Does nest concealment in Wood Thrushes predict predation risk and female stress levels?

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Abstract

The Wood Thrush (*Hylocichla mustelina*) is a long-distance migrant that has declined severely in the last 50 years and is currently listed as a Species at Risk in Canada. This study investigated whether nest concealment from nest predators and brood-parasitic Brown-headed Cowbirds had an influence on the success of Wood Thrush nests. Through visual estimates of concealment in 186 nests over 3 years, results show that Wood Thrushes experience high nest predation (53.2%) and moderate cowbird parasitism (25.3%) in southwestern Ontario. However, nest concealment does not predict probability of having a successful nest or evading parasitism. We also tested if nest concealment impacts an incubating female's flight initiation distance (FID) or corticosterone level (a measure of stress). Although we found no correlation between these variables, this is the first step in understanding if nest site selection affects the female directly, and not just her immediate nesting success.

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Introduction

Predation is an extremely important selective pressure, and animals have evolved a variety of adaptations to defend themselves, which could be behavioral (e.g. hiding, fleeing), morphological (e.g. spines, colouration) or physiological (e.g. toxins) (Kats & Dill 1998). Choosing a safe breeding site is a potential anti-predator strategy for animals that produce stationary offspring, such as insects, reptiles, mammals, and birds (Spencer 2002; Goodnow & Reitsma 2011; Pradhan et al. 2017; Jones & Agrawal 2019). It has been shown that female Monarch butterflies (*Danaus plexipuss*) will choose to avoid laying eggs on host plants that are currently occupied by larvae of the same species, to reduce competition and predation by cannibalism of their offspring (Jones & Agrawal 2019). In freshwater turtles (*Emydura macquarrii*), studies have shown that predation of nests can influence nest site selection, where female turtles consistently build in areas where nests are more likely to survive predation (Spencer 2002). Additionally, in Indian giant squirrels (*Ratufa indica*), it has been shown that squirrels consistently choose taller trees to construct their nests, likely as a way to avoid predators (Pradhan et al. 2017). Choosing a safe nesting site is important for offspring success and fitness of the mother in species where nest site characteristics predict predation risk.

This study tests if a threatened songbird, the Wood Thrush, uses nest placement and concealment as a predator avoidance strategy. Nest predation is a major source of nest failure in many species of birds, accounting for nearly 80% of

nest failures on average (Lack 1954; Ibanez-Alamo et al. 2015; Thys et al. 2019, Jara et al. 2020). Nest predation is a strong evolutionary force in birds (Martin 1993; Willson & Gende 2000; Weidinger 2002) and an important contributor to population declines of birds (Martin 1993). Many birds have evolved a variety of strategies to defend their eggs and young from predators. These strategies can include direct defense of the nest by the parents (Montgomerie & Weatherhead 1988) or more indirect defense through placement of the nest or timing of breeding (Weidinger 2002). To reduce the risk of predation, birds could choose nesting sites in areas with a low predation risk (Martin 1993; Wilson & Cooper 1998) and attempt to conceal their nest (e.g. camouflage, dense vegetation) from diurnal predators.

The nest-concealment hypothesis (Martin & Roper 1988; Holway 1991; Martin 1993; Goodnow & Reitsma 2011; Weidinger 2002; Borgman & Conway 2015;) predicts (1) songbirds should choose nesting sites with more dense foliage than random sites and (2) the probability of nest predation should decrease with increased foliage density (Goodnow & Reitsma 2011). Previous studies in this field have found some support for this hypothesis. For example, Canada Warblers (*Wilsonia canadensis*) choose nesting sites that have significantly greater concealment and vegetation density when compared to randomly selected sites within the birds' territory (Goodnow & Reitsma 2011). Black-throated Blue Warblers (*Setophaga caerulescens*) choose dense shrub patches to build their nests, which could provide better concealment from predators (Holway 1991). However,

other experimental studies have found that high nest concealment with vegetation is not necessarily a significant factor in determining the success of a nest (Howlett & Stutchbury 1996; Burhans & Thompson 1998; Peak 2003; Li et al. 2018; Jara et al. 2020), perhaps because many predators do not hunt visually. For Wood Thrushes, I will test whether greater nest concealment is associated with reduced nest predation rate.

Nesting success of songbirds is strongly impacted by brood parasitism by the Brown-headed Cowbird (*Molothrus ater*), which is both a nest predator (via host egg removal) and a parasite of host parental care. Female Brown-headed Cowbirds lay their eggs in the nest of a host species and typically remove one or more host eggs. Most hosts accept the foreign egg and raise the young cowbirds, which are often much larger than the host young. This heightened food competition typically reduces the reproductive success of the host species by 50% or more (Brittingham & Temple 1983; Hackemack et al. 2016). Brown-headed Cowbirds were found primarily in the Midwestern United States prior to the 1800s, but with extensive deforestation and conversion to agricultural land, Brown-headed Cowbirds have expanded their range all over North America (Brittingham & Temple 1983). Many songbirds within this range have not coevolved with Brown-headed Cowbirds, so they are evolutionarily naïve and lack defense mechanisms against brood parasites. In some studies, rates of parasitism by Brown-headed Cowbirds are not influenced by concealment of the nest, or other nest site characteristics (Hackemack et al.

2016). With Brown-headed Cowbirds being diurnal and visually oriented, increased nest concealment should reduce rates of brood parasitism in Wood Thrushes.

