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Territorial Aggression Increases Along an Urban Gradient in Resident But Not Migratory Song Sparrows

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TERRITORIAL AGGRESSION INCREASES ALONG AN URBAN GRADIENT IN
RESIDENT BUT NOT MIGRATORY SONG SPARROWS

by

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A Thesis Submitted in Partial Fulfillment
of the Requirements for a Degree with Honors
(Zoology)

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Abstract

During the breeding season, birds behave more aggressively toward rivals to maintain and defend territories. Resident birds are thought to be more aggressive than migratory birds because they need to maintain a territory year round. Furthermore, birds in urban environments can exhibit more aggressive behaviors than their rural counterparts because of the bolder behavioral characteristics required to colonize urban habitats. In this study, we investigated how migration strategy and landscape composition interact to affect territory defense in two subspecies of Song Sparrow (*Melospiza melodia*). To evoke an aggressive response, we simulated invasions by broadcasting songs from within a male's territory and recorded the bird's response. We found that neither migration strategy nor landscape composition alone correlated with territorial aggression, but the interaction between these two predictors was significant. Territorial aggression was consistent across landscapes for migratory Song Sparrows but decreased with increasing distance from urban environments for resident Song Sparrows. We hypothesize that migratory Song Sparrows do not spend enough time maintaining their territories to be affected by the landscape composition.

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Introduction

Many bird species defend exclusive space (territories) using aggressive behaviors to increase reproductive success or survival by excluding others from a particular resource. The exact strategy and degree of aggression used is dependent on the species involved and environmental factors. For example, birds in highly disturbed environments may be more aggressive than individuals in more rural settings (Evans et al. 2010, Scales et al. 2011), and migratory birds may be less aggressive than resident (non-migratory) birds because of variation in the length of time the territory is maintained. Investigating how the frequency or form of an aggressive behavior changes in respect to contributing factors can provide valuable insight into how those factors affect territory aggression and how territorial behavior arises and evolves. In this study, we explored how migration strategy and landscape composition together affected territorial aggression in multiple populations of the Song Sparrow (*Melospiza melodia*).

For migratory bird species, territories are maintained during the breeding season but later abandoned as the bird leaves for its non-breeding grounds. As a consequence, interactions with neighbors are season-specific. The same is not true for resident bird species, which may maintain a territory year-round and have the same neighbors for years in a row (Akçay et al. 2009). Though these long-term associations can result in “forgiving” strategies where a territory holder displays less aggressive responses to neighbors than to strangers (Hyman 2002), Song Sparrows show no such effect (Akçay et al. 2009). Unfortunately, no studies on avian populations have explored the direct effects of migration strategy on territorial aggression. However, studies on fish populations have found that territorial aggression is positively correlated with duration of residence

(Bakker and Feuth-de Bruijn 1988, Hutchison and Iwata 2001). Resident fish are thought to be more aggressive because they experience greater selective pressure toward aggressive behaviors that would help them claim and maintain a territory (Hutchison and Iwata 2001). If resident bird populations experience similar selective pressure toward territoriality, then resident bird populations should be more aggressive than migratory bird populations that are only territorial during the breeding season.

To utilize urban environments, urban birds tend to be bolder than their rural counterparts (Evans et al. 2010) and more tolerant of humans (Metcalf et al. 2000, Evans et al. 2010). Boldness often correlates with territorial aggression among different sparrow populations, with urban Song Sparrows being both bolder and more aggressive than rural Song Sparrows (Evans et al. 2010, Scales et al. 2011). This correlation between boldness and aggression however, has not been detected within populations, only between populations with markedly different landscape compositions (Evans et al. 2010, Scales et al. 2011).

The Song Sparrow presents an ideal study species to test whether the effects of migration strategy and landscape composition interact to determine territory behaviors. It is one of the most common sparrows across North America, found as far north as Alaska and as far south as Mexico, and it lives in a variety of habitats from fields, swamps, and forest edges to backyards and parking lots (Arcese et al. 2002). The Song Sparrow also employs differing migration strategies, with populations being either migratory or resident (Erikson et al. 2011). As expected of a species that lives in a variety of habitats, the Song Sparrow shows significant geographic variation in size, color, and behavior (Aldrich 1984). Song, which the males use to claim their breeding territories and attract a

mate, also varies geographically (Searcy et al. 2002). When faced with a rival male, the Song Sparrow will sing in warning (usually a loud song) and attempt to locate the invader. If the invader persists, the Song Sparrow will either flee or increase his flight and song frequency, switch to soft songs (quieter but more aggressive than loud songs: Nice 1943), and potentially even attack the intruder. Both song and flight are easily observed and can be recorded as a measure of aggression (Beecher et al. 2000a).

