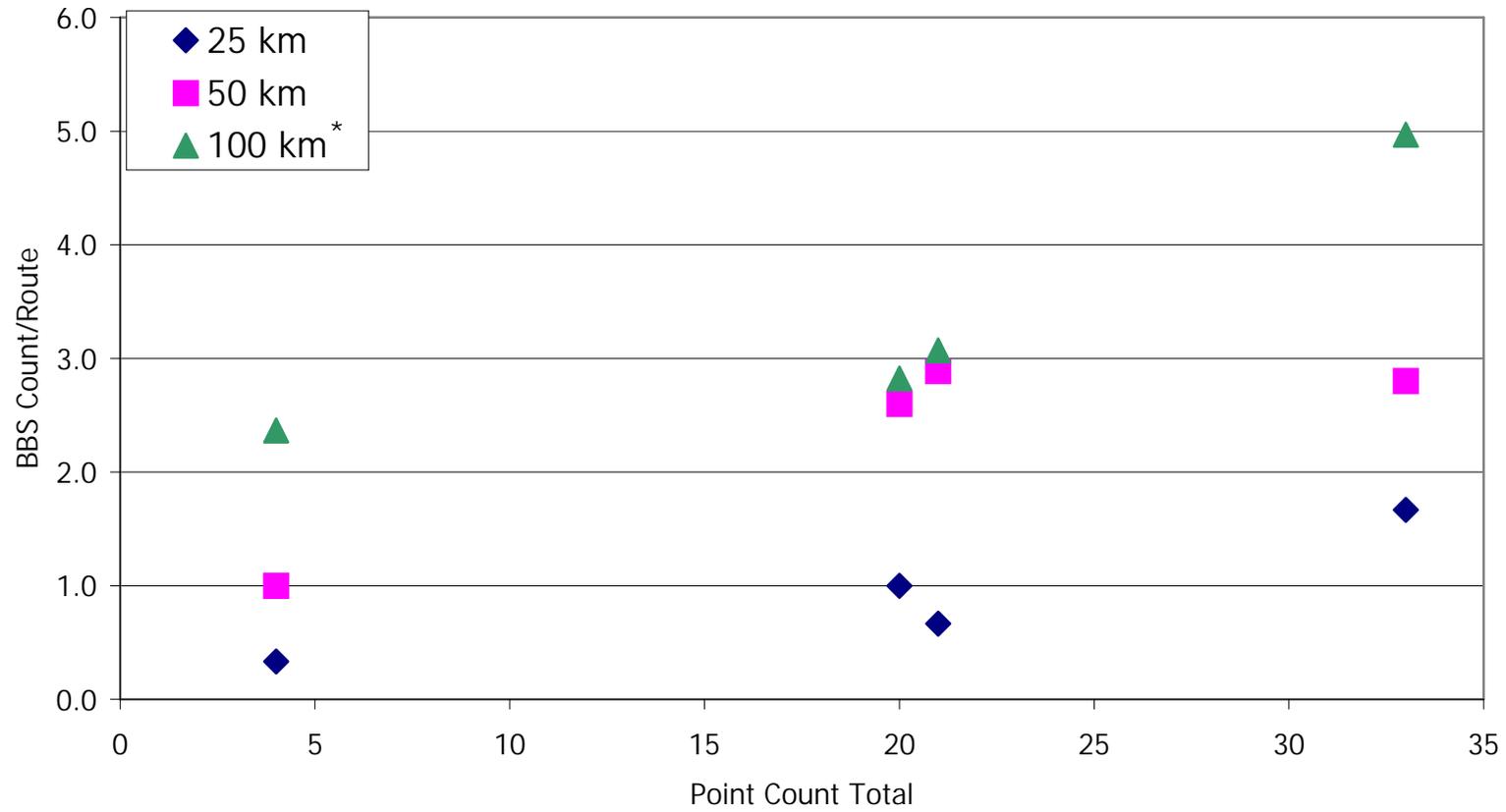
Scarlet Tanager (INT, SEN)



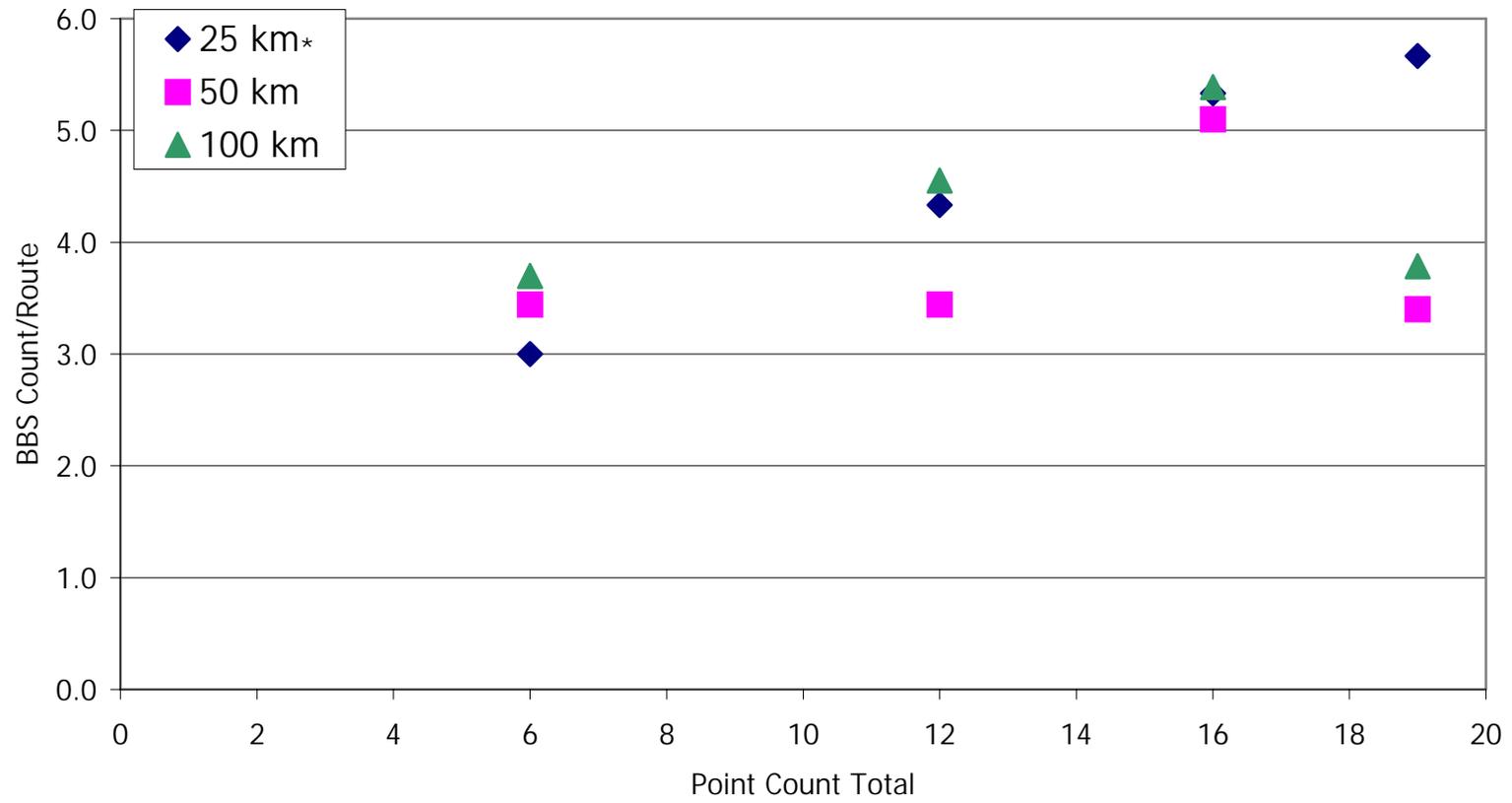
Veery (INT, SEN)



