Roles of Maladaptive Behaviour and Evolutionary Traps in the Decline of a Threatened Woodpecker

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Dedication

This thesis is dedicated to all those that care about making a difference in protecting and conserving our ecosystems and species within them. To my parents, with much love, thank you for your endless support, inspiration, and hope for a brighter future. To the future generations, never stop asking what you can do to make this world a better, more respectful place – then get out and do it!

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Abstract

The Red-headed Woodpecker (*Melanerpes erythrocephalus*) is a widespread, once common but increasingly rare North American bird species. Consistent long-term population declines have resulted in the species' threatened status in Canada and several states in the United States. Throughout most of its range, Red-headed Woodpeckers occupy habitats that have been heavily influenced by human presence and activities. Yet, there is little research quantifying the potential drivers of the species' population decline, which constrains conservation or policy action. The overall objective of this research is to determine why the Red-headed Woodpecker, a once common, widespread species with apparently a high flexibility in habitat use is undergoing such large population declines. I hypothesize that rapid anthropogenic changes and ecological novelties are causing Red-headed Woodpecker fitness and its behavioural choices to have become disjointed. The specific objectives include: (1) to determine if Red-headed Woodpecker habitat use is adaptive or maladaptive, (2) to determine the influence of a non-native interference competitor, the European Starling (*Sturnus vulgaris*), on Red-headed Woodpecker breeding success, and (3) to compare the efficacy of global and local models of the relationships between Red-headed Woodpeckers and two possible competitor species over space and time, and explore local variations of these relationships. To test my hypothesis, I investigated Red-headed Woodpecker multi-scale habitat use and associations, and nest survival near the northern edge of the species range in southern Ontario, where populations are rapidly declining. In addition, I modelled interspecies abundance relationships across southern Canada and east-central United States using 45 years of survey data from the Breeding Bird Survey (BBS) for Red-headed Woodpeckers, European Starlings, and Red-bellied Woodpeckers (*M. carolinus*).

Field-based results demonstrated that Red-headed Woodpeckers exhibit maladaptive habitat use at multiple scales, suggesting the potential for an ecological trap for the species. Specifically habitat characteristics that promoted feeding potential such as canopy openness and greater limb length were consistently associated with Red-headed Woodpecker occupancy from nest tree to woodlot scales, despite correlations with lower reproductive success. Further investigation into Red-headed Woodpecker nest survival by modelling a suite of abiotic, biotic, temporal, and habitat-based drivers showed that European Starling abundance near active woodpecker nest sites was the strongest factors influencing woodpecker nest survival. Logistic-exposure nest success assuming constant survival dropped significantly from 68% to 13% when starling abundance was considered. When interspecies abundance relationships were investigated at a larger spatial scale, they were found to be spatially structured, and suggested evidence for interspecific competition between Red-headed Woodpeckers and starlings, and niche differentiation between Red-headed and Red-bellied Woodpeckers. This research demonstrates the importance of multi-scale, multi-factor studies when determining threats for species-at-risk and will help in the development of conservation, management, and policy-making decisions for the species.

Résumé

Le Pic à Tête Rouge (*Melanerpes erythrocephalus*) est une espèce d'oiseau répandue en Amérique du Nord, autrefois commune mais maintenant de plus en plus rare. Un déclin constant de la population dans les dernières décennies a mené l'espèce à être désignée menacée au Canada et dans plusieurs États américains. Dans la plupart de son aire de répartition, le Pic à Tête Rouge occupe des habitats fortement influencés par la présence et les activités humaines. Il y a cependant peu de recherche quantifiant les causes possibles du déclin de la population de l'espèce. Par conséquent, il manque d'information pour la conservation et l'action politique. L'objectif général de cette recherche est de déterminer pourquoi le Pic à Tête Rouge, une espèce autrefois commune et répandue avec une grande souplesse d'utilisation de l'habitat, connaît-il une diminution dramatique de ses populations. J'émets l'hypothèse que de rapides changements anthropiques et des nouveautés écologiques ont mené la valeur sélective et les choix comportementaux du Pic à Tête Rouge à être devenus disjoints. Les objectifs spécifiques incluent : (1) de déterminer si l'utilisation de l'habitat par le Pic à Tête Rouge est adaptatée ou mésadaptée, (2) de déterminer l'influence d'un compétiteur par interférence exotique, l'Étourneau Sansonnet (*Sturnus vulgaris*), sur le succès de reproduction du Pic à Tête Rouge, et (3) de comparer l'efficacité des modèles global et local du Pic à Tête Rouge versus deux compétiteurs potentiels pour l'espace et le temps, et explorer les variations locales des relations interspecifiques. Pour tester notre hypothèse, nous avons étudié l'utilisation et les associations multiéchelles de l'habitat du Pic à Tête Rouge, et la survie au nid près de la frontière nord de sa distribution dans le sud de l'Ontario, où les populations sont en rapide déclin. De plus, nous avons modélisé l'abondance interspécifique à travers le sud du Canada et le centre-est des États-Unis en utilisant

45 ans de données de recherche du Relevé des oiseaux nicheurs (BBS) pour le Pic à Tête Rouge et deux potentiels compétiteurs (Étourneau Sansonnet et Pic à Ventre Roux (*M. carolinus*).

Des résultats basés sur la recherche sur le terrain ont démontré que le Pic à Tête Rouge présente une utilisation multiéchelles de l'habitat mésadaptée, ce qui suggère la possibilité d'un piège écologique pour l'espèce. De façon spécifique, les caractéristiques de l'habitat qui promouvaient le potentiel alimentaire tels que l'ouverture de la canopée et des membres plus longs étaient systématiquement associés à l'occupation de l'habitat à l'échelle de l'arbre du nid et du boisé par le Pic à Tête Rouge, malgré des corrélations avec un plus faible succès de reproduction. Une étude plus poussée de la survie au nid du Pic à Tête Rouge en modélisant une suite de pilotes abiotiques, biotiques, temporels et basés sur l'habitat a démontré que l'abondance de l'Étourneau Sansonnet près des sites de nids de pic actifs était le plus fort facteur influençant la survie au nid du pic. L'exposition logistique survie des nids en supposant une survie constante (68%) a chuté de façon significative lorsque l'abondance de l'Étourneau était considérée (13%). Lorsque les relations d'abondance interspécifiques ont été examinées à une plus grande échelle spatiale, elles se sont trouvées être structurées spatialement, et suggéraient une preuve de la compétition interspécifique entre le Pic à Tête Rouge et l'Étourneau et de la différentiation de niche entre les Pics à Tête Rouge et à Ventre Roux. Cette recherche démontre l'importance des études multiéchelles et à facteurs multiples lors de la détermination des menaces pour les espèces en péril, et aidera au développement de décisions relatives à la conservation, la gestion et l'élaboration des politiques pour cette espèce.

Contribution of the authors

This thesis consists of three manuscripts, of which the candidate was fully responsible for the design, development and execution of the field-based research studies, collection and analysis of the data, discussion of the results, and writing of the thesis and manuscripts. However, this work could not have been achieved without the contribution of the thesis co-supervisors, Drs. Joseph J. Nocera and James W. Fyles, who provided guidance, advice, and support during the preparation, fieldwork, data analysis, interpretation of findings, and writing of this manuscript, as well as geostatistical input from Dr. Jeffrey Cardille in Chapter 5.

Chapter 3 (Maladaptive Habitat Use of a North American Woodpecker in Population Decline) was co-authored by B. Frei, J.W. Fyles and J.J. Nocera and published in *Ethology*. Chapter 4 (Invasive Species Interference Competition as an Evolutionary Trap for a Threatened North American Woodpecker) was co-authored by B. Frei, J.J. Nocera and J.W. Fyles with planned submission to *Auk*. Chapter 5 (Geographic-Dependency in the Relationship Between a Threatened Species and Two Possible Competitors*)* was co-authored by B. Frei, J.W. Fyles, J. Cardille and J.J. Nocera with planned submission to *Ecography*. Each chapter includes a list of literature cited, with Ch. 3-5 formatted in the style of the published or submitted chapters. All other chapters are in consistent with *Ethology* referencing style.

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Chapter 1

1. Literature Review

1.1 Focal Species: The Red-headed Woodpecker

1.1.1 Red-headed Woodpecker Natural History

The Red-headed Woodpecker (*Melanerpes erythrocephalus*) is a charismatic, easily recognizable North American woodpecker found in eastern-central southern Canada and the United States. Despite the species' conspicuousness, there is surprisingly little past research on the species (Smith et al. 2000). Red-headed Woodpeckers are sexually monomorphic (with both adult males and females head's brilliant red) and are indistinguishable in the field (Smith et al. 2000). Although a migratory species, especially in northern and western portions of the range, yearly migration dynamics are highly variable and driven by hard mast crops (Zimmerman 1993).

Red-headed Woodpeckers are found in deciduous woodlands, sparsely wooded open country habitat such as temperate savannahs or pasturelands, riparian edges, and human-modified habitats such as managed woodlots, parks, and golf courses (Bent 1939; Reller 1972; Conner 1976; Ingold 1994b). During the breeding season, Red-headed Woodpeckers excavate nest cavities in snags or dead branches/portions of live trees (Reller 1972; Sedgwick & Knopf 1990). Male woodpeckers do most of the cavity excavation and typically initiate excavation near a natural crack or crevice, suggesting the species is a relatively 'weak' excavator (Jackson 1976; Ingold

1994b). The species also demonstrates strong site fidelity, returning to the same nest site, nest tree, or even nest cavity for several years in a row (Ingold 1991, 1994a; B. Frei, unpub. data).

The most omnivorous of North American woodpeckers, Red-headed Woodpeckers feed on a wide variety of food items including: seeds and nuts, crops such as corn (*Zea mays*), berries, fruit, insects, and even occasional mice, and other bird eggs and nestlings (Beal 1911; Smith et al. 2000). Unlike a majority of North American woodpeckers that feed on trees by gleaning or excavating insects from on and under the bark, Red-headed Woodpeckers capture insects on the ground by swooping down from a perch or on the wing by 'flycatching' (Short 1982). They are also one of only four woodpeckers in the world (198 spp.) that commonly stores food, and the only species that will cover stored food with wood or bark (Vander Wall 1990). Greater diversity in their foraging techniques and diet may allow Red-headed Woodpecker to inhabit smaller habitat patches than other woodpeckers in North America (Blake 1983; Blake & Karr 1987).

1.1.2 Population Demographics and Reasons for Declines

Consistent, long-term population declines have resulted in the Red-headed Woodepcker being listed as a threatened species in Canada and several states in the United States. There is however little research quantifying the potential drivers of the species' population decline, which fails to serve conservation or policy action. The species' historical population declines (prior to the 1900s) are attributed primarily to loss of vast expanses of mature hardwood following European settlement (Brewer 1853; Skutch 1985). As a species with a well-known affinity for small forest patches and edge-like habitat, historical habitat use was likely confined to forest edges and openings created due to natural disturbances such as fire, wind storms, or beaver (*Castor Canadensis*) activity (Smith et al. 2000). In addition, the species was persecuted as a presumed pest of fruit and nut crops, but crop losses due to the species have been minimal since monocultures have become extensive and the species is no longer hunted (Brewer 1853; Skutch 1985). This presents the perplexing ecological question of how populations of this widely distributed species, which has been shown to occupy and breed in a variety of habitats from expansive forests to small patches are continuing to decline at an increasing rate (Smith et al. 2000). The North American Breeding Bird Survey (BBS) has shown that from 1966-2007 the Red-headed Woodpecker populations have declined -2.7% per year (Sauer et al. 2008). Since 1980 however, this decline has steepened to -4.1%/year (Sauer et al. 2008). Certain areas, such as Ontario, have experienced even more dramatic declines; -5.7%/year from 1968-2008 and -24.2%/year from 1998-2008 (Collins & Downes 2009).

Several factors have been suggested for the more recent declines of Red-headed Woodpeckers populations such as the loss of snags used for nest and roost sites due to deadwood removal in urban areas and fire-wood cutting, clear-cutting, fire suppression and agricultural intensification in rural areas, collision with motor vehicles, and pesticide/chemical exposure (Ehrlich et al. 1992; Graber et al. 1977; Smith et al. 2000), and possible interference competition with other cavity nesters such as European Starlings (*Sturnus vulgaris*) and/or Red-bellied Woodpeckers (*M. carolinus*; Ingold 1989, 1994a). In certain areas, local Red-headed Woodpecker population increases and subsequent decreases paralleled the proliferation of dead American elms, possible nest sites for the species, following the spread of the Dutch elm disease, and subsequent decline of nest sites in the absence of recruitment of new elm snags (Kendeigh 1982; Smith el al. 2000).

1.1.3 Red-headed Woodpecker Habitat Associations

Red-headed Woodpecker habitat use has been described across a variety of environments including: golf courses, savannahs, managed deciduous woodlots, and mixed ponderosa pine (*Pinus ponderosa*) and aspen (*Populus* spp.) woodlands (Conner 1976; Ingold 1994b; Rodewald et al. 2005; Vierling & Lentile 2006; King et al. 2007). Certain habitat associations, such as forest openness and higher densities of standing dead wood are consistent across a variety of habitat types and geographic locations (Conner 1976; Sedgwick & Knopf, 1990; Rodewald et al. 2005; King et al. 2007). Red-headed Woodpeckers use dead trees or dead limbs for nesting, as perches from which to flycatch, and as locations to cache food (Smith et al. 2000). Their relationship to standing dead wood is an integral part of the species' breeding habitat requirements, so much so that their habitat selection seems subject to a decadent-tree threshold that can be accurately measured by the number of trees with dead limbs surrounding nests (King et al. 2007). Other habitat variables associated with Red-headed Woodpecker use or occupancy, including tree species, nest cavity placement in dead tree (snag) vs. dead limb in live tree, nest tree height and width, and understory composition and density do not vary within predictable ranges (Conner 1976; Jackson 1976; Gutzwiller & Anderson 1987; Ingold 1994b; Rodewald et al. 2005; Vierling & Lentile 2006; King et al. 2007).

1.1.4 European Starlings as Interference Competitors

The European Starling was introduced in North America on the east coast in 1890 and was established across most of the continent south of the tree line by the 1970s (Kessel 1953; Cabe

1993). European Starlings are hole-nesting birds but, as they cannot excavate a cavity, they must use existing natural or previously excavated cavities, and/or expropriate a nest cavity from another species. As such, starlings commonly usurp nest cavities and are considered interference competitors for woodpeckers and secondary cavity nesters (e.g. bluebirds) in North America and Europe (Troetschler 1976; Weitzel 1988; Carter et al. 1989; Ingold 1989, 1996; Kerpez & Smith 1990; Vierling 1998; Mazgajski 2000; Smith 2005, 2006; Koch et al. 2012).

European Starlings and Red-headed Woodpeckers have similar small-scale (i.e., nest tree and nest patch) habitat affinities, including a tendency to nest in cavities in dead limbs, an affinity for habitats with a higher density of trees with dead limbs, and greater canopy openness (Sedgwick & Knopf 1990). In an ordination analysis of nest sites of 10 cavity-nesting species in Iowa, Stauffer and Best (1982) found Red-headed Woodpeckers, European Starlings, and Red-bellied Woodpeckers used very similar nest-sites and suggested the potential for competition between these species. Usurpation of active Red-headed Woodpecker nest cavities by European Starlings has been commonly observed (Stauffer & Best 1982; Ingold & Densmore 1992; Ingold 1994a).

Evidence on the influence of interference competition by starlings on Red-headed Woodpecker fitness or populations is limited to observations of aggressive interactions between the two species at active Red-headed Woodpecker nest sites (Ingold & Densmore, 1992; Ingold 1994a) and a comparison of mean densities of Red-headed Woodpeckers before and after starling invasions using Christmas Bird Count (CBC) and BBS data (Koenig 2003). However, support for the hypothesis that starlings negatively influence Red-headed Woodpeckers is modest, as the woodpeckers reportedly win a majority of aggressive interactions with starlings (Ingold &

Densmore 1992; Ingold 1994a), and mean woodpecker densities did not differ pre- and post-starling invasions (Koenig 2003). In comparison, as European Starling populations have decreased in Britain over the last four decades, the native Great-spotted Woodpecker's (*Dendrocopos major*) breeding success and measures of fitness increased (Smith 2005), suggesting a 'release' from interference competition with starlings. If indeed the Great-spotted Woodpecker is negatively influenced by competition with starlings, the consequence of starling competition on the threatened Red-headed Woodpecker is well worth investigating.

1.2 Habitat Use: Exploring Animal-Habitat Association

1.2.1 Quantifying Habitat Use

Breeding habitat use is a hierarchical process (Orians & Wittenberger 1991) in which individuals select landscapes, territories, nest patch, and finally a nest site that should offer them the highest available fitness (i.e., adaptive habitat use; Fretwell & Lucas 1970). The terms 'habitat use' and 'habitat selection' have often been used interchangeably and are mistakenly assumed to be the same. Describing habitat selection requires the understanding of complex behavioural and environmental process, where the use of the habitat is an end product of a complex selection process (Jones 2001). True habitat selection studies would generally be observed in an experimental setting where individuals are allowed to choose among equally accessible options. In comparison, habitat use of a species is most often measured via its occupancy or absence in the habitat under study. This usually involves a comparison of occupied nest plots to unoccupied plots within the same study area (Gutzwiller & Anderson 1987; Li & Martin 1991; Misenhelter & Rotenberry 2000; Newlon & Saab 2011).

1.2.2 Habitat Use and the Importance of Spatial Scale

Habitat use is an inherently a scale-sensitive process, with both temporal and spatial scale influencing how an animal can and will use the landscape and resources (Mayor et al. 2009). As such, habitat use measured at one scale may not necessarily allow for predicting use at another scale (Mayor et al. 2009). Research at multiple spatial scales enables inferences about drivers of habitat use at various scales, and gives a superior portrayal of habitat use patterns compared to single scale studies (Poizat & Pont 1996). Habitat use and association may vary between scales for the same species due to scale-dependent spatial distribution of habitat components (Boyce et al. 2006; Anderson et al. 2005; Mayor et al. 2007), and/or limiting factors (i.e. resources, competition) that vary with scale (Rettie & Messier 2000; Mayor et al. 2009).