The goal of this study was to see how territorial aggression in breeding Song Sparrows changed in response to differing migration strategy and changing landscape composition (with respect to level of urbanization). If territorial aggression changes with migration strategy, we predicted that resident Song Sparrows would sing more often and search more fervently for invading males (i.e. behave more aggressively) than migratory Song Sparrows, which only maintain a territory during the breeding season (Arcese et al. 2002). If territorial aggression changes with urbanization, we predicted urban Song Sparrows would behave more aggressively than rural Song Sparrows because of the bold behaviors required more generally to utilize urban environments (Scales et al. 2011).

Methods

Study Sites & Design

We conducted simulated territory invasions for Song Sparrows in three regions: Maine (Penobscot county), southern New England (Essex and Middlesex counties, Massachusetts; Hillsborough and Rockingham counties, New Hampshire), and Wyoming (Teton county). We selected these sites because they differed along three separate axes: migration strategy (migratory or resident), subspecies (*Melospiza melodia melodia* or *M.*

m. montana), and landscape composition (urban or rural). Song Sparrows are migratory in Maine and Wyoming but are present year-round in southern New England (Erikson et al. 2011). The Song Sparrows in Maine and southern New England are the Eastern subspecies (*M. m. melodia*), but the birds in Wyoming are the Montana subspecies (*M. m. montana*) (Arcese et al. 2002).

Within each of the regions, we surveyed Song Sparrows in both rural and urban settings. In Maine, we surveyed within the town of Orono on the University of Maine campus (18 territories) and on Ayers Island (25 territories), an early successional island in the middle of the Penobscot River. We also surveyed two locations in Wyoming: Karns Meadow Park (22 territories), centrally located in the town of Jackson, and Blacktail Ponds (20 territories), located within Grand Teton National Park near the town of Moose. Survey locations in southern New England were spread out across Massachusetts (15 territories) and New Hampshire (4 territories) and included near equal numbers of urban and rural sites. Surveys took place June through August in 2012 and 2013.

Landscape Composition Definition

We assessed categorical landscape composition to align with previous studies on Song Sparrow behavior by labeling them as either urban or rural (Evans et al. 2010, Scales et al. 2011). We also assessed landscape composition continuously using two different means: 1) the proportion of “urban” (buildings, roads, parking lots, etc.) to “rural” (fields, forests, etc.) land coverages within a 100 meter radius of the survey point and 2) the shortest distance to an “urban” object (buildings, roads, parking lots, etc.) from

the survey point. These continuous metrics offer a more fine-scale differentiation among territories, but they also assess landscape composition on a smaller scale than the categorical metric.

Simulated Territory Invasion

Each simulated territory invasion consisted of two, three-minute phases: silence (the control phase) and playback (the invasion phase). For each invasion phase, we played a recorded song repeatedly throughout the three-minute period with 10 seconds of silence between each song replicate. The playback track was broadcast from a portable speaker and MP3 player that we concealed near a perch used by the territorial male during one of our previous observations. We flagged the area around the speaker at 2, 4, 8, and 16 meter intervals for ease of position estimates (see the following paragraph). Song Sparrow territories within 100 meters of each other were surveyed on separate days to avoid multiple simulated invasions within a small area on the same day. We surveyed males between one and three times throughout the breeding season. During the invasion phase, we recorded the Song Sparrow's perch changes and position and song frequency and type (loud or soft: *sensu* Anderson et al. 2007) using a voice recorder. From these recordings, we calculated a suite of behavioral variables that we thought were indicative of aggression.

Song Recording

To avoid a behavioral bias due to foreign songs (Searcy et al. 2002), we recorded local songs from each Song Sparrow population near the populations we surveyed (but at

least 3 kilometers from the nearest surveyed bird). We recorded the songs using either the internal microphone of a Roland R-09HR recorder or a Sennheiser K6 shotgun-style microphone and sound parabola hooked up to a Marantz PMD660 recorder. We then used these recordings to generate 9-minute tracks used in the simulated territory invasions. The recording used for each survey was selected randomly from the appropriate set (Maine set = 17 songs, Wyoming set = 13 songs, southern New England set = 7 songs) of local male songs (to avoid issues of pseudoreplication: Kroodsma 1989).