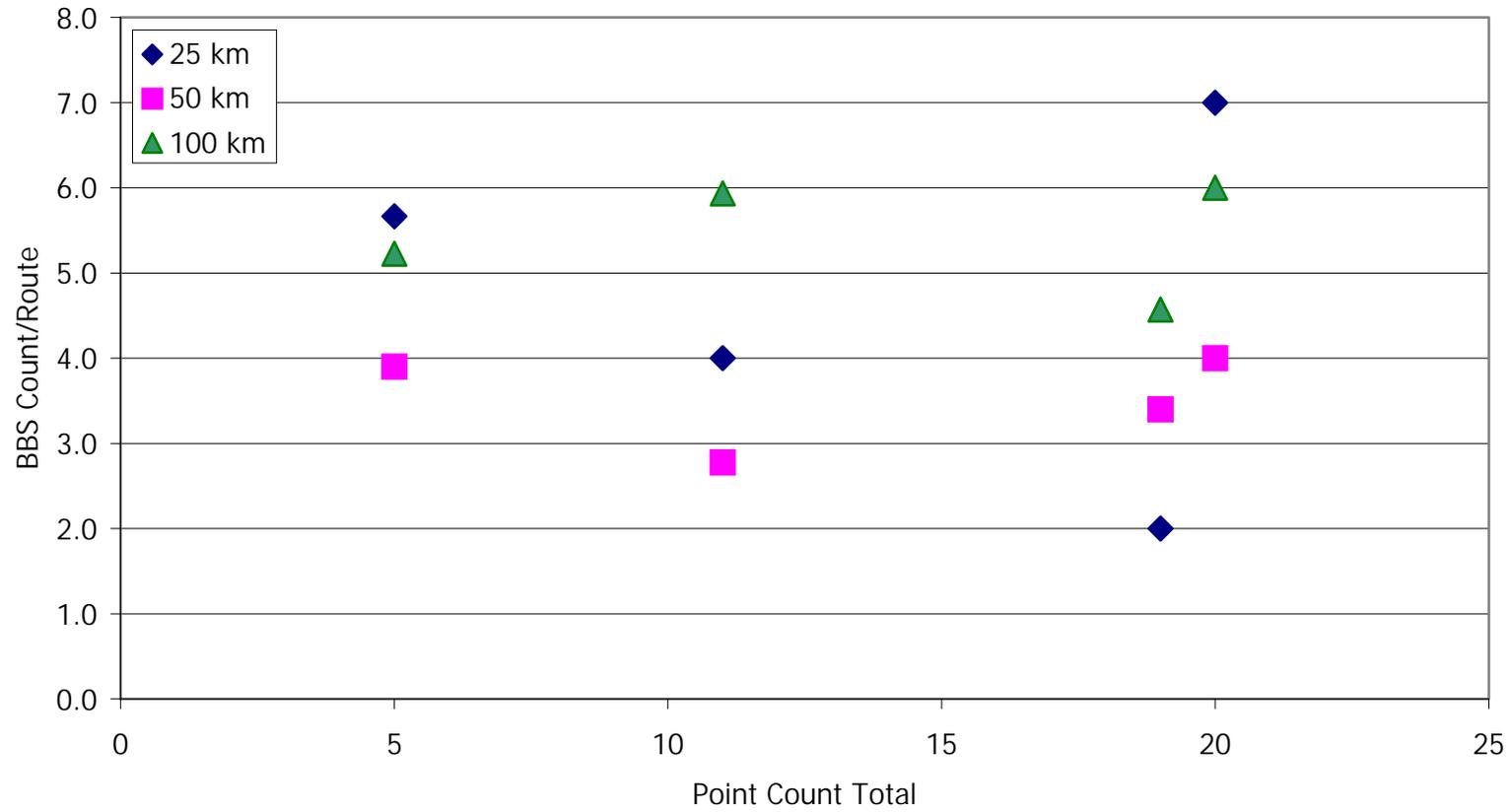
White-breasted Nuthatch (INT, SEN)



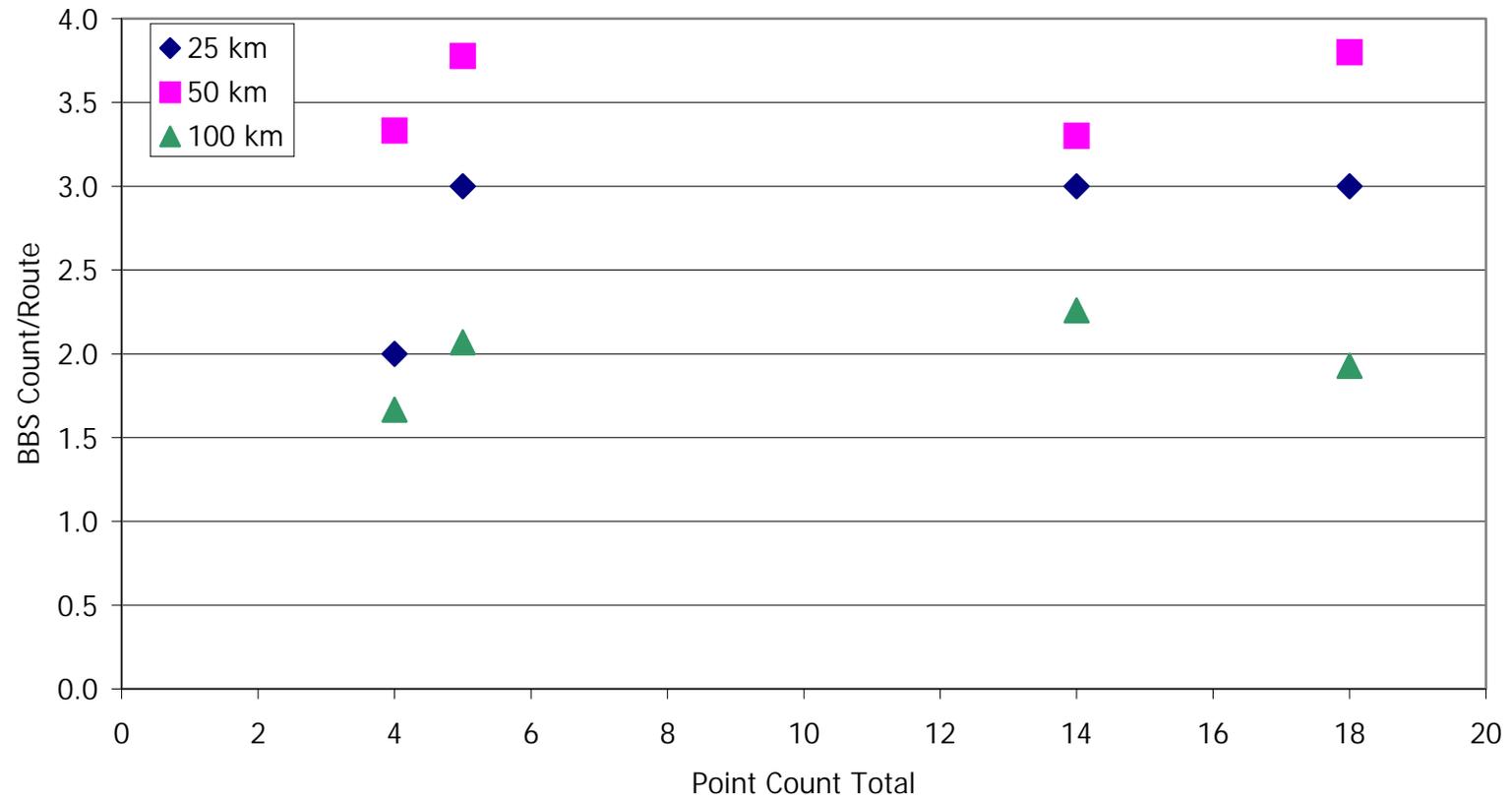
Black-capped Chickadee (IE, INS)