Most habitat use research assumes a hierarchical process of either top-down or bottom-up effects, where habitat use at each scale is nested within another (Johnson 1980). Understanding species breeding ecology or measuring individual fitness necessarily focuses research at smaller spatial scales, yet ecological relationships on small-scales are driven and/or confounded by dynamics on larger-scales. Within a hierarchical framework, this would allow population-limiting factors and habitat use to be linked across spatial scales (Rettie & Messier 2000), or to identify tradeoffs when multiple drivers of habitat use occur on the same scale (Dussault et al. 2005). For example, predator avoidance (a dominant fitness constraint) trumps foraging decisions (e.g., in response to temporary resources shortages) as a driver of habitat use by animals (Bowers & Dooley 1993; Folt et al. 1998; Dussault et al. 2005; Mayor et al. 2009). Although multi-scale research improves our understanding of habitat use, and the findings at each scale are pertinent in driving specific conclusions, each on its own is just a piece of the overall story (Wiens 1989). Research is often influenced by logistics and constraints beyond the ecological aspect, yet whenever possible carefully considered multi-scale research should become the standard. Lastly, multi-scale research on species of conservation concern is especially important, as management opportunities may vary or be limited by the scale at which they can be implemented (Nocera et al. 2008).

1.2.3 Adaptive and Maladaptive Habitat Use

The way animals use habitats is the result of a complex balance of rewards and risks (Mayor et al. 2009). For habitat use to be considered adaptive (balanced) it must include ideal choice, wherein an individual accurately assesses the options and correctly chooses the one offering higher fitness (Fretwell & Lucas 1970). Poor habitat choices (those that are unbalanced) yielding non-adaptive (i.e., no 'reward' of higher fitness due to choice taken) habitat use may arise from imperfect spatial knowledge of available habitat (Lima & Zollner 1996), limited availability of cues used to assess the habitat at the time of choice (Orians & Wittenberger 1991; Schlaepfer et al. 2002), conflicting benefits (e.g., mate choice; Kokko & Sutherland 2001), site fidelity (Pulliam & Danielson 1991), or incorrect social cues (Rieucau & Giraldeau 2011). Non-adaptive habitat choice occurs along a continuum of mismatches between use and fitness, including non-ideal (use fails to influence fitness) and maladaptive habitat use (use lowers fitness) (Kristian 2003; Battin 2004; Arlt & Pärt 2007).

1.3 Novel Habitats and Trap Mechanisms

1.3.1 Ecological Novelty in a Changing World

Humans, and their activities, are now the world's greatest biotic driver of ecological and evolutionary changes (Palumbi 2001). Human-induced rapid environmental changes (HIREC) are driving the vast majority of biodiversity loss worldwide (Czech & Krausman 1997; Dobson et al. 1997; May & Tregonning 1998). Five major types of HIREC are habitat loss and/or fragmentation, interactions with non-native species, harvesting by humans, pollution, and climate change (Gurevitch & Padilla 2004; Rohr et al. 2006; IPCC 2007; Lockwood et al. 2007; Salo et al. 2007; Fabry et al. 2008; Sih et al. 2011). Despite different mechanisms and effects, all HIRECs are alike in creating rapidly changing, ecologically novel conditions unlike those that species have encountered their evolutionary past (Palumbi 2001). Ecosystems resulting from HIRECs are described as ecologically novel as they are different in composition, function, and/or appearance from past ecosystems (Robertson et al. 2013).

A main goal of conservation biology is to discern the factors leading to species' population declines in order to halt or mitigate them. To sustain or enhance populations of threatened species, they must either be protected on native or restored habitat in a near pristine state, or managed on ecologically novel, anthropogenic habitats with their corresponding communities (Schlaepfer et al. 2002). For certain species, native habitats have long since disappeared via extensive land use changes (Kerr & Deguise 2004), and are thus economically unfeasible for necessary restoration. In Canada, the area predominantly modified by human presence is in the southern part of the country, which likewise has the greatest species richness (Kerr & Cihlar

2004). Thus species-at-risk occupying these areas, such as the Red-headed Woodpecker, must be managed in the context of the existing habitat and community.

1.3.2 Evolutionary and Ecological Traps

HIREC is a challenge to which most animals must respond (Sih et al. 2011; Robertson et al. 2013). These rapid and novel changes are responsible for a disjoint between environmental cues and the conditions they were associated with in the past, resulting in an inability by some animals to properly assess the fitness values or costs associated with habitats, resources, and inter-/intra-species interactions (Sih et al. 2011; Robertson et al. 2013). This disjoints of behavioural choices (i.e., the inability of an animal to avoid choices or interactions (or preferentially seek them out) that lower their fitness) is termed an evolutionary trap (Schlaepfer et al. 2002). A well-known type of evolutionary trap is when an animal is preferentially attracted to a (novel) habitat type in which it experiences lower fitness; this specific type of trap is termed an ecological trap (Dwernychuk & Boag 1972; Robertson et al. 2013). Maladaptive habitat use is a component of an ecological trap, an extreme case of use and fitness mismatch assumed to arise as a consequence of rapid environmental change (e.g., anthropogenic) and leading to the disjoint between interpretation of habitat quality cues and the true quality of the habitat (Kokko & Sutherland 2001; Battin 2004; Robertson & Hutto, 2006).

There are three mechanisms in which evolutionary traps occur: (1) Attraction: anthropogenic changes alter environmental cues making options that result in lower fitness appear as or more attractive than those that increase fitness; (2) Degradation: a reduction in the benefit associated with a choice or situation without a parallel reduction in the associated cues, and (3) Combination: a combination of both a greater attraction of the cues and degradation of the choice (Robertson et al., 2013). The degradation mechanism appears to be the most common trap (Robertson et al., 2013), especially in the case of a habitat-based, ecological trap.

Non-native, exotic species (spread purposefully or accidentally by humans) are the prominent drivers of evolutionary traps (Schlaepfer et al. 2005; Rodewald et al. 2011; Robertson et al. 2013). When faced with predation, competition, or other interaction with non-native species, to survive native species must either learn or evolve mechanisms to cope (e.g. avoidance, increased defense mechanisms, and/or improved competition capabilities) and persist in the environment (Ancel Meyers & Bull 2002; Schlaepfer et al. 2005). The ecological impact of non-native species can be compounded by additional HIREC creating novel environments that benefit non-natives (Byers 2002; Schlaepfer et al. 2005). The survival of 'trapped' native species is linked to their potential for genetic variation and behavioural plasticity to respond to novel cues, and/or if the native population is large enough for persistence to reach a point of adaptive shifts in behaviour (Schlaepfer et al. 2002).

1.3.3 Mitigation and Disarming of Traps: What Can Be Done?

Behavioural and evolutionary processes are rarely integrated into conservation and management strategies (Schlaepfer et al. 2005), and are assumed to exist at spatial and temporal scales beyond human capabilities to influence (Ashley et al. 2003). For example, it is costly, and unlikely, to completely exterminate non-native species after establishment, management for native species must proceed with the non-native species in mind and consider the native species' ability to survive given their evolutionary history and behavioural ecology (Shea & Chesson 2002; Schlaepfer et al. 2005). In such cases, survival of the 'trapped' native species can be subsidized until such a time that the species has adapted to the novel environment and/or evolved to persist without human intervention (Schlaepfer et al. 2005). Species with high behavioural plasticity may be the most capable to safely adapt to novel situations or environments while neophilic, exploratory animals may be more susceptible to falling into evolutionary traps (Robertson et al. 2013).

Schlaepfer and colleagues (2005) suggest two approaches to integrating evolutionary concepts into management and conservation efforts. The first is to allow native species to be sufficiently exposed to novel ecological conditions to initiate an evolutionary change in behaviour, but without subjecting the population to local extinctions. Regulated trap exposure might be accomplished using temporal or spatial refugia, and/or by temporarily reducing the abundance of the non-native species (Schlaepfer et al. 2005); both methods would provide short-term relief of the evolutionary trap and allow native species populations to respond. This approach requires the theories of population genetics to be included into traditional management efforts and increases the likelihood that native species populations may successfully progress to surviving in a ecologically novel situation (Rice & Emery 2003; Schlaepfer et al. 2005). A second approach is to introduce experienced (i.e., possibly adapted) members to naïve (i.e., un-adapted) communities to expedite adaptive behaviour in the population (Schlaepfer et al. 2005).

Recent research indicates evolutionary traps are more common than originally assumed, with examples of traps influencing a broad taxonomic range of animals (see Robertson et al. 2013). Understanding the mechanisms underlying the traps, their severity, and the potential to manage the effects of the traps is imperative for future survival of the trapped species.

1.4 Red-headed Woodpeckers in a Novel World

Using a theoretical ecology framework, I explore the possibility that the threatened Red-headed Woodpecker is caught in one or more evolutionary traps, thus contributing to its past and ongoing declines. As a species now found predominantly in human-modified landscapes, Red-headed Woodpeckers are susceptible to the trap of ecologically novel conditions created by HIRECs. In particular, habitat degradation and the introduction of the non-native European Starlings are two possible mechanisms of traps for the species. To answer the specific questions outlined in Chapter 2, I undertook multi-scale field-based studies, as well as employed geospatial statistical techniques using 45 years of citizen science survey data to investigate the roles of maladaptive behaviour and evolutionary traps in the decline of this threatened woodpecker.

1.5 Literature Cited

Ancel Meyers, L. & Bull, J.J. 2002: Fighting change with change: adaptive variation in a uncertain world. Trends in Ecology & Evolution **17**, 551–557.

Anderson, D.P., Turner, M.G., Forester, J.D., Zhu, J., Boyce, M.S., Beyer, H. & Stowell, L. 2005: Scale-dependent summer resource selection by reintroduced elk in Wisconsin, U.S.A. Journal of Wildlife Management **69**, 298–310.

Arlt, D. & Pärt, T. 2007: Nonideal breeding habitat selection : A mismatch between preference and fitness. Ecology **88**, 792–801.

Ashley, M., Willson, M., Pergams, R.W., O'Dowd, D.J., Gende, S.M. & Brown, J.S. 2003: Evolutionarily enlightened management. Biological Conservation **111**, 115–123.

Battin, J. 2004: When good animals love bad habitats: Ecological traps and the conservation of animal populations. Conservation Biology **1**, 1482–1491.

Beal, F.E.L. 1911: Food of woodpeckers of the United States. U.S. Dep. Agricultural Biological Survey Bulletin No. 37., U.S.A.

Bent, A.C. 1939: Life histories of North American woodpeckers. U.S. Natl. Mus. Bull. 174.

Blake, J.G. 1983: Trophic structure of bird communities in forest patches in east-central Illinois. Wilson's Bulletin **95**, 416-430.

Blake, J.G. & Karr, J.R. 1987: Breeding birds in isolated woodlots: area and habitat relationships. Ecology **68**, 1724-1734.

Bowers, M.A. & Dooley, J.L. 1993: Predation hazard and seed removal by small mammals: microhabitat versus patch scale effects. Oecologia **94**, 247–254.

Boyce, M.S. 2006: Scale for resource selection functions. Diversity and Distributions **12**, 244-257.

Brewer, T.M. 1853: Wilson's American Ornithology. Samuels, H.S., ed. New York, N.Y., U.S.A.

Byers, J. 2002: Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. Oikos **97**, 449–458.

Cabe, P.R. 1993: European Starling (*Sturnus vulgaris*). In: The Birds of North America (Poole, A. ed). Cornell Lab of Ornithology, Retrieved from the Birds of North America Online, Ithaca. doi:10.2173/bna.518

Carter, J., Walters, J., Everhart, S. & Doerr, P. 1989: Restrictors for Red-cockaded Woodpecker cavities. Wildlife Society Bulletin **17**, 68–72.

Collins, B.T. & Downes, C.M. 2009: The North American Breeding Bird Survey, Results and Analysis 1966-2007. Version 5.15.2008. USGS Patuxent Wildlife Research Center, U.S.A.

Conner, R.N. 1976: Nesting habitat for Red-headed Woodpeckers in southwestern Virginia. Bird-Banding **47**, 40–43.

Czech, B. & Krausman, P. 1997: Distribution and causation of species endangerment in the United States. Science **277**, 1116–1117.

Dobson, A., Rodriguez, J., Roberts, W., Wilcove & D. 1997 Geographic distribution of endangered species in the United States. Science **275**, 550–553.

Dussault, C., Ouellet, J., Courtois, R., Huot, J., Breton, L. & Jolicoeur, H. 2005: Linking moose habitat selection to limiting factors. Ecography **5**, 619– 628.

Dwernychuk, L.W. & Boag, D.A. 1972: Ducks nesting in association with gulls - an ecological trap? Canadian Journal of Zoology **50**, 559–563.

Ehrlich, P.R., Dobkin, D.S. & Wheye D. 1992: Birds in jeopardy. Standford University Press, Stanford, CA. U.S.A.

Fabry, V.J., Seibel, B.A., Feely, R.A. & Orr, J.C. 2008: Impacts of ocean acidification on marine fauna and ecosystem processes. ICES Journal of Marine Science **65**, 414–432.

Folt, C.L., Nislow, K.H. & Power, M.E. 1998: Implications of temporal and spatial scale for Atlantic salmon (*Salmo salar*) research. Canadian Journal of Fisheries and Aquatic Sciences **55**, 9–21.

Fretwell, S.D. & Lucas, H.R. 1970: On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical Development. Acta. Biotheor. **19**, 16-36.

Graber, J.W., Graber, R.R. & Kirk, E.L. 1977: Illinois birds: Picidae. Illinois Natural History Survey Biological Notes, no. 102.

Gurevitch, J. & Padilla, D.K. 2004: Are invasive species a major cause of extinctions? Trends in Ecology & Evolution **19**, 470–4.

Gutzwiller, K.J. & Anderson, S.H. 1987: Multiscale associations between cavity-nesting birds and features of Wyoming streamside woodlands. Condor **89**, 534–548.

Ingold, D.J. 1989: Nesting phenology and competition for nest sites among Red-headed and Red-bellied Woodpecker and European Starlings. Auk **106**, 209–217.

Ingold, D.J. 1991: Nest-site fidelity in Red-headed and Red-bellied woodpeckers. Wilson's Bulletin **103**, 118-122.

Ingold, D.J. 1994a: Influence of nest-site competition between European Starlings and woodpeckers. Wilson's Bulletin **106**, 227–241.

Ingold, D.J. 1994b: Nest-site characteristics of Red-bellied and Red-headed Woodpeckers and Northern Flickers in east-central Ohio. Ohio Journal of Science **94**, 2–7.

Ingold, D.J. 1996: Delayed nesting decreases reproductive success in Northern Flickers: Implications for competition with European Starlings. Journal of Field Ornithology **67**, 321–326.

Ingold, D.J. & Densmore, R. 1992: Competition between European Starlings and native woodpeckers for cavity nests in Ohio. Sialia **14**, 41–80.

IPCC 2007: Summary for policymakers. In: Climate Change: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (Solomon, S., Qin, D., Manning, M., Chen, Z., & Marquis, M., eds). Cambridge University Press, Cambridge, U.K., pp. 1–18.

Jackson, J.A. 1976: A comparison of some aspects of the breeding ecology of Red-headed and Red-bellied Woodpeckers in Kansas. Condor **78**, 67–76.

Johnson, D.H. 1980 The comparison of usage and availability measurements for evaluating resource preference. Ecology **61**, 65–71.

Jones, J. 2001: Habitat selection studies in avian ecology: a critical review. Auk **118**, 557-562.

Kendeigh, S.C. 1982. Bird populations in east central Illinois: fluctuations, variations, and development over a half-century. Illinois Biological Monograph 52**.**

Kessel, B. 1953 Distribution and migration of the European Starling in North American. Condor **55**, 49-67.

Kerpez, T.A. & Smith, N.S. 1990: Competition between European Starlings and native woodpeckers for nest cavities in Saguaros. Auk **107**, 367–375.

Kerr, J. & Cihlar, J. 2004: Patterns and causes of species endangerment in Canada. Ecological Applications **14**, 743–753.

Kerr, J.T. & Deguise, I. 2004: Habitat loss and the limits to endangered species recovery. Ecology Letters **7**, 1163–1169.

King, R.S., Brashear, K.E. & Reiman, M. 2007: Red-headed Woodpecker nest-habitat thresholds in restored savannas. Journal of Wildlife Management **71**, 30–35.

Koch, A., Martin, K. & Aitken, K. 2012: The relationship between introduced European Starlings and the reproductive activities of Mountain Bluebirds and Tree Swallows in British Columbia, Canada. Ibis **154**, 590–600.

Koenig, W.D. 2003: European starlings and their effect on native cavity-nesting birds. Conservation Biology **17**, 1134–1140.

Kokko, H. & Sutherland, W.J. 2001: Ecological traps in changing environments: Ecological and evolutionary consequences of a behaviourally mediated Allee effect. Evolutionary Ecology Research **3**, 537–551.

Kristian, W.B.I. 2003: The role of habitat selection behaviour in population dynamics : source-sink systems and ecological traps. Oikos **103**, 457–468.

Li, P. & Martin, T.E. 1991: Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. Auk **108**, 405–418.

Lima, S.L. & Zollner, P.A. 1996: Towards a behavioural ecology of ecological landscapes. Trends in Ecology & Evolution **11**, 131–135.

Lockwood, J.L., Hoopes, M.F. & Marchetti, M.P. 2007: Invasion Ecology. Blackwell, Oxford, U.K.

May, R.M. & Tregonning, K. 1998: Global conservation and UK government policy. In: Conservation in a Changing World (Mace, G.M., Balmford, A., Ginsberg, J.R., eds.) Cambridge University Press, Cambridge, UK, pp. 287-301.

Mayor, S.J., Schaefer, J.A., Schneider, D.C., Mahoney, S.P. (2007) Spectrum of selection: New approaches to detecting the scale-dependent response to habitat. Ecology 88: 1634–1640.

Mayor, S.J., Schneider, D.C., Schaefer, J.A. & Mahoney, S.P. 2009: Habitat selection at multiple scales. Ecoscience **16**, 238–247.

Mazgajski, T. 2000: Competition for nest sites between Starling *Sturnus vulgaris* and other cavity nesters - study in a forest park. Acta Ornithologica **35**, 103–107.

Misenhelter, M. & Rotenberry, J.T. 2000: Choices and consequences of habitat occupancy and nest site selection in Sage Sparrows. Ecology **81**, 2892–2901.