Although the nest concealment hypothesis expects females to conceal their nests as much as possible, in most species there is wide variation among nests in extent of concealment. Why do some females not do a better job of hiding their nests? Nest site selection may involve a tradeoff between concealing the nest from predators and having sufficient visibility around the nest to detect approaching predators (Götmark et al. 1995). If a nest is well concealed, the female bird may not be able to detect an approaching predator in time, and risk injury or death to herself. Timing of escape for prey animals is crucial to avoid a lethal encounter, so choosing a partially concealed nest could maintain a sufficient view of the nest site surroundings and reflect the tradeoff between minimizing both nest predation and predation on parents (Götmark et al. 1995).

The distance between the female parent and the approaching predator when escape is initiated is defined as the "flight initiation distance" (FID), which can be adjusted depending on the situation (Javurkova et al. 2012). If the current value of reproduction is high (ie. nestlings would take a great deal of time and energy to replace) the female bird should be reluctant to flush and give away her position to a predator, reducing FID (Montgomerie & Weatherhead 1988). Additionally if the risk of predation is low, many prey animals will lower their FID and flee the nest only when the predator is very close (Javurkova et al. 2012). Nest concealment can also

influence FID by obstructing the bird's view of the surrounding area, obscuring potential predators from the female bird until they are very close to the nest (Javurkova et al. 2012). Wood Thrush females may be placing nests in areas with lower vegetation concealment in order to better detect predators. In this study, I test if the distance at which female Wood Thrushes flush from the nest as a predator approaches is negatively correlated with extent of nest concealment.

Nest placement could also have physiological benefits to nesting females if this reduces their stress levels. Physiologically, a response to stress is caused by the activation of the hypothalamus-pituitary-adrenal (HPA) axis, which increases the secretion of corticosterone (Wingfield et al. 1998; Williams et al. 2008). The level of stress a bird is experiencing can be quantified by measuring the amount of corticosterone in the blood. Previous research has found that birds who experience higher predator abundance also have higher baseline levels of corticosterone (Clinchy et al. 2004). These high corticosterone levels can have long-term effects, such as delayed breeding (Schoech et al. 2009) and reduced reproductive success (Bonier et al. 2009). Females with highly concealed nests may have lower risk of nest predation but at the expense of higher risk of mortality to themselves, which should induce chronic stress. I am aware of only one study that has investigated the relationships between FID, nest concealment, and stress response in birds, which was on nesting Eider Ducks (*Somateria mollissima*) (Seltmann et al. 2014). Female Eider ducks who were less responsive to induced handling stress, as measured by the increase in body temperature, were found to nest in more concealed nesting

sites (Seltmann et al. 2014). This was explained by personality differences among individuals in that bold (low FID) and high risk-taking individuals (low responsiveness to stress) choose concealed nest sites to maximize their reproductive success even if this increases predation risk to themselves. However, corticosterone levels in female eider ducks did not vary significantly with nest concealment, which was unexpected. In this study, I examine the relationship between corticosterone levels in female Wood Thrushes and nest concealment.

The Wood Thrush (*Hylocichla mustelina*) is a long-distance migrant that has declined severely in the last 50 years and is currently listed as a threatened Species at Risk in Canada (Government of Canada 2017). Wood Thrushes are known for nesting in low branches of the shrub layer, usually less than 5m from the ground, making their nests easily accessible for study (Birds of the World 2020). They nest in a variety of habitats ranging from mature forest interior to scrubby forest edge (COSEWIC 2012), they are double brooded, and a breeding pair will continue to re-nest after a nest failure (Newell & Kostalos 2007). The relative abundance and accessibility of Wood Thrush nests make this species an ideal subject for studying nest characteristics and concealment.

Previous work on this species has found mixed results for whether dense vegetation near the nest or nest concealment predicts nesting success. Farnsworth & Simons (1999) found that canopy cover directly above the nest, but not shrub density, was significantly correlated with successful Wood Thrush nests in a large

contiguous forest. Newell & Kostalos (2007) estimated nest concealment, using a scale of 0 – 3, of Wood Thrushes nesting in a highly fragmented landscape. They found no evidence that nest concealment or canopy cover predicted nest success and, surprisingly, that stem density near the nest was associated with higher predation. Further studies of fragmented landscapes, particularly in Canada where Wood Thrushes are threatened, are needed because small fragments can be population sinks due to high nest predation and cowbird parasitism, contributing to overall population declines (Brittingham & Temple 1983).

I hypothesized that Wood Thrushes nesting in fragmented landscapes, where predator risk is generally high, use nest concealment behaviour to reduce the risk of nest predation. I predicted that nests placed in areas of high concealment would be less likely to be depredated, and less likely to be parasitized by Brown-headed Cowbirds, compared with more visible nests. Unlike prior studies on this species, I quantified nest concealment in detail via analysis of images of nests. Additionally, I tested for the first time whether nest concealment influences stress levels in incubating females and their flight initiation distance in response to a predatory threat. I predicted that greater nest concealment would result in shorter flight initiation distances and tested if corticosterone levels of incubating females are related to nest concealment.