Statistical Analysis

From the invasion data, we derived nine behavioral variables (Table 1) that we used to run a Principal Components Analysis (PCA). Principal Component 1 (PC1) negatively correlated with the behavioral variables consistent with aggression, and thus we used PC1 as our aggression response variable.

We ran three Linear Mixed-Effects Models using the PC1 value for each simulated invasion as our dependent variable. To test our primary research hypotheses, we included the fixed effects of the interaction between landscape composition and migration strategy and between landscape composition and subspecies in each of the three models. We also included Julian date nested within subspecies as a fixed effect in all the models to control for the subspecies specific phenologies for changes in territorial behavior. Each of the three models differed in how we defined landscape composition (either as a categorical type, a land coverage proportion, or as a minimum distance). All three models included study year and male identification number as random effects to

control for potential differences where they nested between 2012 and 2013 and between simulated invasions for males we surveyed more than once. All statistical analyses were performed using the statistical program RStudio (2012).

Results

Birds Sampled

In total, we performed 112 simulated territorial invasions with 70 Song Sparrow males. Of these surveys, 53 were conducted in Maine (30 birds), 14 in southern New England (14 birds), and 45 in Wyoming (26 birds). Divided by treatments, we had 56 migratory birds and 14 resident birds, 39 birds in rural landscapes and 31 birds in more urban landscapes, and 44 birds of the Eastern subspecies and 26 birds of the Montana subspecies.

Principal Components Analysis

Of the nine Principal Components generated by the PCA, PC1 explained 45.3% of the variation in the initial dataset (Figure 1). PC1 showed a positive correlation with the minimum approach distance to the speaker, time until first song, and time until first perch change, and a negative correlation with the total number of songs, total number of soft songs, total number of perch changes, time spent within 16 meters of speaker, time spent within 4 meters of speaker, and total time observed during the three minutes of silence prior to playback (Table 1). In other words, PC1 showed a negative correlation with aggression with negative PC1 values indicating more aggression than positive PC1 values.

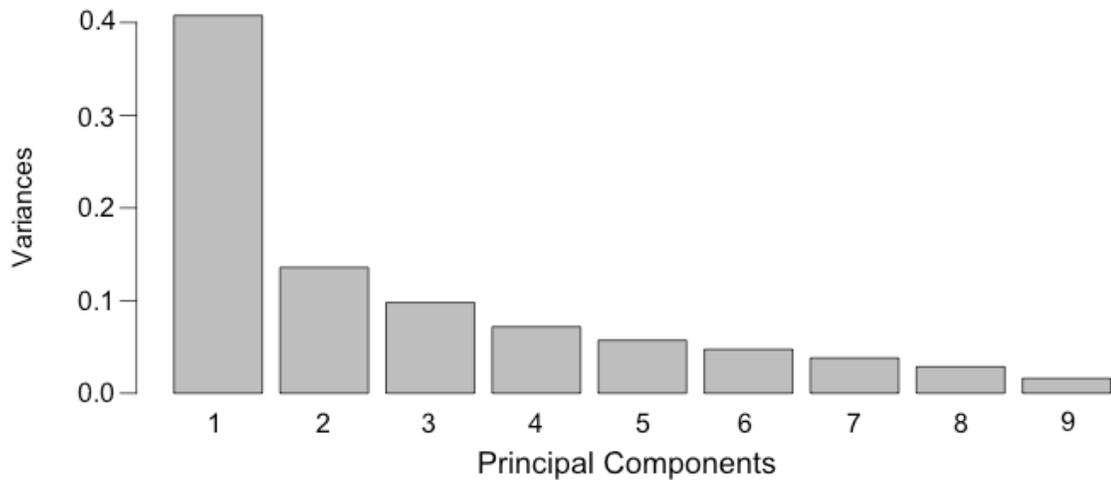


Figure 1. The proportion of data set variance explained by each Principal Component produced by the Principal Components Analysis.

Table 1. Behavioral variables used in Principal Components Analysis and how they correlate with PC1*.