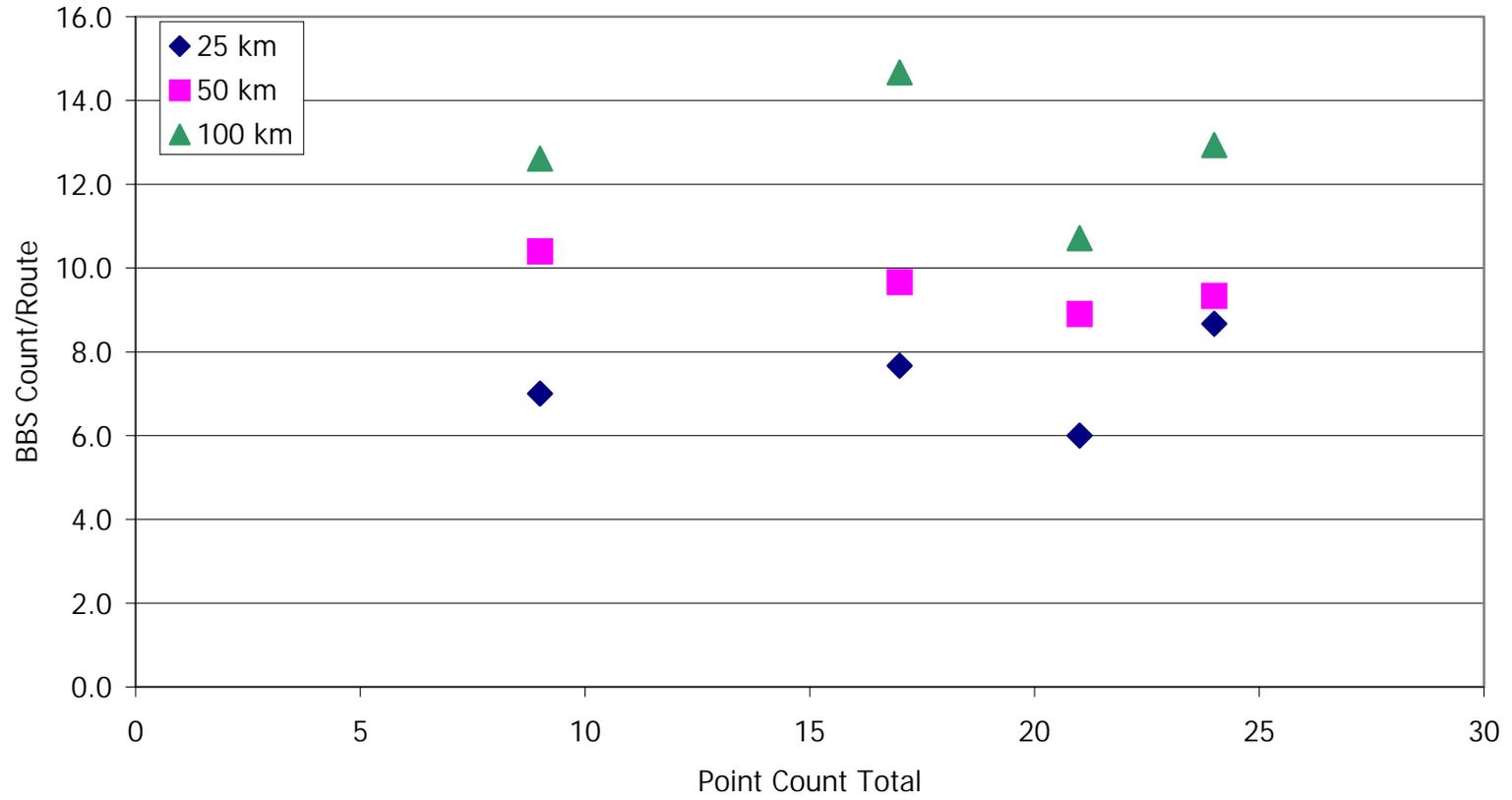
Blue Jay (IE, INS)