Methods

Study sites

In 2017, 2018 and 2019, Wood Thrush nests were found within forest fragments throughout Norfolk County, southwestern Ontario, a region with 17% forest cover located on the north shore of Lake Erie (Eng et al. 2011). Forest fragments were selected based on sufficient forest coverage, land ownership of the forest, and distance between study sites for logistical purposes. Forest fragments were categorized into 10 small fragments (11 – 69 ha) and 10 large fragments (162 – 500 ha) and consisted of deciduous and mixed forest. Within these fragments, forest cover was fairly continuous and only interrupted by walking trails, small streams, and ravines. Video documentation of nest predators of Wood Thrush nests in southwestern Ontario forests include Raccoons (*Procyon lotor*), Cooper's Hawks (*Accipiter cooperii*), American Crows (*Corvus brachyrynchos*), Blue Jays (*Cyanocitta cristata*), Red Squirrels (*Tamiasciurus hudsonicus*), Eastern Chipmunks (*Tamias striatus*), Eastern Gray Squirrels (*Sciurus carolinensis*), Red-tailed Hawks (*Buteo jamaicensis*), Sharp-shinned Hawks (*Accipiter striatus*), and Short-tailed Weasels (*Mustela erminea*) (Friesen et al. 2013).

Locating and monitoring nests

Nests were located May-Aug by (i) finding singing males within the study sites and then intensively searching likely areas within their territories, (ii) by finding females carrying nesting material and following them to their nesting

location, or (iii) searching typical nesting habitats. Nests were checked on average every 8 days. To check the nests in the least invasive way possible, a cellphone with video recording capabilities was attached to a long stick and raised over top of each nest, while standing as far back from the nest as possible. The video would be reviewed away from the nest and allow us to determine if it remained active. Indicators such as eggshells, an empty nest that previously contained eggs, or feathers from nestlings/adults would allow us to mark the nest as depredated. For active nests, when the nestlings survived to be approximately 10 days old, the nestlings were banded with aluminum Canadian Wildlife Service bands and fitted with radio tags by the other researchers also studying this breeding population of Wood Thrushes. Female Wood Thrushes will incubate their eggs for about 13 to 14 days, and young will begin to fledge (leave the nest) around 12 days after hatching (The Cornell Lab of Ornithology 2017). For this study, each nest was checked one final time when the nestlings were 10 days old, and the nest was recorded as successful if nestlings were present, or depredated if nestlings were absent. For this reason, a nest was considered successful if the nestlings survived to be 10 days old. We also noted the presence or absence of Brown-headed Cowbird eggs or nestlings (hereafter "cowbirds") in the nest when it was active.

Nest concealment measurements

The concealment of a nest was measured at least one week after the nestlings fledged to avoid disturbance to the fledglings who may remain in the nest vicinity until they become more mobile. Concealment was measured at three different

heights (at ground level, at nest height, and 1m above nest height), and from the four primary compass directions around the nest. Percentage of concealment was also estimated directly above and below the nest. Concealment scoring was accomplished by taking a photo of the nest and estimating the percentage of the nest that was concealed to the nearest 10%. All concealment scoring was completed by one person (A.I.) to avoid inconsistencies when scoring the concealment values. The overall concealment of each nest was calculated as the average of the 14 estimates of concealment for each nest (similar to Howlett & Stutchbury 1996).

FID measurements

FID measurements were taken in the summer of 2018 and 2019 during regular nest checks, so as not to cause female Wood Thrushes to flush from their nests more than necessary. If a female Wood Thrush was seen sitting on her nest during the incubation period, the nest was approached from a random direction at a steady walking pace, and in a straight line. The point at which the female left her nest was the FID measurement and was recorded in meters.

Blood Sampling

Blood sampling occurred in the summer of 2018 and 2019 on adult female Wood Thrushes that were radio-tagged as part of another ongoing project for this population of Wood Thrushes. All blood sampling was performed by PhD student Brendan Boyd, and most samples were taken in the morning to standardize

sampling (Done et al. 2011). Mist nets were set up around Wood thrush nests and were monitored closely to ensure that baseline blood samples were taken less than three minutes from the moment of capture to reflect baseline conditions. Blood was taken from the brachial vein of one wing; the vein was punctured with a small gauge needle and capillary tubes were used to collect the blood (approximately 100ul of blood was taken). A second blood sample was taken from the other wing after the bird was held for 30 minutes, to measure the induced stress response of the bird. Blood samples were immediately transferred into 400ul Eppendorf tubes and stored on ice. After returning from the field, blood samples were centrifuged within five hours and blood plasma was separated and stored in a freezer. Corticosterone concentration was determined at Dr. Macdougal-Shackleton's lab at Western University by both myself and Brendan Boyd, using the commercially available ENZO Life Sciences Corticosterone ELISA kit in the process described by Washburn et al. (2002).

Statistical analysis

The nest concealment data was not normally distributed; therefore the differences in nest concealment among successful/unsuccessful and non-parasitized/parasitized nests were calculated using non-parametric statistical tests (Mann-Whitney *U*-test and generalized linear models (GLMs)). All statistical tests and figures were generated in RStudio (Version 1.1.456).

Results

Nest concealment and predation/parasitism

Of all nests found, 53.2% (99 of 186) failed due to nest predation and 25.3% (47 of 186) were parasitized by cowbirds.

Overall nest concealment varied widely among females, from <5% hidden to >60% hidden, with an average ~30% (Fig. 1). For nests that had no cowbirds, there was no significant difference in overall concealment between successful (fledged at least one young; mean = 31.0% ± 1.91) or depredated nests (mean = 27.6% ± 1.50; Fig. 1; Mann-Whitney U test, U=2097, n = 139, p=0.201). Even when each nest concealment metric was analyzed individually (concealment from the ground level, nest level and 1m above the nest), there were also no significant differences between successful or depredated nests (P > 20; Table 1). When analyzing the influence of multiple variables (concealment, nest height, fragment size, and year) on the outcome of nests through a binomial generalized linear model (GLM), the fit of the model was insignificant for all variables of overall concealment, concealment at ground level, nest level, and 1m above the nest (Table 2).