Variable	Correlation
Minimum approach distance to the speaker	+
Time until first song	+
Time until first perch change	+
Total number of songs	-
Total number of soft songs	-
Total number of perch changes	-
Time spent within 16 meters of speaker	-
Time spent within 4 meters of speaker	-
Total time observed	-

*PC1 correlates negatively with aggression.

Linear Mixed-Effects Model

Neither migration strategy, subspecies, nor Julian date had a significant relationship with PC1 in any of the models (Tables 2, 3, 4). Landscape composition also did not correlate significantly with PC1 when defined as a categorical type ($n = 112$, $df = 69$, $t = -0.77$, $p = 0.45$, Table 2), a land coverage proportion ($n = 112$, $df = 69$, $t = -0.35$, p

= 0.73, Table 3), or a minimum distance to an urban object (n = 111, df = 68, t = 1.71, p = 0.09, Table 4), although defining landscape composition as a minimum distance had the strongest trend. Only the interaction between landscape composition (defined as a minimum distance) and migration strategy showed a significant correlation with aggression (t = -2.00, p = 0.05, Table 4). The aggression of migratory birds was unrelated to landscape composition, but aggression was positively correlated with degree of urban-ness (as defined by the minimum distance to an urban object) among resident birds (Figure 2).

Table 2. Results of the Linear Mixed-Effects Model with landscape composition defined as a categorical type (n = 112).

Variable	Value	Standard error	DF	t-value	p-value
Intercept	-0.62	3.82	69	-0.16	0.87
Landscape type	-0.97	1.27	69	-0.77	0.45
Migration strategy	-0.09	0.73	69	-0.13	0.90
Subspecies	0.98	4.29	69	0.23	0.82
Interaction between landscape type and migration strategy	0.62	1.11	69	0.55	0.58
Interaction between landscape type and subspecies	0.90	0.81	69	1.10	0.27
Julian date (<i>M. m. montana</i>)	0.01	0.02	34	0.61	0.55
Julian date (<i>M. m. melodia</i>)	-0.01	0.01	34	-0.62	0.54

Table 3. Results of the Linear Mixed-Effects Model with landscape composition defined by the continuous urban proportion value (n = 112).

Variable	Value	Standard error	DF	t-value	p-value
Intercept	-1.02	3.74	69	-0.27	0.79
Proportion urban-ness	-1.61	4.65	69	-0.35	0.73
Migration strategy	-0.21	0.71	69	-0.30	0.77
Subspecies	1.63	4.22	69	0.39	0.70
Interaction between proportion urban-ness and migration strategy	2.55	3.34	69	0.76	0.45
Interaction between proportion urban-ness and subspecies	-0.11	3.38	69	-0.03	0.97
Julian date (<i>M. m. montana</i>)	0.01	0.02	34	0.69	0.49
Julian date (<i>M. m. melodia</i>)	-0.01	0.01	34	-0.66	0.51

Table 4. Results of the Linear Mixed-Effects Model with landscape composition defined by the continuous shortest distance to an urban object value (n = 111*).

Variable	Value	Standard error	DF	t-value	p-value
Intercept	-3.15	3.75	68	-0.84	0.40
Distance to an urban object	0.01	0.00	68	1.71	0.09
Migration strategy	0.90	0.64	68	1.40	0.17
Subspecies	3.14	4.22	68	0.75	0.46
Interaction between distance to an urban object and migration strategy ⁺	-0.01	0.00	68	-2.00	0.05
Interaction between distance to an urban object and subspecies	0.00	0.00	68	-0.93	0.36
Julian date (<i>M. m. montana</i>)	0.02	0.02	34	0.93	0.36
Julian date (<i>M. m. melodia</i>)	-0.01	0.01	34	-0.66	0.51

* We could not measure a minimum distance for one simulated territory invasion so it was removed from the model