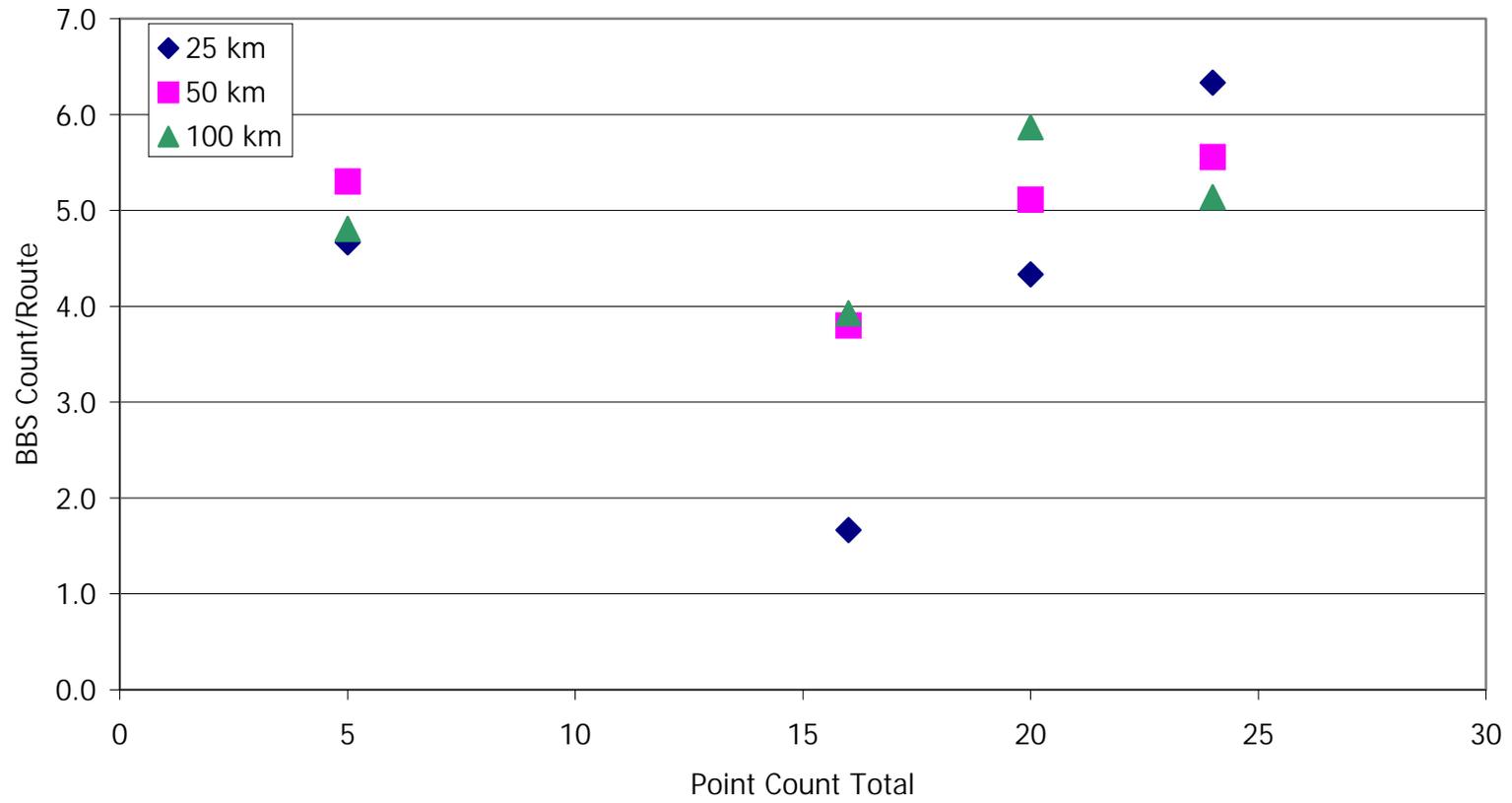
Dark-eyed Junco (IE, unknown)



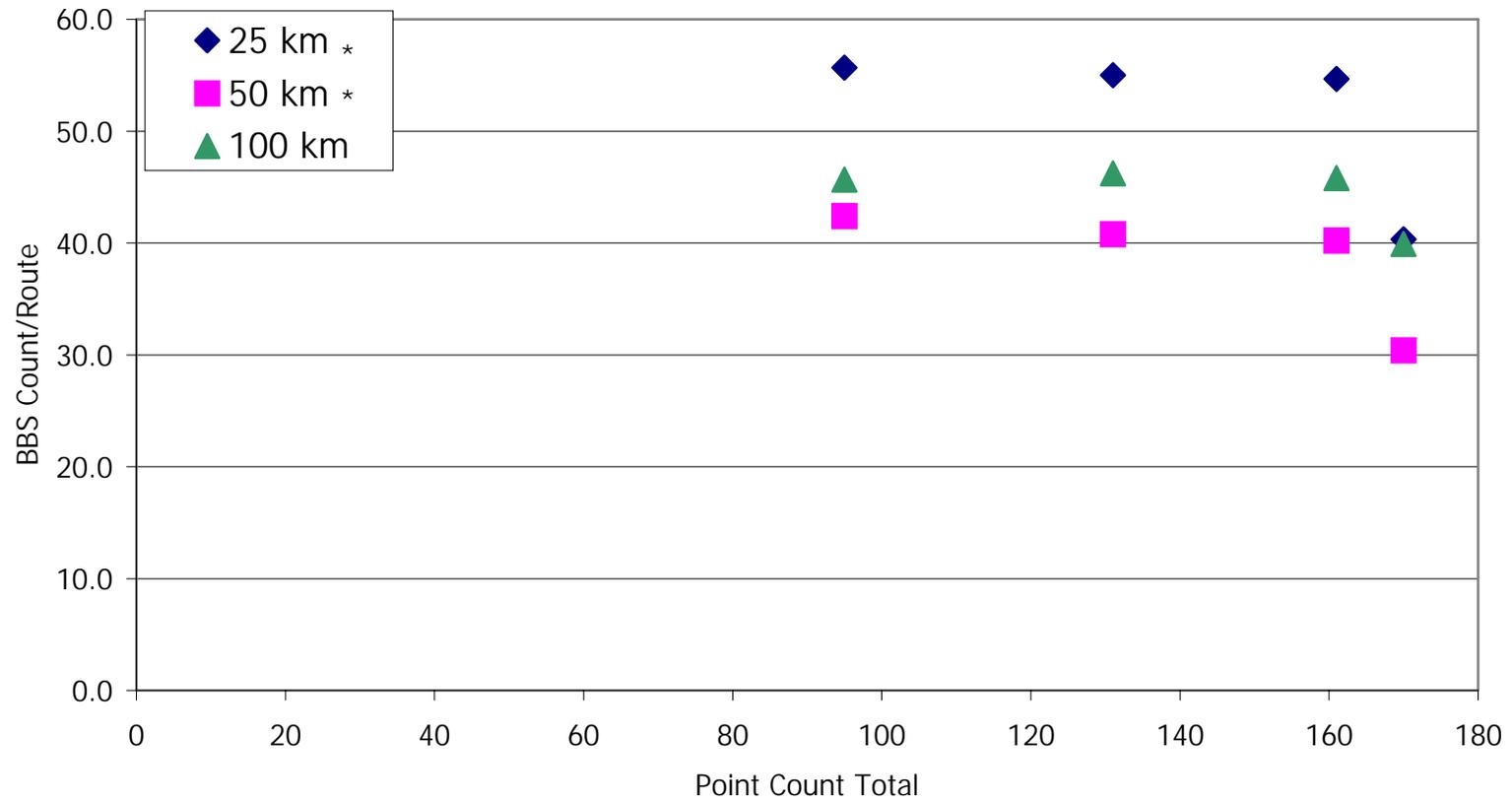
Eastern Towhee (ED, INS)