Newlon, K.R. & Saab, V.A. 2011: Nest-site selection and nest survival of Lewis's Woodpecker in aspen riparian woodlands. Condor **113**, 183–193.

Nocera, J.J., Forbes, G.J., & Milton, G.R. 2008: The relevance of local-scale relationships to habitat management and landscape patterns. Avian Conservation and Ecology **3**, 4 [online] http://www.ace-eco.org/vol3/iss1/art4/

Orians, G.H. & Wittenberger, J.F. 1991: Spatial and temporal scales in habitat selection. American Naturalist **137**, S29–S49.

Palumbi, S.R. 2001: Humans as the world's greatest evolutionary force. Science **293**, 1786–90.

Poizat, G. & Pont, D. 1996: Multi-scale approach to species-habitat relationships: Juvenile fish in a large river section. Freshwater Biology **36**, 611-622.

Pulliam, H.R. & Danielson, B.J. 1991: Sources, sinks, and habitat selection: A landscape perspective on population dynamics. American Naturalist **137**, S50–S66.

Reller, A.W. 1972: Aspects of behavioural ecology of Red-headed and Red-bellied woodpeckers. American Midland Naturalist **88**, 270–290.

Rettie, W.J. & Messier, F. 2000: Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. Ecography **23**, 466–478.

Rice, K. & Emery, N. 2003: Managing microevolution: restoration in the face of

global change. Frontiers in Ecology and the Environment **1**, 469–478.

Rieucau, G. & Giraldeau, L.-A. 2011: Exploring the cost and benefits of social information use: an appraisal of current experimental evidence. Philosophical Transactions of the Royal Society B **366**, 949-957.

Robertson, B.A. & Hutto, R.L. 2006: A framework for understanding ecological traps and an evaluation of existing evidence. Ecology **87**, 1075–1085.

Robertson, B.A., Rehage, J.S. & Sih, A. 2013: Ecological novelty and the emergence of evolutionary traps. Trends in Ecology & Evolution **1696,** 1–9.

Rodewald, A.D., Shustack, D.P. & Jones, T.M. 2011: Dynamic selective environments and evolutionary traps in human-dominated landscapes. Ecology **92**, 1781–8.

Rodewald, P.G., Santiago, M.J. & Rodewald, A.D. 2005: Habitat use of breeding Red-headed Woodpecker on golf courses in Ohio. Wildlife Society Bulletin **33**, 448–453.

Rohr, J.R., Kerby, J.L., Sih, A. (2006) Community ecology as a framework for predicting contaminant effects. Trends in Ecology & Evolution 21: 606–13.

Salo, P., Korpimäki, E., Banks, P.B., Nordström, M. & Dickman, C.R. 2007: Alien predators are more dangerous than native predators to prey populations. Proceedings of The Royal Society **274**, 1237–43.

Sauer, J.R., Hines, J.E. & Fallon, J. 2008: The North American Breeding Bird Survey, Results and Analysis 1966-2007. Version 5.15.2008. USGS Patuxent Wildlife Research Center, U.S.A.

Schlaepfer, M.A., Sherman, P.W., Blossey, B. & Runge, M.C. 2005: Introduced species as evolutionary traps. Ecology Letters **8**, 241–246.

Schlaepfer, M., Runge, M. & Sherman, P. 2002: Ecological and evolutionary traps. Trends in Ecology & Evolution **17**, 474–480.

Sedgwick, J.A. & Knopf, F.L. 1990: Habitat relationships and nest site characteristics of cavity-nesting birds in cottonwood floodplains. The Journal of Wildlife Management **54**, 112–124.

Shea, K. & Chesson, P. 2002: Community ecology theory as a framework for biological invasions. Trends in Ecology & Evolution **17**, 170–176.

Short, L.L. 1982: Woodpeckers of the world. Delaware Museum of Natural History Monographs, series number 4.

Sih, A., Ferrari, M.C.O. & Harris, D.J. 2011: Evolution and behavioural responses to human-induced rapid environmental change. Evolutionary Applications **4**, 367–387.

Skutch, A.F. 1985: Life of the Woodpecker. Ibis Publishing Co., Santa Monica, CA, U.S.A.

Smith, K.G., Withgott, J.H. & Rodewald, P.G. 2000: Red-headed Woodpecker (*Melanerpes erythrocephalus*). In: The Bird in North America. (Poole, A. ed). Cornell Lab of Ornithology, Retrieved from Birds of North America Online, Ithaca, N.Y., U.S.A.

Smith, K. 2005: Has the reduction in nest-site competition from Starlings *Sturnus vulgaris* been a factor in the recent increase of Great Spotted Woodpecker *Dendrocopos major* numbers in Britain? Bird Study **52**, 307–313.

Smith, K.W. 2006: The implications of nest site competition from starlings *Sturnus vulgaris* and the effect of spring temperatures on the timing and breeding performance of great spotted woodpeckers *Dendrocopos major* in southern England. Annales Zoologici Fennici **43**, 177–185.

Stauffer, D. & Best, L. 1982: Nest-site selection by cavity-nesting birds of riparian habitats in Iowa. Wilson's Bulletin **94**, 329–337.

Troetschler, R. 1976: Acorn woodpecker breeding strategy as affected by starling nest-hole competition. Condor **78**, 151–165.

Vander Wall, S.B. 1990: Food hoarding in animals. University of Chicago Press, Chicago, IL, U.S.A.

Vierling, K.T. 1998: Interactions between European Starlings and Lewis' Woodpeckers at nest cavities. Journal of Field Ornithology **69**, 376–379.

Vierling, K.T. & Lentile, L. 2006: Red-headed woodpecker nest-site selection and reproduction in mixed ponderosa pine and aspen woodland following fire. Condor **108**, 957–962.

Weitzel, N.H. (1988) Nest-site competition between the European Starling and native breeding birds in northwestern Nevada. Condor 90: 515–517.

Wiens, J. A. 1989: Spatial scaling in ecology. Functional Ecology **3**, 385–397.

Winkler, H., Christie, D.A. & Nurney, D. 1995: Woodpeckers. A guide to woodpeckers, piculets and wrynecks of the world. Pica Press, Russel Friedman Books, South Africa.

Zimmerman, J. L. 1993: The birds of Konza. Univ. Press of Kansas, Lawrence.

Chapter 2

2. Research Questions and Objectives

This doctoral research seeks to answer the question: *Why is the Red-headed Woodpecker, a once common, widespread species with apparently a high flexibility in habitat use undergoing such large population declines?* We hypothesized that due to rapid anthropogenic changes and ecological novelties such as non-native competitors, Red-headed Woodpecker fitness and its behavioural choices and actions have become disjointed and as such the species is vulnerable to evolutionary traps. To answer this principal question, four underlying questions need to be considered:

1. **Is Red-headed Woodpecker habitat use adaptive or non-adaptive?**
    - In this research question we assume that when habitat occupancy increases fitness it is adaptive for the species, whereas occupancy that reduces fitness is non-adaptive.
    - As Red-headed Woodpecker's are predominantly using anthropogenically-altered habitats, we suspect the species may be vulnerable to non-adaptive habitat use.
    - The specific objectives of this research question can be found in Chapter 3. In this chapter our objectives were to: (1) perform a multi-scale analysis of habitat use and nesting success of Red-headed Woodpeckers in the northern edge of their range, and (2) test the prediction that the species will demonstrate non-adaptive habitat use at one or more scales.

2. **Are European Starlings a potential evolutionary trap for Red-headed Woodpeckers and influencing their fitness in ecologically novel landscapes?**
    - As European Starlings are a well-known, non-native interference competitor for nest cavities with Red-headed Woodpeckers, we suspect that the presence and/or abundance of the non-native competitor may reduce the Red-headed Woodpecker's fitness if the species struggles to evolve improved competitive abilities.
    - This question was explored in Chapter 4, where objectives included: (1) to determine the relative importance of abiotic, temporal biotic and habitat variables as drivers of Red-headed Woodpecker nest survival in southern Ontario, with particular interest of European Starling presence and/or abundance at Red-headed Woodpecker nest sites as biotic drivers, and (2) to determine nest survival of Red-headed Woodpeckers at the northern edge of their range in southern Ontario, which will assist with conservation of the species.

3. **As previous research using large-scale population demographics suggests that European Starling abundances do not have adverse effects on Red-headed Woodpeckers, is a global model analysis effective, or do local variations in the interspecies relationships exist over space and time?**
    - As Red-headed Woodpeckers and European Starlings share habitat affinities, an overall correlation between these species is expected on a global scale, but local variations may exist due to interference competition and/or habitat heterogeneity. A comparison using the Red-headed Woodpecker's congener, the Red-bellied Woodpecker enables differentiation of drivers between species relationships.

- This question was explored in Chapter 5, where objectives included: (1) to discover whether Red-headed Woodpecker, Red-bellied Woodpecker, and European Starling abundance (using North American Breeding Bird Survey data) were spatially variable (i.e., data autocorrelation or non-stationarity) and assess the validity of a global model, (2) to determine if spatially variable modelling (geographically weighted regression) captured local variation in species relationship, producing more accurate comparisons, and (3) determine species relationship over space and time (for a 45-year period).

4. **Can Red-headed Woodpeckers persist despite the challenges of rapid anthropogenic changes and ecological novelties?**
    - As it is unfeasible to return the landscape Red-headed Woodpeckers' inhabit to its pristine state, and exterminate the ubiquitous non-native European Starlings, management and recovery for this species-at-risk must take into context the species' behavioural ecology and susceptibility to evolutionary traps.
    - In Chapter 6, I explore this question through a summary of the research findings and provide recommendations for future research.

Preface to Chapter 3

Chapter 3 describes the rationale behind the project hypotheses, and focuses on Red-headed Woodpecker habitat use and occupancy in woodlots of southern Ontario and their corresponding nesting success on five spatial scales. Emphasis was placed on investigating the mismatches between use and fitness as a result of non-adaptive habitat use. This was accomplished by comparing logistic regression models of habitat variables for occupied vs. unoccupied and successful vs. unsuccessful sites at the cavity, nest tree, nest patch, woodlot, and landscape scales. Chapter 3 was co-authored by the candidate's supervisors, Drs. James W. Fyles and Joseph J. Nocera, and published in *Ethology* in March 2013.

Frei, B., Fyles, J.W., Nocera, J.J. (2013) Maladaptive Habitat Use of a North American Woodpecker in Population Decline. Ethology: 119: 377-388.

Chapter 3

3. Maladaptive Habitat Use of a North American Woodpecker in Population Decline

3.1 Abstract

Rapid anthropogenic habitat changes can lead to non-ideal habitat use by animals, often resulting in lower fitness and population declines. An extreme case of use and fitness mismatch is an ecological trap where habitat quality cues are disjointed from the true quality of the habitat. Species primarily associated with anthropogenically-altered habitat, such as Red-headed Woodpeckers (*Melanerpes erythrocephalus*), may be especially vulnerable to use and fitness mismatch as they encounter novel environmental challenges. We investigated multi-scale habitat use and nesting success of Red-headed Woodpeckers to assess their vulnerability to mismatches between use and fitness as a result of non-ideal habitat use across multiple scales. We found that habitat characteristics that promote feeding potential, such as canopy openness and greater dead limb length appeared paramount and were consistent in use across several spatial scales although reproductive fitness suffered. This contrasts with the assumption that habitat use by nesting birds should instead favor predation avoidance at smaller scales to improve reproductive fitness, and suggests that maladaptive, food-based habitat use by Red-headed Woodpeckers in southern Ontario may result in ecological traps for the species. Whether due to poor habitat choices or costly ones in favor of feeding potential, it is vital to consider this behaviour in conservation and management plans for this and similar species. We suggest multi-scale habitat use studies that consider fitness outcomes are critical for species-at-risk in human-modified landscapes.

Keywords: *Melanerpes erythrocephalus*, habitat use, maladaptive, ecological trap, multi-scale, species-at-risk

3.2 Introduction

An unprecedented rate of landscape change is a challenge to which many animals must respond, but must also correctly detect and assess habitat alterations and their subsequent effects. To be effective, conservation plans must recognize the severity and reasons surrounding species' declines and address them accordingly. Despite a wealth of knowledge generated from habitat-based studies (Mayor et al. 2009), two critical caveats are often overlooked in management plans and policies: (1) that habitat use is a scale-sensitive process (Mayor et al. 2009), and (2) that habitat selection and use may not be ideal or adaptive (Kristian 2003; Battin 2004; Chalfoun & Martin 2007).

For habitat use to be considered adaptive it must include ideal choice, wherein an individual accurately assesses the options and correctly chooses the one offering higher fitness (Fretwell & Lucas 1970). Many conditions may render a choice non-ideal, including flawed spatial knowledge of the habitat (Lima & Zollner 1996), inadequate cues to assess at the correct time (Orians & Wittenberg 1991), and conflicting benefits (Kokko & Sutherland 2001). Non-adaptive habitat choice occurs along a continuum of mismatches between use and fitness, including non-ideal (use fails to influence fitness) and maladaptive habitat use (use lowers fitness) (Kristian 2003; Battin 2004; Arlt & Pärt 2007). The latter is a component of an ecological trap, an extreme case of use and fitness mismatch assumed to arise as a consequence of rapid environmental change (e.g., anthropogenic) and leading to the disjoint between interpretation of habitat quality cues and the true quality of the habitat (Kokko & Sutherland 2001; Battin 2004; Robertson & Hutto 2006).

As critical resources may vary spatially and temporally, habitat use may be a tradeoff or maximization of different resources (Crampton & Sedinger 2011). Therefore, it is not surprising that habitat use may commonly be seen as non-ideal when investigated within a single spatial scale. Due to the intrinsic spatial aspect of habitat use (Mayor et al. 2009) it is essential for future habitat-based research to be multi-scale, especially for species of conservation importance. Recently, non-ideal selection has been demonstrated within several multi-scale studies (Misenhelter & Rotenberry 2000; Arlt & Pärt 2007; Chalfoun & Martin 2007; Sadoti & Vierling 2010).

The Red-headed Woodpecker (*Melanerpes erythrocephalus* L.) is a once common but declining bird species found in southern Canada and east-central United States (Smith et al. 2000). Consistent long-term population declines have resulted in Red-headed Woodpecker's threatened status in Canada and several states in the U.S. Throughout most of its range, the species often inhabits areas that have been heavily altered by humans and as such may be susceptible to non-ideal habitat choices. In Canada, the area predominantly modified by human presence is in the southern part of the country, which also includes the area with the mildest climate, highest habitat heterogeneity, and greatest species richness (Kerr & Cihlar 2004). The majority of at-risk species in Canada, including Red-headed Woodpeckers, are in areas best suited for and most altered by agricultural activities (Kerr & Deguise 2004). Factors suggested for substantial population declines of Red-headed Woodpeckers include: loss of standing dead wood and overall habitat, pesticide and chemical exposure (Smith et al. 2000), and possible nest-site competition with other cavity nesters such as European Starlings (*Sturnus vulgaris*) or Red-bellied Woodpeckers (*M. carolinus*) (Ingold 1989, 1994). However, no formal tests of these proposed factors have been made and very little is known of Red-headed Woodpecker's feeding habits, breeding ecology, habitat selection process, and inter- and intraspecific competition.

We chose to study Red-headed Woodpeckers in Ontario, at the northern edge of the species' range. Studying factors relevant to population decline of a species at its range edge is ecologically important as: (a) variables influencing the decline may be more visible, as the species is already facing population limitations (Thomas & Kunin 1999) and (b) peripheral populations may have strong conservation value due to their genetic diversity (Shreeve et al. 1996). In addition, according to the North American Breeding Bird Survey, Red-headed Woodpecker populations have declined > 60% over the last 20 years in Ontario, making this one of the areas with the steepest declines across the species range (COSEWIC 2007). The overall goal of this study is to determine why a once common, widespread species with an apparently high degree of flexibility in habitat use is undergoing such large population declines. The main objective of our study was to perform a multi-scale analysis of habitat use and nesting success of Red-headed Woodpeckers in the northern edge of their range, and test the prediction that the species will demonstrate non-ideal habitat use at one or more scales.

3.3 Material and Methods

3.3.1 Study Area

Our study area included two sites encompassing Elgin (1,880 km^2), Norfolk (1,607 km^2), and Northumberland (1,905 km^2) counties of southern Ontario (range: 42-43° N/81-78° W). The southern site (Elgin and Norfolk) is within the Deciduous Forest zone on the north shore of Lake Erie in southwestern Ontario, which is the mildest and most fertile part of the province (OMAFRA 2006). The northern site (Northumberland) is on the north shore of Lake Ontario in southeastern Ontario, and is characterized by undulating topography and a lower density of cash crops (e.g., corn and soybean) than other regions of southern Ontario (OMAFRA 2006).

3.3.2 Nest Monitoring

We surveyed for Red-headed Woodpecker nests for two breeding seasons (May-August of 2010-2011) at the northern site and in 2011 only in the southern site. We focused our searches by inspecting possible habitats identified from topographic maps and satellite imagery and focusing on deciduous or mixed woodlots, open woodlands, and treed agricultural or rural areas, and by following up on reports from birders and landowners. We surveyed potential sites by eliciting responses from territorial pairs by broadcasting recordings of the species' territorial calls obtained from the Cornell Lab of Ornithology's Macaulay Library collection. We broadcast calls using a handheld game call unit (FOXPRO NX3, FOXPRO Inc.) and played looped 20-sec sound clips for 1-2 minutes with a 5-min break three times at each potential site, and we visited each site twice. Through observations of breeding pairs' behaviour (copulation, cavity excavation, incubation, feeding of young) we located and determined nest stage. We used an Elevated Video Inspection System (based on Huebner & Hurteau 2007) to inspect a subset of cavity nests (≤13 m in height). We obtained geographic coordinates for each nest using a handheld GPS with ±7 m accuracy and monitored nests every 2-5 days until the nest failed (due to predation and/or abandonment) or young fledged (≥1 nestling left the nest). We confirmed fledging by observing fledglings within the breeding territory or by observing adults bringing food to locations other than the nest cavity. We considered a nest to be failed if the cavity was empty or adults abandoned the area before the earliest possible date of fledging.