For cowbird parasitism, there was also no significant difference in overall concealment between non-parasitized (mean = 29.2% ± 1.20) or parasitized nests (Fig. 2; mean = 27.8% ± 2.45; U=3492.5, n= 186, p=0.48), and there were no significant differences for any individual concealment metric (P > 0.40; Table 1). A

binomial GLM including nest height, fragment size, and year found the model for overall concealment was also insignificant (Table 2).

Concealment, corticosterone and flight initiation distance

There was no relationship found between overall nest concealment and corticosterone (CORT) concentrations at either the baseline sampling time (immediately after capture) or the 30-minute sampling time (Fig 3) in either year. As expected, CORT concentrations were significantly higher after the induced 30-min stress protocol (Table 3).

Unexpectedly, the vast majority (88%) of FID measurements were 0m in 2018 (Fig. 4A), but FID measurements were more variable in 2019 (Fig 4B). There was no relationship between FID and overall concealment (Table 3).

Table 1. Comparisons of Mann-Whitney *U*-test values for different measures of nest concealment of successful vs. depredated nests (n = 139) and non-parasitized vs. parasitized nests (n = 186). Ground concealment includes the concealment scores from all 4 cardinal directions at the ground level, and also the concealment score for directly under the nest. Additionally, 1m concealment includes the concealment scores from all 4 cardinal directions at 1m above the nest, and also the concealment score for directly 1m over the nest.

	Concealment variables			
	Ground	**Nest**	**1m above**	**Overall**
Successful versus depredated	*U*=2153, *p*=0.297	*U*=2462, *p*=0.7941	*U*=2207, *p*=0.4157	*U*=2097, *p*=0.201
Non-parasitized versus parasitized	*U*=3351.5, *p*=0.7909	*U*=3320.5, *p*=0.8664	*U*=3393, *p*=0.6928	*U*=3492.5, *p*=0.4796

Table 2. The *z*-values and *p*-values for a binomial generalized linear model (GLM) predicting nest predation (n = 139) using multiple different predictors (overall concealment, nest height, fragment size, and year).

Predictors	z value	p value
Overall concealment	1.322	0.186
Nest height	-0.051	0.959
Fragment size	1.130	0.258
Year	-1.132	0.258
Overall ground-level concealment	1.556	0.120
Nest height	-0.099	0.921
Fragment size	1.296	0.195
Year	-1.261	0.207
Overall nest-level concealment	0.197	0.844
Nest height	0.025	0.980
Fragment size	1.271	0.204
Year	-1.101	0.271
Overall concealment 1m above nest	0.659	0.510
Nest height	0.035	0.972
Fragment size	1.072	0.284
Year	-1.074	0.283

Table 3. The *t*-values and *p*-values for a gamma generalized linear model (GLM) predicting base-level (3 min) CORT levels using multiple different predictors (nest concealment, nest height, fragment size, and year). Additionally, *z*-values and *p*-values for a poisson generalized linear model (GLM) is shown, predicting FID using the same predictors.

	Baseline CORT		**30 minute CORT**		**FID**	
	t value	p value	t value	p value	z value	p value
Overall concealment	0.001	0.999	-0.272	0.787	0.387	0.699
Nest height	-1.094	0.281	-0.659	0.514	-1.623	0.105
Fragment size	1.074	0.289	-0.396	0.694	-0.567	0.570
Year	1.783	0.082	0.426	0.673	2.231	**0.026**