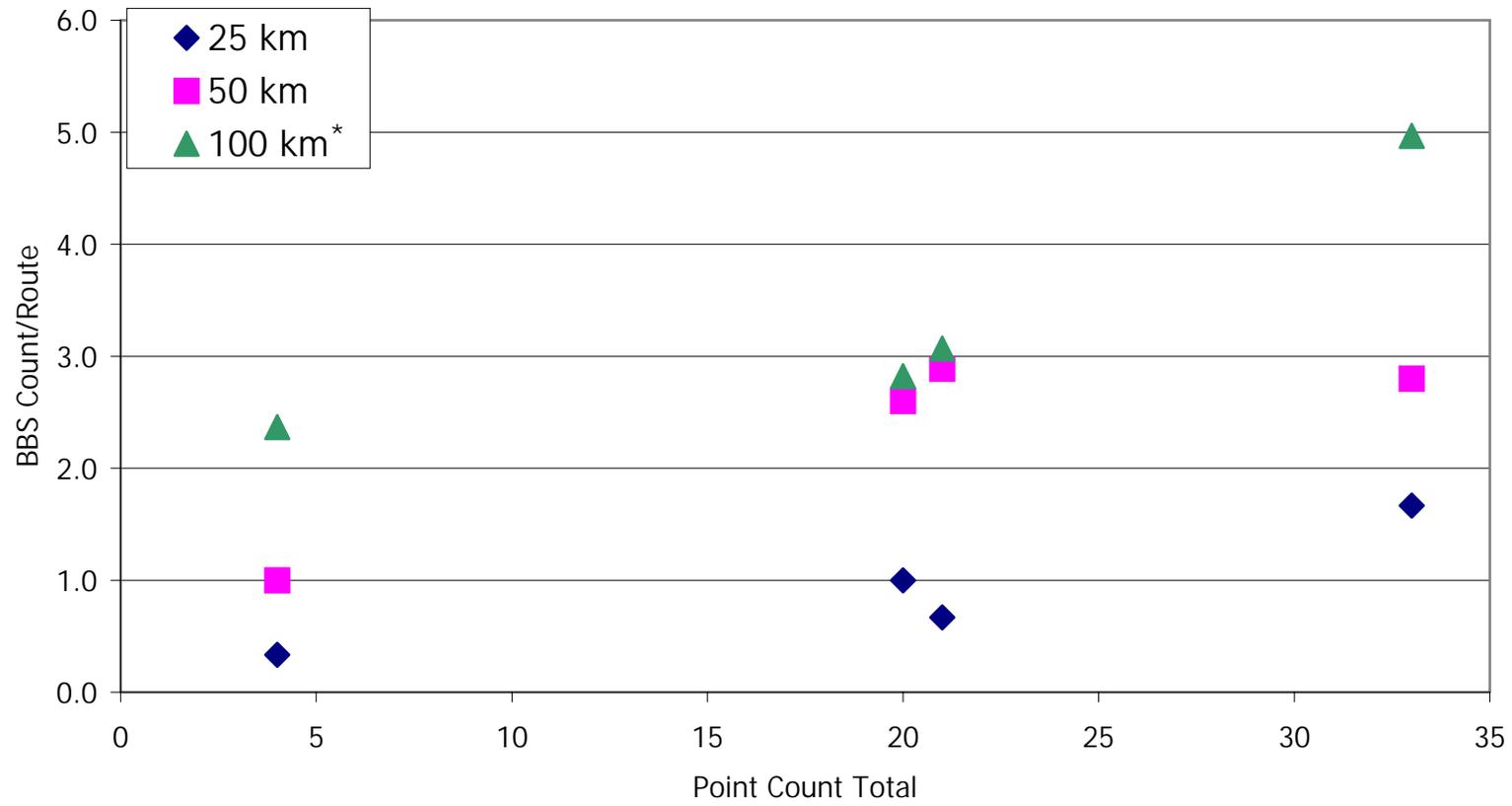
Eastern Wood-pewee (IE, INS)



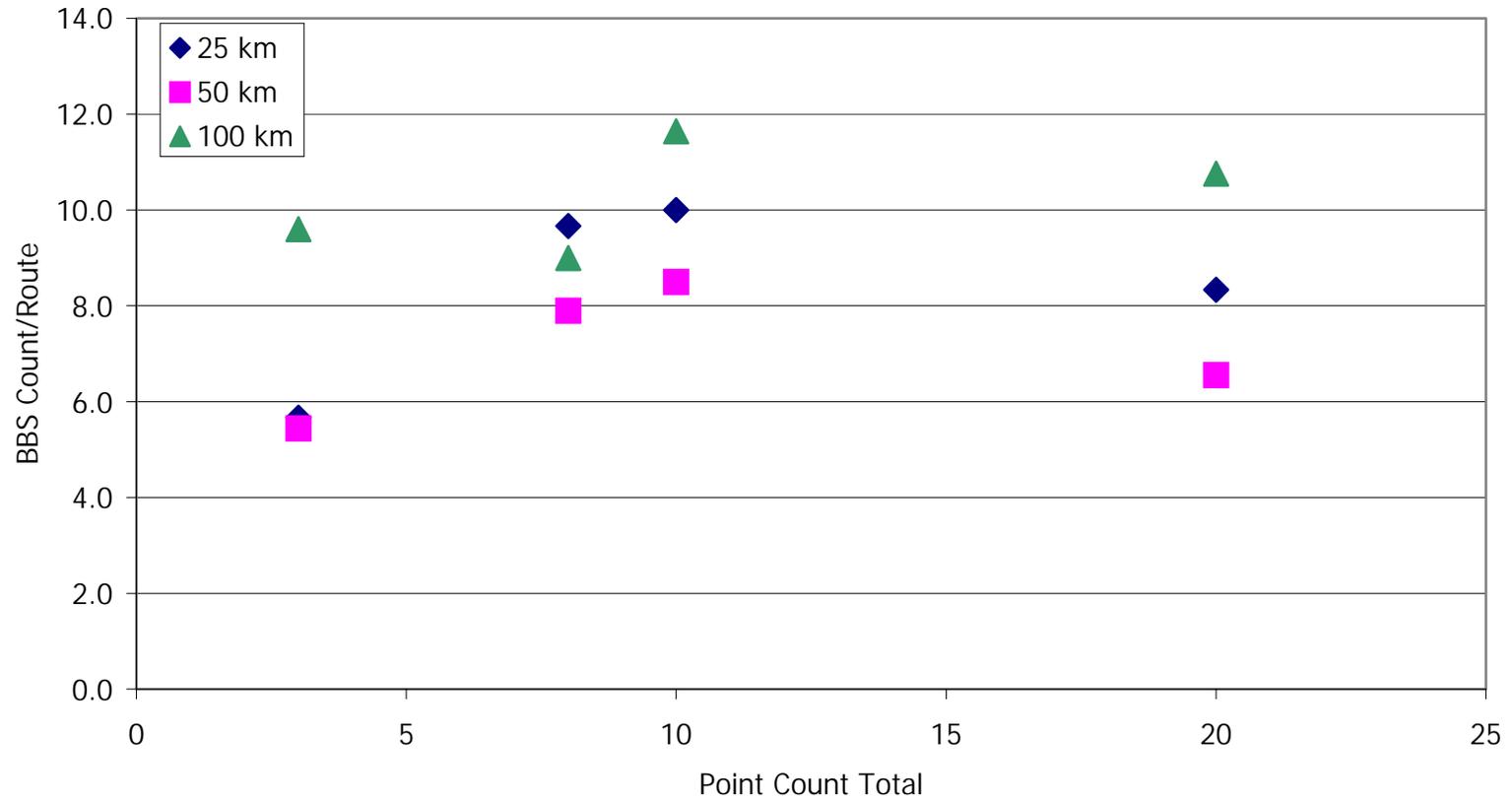
Red-eyed Vireo (IE, SEN)