3.3.3 Habitat Sampling

We measured habitat variables at five spatial scales: cavity, tree, patch, woodlot, and landscape. We chose these scales to represent the range from micro- to macro-habitat scales. After nest completion or failure, we recorded cavity, tree, patch, and woodlot characteristics (Table 3.1). We created random nest orientations (*n* = 60) by assigning computer-generated numbers from 1-8 to cardinal directions (N, NE, E, SE, S, SW, W, NW) for comparison with nest data. For tree, patch, and woodlot scales we used a constrained habitat design: (1) an unoccupied tree (deciduous tree ≥25 cm dbh) was selected randomly within each nest-patch, (2) an unoccupied patch was selected randomly within each occupied woodlot, (3) and unoccupied woodlots were selected randomly in the same study area. At each random site/scale, we measured the same independent variables as at the nest sites. We measured the patch habitat variables in a 11.3-m-radius circular plot around nest or random trees following forest bird protocols such as Martin et al. (1997) and Saab et al. (2009) with modifications (see Table 3.1). Woodlot measurements consisted of multiple patches randomly selected within the woodlot, with 1 patch/ha up to 5 ha and ≥50 m from the woodlot edge.

We measured landscape attributes within 200 m and 1000 m-radius circles centered on a nest or random unoccupied locations. We chose these sizes because: (1) the smaller scale was similar to the largest Red-headed Woodpecker territory found in South Carolina (11.4 ha; Kilgo & Vukovich 2012), and (2) we consistently observed Red-headed Woodpeckers feeding ≤1 km from their nest (B. Frei, pers. obs.). The habitat variables we measured included land cover composition, length of forest-open edge, and road length within the landscapes. We derived landscape attributes from a 30m resolution spatial data set of Geobase LCC2000-V. These 26-class data were derived from Landsat 5 and Landsat 7 imagery collected in 1996-2005.

3.3.4 Hypotheses for Statistical Analyses

We generated two hypotheses to undergo null-hypothesis testing and determine if Red-headed Woodpeckers cavity and tree use followed classical assumptions of cavity nesters. Specifically, we predicted that:

1. Nest cavities will favor a south-facing direction, and this choice will correlate with successful nests (Red-headed and Red-bellied Woodpecker, Reller 1972)
2. Nest cavities higher from the ground (woodpecker sp., Li & Martin 1991; Martin & Li 1992) and in trees that lack bark (Red-cockaded Woodpeckers (*Picoides borealis*); Saenz et al. 1999) are associated with successful nests due to safety from ground predators.

To examine two further hypotheses, we used an information-theoretical approach in evaluating whether (3) at smaller spatial scales (e.g., tree and patch) habitat features are selected that favor ‘safer’ nest sites (Martin & Roper 1988; Martin 1993) as predation is the primary cause of nest failure (Ricklefs 1969), and (4) at larger spatial scales (e.g., patch and woodlot) habitat features are selected that promote feeding potential for adults and nestlings (Parker 1986; Martin 1993). Specifically, we predicted that:

3a. Taller (TREE) and wider (DBH) nest trees offer greater protection from predation risk and thermal stress (Nilsson 1984; Li & Martin 1991), additional cavities (TCAVITY) will reduce the probability of predation as it lengthens a predator’s search duration (Martin 1988, Martin & Roper 1988).

3b. Higher cavity density (PCAVITY), lower canopy openness (OPEN), snag density (SNAG), and dead limb length (PLENGTH) will provide greater concealment from aerial predators (Martin 1993, Kilgo & Vukovich 2012), and a lower density of small trees (SMALL) may allow earlier detection of ground predators by adults (Kozma & Kroll 2012).

4a. An open canopy (OPEN) with small trees (SMALL) and coarse woody debris (CWD) is associated with a higher abundance of arthropods (Hanula et al. 2006) and aerial maneuverability for flycatching (Saab et al. 2009); snags (SNAG) and dead limbs (PLENGTH) provide perching and food caching potential (Smith et al. 2000).

4b. A landscape composed of deciduous or mixed forests, pasture, and grasslands may provide a variety of food sources for Red-headed Woodpeckers (Smith et al. 2000), and a greater forest to open edge (EDGE) length, and telephone poles along roads (ROAD) provide flycatching, perching, and food caching potential (Smith et al. 2000).

3.3.5 Statistical Analyses

We performed all statistical analyses with R version 2.13.2 (R Development Core Team 2011). We used a mix of null-hypothesis testing and an information-theoretical approach. The classical technique of null-hypothesis is well suited to simple univariate tests, while information-theoretics (IT) are appropriate for model selection and drawing inferences from multivariate ecological data. IT also minimizes loss of information, which is especially relevant in our work with an uncommon species-at-risk.

At the cavity scale, only cavity orientation allowed comparison between observed and random data. We used Chi-square tests to analyze cavity substrate and orientation (occupied vs. unoccupied) and breeding success (successful vs. unsuccessful) whereas we used Welch's t-test to compare breeding success and cavity height. Null hypothesis testing is useful for univariate causality analysis (Stephens et al. 2005), with Chi-square tests differentiating distributions of categorical (e.g., tree species) variables (Margolin & Light 1974), and Welch's t-test for comparing two populations with unequal variances (Ruxton 2006).

At the tree, patch, woodlot, and landscape scales, we used mixed-effects logistic regression (R library lme4, function lmer; R Development Core Team 2011) to model habitat use (occupied vs. unoccupied) and breeding success (successful vs. unsuccessful). Before generating a set of *a priori* candidate models, we looked for statistical correlation between habitat variables in tree and patch/woodlot scales. We accounted for possible temporal and spatial variation in our data by including study site and year as random effects. We framed our *a priori* candidate models first by different forest structures (BASAL, SMALL, MED, BIG), then adding canopy cover (OPEN), standing dead wood and existing cavities (SNAG, PLENGTH, PCAVITY), and lastly coarse woody debris (CWD).

We evaluated models using Akaike's Information Criterion adjusted for small sample sizes (AICc; Hurvich & Tsai 1989). We investigated the model set and removed similar models in which uninformative parameters increased the number of parameters without reducing the deviance (Anderson 2008; Arnold 2010). Models were then ranked according to the strength of support of each model, as determined by the difference in AICc between a given candidate model and the model with the lowest AICc (ΔAICc), and AICc weight (Anderson et al. 2001). Next, we calculated model-averaged parameter estimates (R library 'AICcmodavg', function 'modavg'; R Development Core Team 2011) with unconditional standard errors and confidence intervals (Anderson 2008). We used model averaging to eliminate information loss that may result from using only single (top) model parameter estimates (Burnham & Anderson 2002). Through post hoc exploration we considered alternative models, and by selectively removing or adding parameters to top models (lowest ΔAICc), we created post hoc models to add to the candidate set (Burnham & Anderson 2002). Lastly, additional model discrimination was evaluated with model-wide Area Under Curve (AUC) (R library 'epicalc', function 'lroc'; R Development Core Team 2011) as defined by the Receiver Operating Characteristic (ROC) (Hanley & McNeil 1982, Hosmer & Lemeshow 2000), which originates from signal theory and measures a model's ability to discriminate between a true signal and false 'noise' (Hosmer & Lemeshow 2000).

3.4 Results

3.4.1 Nest Phenology and Characteristic of Nest Cavities and Trees

We found 60 Red-headed Woodpecker nests in southern Ontario during the 2010-2011 breeding seasons: 30 nests in Elgin/Norfolk in 2011 and 30 nests in Northumberland 2010-2011. Overall, 46 nests were successful in fledgling ≥ 1 young. Because we could not access most nest cavities with the Elevated Video Inspection System, specific causes of nest failures (i.e., predation, nest usurpation, abandonment) could not be ascertained. All 60 nests were used for cavity scale analysis, and nests found in woodlots only (n = 42) for tree, patch, woodlot, and landscape scales.

As predicted (H1), cavity orientation differed between excavated nests and randomly generated aspects ($x^2 = 14.2$, df = 7, $p = 0.04$), with excavated nests favoring south-facing orientations. There was no orientation difference between successful and unsuccessful nests. Despite the variation in cavity heights ($t = -0.8$, df = 28.4, $p = 0.40$) and substrates (bark vs. no bark; $x^2 = 2.0$, df = 1, $p = 0.65$), there were no differences for breeding outcomes based on these characteristics, contrary to our predictions (H2). Nest tree mean height was 21.0 ± 1.2 m (SE), with a range from 8.0 – 42.9 m.

3.4.2 Habitat Occupation vs. Breeding Success at Multiple Scales

At the tree scale, the top two occupancy models (TLENGTH; DBH + TLENGTH) together account for 99% of the AICc weight and have good discrimination ability (Table 3.S1). Breeding success was best described by a single top model (DBH + TREE + TLENGTH) that accounts for 70% of the

AICc weight and also has good discriminatory power. Red-headed Woodpeckers predominantly occupied nest trees with lower dbh and greater dead limb length (although this was the only parameter estimate whose 95% CI did not include zero), however, successful nests trees tended to be in trees with higher dbh, greater tree height, and lesser dead limb length (Fig. 3.1, Table 3.S2).

Habitat occupancy at the patch scale was best described by two models (BASAL + SMALL + BIG + OPEN + SNAG + PLENGTH + PCAVITY + CWD; SMALL + BIG + SNAG + PLENGTH) which together account for 72% of the AICc weight and possess good to excellent model discrimination ability (Table 3.2). Model uncertainty was higher for breeding success at the patch scale, as the top model (SMALL + BIG + OPEN) accounts for 39% of the AICc weight, with the intercept-only model the sole model within a ΔAICc of 2 (Table 3.2). Despite the lower information-theoretic support, the top model had good model discrimination ability via AUC. Thus Red-headed Woodpeckers typically occupied patches with higher basal area, small and big trees, coarse woody debris and canopy openness, and a lower density of snags when to compared to random unoccupied patches in the same woodlot. Successful patches had lower basal, fewer small and big trees, less coarse woody debris and canopy openness compared to unsuccessful nests (Fig. 3.1). Dead limb length and cavity density were the only variables positively associated with both occupancy and breeding success at the patch scale (Table 3.3).

Habitat occupancy at the woodlot scale is best described by two models (SMALL + MED + OPEN + SNAG + PLENGTH; SMALL + MED + OPEN) that together account for 70% of the AICc weight and have good discrimination ability (Table 3.4). Breeding success at the woodlot scale is best described, with low model uncertainty, by a single top model (SMALL + BIG + OPEN + SNAG + PLENGTH + PCAVITY) accounting for 84% of the AICc weight with acceptable discrimination (Table 3.4). Thus Red-headed Woodpeckers occupied woodlots characterized by less basal area of medium and big trees with greater dead limb length, lower cavity density, more snags and canopy openness compared to unoccupied woodlots. Woodlots in which Red-headed Woodpeckers bred successfully had lower basal area, greater cavity density, fewer big trees, snags, and less canopy openness than woodlots with unsuccessful nests (Fig. 3.1). Dead limb length was the only significant variable positively associated with both occupancy and breeding success in woodlots (Fig. 3.1, Table 3.5).

Habitat occupancy at the landscape scale was best described by two models (EDGE1000; COMPOSITITON + EDGE1000) that together account for 95% of the AICc weight with fair and excellent discrimination abilities, respectively (Table 3.S3). All models at the 1000 m scale had considerably better fit than those at the 200 m scale. We observed high model uncertainty for breeding success at the landscape scale, because the intercept-only model (with 41% AICc weight) was ranked as the top model, followed closely with the similar weighted 200 m and 1000 m edge and the road lengths (which possessed a combined AICc weight of 46%) (Table 3.S3). All breeding success models in the candidate set had no discrimination ability. All model parameters for both habitat occupancy and breeding success on the landscape scale had CI that crossed zero. As model uncertainty for habitat occupancy models was low, we examined model-specific variable estimates for the edge 1000 m and composition + edge 1000 m models (Table 3.S4). Both the grassland and mixed forest area in the landscape are significant variables guiding Red-headed Woodpeckers landscape use at 1000 m. We assumed biological significance at $\alpha \leq$

0.1 to reduce Type I error and acknowledge the consequences of Type II error for a rare species of conservation concern. Forest to open edge length appeared to differ between occupied and random unoccupied landscapes, but with an estimate of zero, we assume these differences were extremely variable and thus difficult to quantify.

3.5 Discussion

We found Red-headed Woodpeckers exhibit maladaptive habitat use across three spatial scales, supporting the hypothesis that rapid anthropogenic changes in the landscape may render the species vulnerable to the consequences of poor habitat choices and may contribute to ongoing population declines. The habitat occupancy patterns we observed suggest food-based choices supersede those of predator avoidance across micro- to macro-scales, independent of breeding success. Several of the key habitat characteristics that we identified as important, but maladaptive at several scales, in Red-headed Woodpecker's habitat use in Ontario (such as forest openness and standing dead wood) have been shown to be central features in other studies, despite geographic and habitat type differences (Conner 1976; Sedgwick & Knopf 1990; Rodewald et al. 2005; King et al. 2007). This suggests the species is experiencing heretofore unrecognized population stressors across their range. Given this, it would appear that cavity-scale choices and use of species-specific nest trees is non-ideal but unlikely to be limiting Red-headed Woodpecker populations in southern Ontario.

Habitat use has been shown to be maladaptive for several species at territorial and landscape scales (Misenhelter & Rotenberry 2000; Weldon & Haddad 2005; Chalfoun & Martin 2007;

Hollander et al. 2011), but often remains ideal at smaller scales (i.e., nest patch; Misenhelter & Rotenberry 2000; Chalfoun & Martin 2007). Canopy openness at the woodlot scale had the strongest statistical support for describing habitat use, which indicates Red-headed Woodpeckers occupy more open woodlots; however, we found fewer successful nests in open woodlots than those with more canopy closure.

Recent research in South Carolina identified Sharp-shinned (*Accipiter striatus*) and Cooper's Hawk (*A. cooperii)* as dominant predators of adult Red-headed Woodpeckers, and determined that adult survival was positively associated with the number of cover patches available to woodpeckers within 191 m of a territory center (Kilgo & Vukovich 2012). Increased adult predation in open woodlots may contribute to unsuccessful nests by inducing abandonment. Northern Flickers (*Colaptes auratus*), Red-bellied Woodpeckers, and European Starlings have been suggested to be potential interference competitors for both nest sites and nest cavities (Ingold 1989, 1994). As Northern Flickers and European Starlings share similar habitat affinities with Red-headed Woodpeckers (Sedgwick & Knopf 1990), this may increase confrontations with Red-headed Woodpeckers in habitats with an open canopy and/or nest trees with dead limbs, leading to nest cavity or site usurpation or nest predation as a result of absence during aggressive interactions.

Contrary to our predictions and suggestions from other studies (Martin & Roper 1988, Martin 1993), habitat features that promote safer nests were not selected at smaller scales (tree and patch). Instead, dead limb length, a trait serviceable for flycatching, perching, and food-caching potential (Smith et al. 2000) is consistent with use across tree, patch, and woodlot scales.

Characteristics of used forest patches include small tree density and coarse woody debris, both associated with higher abundance of arthropods (Hanula et al. 2006, Saab et al. 2009). Thus, habitat occupancy at smaller scales (tree and patch) is consistent with the larger woodlot scale where, as predicted, habitat use favored characteristics related to feeding potential such as standing dead wood, canopy openness, and coarse woody debris. Lastly, at the landscape scale, forest to open edge length and habitat composition (especially greater grassland and mixed forest composition) at 1000 m from the nest were strong determining characteristics of habitat occupancy. In addition, grassland and mixed forest habitat patches in the landscape may increase both the edge length and the feeding habitats in a woodpecker's breeding territory. These habitat patterns suggest that comparing the relative importance of food vs. predators as population limiting factors (Martin 1995) is important for Red-headed Woodpeckers in our study area, where food-based territory choice (Burke & Nol 1998) is prevalent across micro-macro scales. This finding contrasts with several studies where predation avoidance at smaller scales is paramount, suggesting predation is a greater impediment to fitness than food shortages (Parker 1986; Bowers & Dooley 1993; Martin 1993; Misenhelter & Rotenberry 2000; Dussault et al. 2005; Fisher & Wiebe 2006; Chalfoun & Martin 2007; Cornelius 2008; Saab et al. 2009). A review of North American and European woodpecker species found predation to be the dominant cause of nest failures, similar to open-cup nesting birds (Paclík et al. 2009).

In general, Red-headed Woodpecker habitat use in southern Ontario corresponds with findings in other studies across the species range. Particularly, a strong association with forest openness (Conner 1976; Rodewald et al. 2005) and higher densities of standing dead wood (Sedgwick & Knopf 1990; Rodewald et al. 2005; King et al. 2007) are apparent at nest tree and nest patch scales. Our findings of greater small tree density at used nest patches contradicts findings where Red-headed Woodpeckers nest sites had significantly lower small tree density in (a) restored savannas in Wisconsin (King et al. 2007), and (b) Colorado cottonwood floodplains (Sedgwick & Knopf 1990). Conversely, work in South Dakota (Vierling & Lentile 2006) found higher shrub density within nest landscapes. As small trees and shrubs are conceivably similar in their microhabitat function and in provision of higher arthropod densities, these characteristics may be important for feeding potential. Yet, all three studies are in unique locations and habitats, and understory composition may be an artifact of forest age and management, thus accounting for such differences.

The predisposition of maladaptive, food-based habitat use by Red-headed Woodpeckers in southern Ontario may be resulting in an ecological trap for the species. We make this statement with caution, as ecological traps are most reliably examined using multiple proxies for preference, including settlement patterns, dominant individual distribution, site fidelity, temporal variation in population size, and choice experiments (Robertson & Hutto 2006). Although we detected marked signals of maladaptive habitat use, working with an uncommon, cavity nesting, species-at-risk presents challenges for collecting such information, so future work in this area would prove valuable. Maladaptive habitat use may result from habitat changes and resulting cues being 'misread' by animals leading to poor choices, or that the choice made, although maladaptive, is the best of a set of poor options available (Wheelwright et al. 1997; Kristian 2003). In addition, maladaptive habitat use may also occur in sink populations due to despotic distributions (Pulliam 1988; Remes 2000). We suggest that maladaptive habitat use by Red-headed Woodpeckers in southern Ontario is neither due to source-sink dynamics nor the 'best of poor choices' but is a weak ecological trap for the species. Red-headed Woodpeckers have undergone steep range-wide population declines, with declines in Ontario in the last two decades being among the most severe (Smith et al. 2000; COSEWIC 2007). In a source-sink dynamic, the proportion of occupied source habitat should increase as a population shrinks (Kristian 2003), leading to less maladaptive habitat use. Likewise, as a population shrinks, the landscape should be unsaturated and allow more of the 'best' habitats to be occupied. Most historical Red-headed Woodpeckers habitat (American chestnut (*Castanea dentate*)) and beech woodlands and savannahs) has disappeared, and the species has since used surrogate habitat such as treed rural farmland, deciduous woodlots, and a variety of anthropogenic open habitat such as campgrounds, golf courses, and parks (Smith et al. 2000). In these habitats, the birds may encounter novel challenges such as exotic competitors (European Starlings, Ingold 1989; 1994), unexpected removal of dead wood by humans, and collision with vehicles (Smith et al. 2000). Such challenges may all contribute to the creation of an ecological trap.