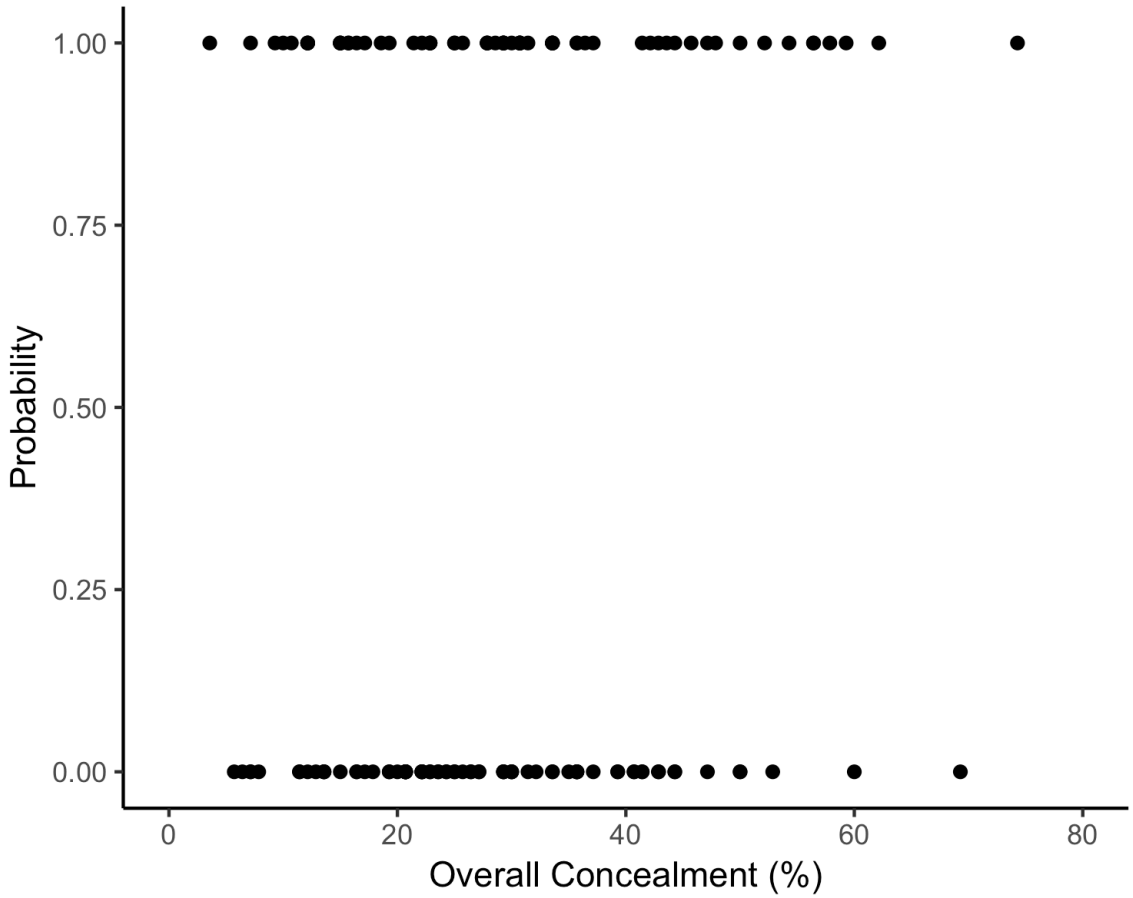

Figure 1. Logistic regression plot showing the probability of nest success in Wood thrushes (0 = unsuccessful, 1 = successful; n=139) in relation to overall nest concealment (%). Only nests that were not parasitized by Brown-headed cowbirds are included.

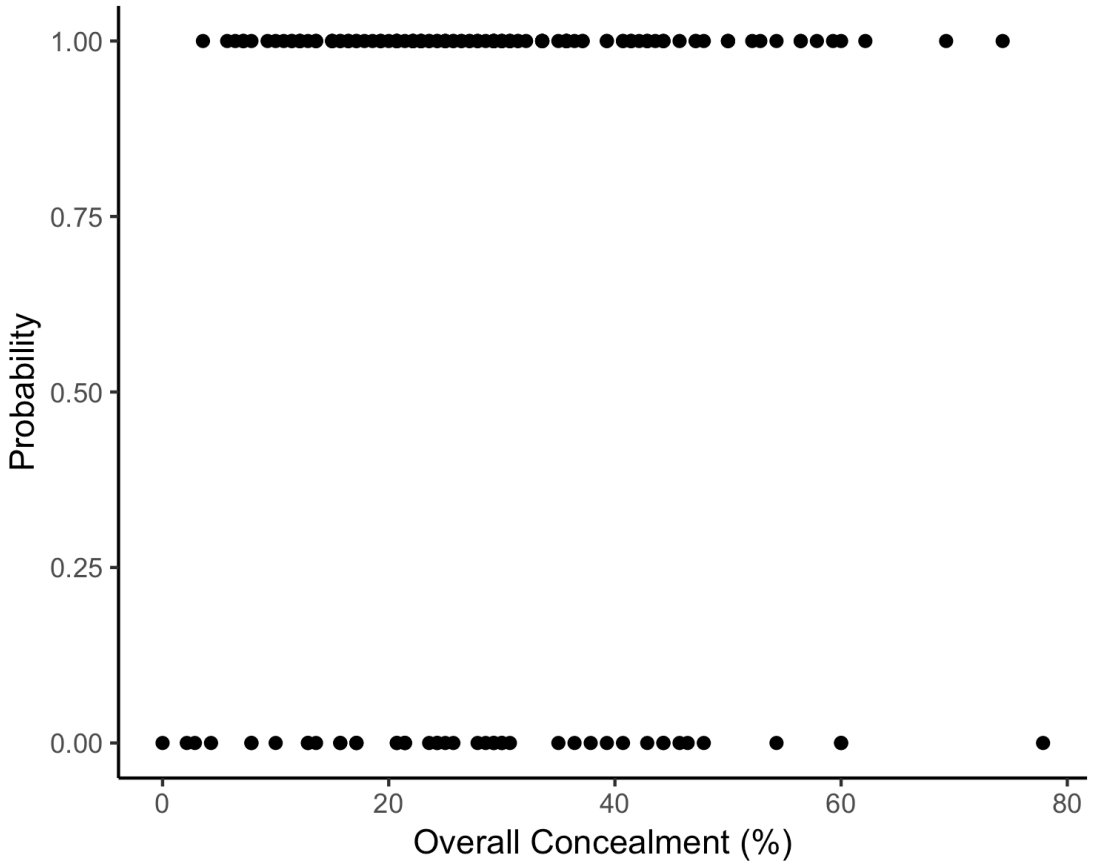

Figure 2. Logistic regression plot showing the probability of cowbird eggs present in Wood thrush nests (0 = cowbird eggs present, 1 = no cowbird eggs; n = 186) in relation to overall nest concealment (%).