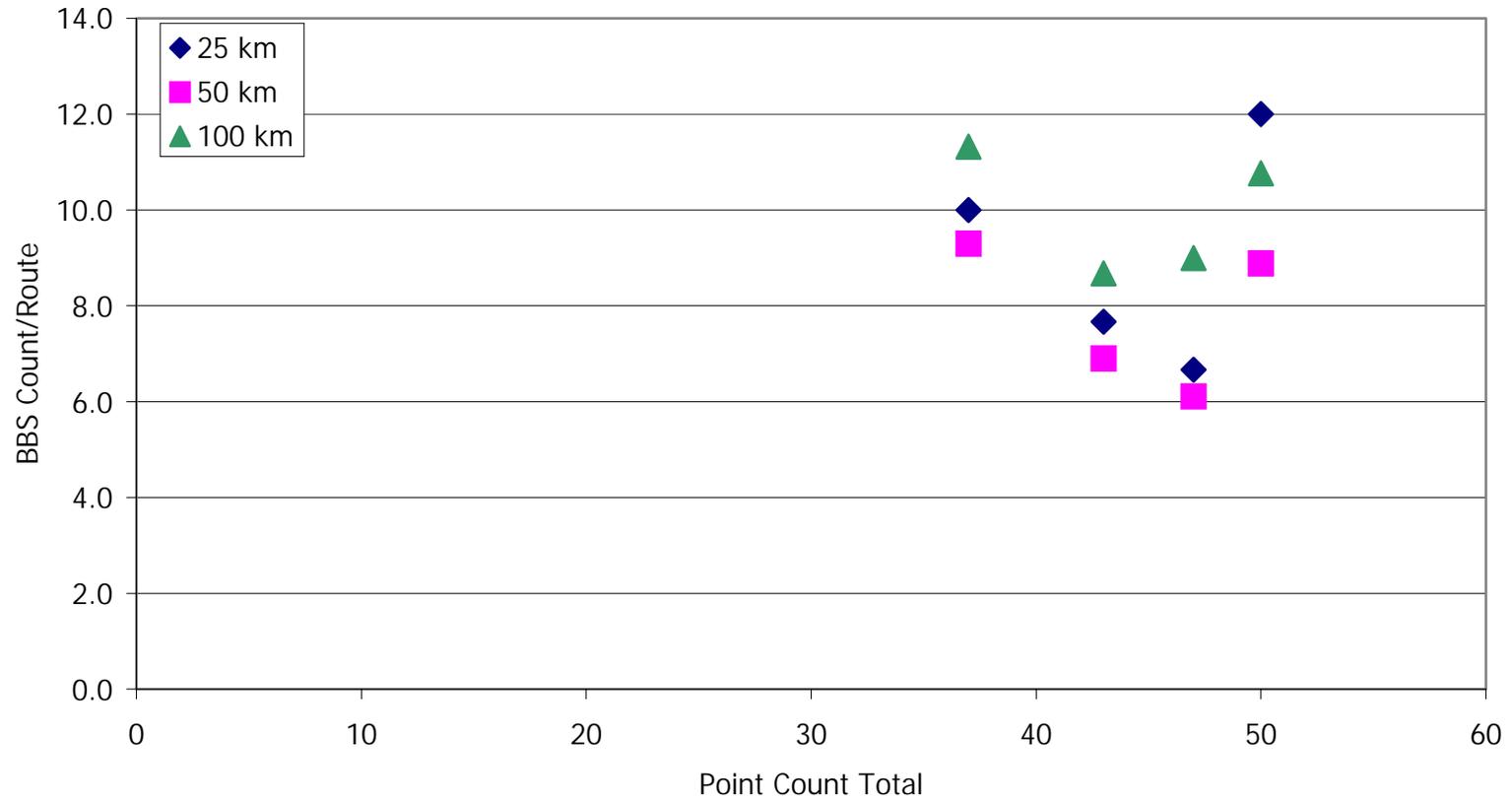
Rose-breasted Grosbeak (IE, SEN)



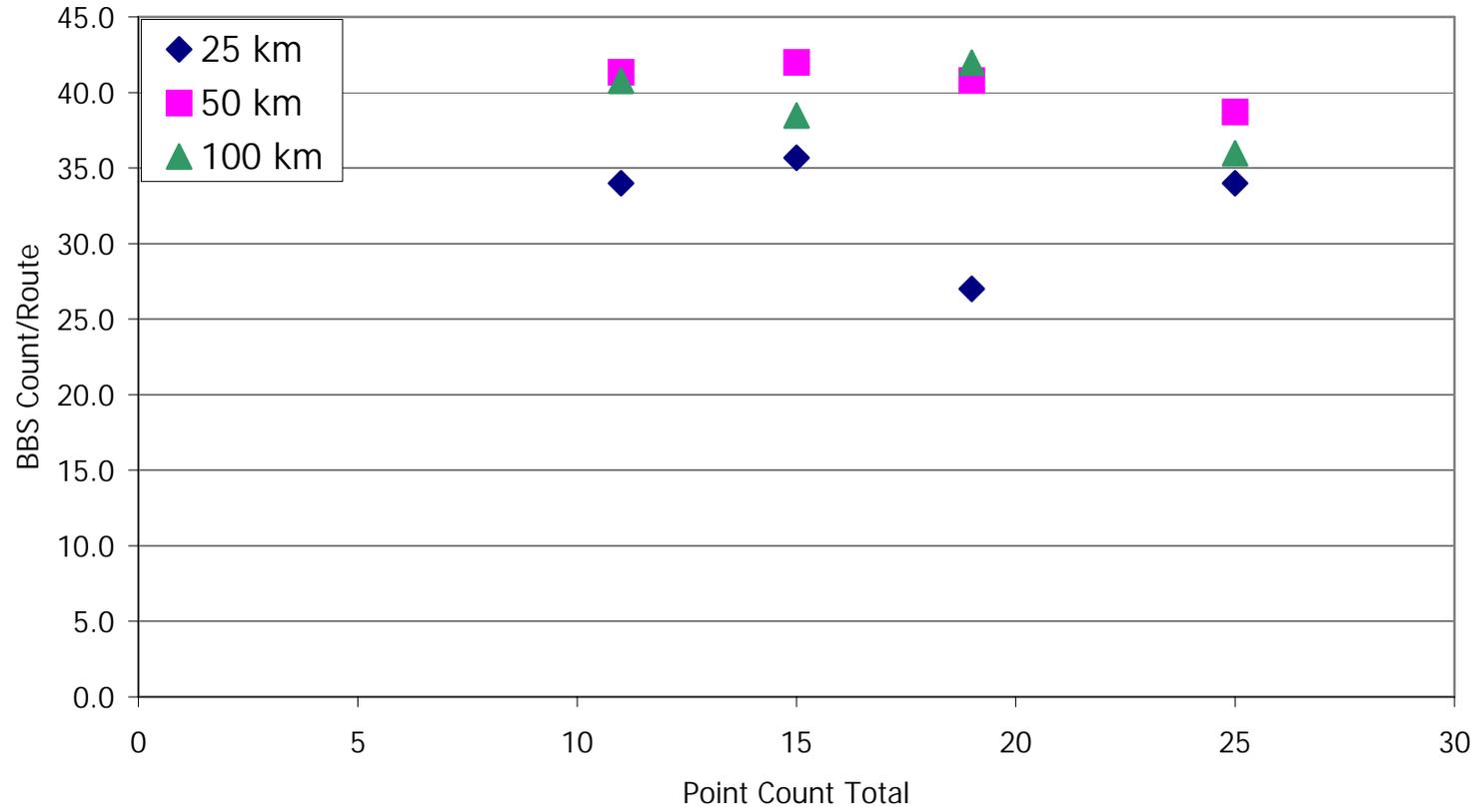
Tufted Titmouse (IE, SEN)