Habitat use that maximizes feeding potential, at the cost of lowering nest success, may be offset by other factors, such as higher re-nesting potential during periods of elevated predation pressure while permitting better breeding potential during relaxed predation periods (Holmes et al. 1992; Nagy & Holmes 2004; Grzybowski & Pease 2005) and larger offspring, increasing future survival and fitness (Sinervo 1990; Lindström 1999). Conversely, individuals may also reduce reproductive outputs and provisioning when nest predation is high (Eggers et al. 2006, Dunn et al. 2010). Red-headed Woodpeckers have been considered foraging generalists, feeding on a variety of plant and animal matter (Smith et al. 2000), but quantitative dietary data are limited to one antiquated study of stomach contents (Beal 1911). During the breeding season in southern

Ontario, flycatching was the dominant feeding strategy, especially as the season progressed (B. Frei, pers. obs.) As a guild, aerial insectivores have been experiencing population declines (Böhning-Gaese et al. 1993; Nebel et al. 2010), which suggests that declining populations of insect prey may explain the dominance of food-based habitat choices for Red-headed Woodpeckers in our study.

Whether habitat use by Red-headed Woodpeckers in southern Ontario is currently maladaptive, or food-based choices trump safer nest choices due to feeding constraints, it is imperative that management of this species is carefully considered at relevant spatial scales. We found that Red-headed Woodpeckers use habitat at multiple scales, while the characteristics that define those habitats may or may not be consistent across scales. The importance of standing dead wood, especially dead limbs, appears paramount to the species across several scales. Likewise canopy openness and coarse woody debris in deciduous woodlots targeted in landscapes with mixed forest stands and grassland appear to be choice habitat features. Persistence of Red-headed Woodpeckers in Ontario is tentative, given ongoing population declines, the apparent ecological trap of a rapidly changing landscape, possible food shortages, and the lack of a provincial management plan. Determining the habitat features used and their influence on the species' success across different, ecologically relevant, spatial scales will improve the understanding and assessment of habitat quality so as to assist with managing populations to make them sustainable.

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3.7 Literature Cited

Anderson, D. 2008: Model based inference in the life sciences: a primer on evidence. Springer, New York.

Anderson, D., Link, W., Johnson, D. & Burnham, K.P. 2001: Suggestions for presenting the results of data analyses. Journal of Wildlife Management **65**, 373-378.

Arlt, D. & Pärt, T. 2007: Nonideal breeding habitat selection: a mismatch between preference and fitness. Ecology **88**, 792-801.

Arnold, T.W. 2010: Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management **74**, 1175-1178.

Battin, J. 2004: When good animals love bad habitats: ecological traps and the conservation of animal populations. Conservation Biology **18**, 1482-1491.

Beal, F.E.L. 1911: Food of the woodpeckers of the United States. U.S. Department of Agriculture Biological Survey Bulletin no 7.

Böhning-Gaese, K., Taper, M. & Brown, J. 1993: Are declines in North American insectivorous songbirds due to causes on the breeding range? Conservation Biology **7**, 76-86.

Bowers, M.A. & Dooley, J.L. 1993: Predation hazard and seed removal by small mammals: microhabitat versus patch scale effects. Oecologia **94**, 247-254.

Burke, D.M. & Nol, E. 1998: Influence of food abundance, nest-site habitat, and forest fragmentation on breeding ovenbirds. Auk **115**, 96-104.

Burnham, K.P. & Anderson, D.R. 2002: Model selection and multimodel inference: a practical information-theoretic approach, 2nd Ed. Springer, New York.

Chalfoun, A.D. & Martin, T.E. 2007: Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness. Journal of Applied Ecology **44**, 983-992.

Conner, R.N. 1976: Nesting habitat for Red-headed Woodpeckers in southwestern Virginia. Bird-Banding **47**, 40-43.

Cornelius, C. 2008: Spatial variation in nest-site selection by a secondary cavity-nesting bird in a human-altered landscape. Condor **110**, 615-626.

COSEWIC. 2007: COSEWIC assessment and update status report on the Red-headed Woodpecker *Melanerpes erythrocephalus* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa.

Crampton, L.H. & Sedinger, J.S. 2011: Nest-habitat selection by the Phainopepla: congruence across spatial scales but not habitat types. Condor **113**, 209-222.

Dunn, J.C., Hamer, K.C. & Benton, T.G. 2010: Fear for the family has negative consequences: indirect effects of nest predators on chick growth in a farmland bird. Journal of Applied Ecology **47**, 994-1002.

Dussault, C., Ouellet, J.-P., Courtois, R., Huot, J., Breton, L. & Jolicoeur, H. 2005: Linking moose habitat selection to limiting factors. Ecography **5**, 619-628.

Eggers, S., Griesser, M., Nystrand, M. & Ekman, J. 2006: Predation risk induces changes in nest-site selection and clutch size in the Siberian Jay. Proceedings of the Royal Society B **273**, 701-706.

Fisher, R.J. & Wiebe, K.L. 2006: Nest site attributes and temporal patterns of Northern Flicker nest loss: effects of predation and competition. Oecologia **147**, 744-753.

Fretwell, S.D. & Lucas, H.R. 1970: On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical Development. Acta Biotheoretica **19**, 16-36.

Grzybowski, J. & Pease, C. 2005: Renesting determines seasonal fecundity in songbirds: what do we know? What should we assume? Auk **122**, 280-291.

Hanley, J.A. & McNeil, B.J. 1982: The meaning and use of the area under a receiver operating characteristic (ROC) curve. Radiology **143**, 29–36.

Hanula, J., Horn, S. & Wade, D.D. 2006: The role of dead wood in maintaining arthropod diversity on the forest floor. In: Grove SJ, Hanula JL (eds) Insect biodiversity and dead wood: proceedings of a symposium for the 22nd International Congress of Entomology. Gen. Tech. Rep. SRS-93. Asheville, NC: US Department of Agriculture Forest Service.

Hollander, F.A., Van Dyck, H., San Martin, G. & Titeux, N. 2011: Maladaptive habitat selection of a migratory passerine bird in a human-modified landscape. PLoS One **6**: e25703.

Holmes, R., Sherry, T.W., Marra, P.P. & Petit, K.E. 1992: Multiple brooding and productivity of a Neotropical migrant, the Black-throated Blue Warbler (*Dendroica caerulescens*), in an unfragmented temperate forest. Auk **109**, 321-333.

Hosmer, D.W. & Lemeshow, S. 2000: Applied logistic regression. John Wiley & Sons, Inc., Hoboken.

Huebner, D.P. & Hurteau, S.R. 2007: An economical wireless cavity-nest viewer. Journal of Field Ornithology **78**, 87-92.

Hurvich, C. & Tsai, C.-L. 1989: Regression and time series model selection in small samples. Biometrika **76**, 297-307.

Ingold, D.J. 1989: Nesting phenology and competition for nest sites among Red-headed Woodpeckers and European Starlings. Auk **106**, 209-217.

Ingold, D.J. 1994: Influence of nest-site competition between European Starlings and woodpeckers. Wilson Bulletin **106**, 227-241.

Kerr, J. & Cihlar, J. 2004: Patterns and causes of the species endangerment in Canada. Ecological Applications **14**, 743-753.

Kerr, J. & Deguise, I. 2004: Habitat loss and the limits to endangered species recovery. Ecology Letters **7**, 1163-1169.

Kilgo, J.C. & Vukovich, M. 2012: Factors affecting breeding season survival of Red-headed Woodpeckers in South Carolina. Journal of Wildlife Management **76**, 328-335.

King, R.S., Brashear, K.E. & Reiman, M. 2007: Red-headed Woodpecker nest-habitat thresholds in restored savannas. Journal of Wildlife Management **71**, 30-35.

Kokko, H. & Sutherland, W.J. 2001: Ecological traps in changing environments: ecological and evolutionary consequences of a behaviourally mediated Allee effect. Evolutionary Ecology Research **3**:537-551.

Kozma, J.M. & Kroll, A.J. 2012: Woodpecker nest survival in burned and unburned managed ponderosa pine forests of the northwestern United States. Condor **114**, 173-184.

Kristian, W.B. III 2003: The role of habitat selection behaviour in population dynamics: source-sink systems and ecological traps. Oikos **102**, 457-468.

Li, P. & Martin, T.E. 1991: Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. Auk **108**, 405-418.

Lima, S.L. & Zollner, P.A. 1996: Towards a behavioural ecology of ecological landscapes. Trends in Ecology and Evolution **11**, 131-135.

Lindström, J. 1999: Early development and fitness in birds and mammals. Trends in Ecology and Evolution **14**, 343-348.

Margolin, B.H. & Light, R.J. 1974: An analysis of variance for categorical data II: small sample comparisons with chi-square and other competitors. Journal of the American Statistical Association **69**, 755-764.

Martin, T.E. 1988: On the advantages of being different: nest predation and coexistence of bird species. Proceedings of the National Academy of Science USA **85**, 2196-2199.

Martin, T.E. 1993: Nest predation and nest sites. BioScience **43**, 523-532.

Martin, T.E. 1995: Avian life history evolution in relation to nest sites, nest predation, and food. Ecological Monographs **65**, 101-127.

Martin, T.E. & Li, P. 1992: Life history of open- vs. cavity-nesting birds. Ecology **73**, 579-592.

Martin, T.E., Paine, C.R., Conway, C.J., Hochachka, W.M., Allen, P. & Jenkins, W. 1997: BBIRD field protocol. Biological Resources Division, Montana Cooperative Wildlife Research Unit, University of Montana, Missoula.

Martin, T. & Roper, J.J. 1988: Nest predation and nest-site selection of a western population of the Hermit Thrush. Condor **90**, 51-57.

Mayor, S.J., Schneider, D.C., Schaefer, J.A. & Mahoney, S.P. 2009: Habitat selection at multiple scales. Ecoscience **16**, 238-247.

Misenhelter, M. & Rotenberry, J.T. 2000: Choices and consequences of habitat occupancy and nest site selection in Sage Sparrows. Ecology **81**, 2892- 2901.

Nagy, L.R. & Holmes, R.T. 2004: Factors influencing fecundity in migratory songbirds: is nest predation the most important? Journal of Avian Biology **35**, 487-491.

Nebel, S., Mills, A., McCracken, J.D. & Taylor, P.D. 2010: Declines of aerial insectivores in North America follow a geographic gradient. Avian Conservation and Ecology **5**: article 1.

Nilsson, S.G. 1984: The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. Ornis Scandinavica **15**, 167–175.

OMAFRA. 2006: Agricultural census 2006. Agricultural and Strategic Policy Branch, Ontario Ministry of Agriculture, Food and Rural Affairs, Guelph.

Orians, G.H. & Wittenberger, J.F. 1991: Spatial and temporal scales in habitat selection. American Naturalist **137**, S29-S49.

Paclík, M., Misík, J. & Weidinger, K. 2009: Nest predation and nest defence in European and North American woodpeckers: a review. Annales Zoologici Fennici **46**, 361- 379.

Parker, K. 1986: Partitioning of foraging space and nest sites in a desert shrubland bird community. American Midland Naturalist **115**, 255-267.

Pulliam, H. 1988: Sources, sinks, and population regulation. American Naturalist **132**, 652-661.

Reller, A.W. 1972: Aspects of behavioural ecology of Red-headed and Red-bellied Woodpeckers. American Midland Naturalist **88**, 270-290.

Remes, V. 2000: How can maladaptive habitat choice generate source-sink population dynamics? Oikos **9**, 579-582.

Ricklefs, R.E. 1969: An analysis of nesting mortality in birds. Contributions to Zoology **9**, 1-48.

Robertson, B.A. & Hutto, R.L. 2006: A framework for understanding ecological traps and an evaluation of existing evidence. Ecology **87**, 1075-1085.

Rodewald, P., Santiago, M. & Rodewald, A.D. 2005: Habitat use of breeding Red-headed Woodpeckers on golf courses in Ohio. Wildlife Society Bulletin **33**, 448-453.

Ruxton, G.D. 2006: The unequal variance t-test is an underused alternative to Student's t-test and the Mann-Whitney U-test. Behavioural Ecology **17**, 688-690.

Saab, V., Russell, R.E. & Dudley, J.G. 2009: Nest-site selection by cavity-nesting birds in relation to postfire salvage logging. Forest Ecology and Management **257**, 151-159.

Sadoti, G. & Vierling, K.T. 2010: Nonideal habitat selection by a North American cavity excavator: pecking up the wrong tree? Canadian Journal of Zoology **88**, 527-535.

Saenz, D., Collins, C.S. & Conner, R.N. 1999: A bark-shaving technique to deter rat snakes from climbing red-cockaded woodpecker cavity trees. Wildlife Society Bulletin **27**, 1069-1073.

Sedgwick, J.A. & Knopf, F.L. 1990: Habitat relationships and nest site characteristics of cavity-nesting birds in cottonwood floodplains. Journal of Wildlife Management **54**, 112-124.

Shreeve, T., Dennis, R. & Pullin, A.S. 1996: Marginality: scale determined processes and the conservation of the British butterfly fauna. Biodiversity and Conservation **5**, 1131-1141.

Sinervo, B. 1990: The evolution of maternal investment in lizards: an experimental and comparative analysis of egg size and its effects on offspring performance. Evolution **44**, 279-294.

Smith, K.G., Withgott, J.H. & Rodewald, P.G. 2000: Red-headed Woodpecker (*Melanerpes erythrocephalus*). In: (Poole A, Ed) The Birds of North America. Cornell Lab of Ornithology, Retrieved from the Birds of North America Online, Ithaca.

Stephens, P.A., Buskirk, S.W., Hayward, G.D. & Martínez del Rio, C. 2005: Information theory and hypothesis testing: a call for pluralism. Journal of Applied Ecology **42**, 4-12.

Thomas, C. & Kunin, W.E. 1999: The spatial structure of populations. Journal of Animal Ecology **68**, 647-657.

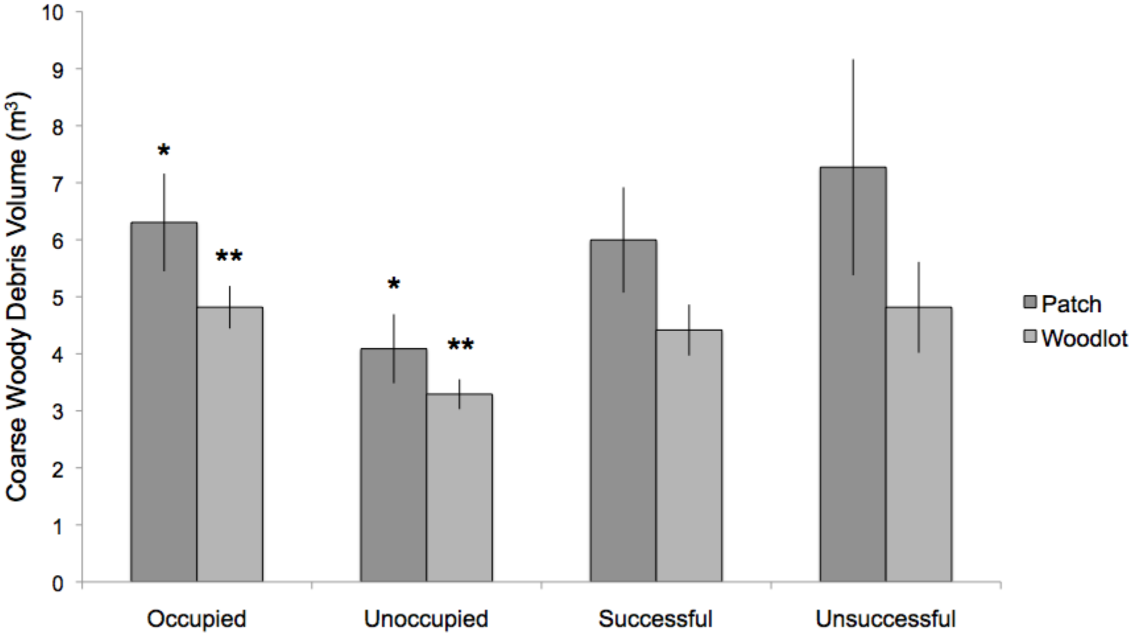
Vierling, K. & Lentile, L. 2006: Red-headed Woodpecker nest-site selection and reproduction in mixed ponderosa pine and aspen woodland following fire. Condor **108**, 957-962.

Weldon, A.J. & Haddad, N.M. 2005: The effects of patch shape on Indigo Buntings: evidence for an ecological trap. Ecology **86**, 1422-1431.