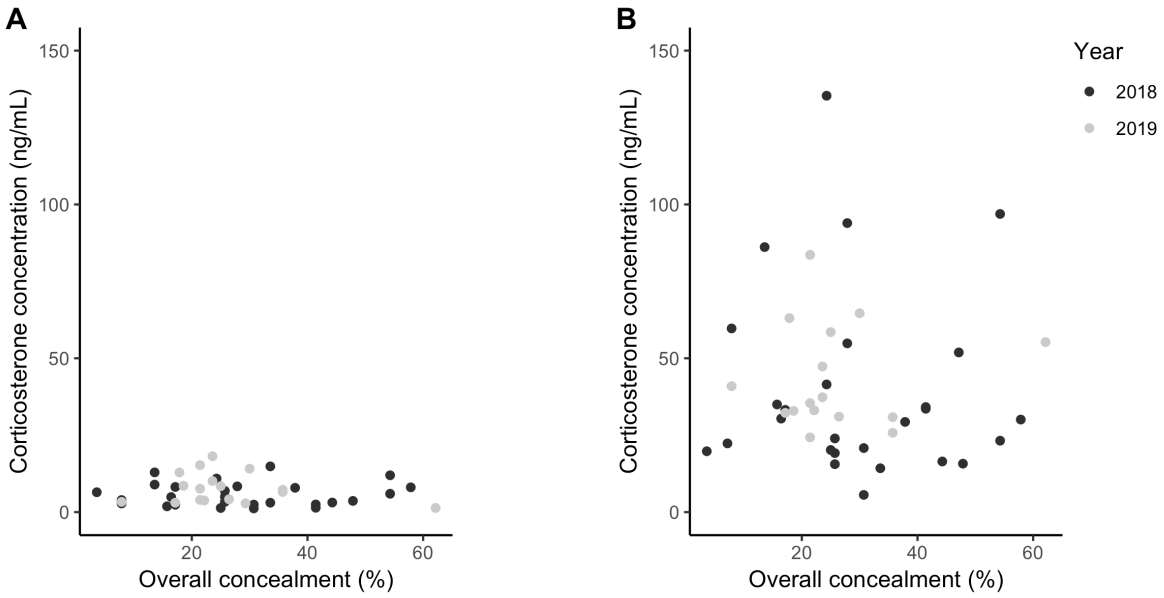

Figure 3. The relationship between corrected corticosterone concentration (ng/mL) and overall concealment, from baseline stress blood samples (A; n = 44) and from 30-minute samples (B; n = 43), for 2018 and 2019.

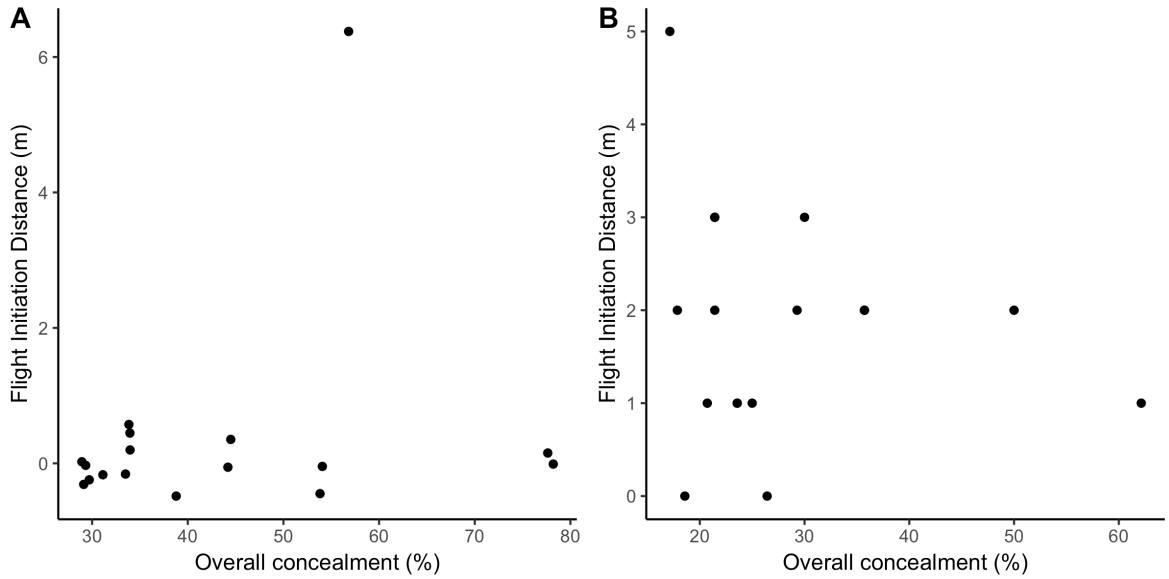

Figure 4. The relationship between overall concealment and FID from 2018 (A; n = 31) and 2019 (B; n = 24). Many points were overlapping at 0m FID in 2018, and so they have been staggered.

Discussion:

Nest Failure and Brood Parasitism

In this study, Wood Thrushes experienced high nest predation (53.2%) in the fragmented forests of southwestern Ontario. Despite the large variability in nest concealment of this species, this does not predict likelihood of predation (Fig. 1, Tables 1-2). Although several studies of North American songbirds have found that nest concealment does not reduce nest predation (Howlett & Stutchbury 1996, Burhans & Thompson 1998), for some species nest concealment is effective (Goodnow & Reitsma 2011, Matsui & Takagi 2012, Mote et al. 2019). Matsui & Takagi (2012) found that nest height and nest concealment were important factors affecting nest predation in Bull-headed shrikes (*Lanius bucephalus*), especially during the nestling stage. They suggest that increased concealment and height of the nest can reduce predation of Bull-headed shrike nests because their primary predator (weasels) mainly hunt using visual cues (Matsui & Takagi 2012). Mote et al. (2019) found that success of Mourning dove (*Zenaida macroura*) nests heavily depended on habitat type and vegetation density below the nest, suggesting that terrestrial animals are the primary predator. One key reason that nest concealment may not reduce nest failure in some birds is because their key predators may not rely on visual cues and may use other modalities for hunting. For instance, concealment of waterfowl nests did not predict nest predation most likely because of nocturnal predators such as raccoons and skunks that rely on olfactory cues (Borgo & Conover 2016). Nest feces, eggs, and incubating birds are all important

sources of olfactory cues that predators may be using to locate nests (cited in Borgo & Conover 2016). In addition to the different strategies that predators use to find nests, nest predation can also occur at random, with some nests being found by predators completely by chance (Staller et al. 2005). Understanding how nest success is affected by nest concealment therefore requires good information on the identity and abundance of the key predators (Schaefer 2004, Staller et al. 2005, Friesen et al. 2013, Goguen and Murray 2020) but such data are scarce due to high cost of video surveillance equipment in the quantities necessary to monitor many nests per season.