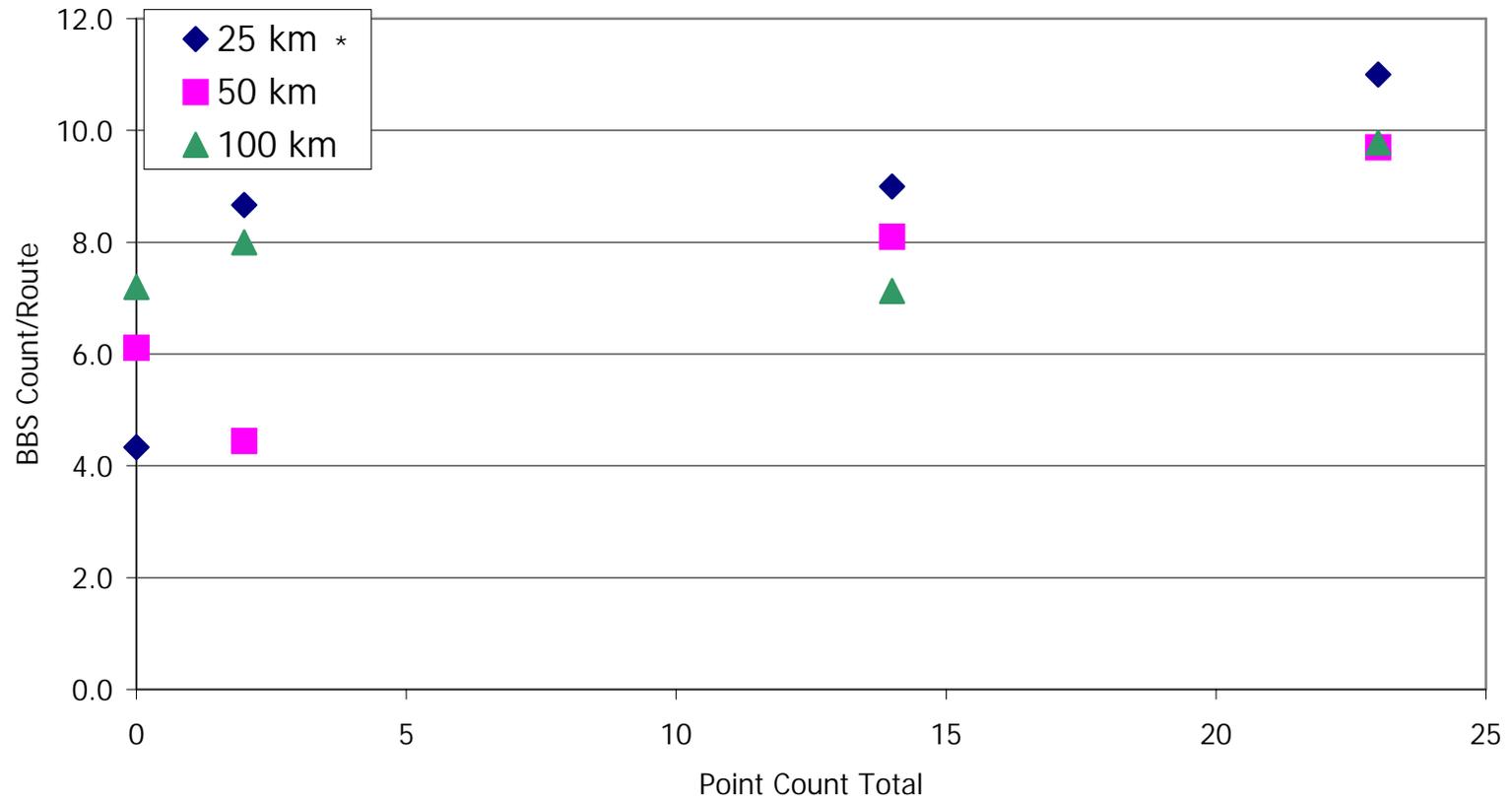
Wood Thrush (IE, SEN)



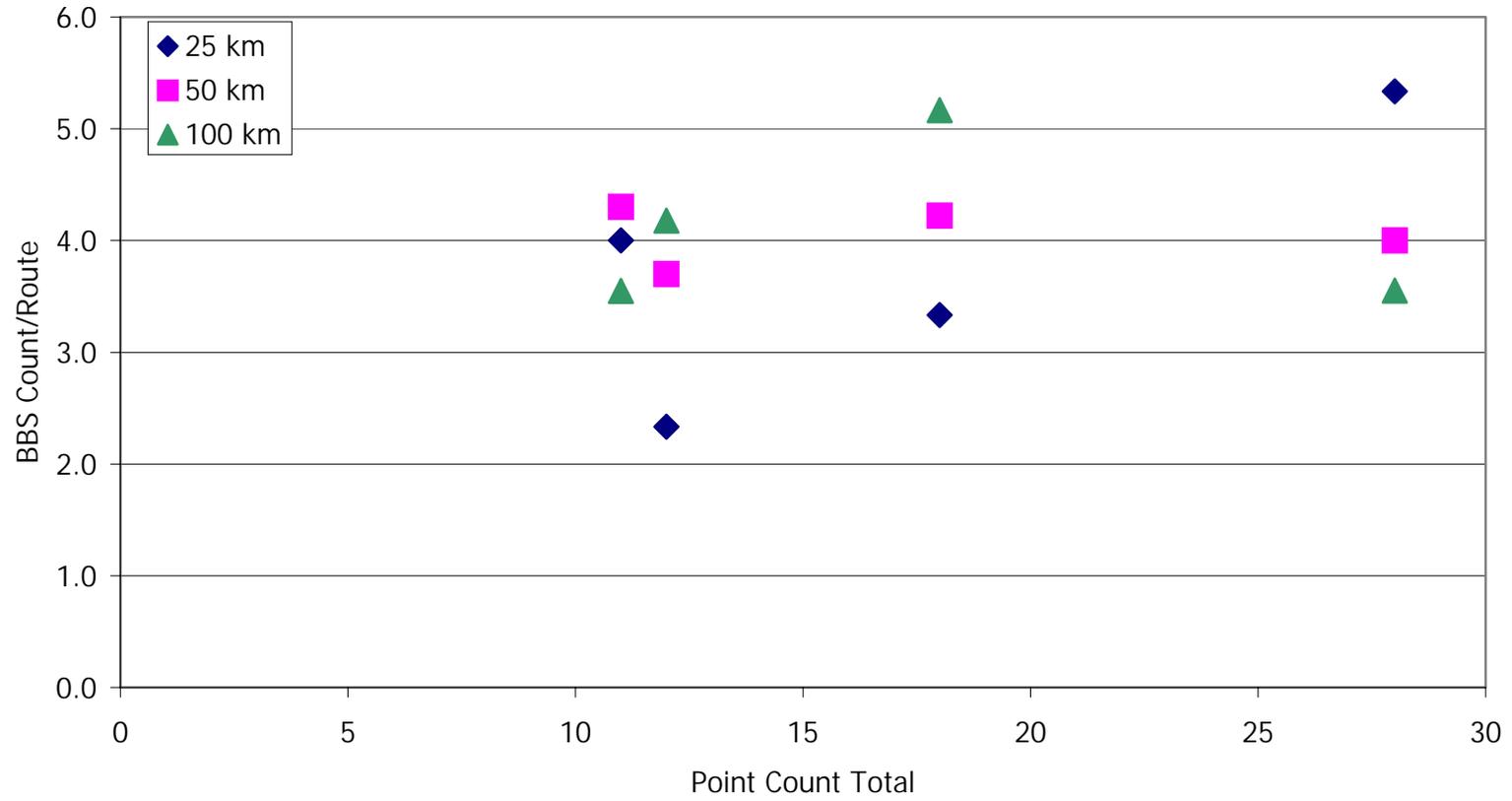
American Robin (ED, INS)