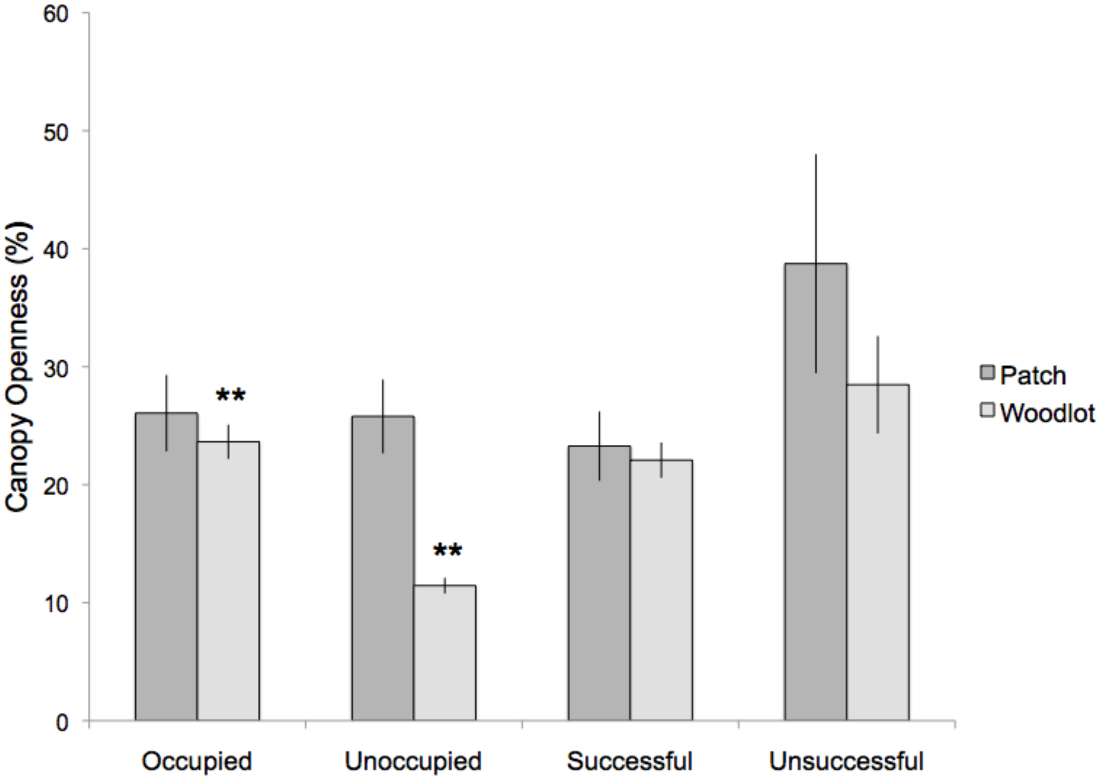
Wheelwright, N., Lawler, J. & Weinstein, J. 1997: Nest-site selection in Savannah Sparrows: using gulls as scarecrows? Animal Behaviour **53**, 197-208.

3.8 Tables and Figures

(a)


Coarse Woody Debris Volume (m^3)
10
9
8
7
6
5
4
3
2
1
0
*
**
*
**
Occupied
Unoccupied
Successful
Unsuccessful
Patch
Woodlot

(b)



60
50
40
30
20
10
0
Canopy Openness (%)
**
**
Occupied
Unoccupied
Successful
Unsuccessful
Patch
Woodlot

(c)

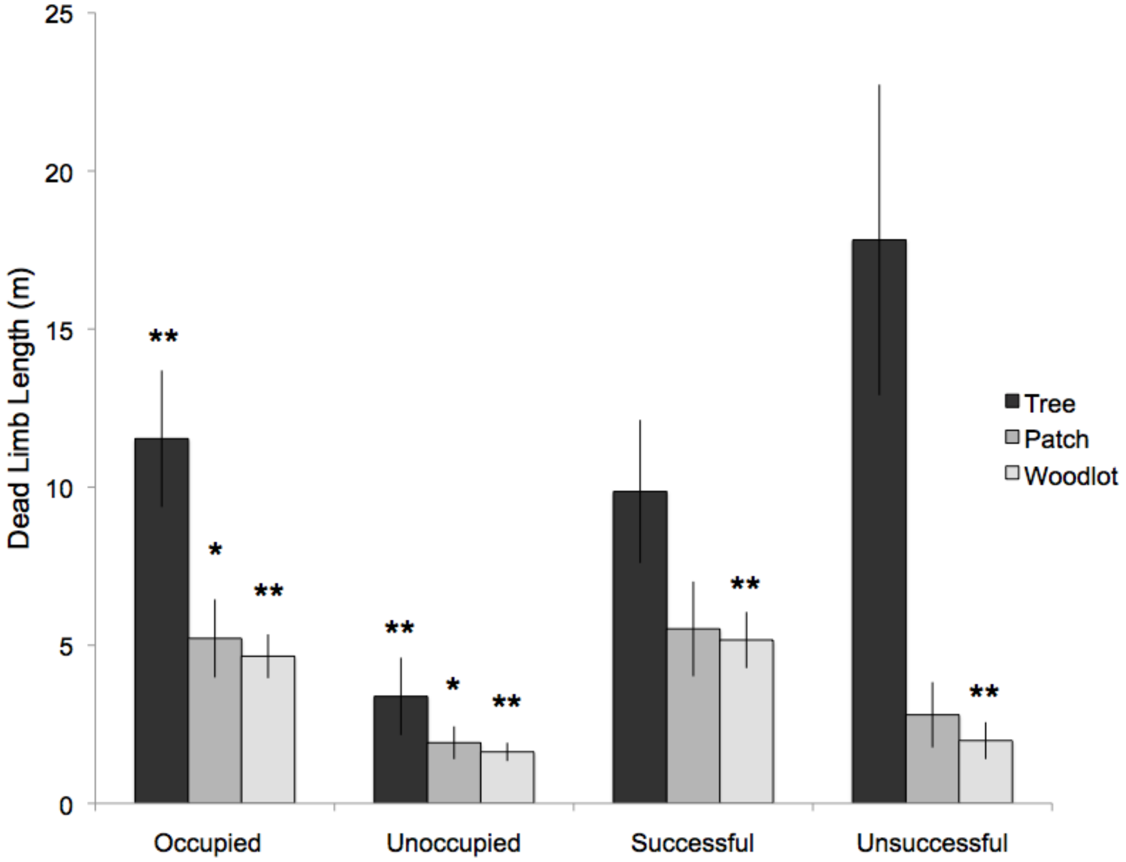


Figure 3.1 Red-headed Woodpecker maladaptive and congruent habitat use characteristics and standard error (SE) including: (a) canopy openness (%) at patch and woodlot, (b) coarse woody debris (m^3) at patch and woodlot, and (c) dead limb length (m) at tree, patch, and woodlot scale. * $p \leq 0.05$; ** $p \leq 0.001$ based on Welch's t-test comparisons between occupied/unoccupied and successful/unsuccessful.

Table 3.1 Description of cavity, tree, patch/woodlot and landscape variables measured at Red-headed Woodpecker nest sites and random sites in southern Ontario, 2010-2011.

Habitat variables	Model code	Description
Cavity		
Cavity height	--	Measured with clinometer
Cavity orientation	--	Determined one of the 8 orientations (N, NE, E, SE, S, SW, W, NW) using compass
Substrate	--	Exterior appearance (bark or no bark)
Tree		
DBH	DBH	Tree dbh; measured with dbh tape in cm
Tree height	TREE	Measured with clinometer in m
Dead-limb length	TLENGTH	Visually estimated length in m of dead limbs ≥ 10 cm diam
Additional cavities	TCAVITY	Number of additional cavities
Patch/Woodlot		
Basal area	BASAL	Measured using a 10-m^2/ha/tree basal area factor prism
Small-tree density	SMALL	No. of trees 3-23-cm dbh
Medium-tree density	MED	No. of trees 23-69-cm dbh
Big-tree density	BIG	No. of trees > 69-cm dbh
Limb-tree density	LIMB	No. of limb trees (those with ≥1-m dead limbs ≥ 10-cm diam)
Dead limb length	PLENGTH	Visually estimated length in m of dead limbs ≥10-cm diam
Canopy openness	OPEN	Percentage open sky from digital cover image taken at tree base
Cavity density	PCAVITY	No. of cavities (measured in a 0.04-ha circle around the nest tree or random site center tree)
Snag density	SNAG	No. of dead trees (0.04-ha circle)

Coarse woody debris	CWD	Total volume of coarse woody debris on the ground > 3 cm in diameter and > 30 cm in length
Landscape		
Composition at 200m	COMP200	Within a 200 m radius circle of focal point, the percentage of: deciduous forest, coniferous forest, mixed-wood forest, row crop, pasture, bare, developed, water, shrubs, and grassland
Composition at 1000m	COMP1000	Same as COMP200 for 1000m
Road length at 200m	ROAD200	Total road length within a 200 m radius circle of focal point
Road length at 1000m	ROAD1000	Same as ROAD200 for 1000m
Edge length at 200m	EDGE200	Forest (deciduous and mixed-wood) to open (row crop, pasture, grasslands) within a 200m radius circle of focal point
Edge length at 1000m	EDGE1000	Same as EDGE200 for 1000m

Table 3.2 Summary of rankings of candidate models from multiple logistic regressions assessing differences for occupancy and breeding success for Red-headed Woodpecker at the patch scale in southern Ontario woodlots, 2010 – 2011. See Table 3.1 for model code descriptions. *K* = number of parameters, w_i = Akaike weight, Cw_i = Cumulative Akaike weight, AUC = Area Under Curve.

Model	Deviance	K	ΔAICc	w_i	Cw_i	AUC
Occupancy (*n* = 67)						
BASAL + SMALL + BIG + OPEN + SNAG + PLENGTH + PCAVITY + CWD	60.30	11	0.00	0.39	0.39	0.86
BASAL + SMALL + BIG + CWD	71.5	7	0.33	0.33	0.72	0.80
BASAL + SMALL + MED + OPEN + SNAG + PLENGTH + PCAVITY + CWD	62.86	11	2.57	0.11	0.83	0.73
BASAL + SMALL + MED + BIG + OPEN + SNAG + PLENGTH + PCAVITY + CWD	59.95	12	2.6	0.11	0.94	0.79
Breeding success (*n* = 40)						
BASAL + SMALL + BIG + OPEN	33.48	7	0.00	0.39	0.39	0.80
Intercept only	44.98	3	0.68	0.28	0.67	NA
BASAL + SMALL + BIG + OPEN + CWD	32.6	8	2.28	0.12	0.79	0.82
BASAL + SMALL + MED + BIG + OPEN	33.14	8	2.82	0.09	0.89	0.80
BASAL + SMALL + MED + OPEN	35.8	7	5.04	0.03	0.92	0.69

Table 3.3 Model averaged parameter estimates Red-headed Woodpecker nest sites at the patch scale in southern Ontario woodlots, 2010 – 2011. See Table 3.1 for model code descriptions. Parameters with opposing value estimates (+/-) between occupancy and breeding success at the patch scale are italicized; parameters in which the CI does not cross zero are bolded.

Model	Variable	Estimate	Unconditional SE	Unconditional CI	
Patch use					
	BASAL	0.07	0.05	-0.03	0.17
	SMALL	0.13	0.06	0.02	0.25
	MED	-0.19	0.31	-0.08	0.41
	BIG	17.23	3035.58	5932.41	5966.87
	PLENGTH	0.15	0.09	-0.4	0.33
	PCAVITY	1.53	1.14	-0.7	3.76
	SNAG	-0.89	0.44	-1.76	-0.03
	OPEN	0.02	0.02	-0.02	0.05
	CWD	0.22	0.10	0.03	0.41
Patch outcome					
	BASAL	-0.09	0.08	-0.24	0.06
	SMALL	-0.01	0.05	-0.12	0.09
	MED	0.43	0.46	-0.48	1.34
	BIG	-3.56	2.04	-7.57	0.44
	PLENGTH	0.12	0.12	-0.12	0.36
	PCAVITY	0.66	0.67	-0.65	1.97
	SNAG	0	0.91	-1.78	1.78
	OPEN	-0.08	0.03	-0.14	-0.01
	CWD	-0.12	0.11	-0.34	0.09

Table 3.4 Summary of rankings of candidate models from multiple logistic regressions assessing differences for occupancy and breeding success for Red-headed Woodpecker at the woodlot scale in southern Ontario woodlots, 2010 – 2011. See Table 3.1 for model code descriptions. *K* = number of parameters, w_i = Akaike weight, Cw_i = Cumulative Akaike weight, AUC = Area Under Curve.

Model	Deviance	K	ΔAICc	w_i	Cw_i	AUC
Woodlot use (*n* = 258)						
BASAL + SMALL + MED + OPEN + SNAG + PLENGTH + PCAVITY	272.40	10	0.00	0.55	0.55	0.81
BASAL + SMALL + MED + OPEN	281.40	7	2.56	0.15	0.70	0.81
BASAL + SMALL + BIG + OPEN + SNAG + PLENGTH + PCAVITY + CWD	273.38	11	3.15	0.11	0.81	0.81
BASAL + SMALL + MED + BIG + OPEN	280.32	8	3.6	0.09	0.90	0.81
Woodlot outcome (*n* = 130)						
BASAL + SMALL + BIG + OPEN + SNAG + PLENGTH + PCAVITY	104.16	10	0.00	0.84	0.84	0.78
BASAL + SMALL + BIG + OPEN + CWD	114.38	8	5.51	0.05	0.89	0.70
BASAL + SMALL + MED + BIG + OPEN	114.64	8	5.77	0.05	0.94	0.69

Table 3.5 Model averaged parameter estimates for Red-headed Woodpecker nest sites at the woodlot scale in southern Ontario woodlots, 2010 – 2011. See Table 3.1 for model code descriptions. Parameters with opposing value estimates (+/-) between occupancy and breeding success at the woodlot scale are italicized; parameters in which the CI does not cross zero are bolded.

Model	Variable	Estimate	Unconditional SE	Unconditional CI	
Woodlot use					
	BASAL	-0.02	0.02	-0.06	0.01
	SMALL	0	0.02	-0.05	0.04
	MED	0.18	0.13	-0.08	0.43
	BIG	0.35	0.78	-1.19	1.89
	PLENGTH	0.09	0.03	0.02	0.16
	PCAVITY	-0.02	0.13	-0.27	0.23
	SNAG	0.05	0.16	-0.25	0.35
	OPEN	0.12	0.02	0.08	0.17
	CWD	0.03	0.05	-0.06	0.12
Woodlot outcome					
	BASAL	-0.02	0.03	-0.07	0.03
	SMALL	-0.06	0.03	-0.12	0.01
	MED	0.04	0.22	-0.40	0.48
	BIG	-2.85	1.09	-4.98	-0.71
	PLENGTH	0.15	0.07	0.01	0.28
	PCAVITY	0.20	0.38	-0.54	0.95
	SNAG	-0.50	0.27	-1.03	0.95
	OPEN	-0.04	0.01	-0.06	-0.01
	CWD	0.05	0.06	-0.07	0.16

Table 3.S1 Summary of rankings of candidate models from multiple logistic regressions assessing differences for occupancy and breeding success for Red-headed Woodpecker at the tree scale in southern Ontario woodlots, 2010 – 2011. See Table 3.1 for model code descriptions. *K* = number of parameters, w_i = Akaike weight, Cw_i = Cumulative Akaike weight, AUC = Area Under Curve.

Model	Deviance	K	ΔAICc	w_i	Cw_i	AUC
Occupancy (*n* = 71)						
TLENGTH	86.16	4	0.00	0.55	0.55	0.81
DBH + TLENGTH	82.26	5	0.43	0.44	0.99	0.76
Breeding success (*n* = 42)						
DBH + TREE + TLENGTH	34.62	6	0.00	0.70	0.70	0.80
Intercept only	46.10	3	3.72	0.11	0.81	NA
TLENGTH	43.72	4	3.80	0.10	0.91	0.67

Table 3.S2 Model averaged parameter estimates for Red-headed Woodpecker nest sites at the tree scale in southern Ontario woodlots, 2010 – 2011. See Table 3.1 for model code descriptions. Parameters with opposing value estimates (+/-) between the occupancy and breeding success at the tree scale are italicized, parameters in which the CI does not cross zero are bolded.

Model	Variable	Estimate	Unconditional SE	Unconditional CI	
Occupancy	*DBH*	-0.03	0.02	-0.08	0.02
	TLENGTH	0.11	0.05	0.02	0.20
Breeding success	*DBH*	0.14	0.08	-0.02	0.29
	TREE	0.15	0.13	-0.10	0.39
	TLENGTH	-0.16	0.09	-0.33	0.01
	TCAVITY	0.22	0.19	-0.14	0.59

Table 3.S3 Summary of rankings of candidate models from multiple logistic regressions assessing differences for occupancy and breeding success for Red-headed Woodpecker at the landscape scale in southern Ontario woodlots, 2010 – 2011. See Table 3.1 for model code descriptions. *K* = number of parameters, w_i = Akaike weight, Cw_i = Cumulative Akaike weight, AUC = Area Under Curve.

Model	Deviance	K	ΔAICc	w_i	Cw_i	AUC
Occupancy ($n = 63$)						
EDGE_1000	71.60	4	0.00	0.63	0.63	0.72
COMP_1000 + EDGE_1000	41.48	15	1.39	0.32	0.95	0.91
COMP_1000	48.96	14	5.41	0.04	0.99	0.88
Breeding success ($n = 39$)						
Intercept only	44.40	3	0.00	0.41	0.41	NA
EDGE_200	43.76	4	1.85	0.16	0.57	0.52
ROAD_200	44.40	4	2.48	0.12	0.69	0.54
EDGE_1000	44.88	4	2.97	0.09	0.78	0.59
ROAD_1000	44.9	4	2.98	0.09	0.88	0.52
ROAD_1000 + EDGE_1000	42.62	5	3.35	0.08	0.95	0.60

Table 3.S4 Significant ($\alpha \leq 0.1$) parameter estimates for the top two models for Red-headed Woodpecker occupancy at the landscape scale in southern Ontario woodlots, 2010 – 2011. See Table 3.1 for model code descriptions.

Model	Variable	Estimate	Std. Error	z-value	P-value
EDGE_1000	Forest/open edge length	0.00	0.00	-2.96	< 0.01
COMP_1000+	Mixed forests	0.58	0.31	1.90	0.05
EDGE_1000	Grassland	3.28	1.79	1.82	0.06
	Forest/open edge length	0.00	0.00	-2.33	0.02

Preface to Chapter 4

In Chapter 3, I showed that Red-headed Woodpeckers in southern Ontario exhibit maladaptive habitat use at the tree, patch, and woodlot scales. Specifically, habitat characteristics that promote feeding potential (for catching aerial insects) such as canopy openness and greater dead limb length were consistently related to site occupancy, despite these same features corresponding to lower fitness via decreased nesting success. Whether the maladaptive habitat use is due to an ecological trap or a costly choice in favor of increased feeding potential is unknown.

Chapter 4 further investigates the nest success of Red-headed Woodpeckers in southern Ontario, given a suite of possible drivers. Of particular interest is the role of the non-native European Starling as a driver of Red-headed Woodpecker nest success and, as such, a possible mechanism in driving the maladaptive habitat use seen in Chapter 3. Competition with starlings, to which Red-headed Woodpeckers are not adapted, has the potential of serving as an evolutionary trap. Chapter 4 was co-authored by the candidate's supervisors, Drs. Joseph J. Nocera and James W. Fyles and will submitted for publication in *Auk*.