For Wood Thrushes, the nest predators have been identified for a population near Waterloo, Ontario (Friesen et al. 2013), which is only 85 km from my study area. Four of the five top nest predators were diurnal birds (Brown-headed cowbird, Cooper's hawk, American crow, and Blue Jay) and these accounted for 77% of all documented nest predation events (Friesen et al. 2013). Cowbird predation refers to the removal of eggs at the incubation stage and is distinct from nest parasitism, which occurs at egg-laying. The only major nocturnal predator was the raccoon, which destroyed the second-most number of nests and accounted for 18% of nest predation (Friesen et al. 2013). Friesen et al.'s study was conducted in a suburban woodlot, so this may not fully reflect the predator communities occurring in my study sites in Norfolk County, which is rural and agricultural. But even if most nest predators were diurnal avian predators that rely on visual cues, nest concealment by Wood Thrushes may have been ineffective because it rarely exceeded 60% (Fig.

1). Wood Thrushes are large-bodied songbirds and have large, leafy nests, which may be inherently difficult to conceal from sharp-eyed predators.

Future research on nest concealment should take into account landscape level differences in predator abundance. Some studies have found that predator density increases as landscapes become more fragmented and interspersed with agricultural land (Andren 1992). Given the variety of forest fragment sizes that were used in this study, different sites may represent different densities and types of predators. With different predators having different strategies, it may not be feasible for nesting females to assess an optimal level of nest concealment in a given forest site. The experience of the nesting female may also be important in nest site selection and concealment, both within and between years. A study by Hatchwell et al. (1999) found that nest height and breeding experience was an important determining factor in the success of cooperative-breeding Long-tailed Tit (*Aegithalos caudatus*) nests, where low nests were more successful than higher nests. Moreover, they found that failed breeders who assisted conspecifics with successful nests built their subsequent nests lower than nests built prior to their helping experience (Hatchwell et al. 1999). A new avenue to explore could be examining whether Wood Thrushes also learn from previous failed nesting attempts and whether older and more experienced females build more concealed nests than first-time breeders. The former would likely require continuous radio-tracking of females during the breeding season to find their multiple nesting attempts.

This study determined that Wood Thrushes experience moderate cowbird parasitism (25.3%) in the fragmented forests of southwestern Ontario and that nest concealment does not reduce the likelihood of parasitism (Fig. 2, Table 1). These findings contrast with previous studies in other species that have found evidence for nest concealment reducing cowbird parasitism. Sharp & Kus (2006) found that increased microhabitat vegetation cover around Least Bell's vireo (*Vireo bellii*) nests was correlated with reduced cowbird parasitism. Additionally, Saunders et al. (2003) determined that concealment played an important role in nesting Song sparrows (*Melospiza melodia*), where nests that were well concealed, especially from the side-view, encountered less parasitism by cowbirds. Despite this, other studies have found no correlation between parasitism and concealment in other cowbird hosts (Burhans & Thompson 1998, Banks and Martin 2000). Female cowbirds have many strategies for locating host nests, which is not surprising given that one female can potentially parasitize dozens of nests in one season. Cowbirds have been shown to repeatedly visit many host nests during the breeding season to optimize the timing of when to lay their eggs (Norman and Robertson 1975). Banks and Martin (2000) showed that cowbirds were more likely to parasitize nests of host species that spent more time at the nesting site during the nest-building process, and also host species whose males vocalized more frequently. If cowbirds are relying on the movements of the parents to find host nests, vegetation concealment may not impact their ability to locate nests. A recent experimental study by White (2020) found that once female cowbirds found a nest, they have the ability to recognize the amount of time that has elapsed between nest visits, and also

remember the number of host eggs added to the nest each day. White (2020) showed evidence that female cowbirds use this information to optimally select the best nest for parasitism during the host's egg-laying period. Concealing a nest after it has already been found by a cowbird obviously would not be effective. A future behavioural study could monitor nest building at individual Wood thrush nests and test if parental secretiveness, rather than nest concealment, better predicts risk of cowbird parasitism.

Corticosterone analysis and flight initiation distance

The results of this study provide new insights for the relationship between nest concealment and how this might influence the corticosterone levels of a nesting female songbird. To my knowledge, no other study has explored this relationship for a songbird and so it is difficult to make a priori predictions. Concealment could reduce stress because there is lower risk of predation, in theory, or could increase stress because the female cannot detect predators approaching, which pose a threat to her own life. Although I found that nest concealment had no effect on the baseline or 30-minute corticosterone concentration of nesting females (Fig. 3), this is the first step in understanding if nest site selection affects the female directly, and not just her immediate nesting success. Clinchy et al. (2004) used experimental predator sound playbacks to create a simulated high risk of nest predation for ground-nesting Song sparrows and found that this increased female chronic stress levels. For songbirds in general, it remains unknown to what extent female nest site

selection and concealment decisions are influenced by female attempts to reduce their chronic stress.