⁺ Interaction displayed in Figure 2

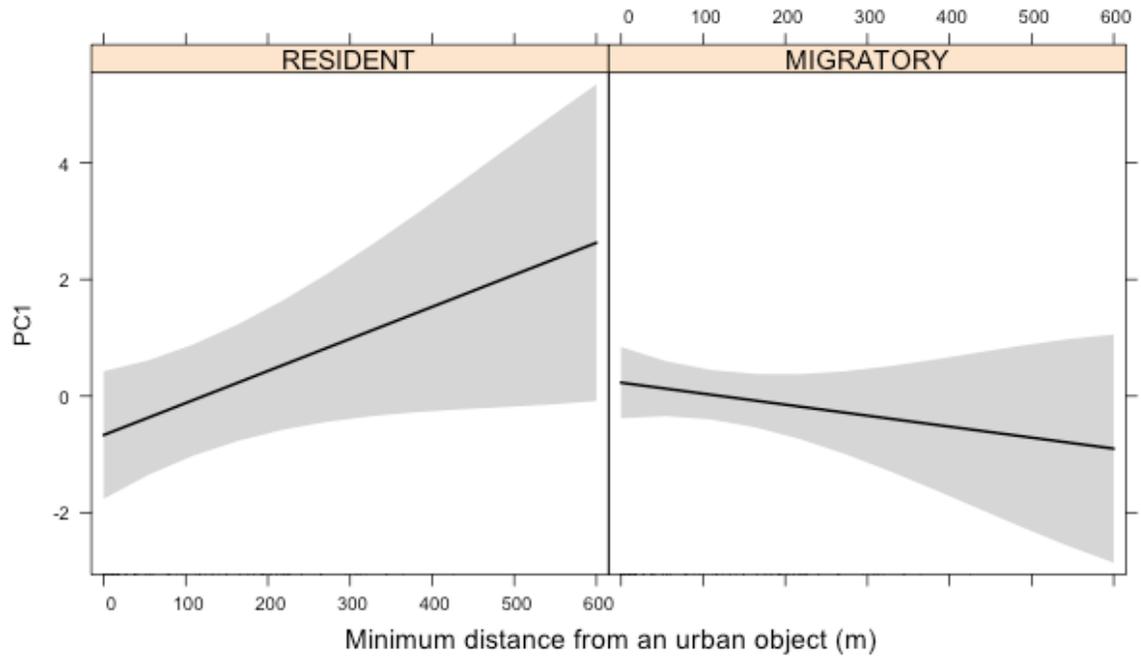


Figure 2. The interaction between migration strategy and landscape composition defined as the minimum distance to an urban object from the survey point ($p = 0.05$). A negative PC1 value was considered more aggressive than a positive PC1 value.

Discussion

Our findings did not support either of our hypotheses in their entirety. There was no consistent difference in territorial aggression between the migratory and the resident Song Sparrow populations nor did territorial aggression consistently increase as the landscape became more urban. However, there were differences in how landscape affected aggression between migratory and resident birds. Territorial aggression correlated with landscape composition within the resident Song Sparrows but not within migratory sparrows. Notably, this interaction between migration strategy and landscape composition was only significant when we defined landscape composition as the minimum distance to an urban object (not defined by previous studies: Evans et al. 2010, Scales et al. 2011).

We did not detect a correlation between territorial aggression and migration strategy as has been reported within fish populations (Bakker and Feuth-de Bruijn 1988, Hutchison and Iwata 2001). This may be because Song Sparrows employ a conditional retaliation strategy when dealing with neighbors and intruders, behaving more aggressively towards aggressive neighbors or males that have recently invaded the holder's territory than neutral neighbors (Ackay et al. 2009). This kind of strategy is dependent on interactions between neighbors, not whether or not the population migrates. Our results suggest that differences between migratory and resident populations may simply be symptomatic of differences between populations in general and not related directly to migration strategy. Year-round territory defense does not consistently result in higher aggression levels relative to migratory Song Sparrows.

However, we may not have been able to detect a correlation between territorial aggression and migration strategy because of the relatively small sample sizes of the two treatment groups. An existing correlation might not have been detectable because of the resulting large variation in aggression seen within the resident sample group. Despite this power issue, variation in aggression within migratory strategy appears larger than any consistent variation between migratory strategies, if it exists.

Landscape composition alone did not correlate with observed territorial aggression, which indicates that patterns found in previous studies about landscape composition (Evans et al. 2010, Scales et al. 2011) may be localized occurrences and not descriptive of the entire species. Another explanation for why we did not detect the previously found patterns is that we measured aggressive response differently. In the prior two studies, aggressive response was identical to bird's average distance from the

speaker during playback (Evans et al. 2010, Scales et al. 2011). We suggest that any single metric is only one part of territorial defense; average distance from speaker does not describe a male's attempt to locate the intruder, how often he challenges the rival through song, or how long such challenges might last. Though correlations have been found using single territorial defense behaviors, they demonstrate significant individual variation relative to suites of behaviors (Nowicki et al. 2002). The individual variation suggests there are different defense strategies the bird can utilize, so that measuring a single defense behavior may only work with birds that use that particular defense strategy, an unlikely assumption given the variation observed within and across populations. Principal components, like the one constructed here, can better summarize a suite of behaviors indicative of aggression to describe correlated aggression strategies more accurately.