Frei, B., Nocera, J.J., Fyles, J.W. Invasive Species Interference Competition as an Evolutionary Trap for a Threatened North American Woodpecker. Target journal: Auk

Chapter 4

4. Invasive Species Interference Competition as an Evolutionary Trap for a Threatened North American Woodpecker

4.1 Abstract

European Starlings (*Sturnus vulgaris*) are abundant non-native competitors for nest cavities with North American birds. Detrimental effects of exotic species on native fauna are well known, yet few studies have quantified negative fitness outcomes from competition with starlings. Red-headed Woodpeckers (*Melanerpes erythrocephalus*), a threatened species found in human-modified habitat, share habitat affinities with starlings and we hypothesize they may be experiencing population depression as a result. To test this hypothesis, we investigated Red-headed Woodpecker nest survival near the northern edge of the species' range, where populations are rapidly declining. We modeled the relevance of a suite of abiotic, biotic, temporal, and habitat-based drivers on woodpecker nesting success. European Starling presence near active woodpecker nest sites was the strongest factor influencing Red-headed Woodpecker nest survival. Logistic-exposure nest success assuming constant survival (68%) dropped significantly when starling abundance was considered (to 13%). We suggest this is evidence of an evolutionary trap where a native species habitat use overlaps that of an exotic species with which it is not adapted to compete. Red-headed Woodpecker nest survival increased later in the breeding season, apparently in response to lessening competition pressure. Nesting success increased with the availability of snags and dead branches, which may increase foraging opportunities and parental attentiveness at the nest, leading to more effective nest defense. This research is contrary to previous reports that starlings do not negatively affect North American primary cavity nesters, and demonstrates the importance of considering multiple ecological, temporal, and spatial factors when determining threats for species-at-risk.

Keywords: *Melanerpes erythrocephalus*, *Sturnus vulgaris*, interference competition, nest success, evolutionary trap

4.2 Introduction

Evolutionary traps are a broad phenomenon of a disjoint between behaviour and resulting fitness that rely on social or environmental cues, due to anthropogenic change (Schlaepfer et al. 2002). Introduced species have a potential of serving as evolutionary traps for native species, as they create novel ecological conditions or interactions for which native species may not be adapted (Shea and Chesson 2002; Schlaepfer et al. 2005). The introduction of species beyond their historical ranges is a common result of anthropogenic change (Schlaepfer et al. 2005). The ecological impact of non-native species is often compounded by further anthropogenic disturbances to the habitat that can create novel environments that benefit non-native species (Byers 2002). An ecological trap is a specific type of evolutionary trap that occurs when the social or environmental cues that a species uses to identify fitness-enhancing habitat characteristics become decoupled from the true state of that habitat (Schlaepfer et al. 2002). Such ‘traps’ are inherently difficult to predict and mitigate as they continue to attract susceptible animals that fail to react to the negative fitness outcomes of the trap and avoid them. In the case of an evolutionary trap driven by a non-native species (which is costly and highly unlikely to be completely removed from a community following establishment) management for native species must proceed with the non-native species in mind and consider the native species' ability to survive given their evolutionary history and behavioural ecology (Shea and Chesson 2002; Schlaepfer et al. 2005).

A prominent non-native species in North America is the European Starling (*Sturnus vulgaris*), which was introduced to the east coast in 1890 and swiftly established across most of the continent south of the tree line by 1970s (Kessel 1953; Cabe 1993). Starlings are interference competitors and usurp nest cavities from woodpeckers and secondary cavity nesters (e.g., chickadees) in North America and Europe (Troetschler 1976; Weitzel 1988; Carter et al. 1989; Ingold 1989, 1996; Kerpez and Smith 1990; Vierling 1998; Mazgajski 2000; Smith 2005, 2006; Koch et al. 2012). While aggressive interactions and cavity usurpations by starlings are commonly observed, few studies clearly quantify a negative impact on cavity nester fitness or breeding success. In addition, a comparison by Koenig (2003) of mean densities of 27 native cavity nesters before and after starling invasions failed to support the hypothesis that starlings have a severe impact on the native bird community. However, the effect of starlings on some populations may only begin to be detectable via statistical analysis (Koenig 2003), and several additional ecological and spatially-explicit factors were not considered in this analysis. The effect of non-native species such as starlings may be most obvious in areas where native cavity nesters are particularly vulnerable to disturbance, such as at range edges. As such, studying threatened populations, like those of the Red-headed Woodpecker (*Melanerpes erythrocephalus*) in southern Canada which are at the northern edge of their range and listed as threatened federally, should reveal population effects more so than in areas where abundance of a native species may buffer interference competition.

In this study, we focus on Red-headed Woodpeckers nesting in southern Ontario in attempt to quantify the fitness consequences (especially nesting success) of potential European Starling interference competition. Red-headed Woodpecker's maladaptive habitat use was previously reported, where occupancy was correlated with habitat features that resulted in poorer reproductive success, suggesting an ecological trap (Frei et al. 2013). This ecological trap may be a consequence of the species favoring habitat features promoting feeding potential at the cost of nest safety, and/or rapid anthropogenic changes resulting in nesting habitat use that elicits greater predation or competition pressure (Frei et al. 2013). However, neither of these hypotheses has been explored quantitatively. European Starlings and Red-headed Woodpeckers share similar small-scale habitat affinities (Stauffer and Best 1982; Sedgwick and Knopf 1990), with the starling being a common interference competitor for nest cavities (Ingold and Densmore 1992; Ingold 1994). Despite reports that Red-headed Woodpeckers 'win' most aggressive encounters with starlings, thus seemingly avoiding fitness consequences (Ingold and Densmore 1992; Ingold 1994), we hypothesize that competition with non-native starling may be part of an evolutionary trap (Schlaepfer et al. 2005) whose effects are compounded by anthropogenic changes to the landscape.

The goal of this study is to determine the relative importance of abiotic, temporal biotic and habitat variables as drivers of Red-headed Woodpecker nest survival in southern Ontario. Our second objective is to determine nest survival of Red-headed Woodpeckers at the northern edge of their range in southern Ontario, which will assist with conservation of the species. Such peripheral populations of species-at-risk may be critical to conservation efforts (Channell and Lomolino 2000), yet they are often dedicated less attention or resources for management and/or protection. Based on data from the Breeding Bird Survey, Red-headed Woodpecker populations have declined > 60% over the last two decades in the province, making this one of the areas with the steepest declines across the species' range (COSEWIC 2007). Researching the factors pertinent to a species' population decline at its range edge is ecologically important as: (1) the factors driving the decline may be more visible, as the species is already facing population limitations (Thomas and Kunin 1999), and (2) peripheral populations have strong conservation value due to their genetic diversity (Shreeve et al. 1996).

4.3 Methods

4.3.1 Study Area

Our study area included two sites encompassing Elgin (1,880 km^2), Norfolk (1,607 km^2), and Northumberland (1,905 km^2) counties of southern Ontario (range: 42-43° N/81-78° W). The southern site (Elgin and Norfolk) is within the Deciduous Forest zone on the north shore of Lake Erie in southwestern Ontario, which is the mildest and most fertile part of the province (OMAFRA 2006). The northern site (Northumberland) is on the north shore of Lake Ontario in southeastern Ontario, and is characterized by an undulating topography and a lower density of cash crops (e.g., corn and soybean) than other regions of southern Ontario. Northumberland straddles the transition between the Deciduous and Great-Lakes St.-Lawrence Forests and thus has a mix of the two forest types.

4.3.2 Nest Monitoring

We surveyed for Red-headed Woodpecker nests for two breeding seasons (May-August of 2010-2011) at the northern site and in 2011 only in the southern site. We delineated possible Red-headed Woodpecker habitats to survey from topographic maps and satellite imagery. We also collected reports from birders and landowners via numerous outreach methods. Using a handheld game call unit (FOXPRO NX3, FOXPRO Inc.), we surveyed all potential sites by broadcasting recordings of the species' territorial calls, obtained from the Cornell Lab of Ornithology's Macaulay Library collection, and eliciting responses from territorial pairs in the area. Recordings were played in looped 20-sec sound clips for 1-2 minutes with a 5-min break, which was done three times at each potential site, and we visited each site twice. We used behavioral cues (e.g., incubation, brooding of younger nestlings, feeding of young, and visual sightings of older nestlings at the nest cavity entrance) to deduce nest status, and used an Elevated Video Inspection System (based on Huebner and Hurteau 2007) to inspect a subset of cavity nests (≤13 m in height). We obtained geographic coordinates for each nest using a handheld GPS with ±7 m accuracy and monitored nests every 2-5 days until the nest failed (due to predation and/or abandonment) or young fledged (≥1 nestling left the nest). During each nest visit we counted feeding events, and the number of European Starlings seen or heard within approximately 100 m of the nest site over a 20 min sampling period. We confirmed fledging by observing fledglings within the breeding territory or by observing adults bringing food to locations in the territory other than the nest cavity. We considered a nest to have failed if the cavity was empty or adults abandoned the area before the earliest possible date of fledging. A nest site was visited several times to ensure there was no activity after it was considered failed.

4.3.3 Nest Survival Model Covariates

We hypothesize (Table 4.1) that nest survival is a product of temperature, precipitation, nest initiation timing, cavity height, habitat structure, the presence/abundance of European Starlings, and/or feeding rates. We further hypothesize (Table 4.1) that feeding rates are influenced by many of the same variables, especially temperature, precipitation, and/or habitat structure. To explore these hypotheses, we developed candidate models (Table 4.1) that investigated the influence of 19 variables on the daily survival rate (DSR) of Red-headed Woodpeckers (Table 4.2). We grouped these variables into four categories: abiotic, biotic, temporal, or habitat (small- and large-scale) factors. Abiotic factors included maximum and minimum daily temperature and precipitation from the National Climate Data and Information Archive from Environment Canada (Table 4.2). Biotic factors included the presence/absence and average abundance of European Starlings near Red-headed Woodpecker nest sites (within visual range of ~ 100 m), as well as the average adult Red-headed Woodpecker feeding rates of their young, which we determined by 20-min behavioural sampling sessions at each nest visit. Temporal factors included the study year, nest initiation date, and nest age as determined by behavioural cues or use of the Elevated Video Inspection System at each nest visit. Lastly, habitat factors include habitat characteristics at small (nest cavity and tree) and large (nest patch and woodlot) spatial scales that significantly differed between occupancy or breeding success in a previous study (see Frei et al. (2013) for a detailed description of habitat measurements). All variables were tested for correlation prior to being used in the analysis, and if variables were strongly correlated, only one variable was used (e.g., Julian date omitted in favor of nest initiation date).

4.3.4 Statistical Analysis

Modelling Nest Success

We performed all statistical analyses with R version 2.13.2 (R Development Core Team 2011). We used the logistic-exposure link function in R (R library mass, function logexp) to calculate nest survival (Shaffer 2004). The logistic-exposure method estimates the probability of daily nest survival as a logistic function of independent covariates on a given day within an exposure period between nest visits (Shaffer 2004). The two main assumptions of the logistic-exposure method are: (1) nest fates are independent of each other, and (2) that daily nest survival probabilities are the same for nest-days with equal values of the explanatory variables (Shaffer 2004). Each interval of exposure between nest visits is treated as an observation. Using the logistic-exposure regression equation we derived daily survival rates (DSR) that could then be extrapolated across the 47-day nesting period (Smith et al. 2000) to calculate nest survival.

We performed analysis on all sites together (n = 60), as well as separate analyses for open sites (n = 18) and woodlot (n = 42) sites. Open sites included nests found in sparsely treed areas (i.e., campgrounds, pastures, golf courses, urban streets), while woodlot sites were deciduous forest patches. We later removed one woodlot nest from the analysis, as we suspected nest failure due to infertile eggs. In open and all sites, only small-scale habitat variables could be characterized, while in woodlots both small- and large-scale habitat variables were measured. We evaluated 21 and 28 models of nest survival for all open nests and woodlot sites respectively, based on *a priori* hypotheses on the influence of abiotic, biotic, temporal, and habitat factors (Table 4.1). Models included each of the factor groups as well as each factor individually for parsimony, a global model, and an intercept-only model. We tested for site effects by including north/south study area as a factor in preliminary models, but as there was no significant difference for nest survival between study areas (F-statistic = 1.25; $p = 0.26$) and this variable was later removed to reduce the number of models.

Model Selection

We evaluated models using Akaike's Information Criterion adjusted for small sample sizes (AICc; Hurvich and Tsai 1989). We developed a set of candidate models based on *a priori* biological hypotheses for variation in Red-headed Woodpecker nest survival, which we derived from previous work on the species and published data on numerous woodpecker species (Table 4.2). Models were ranked according to the strength of support of each model, as determined by the difference in AICc between a given candidate model and the model with the lowest AICc (ΔAICc), and AICc weight (Anderson et al. 2001). We used the intercept-only model and top model(s) to calculate the DSR and Red-headed Woodpecker nest survival with 95% confidence intervals. We calculated the values of covariates across all candidate models and included their relative importance and influence on nest survival in the evaluation of our results. We assumed biological significance at $\alpha \leq 0.1$ to reduce Type I error and acknowledge the consequences of Type II error for a rare species of conservation concern.

4.4 Results

We monitored 60 Red-headed Woodpecker nests over a two-year period in southern Ontario: 30 nests in Elgin/Norfolk in 2011 and 30 nests in Northumberland 2010-2011. Overall, 46 nests were successful in fledgling ≥1 young. Because we could not access a majority (78%) of the nest cavities with the Elevated Video Inspection System due to their height (>13 m in height), specific causes of nest failures (i.e., predation, nest usurpation, abandonment) could not always be ascertained. We found 18 nests during the cavity excavation stage, 30 nests during egg-laying or incubation, and 12 nests during the nestling stage with the phenology at the southern site being approximately a week ahead of the northern site (Table 4.3). European Starlings were present (seen at least 1 time during the nest visits) at 27 nests, of which 12 or 44% failed, compared to a 6% failure rate at Red-headed Woodpecker nest sites without starlings. Successful woodpecker nests with starlings present had an average starling abundance of 0.27 ± 0.04 SE, while failed nests had an average starling abundance of 1.60 ± 0.34 SE. Ultimately of the 12 failed nests with starlings present, a minimum of half (6/12) of the nests were occupied by starlings immediately following the woodpecker nest failure.

4.4.2 Drivers of Red-headed Woodpecker Nest Success

The model that received the most support given our data, for all sites together as well as for woodlot and open sites individually, is European Starling abundance (AEUST) (Table 4.4). In all cases, the second best model is a combination of the three biotic variables (PEUST (presence/absence of starlings), AEUST (abundance of starlings), feeding), with the two top models accounting for 100% of the AICc weight (Table 4.4). Across all sites categories, DSR was significantly (F-statistic = 77.23; p <0.0001) negatively related to AEUST, and for all sites and woodlots sites there was also a significantly negative relationship with PEUST (F-statistic = 6.60; *p*= 0.0105, F-statistic = 7.51; *p*=0.0064, respectively; Table 4.5). Remaining variables, all exhibiting positive correlations, that influence Red-headed Woodpecker DSR include: (1) All sites: Initiation and Initiation^2, (2) Woodlot sites: PSNAG (number of dead trees in nest patch; 0.04-ha circle) and WLIMB (total length of dead branches in woodlot), and (3) Open sites: Age^2, Initiation, and Max_temp (Table 4.5). To assess the effects of AEUST and Initiation on the daily survival of Red-headed Woodpecker nests, we plotted the DSR as a function of the two variables (Fig. 4.1 and 4.2).

Using the intercept-only model, that assumed a constant DSR, Red-headed Woodpecker nest survival calculated using all nest sites is $0.992^{47} = 0.684$ (95% CI = 0.538, 0.793), or 68.4% (Table 4.6). Nest survival for woodlot nests only is slightly higher at 0.691 (95% CI = 0.513, 0.815), and lower for open nests only at 0.636 (95% CI = 0.389, 0.806; Table 4.6). In comparison, nest survival calculated from the top model, AEUST, is 0.132, 0.101 and 0.192 for all, woodlot, and open nest sites respectively (Table 4.6).

4.5 Discussion

The abundance of non-native European Starlings near Red-headed Woodpecker nests in southern Ontario is overwhelmingly the strongest predictor of woodpecker nest survival among biotic, abiotic, temporal, and habitat features. Across woodlot and open nesting sites the abundance of European Starlings drastically lowers Red-headed Woodpecker breeding success. As starlings are well-documented nest competitors for woodpecker nest cavities (Ingold 1989ab, 1994), and several cases of starlings successfully usurping Red-headed Woodpecker nests occurred in the study area (B. Frei, unpub. data), we suggest starling abundance as a proxy measure of interference competition for nest cavities (e.g., harassment leading to nest usurpation). Red-headed Woodpecker nests that are initiated later in the season are more likely to be successful than those initiated earlier in the season, the contrary of many other species for which early nests are more successful (Badyaev et al. 1996; Brown and Brown 1999; Blums et al 2002; Newlon and Saab 2011). Despite Red-headed Woodpeckers demonstrating specific habitat use patterns at multiple spatial scales (Frei et al. 2013), neither small- or large-scale habitat characteristics are strong drivers of the species' nest survival when interspecific competition is considered. Yet, for woodlot nest sites, two measures of standing dead wood at the large spatial scale (1) number of snags in the nest patch, and (2) total dead limb length in the woodlot, are significantly positively correlated with DSR.

Although other studies have reported decreases to woodpecker fitness (e.g., fledglings per nest) correlated with competition with starlings, we are unaware of any other studies that have modeled the effects of starling abundance near nest sites on the nest survival of a North American woodpecker. Interference competition has been observed between European Starlings and native North American woodpeckers (e.g., Acorn Woodpecker (*M. formicivorus*), Troetschler 1976; multiple spp, Weitzel 1988; Red-cockaded Woodpecker (*Picoides borealis*), Carter et al. 1989; Red-headed and Red-bellied Woodpecker, Ingold 1989a, Northern Flicker (*Colaptes auratus*), Ingold 1996; Gila Woodpecker (*M. uropygialis*), Kerpez and Smith 1990; Lewis' Woodpecker (*M. lewis*), Vierling 1998). Ingold (1989a) reported that competing Red-bellied Woodpeckers in

Mississippi had significantly lower numbers of fledglings per nest than those woodpeckers in the absence of starlings. Likewise, Northern Flickers in Ohio and British Columbia suffered higher nest failure early in the season due to interference competition by starlings, and may suffer fitness consequences to clutch size (Ingold 1996; Wiebe 2003).