We expected to find a negative trend between concealment and flight initiation distance (FID) in nesting female Wood thrushes because previous studies have found evidence that females with well-concealed nests flush at shorter distances (Albrecht & Klvana 2004, Javurkova et al. 2012). We did not find any correlation between FID and nest concealment, in part because there was so little variation in FID (Fig. 4). The majority of the FIDs measured in 2018 resulted in a measurement of 0m as females did not flee until literally the last second, but in 2019 measurements were more variable. Previous studies found that increased vegetation cover around the nest decreases the FID of songbird species (Javurkova et al. 2012), suggesting that females sit tight on their nests as a secretive strategy to not give away their location to nearby predators. Given that nest concealment rarely exceeded 60%, nesting female Wood Thrushes may rely on their cryptically coloured plumage and not flush in order to avoid detection by predators. Møller et al. (2019) recently published a study on 93 European bird species and found that birds who were more cryptically coloured had consistently shorter FIDs. Wood Thrush females may be purposefully placing nests in areas with lower vegetation concealment, to safely be able to detect predators at a greater distance from the nest, and to assess the most optimal time to flee if this becomes necessary.

Conclusion

With dozens of migratory songbirds in decline, and increasing numbers joining the Species at Risk list, it is critical to understand what influences nesting success. Predation and brood parasitism are the leading causes of nest failure in Wood Thrushes, so testing whether nest concealment is an effective countermeasure is important for informing future conservation efforts for this declining species. Understanding what influences success of nests is also important for adding to the growing knowledge of this bird's life history strategies, and warrants further research on whether Wood Thrushes can adapt to changing anthropogenic threats and predator communities. Many woodland songbirds share the same habitat requirements as Wood Thrushes, and therefore conserving habitat that provides the highest chance of breeding success for Wood Thrushes will in turn provide ideal habitat for many other species in need.

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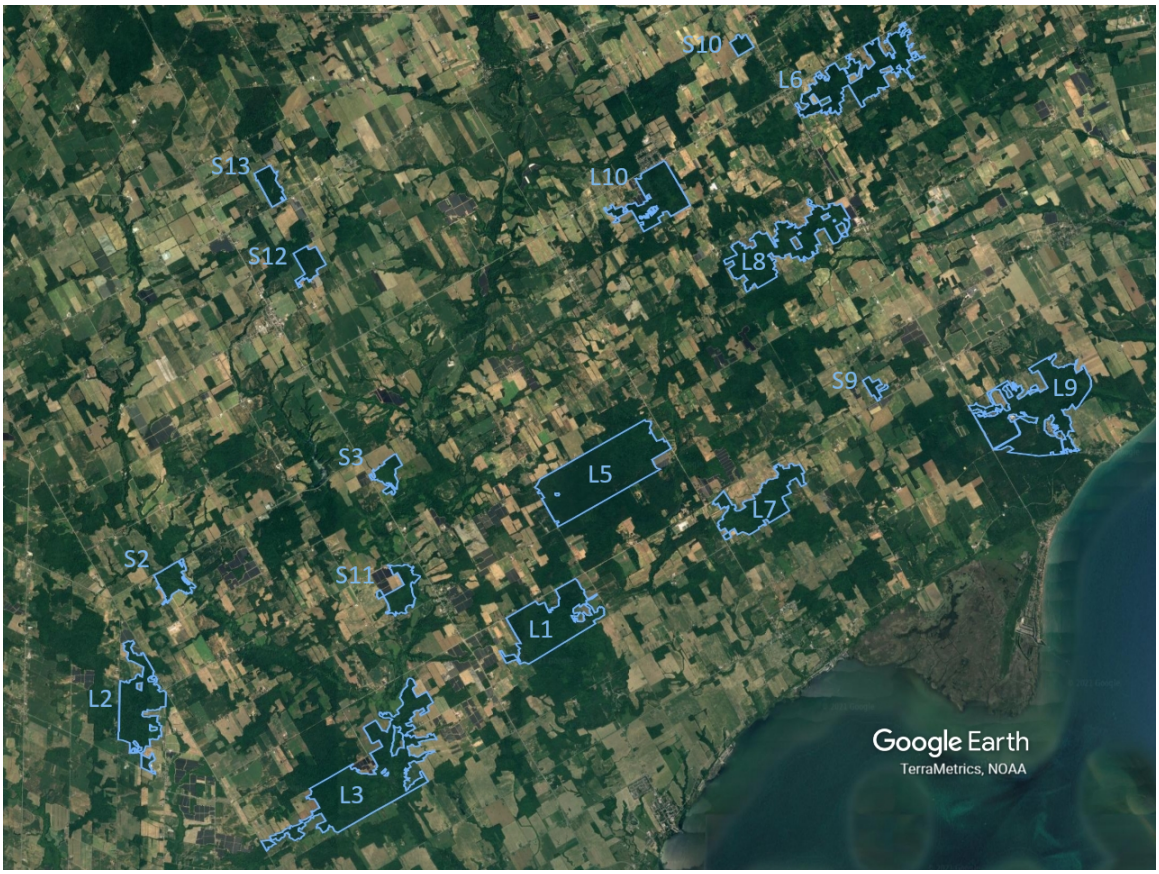
Appendices



Appendix A: Map showing the various small (S) and large (L) study sites used in this project.