We found that landscape composition has an effect on territorial aggression in resident Song Sparrows but not in migratory Song Sparrows, and that resident Song Sparrows become less aggressive the further they are from an urban object. We hypothesize that the difference between the effect of landscape on birds exhibiting the two migratory strategies is caused by the difference in time that migratory versus resident Song Sparrows spend within a particular environment. Migratory Song Sparrows will only maintain a specific territory for the breeding season's duration before migrating back to their non-breeding grounds. Thus, any effects caused by their environment may not manifest during this short period of time. Resident Song Sparrows, which maintain territories year around, can remain within the same environment for five years or longer (Hiebert et al. 1989, Beecher et al. 2000b), an adequate amount of time for environmental

effects to manifest in the bird's behavior. The correlation that territorial aggression decreases among resident Song Sparrows as distance from an urban object increases ties in with previous research: animals in urban environments tend to be bolder and thus more aggressive than their rural counterparts (Huntingford 1976, Dochtermann and Jenkins 2007, Kortet and Hedrick 2007, Reaney and Backwell 2007). Resident Song Sparrows, it seems, are no exception, although migratory Song Sparrows are.

Alternatively, resident birds with different aggression tendencies may be more likely than migratory birds to self-sort themselves on a landscape. Highly aggressive, resident sparrows may be better able to locate prime urban habitats with higher food resources (Scales et al. 2013) than migratory individuals because of their increased fine-scale knowledge of the landscape. Migratory males are under heavy selective pressure to establish territories soon after arrival from the non-breeding grounds in order to secure higher-quality territories (Smith and Moore 2004). Time-limited decisions may constrain information gathering and result in less-informed decisions (Scales et al. 2013).

As to why the interaction between migration strategy and landscape composition was only significant when landscape composition was defined as a minimum distance is best explained by the methods used to calculate the three different landscape composition values. The first definition of landscape composition involved assigning each sample one of two possible categorical types even though the landscapes we surveyed covered a gradient of compositions. There were also potential discrepancies in the categorizations (i.e. what may be considered urban in Wyoming is not the same as what would be considered urban in southern New England). The second definition of landscape composition involved calculating the proportion of urban land coverage within 100-m of

the survey point, an area far larger than the bird's territory (Nice 1937). The third definition of landscape composition provided the most significant and accurate description because by calculating the distance to the nearest urban object from the survey point, we also, arguably, calculated how far the bird's territory was from a town or city. The simplicity of this measurement is its strong point since it is unknown what exactly about urban environments results in higher aggression levels in Song Sparrows (Evans et al. 2010, Scales et al. 2011). By only measuring the distance, we ignored the specifics about the urban environments surveyed and thus were able to detect an established correlation.

Migration strategy and landscape composition alone were not correlated with territorial aggression in Song Sparrows, but the interaction between the two showed a significant correlation. Territorial aggression was consistent across the landscape composition gradient in migratory Song Sparrows but decreased as distance from an urban object increased in resident Song Sparrows. Further research should involve collecting a larger sample size of resident Song Sparrows to make sure any correlation detected (or not detected) was not distorted by our small sample size of resident Song Sparrows.

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Author's Biography

Darlene M. Turcotte was born in Lowell, Massachusetts on May 2, 1992. She grew up in the neighboring town of Dracut, Massachusetts, and graduated from Dracut Senior High School in May 2010. Darlene majored in Zoology while attending the University of Maine but took many courses required for a Wildlife Ecology major. She is a member of Alpha Lambda Delta Honor Society and the National Society for Collegiate Scholars. Darlene also served one term as Secretary of the university's student chapter of The Wildlife Society and participated in the Maine Learning Assistant program for two semesters.

Upon graduation, Darlene will attend the Graduate School at the University of Maine in pursuit of a Master of Science in Teaching degree, where she will earn the certification required to teach biology and science at public secondary schools in Maine.