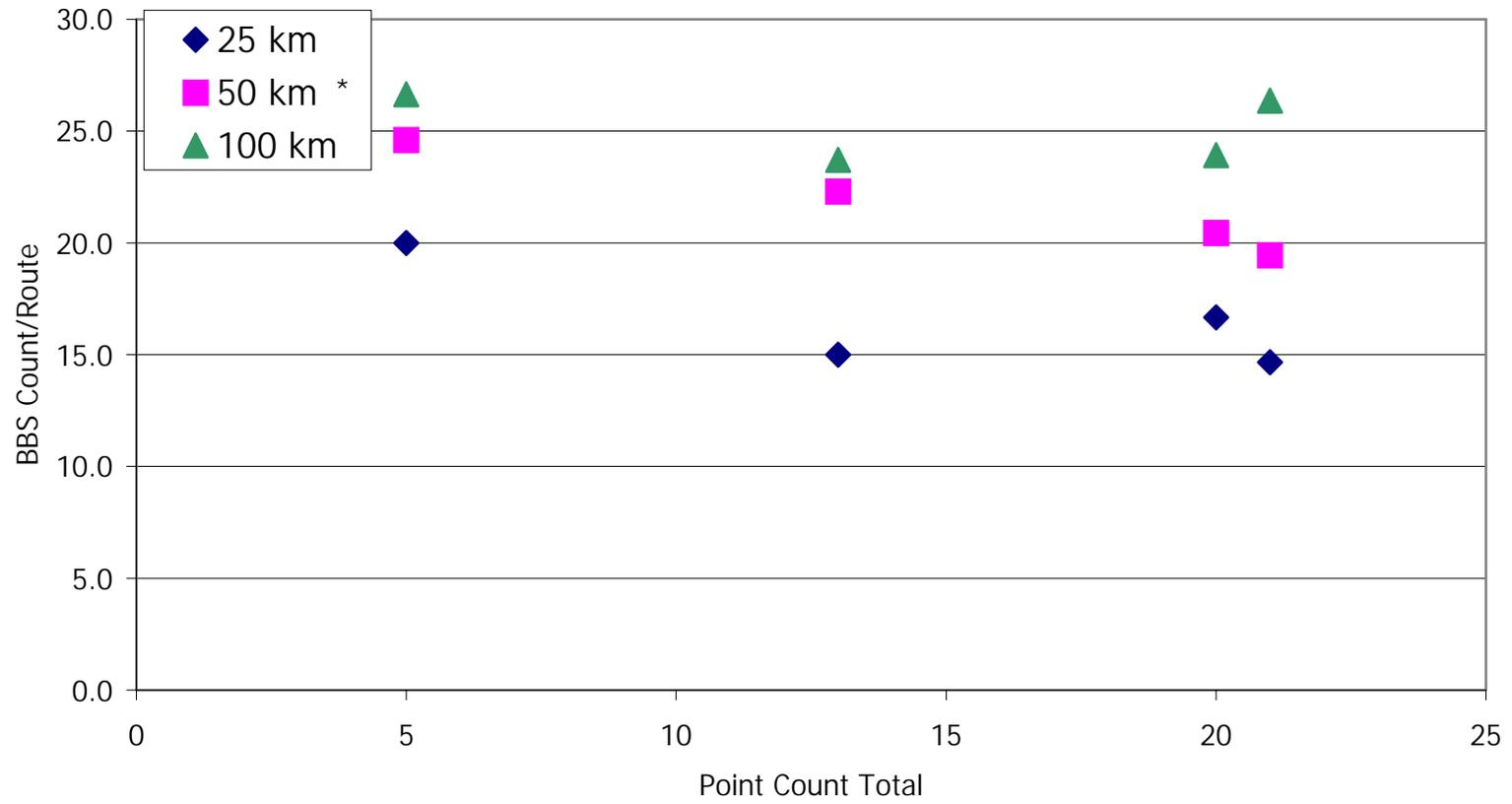
Cedar Waxwing (ED, INS)



Chestnut-sided Warbler



Indigo Bunting (ED, INS)



VITA

Gary E. Williams, Jr.

Gary Williams was born in Ocala, Florida and spent his childhood on the family farm near Oxford, Florida. Upon graduation from Wildwood High School, he enrolled at the University of Florida. After much frustration and many changes in major, Gary had an epiphany one day while snorkeling down Itcheetucknee Run in northern Florida. It was at that point that he decided to pursue a career in wildlife biology. He graduated from the University of Florida in 1993 with a B.S. in Forest Resources and Conservation. After working as a research assistant for eight months, Gary entered the M.S. program in Wildlife Ecology and Conservation at the University of Florida under the direction of advisor, Peter Frederick. Gary's M.S. research centered upon the effects of environmental mercury on the already declining wading bird populations in the Florida Everglades. Gary received his M. S. in 1997 and enrolled that same year in the doctoral program in Forest Resource Science at West Virginia University under advisor, Petra Bohall Wood. While conducting his songbird research at West Virginia University, Gary taught, co-taught, or moderated Vertebrate Natural History, Conservation Biology, Wildlife Discussion Group, and the Wildlife and Fisheries Seminar Series. He graduated in August 2002 with his PhD. Gary is currently pursuing a career in academia.