Past research on competition between starlings and Red-headed Woodpeckers has focused on observed interactions and nest usurpations (Ingold 1989a, Ingold and Densmore 1992), and concluded that because the highly aggressive woodpecker won most interactions, it must be unaffected by competition. However, our nest success models indicate that European Starling abundance supersedes any other factor in accounting for nest success patterns in southern Ontario. This is corroborated that a majority (80%) of failed nests had starling present at the nest site, and there was a clearly higher abundance of starlings at failed nests than at successful nets, out of those nest with starlings present. We suggest our models account for a more general relationship, unlike behavioral observation that focuses exclusively on individual interactions, and as such are superior in capturing the dynamics between Red-headed Woodpeckers and starlings. We suspect that for any observed aggressive interaction, many more go unnoticed, while using modeling techniques allows the inclusion of latent or subtler effects of interference competition in the correlation.

Compared to previous research in central-southern United States, Red-headed Woodpeckers in southern Ontario may be faced with higher rates of direct competition as the starling's nesting period overlaps more with that of the woodpecker at higher latitudes. Continual harassment by multiple starlings increases the potential of nest usurpation (Ingold 1989b), which supports our finding that abundance, not just presence, of starlings is a strong driver of lower nest survival of woodpeckers in southern Ontario. As the average abundance of starlings seen near an active woodpecker nest during monitoring activities approached two individuals, Red-headed Woodpecker DSR decreased substantially (Fig. 4.1).

Several species have shown delayed nesting and/or higher nest failures earlier in the breeding season via nest usurpation by starlings, particularly Northern Flickers in North America and Great-spotted Woodpeckers (*Dendrocopos major*) in Europe (Ingold 1996; Wiebe 2003; Smith 2005, 2006). Likewise, in our study, nests initiated later in the season experienced higher nest success (Fig. 4.2). As aggressive interactions between the two species were commonly observed during our study, as well as several cases of failed Red-headed Woodpecker nests due to takeover of the freshly excavated cavities by starlings (B. Frei, unpub. data), we attribute Red-headed Woodpecker nest survival depression early in the season to be a result of nest usurpation and interference competition in this period. Following the loss of a cavity, woodpeckers may excavate anew and reproduce successfully later in the season, partially mitigating starling competition (Troetschler 1976, Ingold 1994, Wiebe and Moore 2008). But, delayed laying is costly to breeding birds, as clutch size and number of successful fledglings decrease over time (Ingold 1996, Wiebe 2003, Zhu et al. 2012), and as such is likely not a suitable mitigation strategy (Wiebe 2003; Smith 2006). Species with breeding season flexibility (e.g., Acorn Woodpeckers; Troetschler 1976) or those which can excavate a new nest relatively quickly, may tolerate delayed nesting better than Red-headed Woodpeckers, which are relatively weak excavators and late nesters (Smith et al. 2000). Unlike populations in the central and southern United States that commonly double-brood, Red-headed Woodpeckers in southern Ontario at the northern edge of their range thought to be single-brooded due to a shorter breeding season, and thus have a smaller window of opportunity to re-nest following failure or usurpation (Ingold 1989a, 1994; Smith et al. 2000).

In a previous study, we found Red-headed Woodpeckers exhibited maladaptive habitat use; i.e., aspects of habitat use correlated with unsuccessful nests across multiple spatial scales (Frei et al. 2013). There are strong habitat similarities between active Red-headed Woodpecker and European Starling nest cavities, reflecting the degree to which interference competition may be realized (Stauffer and Best 1982, Sedgwick and Knopf 1990). Therefore the same habitat that attracts Red-headed Woodpeckers also attracts starlings (e.g., open canopy and/or nest trees with dead limbs), and may lead to increased interference competition contributing to maladaptive effects (Frei et al. 2013). Mismatches between habitat use and reproductive success are often driven by ecological factors (including interference competition), temporal, and/or abiotic effects, that countermand the benefits of the habitat used (Martin 1998, Zhu et al. 2012). To sustain Red-headed Woodpecker populations, land managers should provide attractive breeding habitat in a spatially explicit way by focusing on areas with few or no European Starling populations. Although the two species have similar small-scale habitat associations, different habitat use at large-scales would allow land managers or conservation planners to focus or manage areas that provide Red-headed Woodpecker habitat in areas that are less attractive to starlings. This may include habitats a distance from building and livestock, and creating suitable nest sites inside a woodlot (i.e., open canopy and standing dead wood) to preempt suitable habitat being restricted for woodlot edges.

Despite our finding that starling presence and abundance is the dominant factor affecting Red-headed Woodpecker nest survival, two measures of standing dead wood at the large habitat scale (1) number of snags in the nest patch, and (2) total dead limb length in the woodlot, are significantly positively correlated with DSR. The presence of dead tree limbs at or surrounding the nest tree or habitat is a well-documented habitat feature of Red-headed Woodpecker territories (Sedgwick and Knopf 1990, Rodewald et al. 2005, King et al. 2007, Waldstein 2012, Frei et al. 2013). Dead limbs are frequently used by the species as a perch from which to flycatch or as a location to cache food (Smith et al. 2000, B. Frei, unpub. data). We hypothesize that nest survival for Red-headed Woodpeckers is enhanced by a higher density of dead limbs as it increases foraging opportunities and parental attentiveness (Hollenbeck et al. 2011). The latter may be especially relevant given interference competition by starlings as a major driver of nest failures, and may be used as a management tool in favor of increasing potential Red-headed Woodpecker fitness.

Whether interference competition has a dramatic effect on nest survival of Red-headed Woodpeckers in other habitat and/or part of the species' range is debatable, as our results contrast with studies concluding that starlings have little negative effects on native North American cavity nesters (Koenig 2003). Assuming constant survival, nest survival for Red-headed Woodpeckers at the northern edge of their range (68%) is slightly lower than expected for a primary excavator (70-100%; Winkler et al. 1995). The dominant nest success model explaining Red-headed Woodpecker nest success in our study area (starling abundance) results in a far lower estimate of nest success of 13%, than the constant survival model. Red-headed Woodpecker nest survival in southern Ontario (assuming constant survival) is considerably higher than the two other studies reporting logistic-exposure nest survival: (1) 47% nest success in mixed-ponderosa and aspen woodlands in South Dakota (Vierling and Lentile 2006), and (2) 56% nest success in golf course and woodlots in Illinois (Hudson and Bollinger 2013). Both these studies reported a majority of nest failures being attributed to predation (78%; Vierling and Lentile 2006, 71%; Hudson and Bollinger 2013), with no mention of starling usurpation, although neither study collected data on starling presence or abundance at nest sites. This contrasts with our study, where at least 43% of failed nests were due to starling usurpation. Interference competition alone likely does not account for the severe population declines of Red-headed Woodpeckers in Ontario (COSEWIC 2007), thus we propose that the evolutionary trap of interference competition with European starlings as well as habitat loss and degradation (Smith et al. 2000) precipitate the declines.

To facilitate our understanding of Red-headed Woodpecker breeding ecology our research necessarily focused on a smaller spatial scale, yet ecological relationships on small-scales are driven and/or compounded by dynamics on larger-scales. Red-headed Woodpeckers in Canada, as well as the majority of Canadian species-at-risk, are found in areas best suited for and most altered by agricultural activities (Kerr and Deguise 2004). As starlings favor open agricultural areas and suburban development for foraging (Feare 1984, Cabe 1993), it is the land-use surrounding Red-headed Woodpecker habitat that has the greatest influence on the level of interference competition in the system. Thus the anthropogenic activities of agricultural expansion and intensification, urbanization, and habitat fragmentation are all driving factors that may influence Red-headed Woodpecker nest success from a distance, via ecological and/or evolutionary traps. Multi-scale and ecosystem-based conservation action and policy development are needed to stabilize or recover populations of Red-headed Woodpeckers, and likely many other species-at-risk, in anthropogenically-altered habitats that are near impossible to return to pristine states. As starling abundance (as a proxy for an evolutionary trap based on interference competition for nest cavities) is strongly correlated with lower and delayed nest success, we suggest managing habitat to increase woodpecker fitness (i.e. increasing standing dead wood), in areas with lower starling abundance or those made less attractive to starlings.

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4.7 Literature Cited

ANDERSON, D.R., W.A. LINK, D.H. JOHNSON, AND K.P. BURNHAM. 2001. Suggestions for presenting the results of data analyses. Journal of Wildlife Management 65:373–378.

BADYAEV, A.V., T.E. MARTIN, AND W.J. ETGES. 1996. Habitat sampling and habitat selection by female Wild Turkeys: Ecological correlates and reproductive consequences. Auk 113:636–646.

BLUMS, P., R.G. CLARK, AND A. MEDNIS. 2002. Patterns of reproductive effort and success in birds: Path analyses of long-term data from European ducks. Journal of Animal Ecology 71:280–295.

BONNOT, T.W., M.A. RUMBLE, AND J.J. MILLSPAUGH. 2008. Nest success of Black-Backed Woodpeckers in forests with Mountain Pine Beetle outbreaks in the Black Hills, South Dakota. Condor 110: 450–457.

BROWN, C.R. AND M.B. BROWN. 1999. Fitness components associated with laying date in the Cliff Swallow. Condor 101:230–245.

BYERS, J.E. 2002. Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. Oikos 97:449–458.

CABE, P.R. 1993 European Starling (*Sturnus vulgaris*). *In* The Birds of North America, no. 48 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington D.C.

CARTER, J.H., J.R. WALTERS, S.H. EVERHART, AND P.D. DOERR. 1989. Restrictors for Red-cockaded Woodpecker cavities. Wildlife Society Bulletin 17:68–72.

CHANNELL, R., AND M.V. LOMOLINO. 2000. Dynamic biogeography and conservation of endangered species. Nature 403:84–86.

CHARMAN, E.C., K.W. SMITH, I.A. DILLON, S. DODD, D.J. GRUAR, A. CRISTINACCE, P.V. GRICE, AND R.D. GREGORY. 2012. Drivers of low breeding success in the Lesser Spotted Woodpecker Dendrocopos minor in England: Testing hypotheses for the decline. Bird Study 59:255–265.

COSEWIC. 2007. COSEWIC assessment and update status report on the Red-headed Woodpecker *Melanerpes erythrocephalus* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa.

FEARE, C. 1984. The Starling. Oxford University Press. Oxford, U.K.

FISHER, R.J., AND K.L. WIEBE. 2006. Nest site attributes and temporal patterns of Northern Flicker nest loss: Effects of predation and competition. Oecologia 147:744–53.

FREI, B., J.W. FYLES, AND J.J. NOCERA. 2013. Maladaptive habitat use of a North American woodpecker in population decline. Ethology 119:377–388.

HOLLENBECK, J.P., V.A. SAAB, AND R.W. FRENZEL. 2011. Habitat suitability and nest survival of White-headed Woodpeckers in unburned forests of Oregon. Journal of Wildlife Management 75:1061–1071.

HUEBNER, D.P., AND S.R. HURTEAU. 2007. An economical wireless cavity-nest viewer. Journal of Field Ornithology 78: 87–92.

HURVICH, C., AND C.-L.TSAI. 1989. Regression and time series model selection in small samples. Biometrika 76: 297-307.

INGOLD, D.J. 1989a. Nesting phenology and competition for nest sites among Red-headed and Red-bellied Woodpeckers and European Starlings. Auk 106:209–217.

INGOLD, D.J. 1989b. Nesting phenology and competition for nest-sites among Red-headed and Red-bellied Woodpeckers and European Starlings in east-central Mississippi. PhD dissertation, Department of Biological Sciences, Mississippi State University, Starkville, Mississippi, USA.

INGOLD, D.J. 1994. Influence of nest-site competition between European Starlings and woodpeckers. Wilson Bulletin 106:227–241.

INGOLD, D.J. 1996. Delayed nesting decreases reproductive success in Northern Flickers: Implications for competition with European Starlings. Journal of Field Ornithology 67:321–326.

INGOLD, D.J., AND R. DENSMORE. 1992. Competition between European Starlings and native woodpeckers for cavity nests in Ohio. Sialia 14:41–80.

KERPEZ, T.A., AND N.S. SMITH. 1990. Competition between European Starlings and native woodpeckers for nest cavities in Saguaros. Auk 107:367–375.

KERR, J.T., AND I. DEGUISE. 2004. Habitat loss and the limits to endangered species recovery. Ecology Letters 7:1163–1169.

KESSEL, B. 1953. Distribution and migration of the European Starling in North American. Condor 55:49-67.

KING, R.S., K.E. BRASHEAR, AND M. REIMAN. 2007. Red-headed Woodpecker nest-habitat thresholds in restored savannas. Journal of Wildlife Management 71:30–35.

KOCH, A., K. MARTIN, AND K. AITKEN. 2012 The relationship between introduced European Starlings and the reproductive activities of Mountain Bluebirds and Tree Swallows in British Columbia, Canada. Ibis 154:590–600.

KOENIG, W.D. 2003 European Starlings and their effect on native cavity-nesting birds. Conservation Biology 17:1134–1140.

LI, P., AND T.E. MARTIN. 1991. Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. Auk 108:405–418.

MARTIN, T.E. 1998. Are microhabitat preferences of coexisting species under selection and adaptive? Ecology 79:656–670.

MAZGAJSKI, T. 2000 Competition for nest sites between Starling *Sturnus vulgaris* and other cavity nesters - study in a forest park. Acta Ornithologica 35:103–107.

NEWLON, K.R., AND V.A. SAAB. 2011. Nest-site selection and nest survival of Lewis's Woodpecker in aspen riparian woodlands. Condor 113:183–193.

OMAFRA (2006) Agricultural census 2006. Agricultural and Strategic Policy Branch, Ontario Ministry of Agriculture, Food and Rural Affairs, Guelph, Canada.

R DEVELOPMENT CORE TEAM. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN: 3-900051-07-0, URL http://www.R-project.org/

RODEWALD, P.G., M.J. SANTIAGO, AND A.D. RODEWALD. 2005. Habitat use of breeding Red-headed Woodpecker on golf courses in Ohio. Wildlife Society Bulletin 33:448–453.

SAAB, V.A., R. RUSSELL, J. ROTELLA, AND J.G. DUDLEY. 2011. Modeling nest survival of cavity-nesting birds in relation to postfire salvage logging. Journal of Wildlife Management 75:794–804.

SCHLAEPFER, M.A., M.C. RUNGE, AND P.W. SHERMAN. 2002. Ecological and evolutionary traps. Trends of Ecology and Evolution 17:474-480.

SCHLAEPFER, M.A., P.W. SHERMAN, B. BLOSSEY, AND M.C. RUNGE. 2005. Introduced species as evolutionary traps. Ecology Letters 8:241–246.

SEDGWICK, J., AND F. KNOPF. 1990. Habitat relationships and nest site characteristics of cavity-nesting birds in cottonwood floodplains. Journal of Wildlife Management 54:112–124.

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

SHEA, K., AND P. CHESSON. 2002. Community ecology theory as a framework for biological invasions. Trends of Ecology and Evolution 17:170–176.

SHREEVE, T., R. DENNIS, AND A.S. PULLIN. 1996. Marginality: scale determined processes and the conservation of the British butterfly fauna. Biodiversity and Conservation 5:1131-1141.

SMITH, K. 2005. Has the reduction in nest-site competition from Starlings *Sturnus vulgaris* been a factor in the recent increase of Great Spotted Woodpecker *Dendrocopos major* numbers in Britain? Bird Study 52:307–313.

SMITH, K.W. 2006. The implications of nest site competition from Starlings *Sturnus vulgaris* and the effect of spring temperatures on the timing and breeding performance of Great Spotted Woodpeckers *Dendrocopos major* in southern England. Annales Zoologici Fennici 43:177–185.

SMITH, K.G., J.H. WITHGOTT, AND P.G. RODEWALD. 2000. Red-headed Woodpecker (*Melanerpes erythrocephalus*). *In* The Birds of North America, no. 518 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington D.C.

STAUFFER, D., AND L. BEST. 1982. Nest-site selection by cavity-nesting birds of riparian habitats in Iowa. Wilson Bulletin 94:329–337.

THOMAS, C., AND W.E. KUNIN. 1999. The spatial structure of populations. Journal of Animal Ecology 68:647-657.

TOZER, D.C., E. NOL, D.M. BURKE, K.A. ELLIOTT, AND K.J. FALK. 2009. Predation by bears on woodpecker nests: Are nestling begging and habitat choice risky business? Auk 126:300–309.

TROETSCHLER, R. 1976. Acorn Woodpecker breeding strategy as affected by starling nest-hole competition. Condor 78:151–165.

VIERLING, K.T. 1998 Interactions between European Starlings and Lewis' Woodpeckers at nest cavities. Journal of Field Ornithology 69:376–379.

WALDSTEIN, A. 2012. Nest-site selection and nesting ecology of Red-headed Woodpeckers. MSc dissertation, Department of Natural Resources Sciences and Management, University of Minnesota, MI, U.S.A.

WEITZEL, N.H. 1988. Nest-site competition between the European Starling and native breeding birds in northwestern Nevada. Condor 90:515–517.

WIEBE, K.L. 2003. Delayed timing as a strategy to avoid nest-site competition : Testing a model using data from starlings and flickers. Oikos 100:291–298.

WIEBE, K.L., AND W.S. MOORE. 2008. Northern Flicker (*Colaptes auratus*). *In* The Birds of North America, no. 166a (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington D.C.

WINKLER, H., D.A. CHRISTIE AND, D. NURNEY. 1995. Woodpeckers: A Guide to Woodpeckers, Piculets and Wrynecks of the World. Pica Press, Russel Friedman Books, South Africa.

ZHU, X., D.S. SRIVASTAVA, J.N.M. SMITH, AND K. MARTIN. 2012. Habitat selection and reproductive success of Lewis's Woodpecker (*Melanerpes lewis)* at its northern limit. PloS ONE 7:e44346.

4.8 Tables and Figures

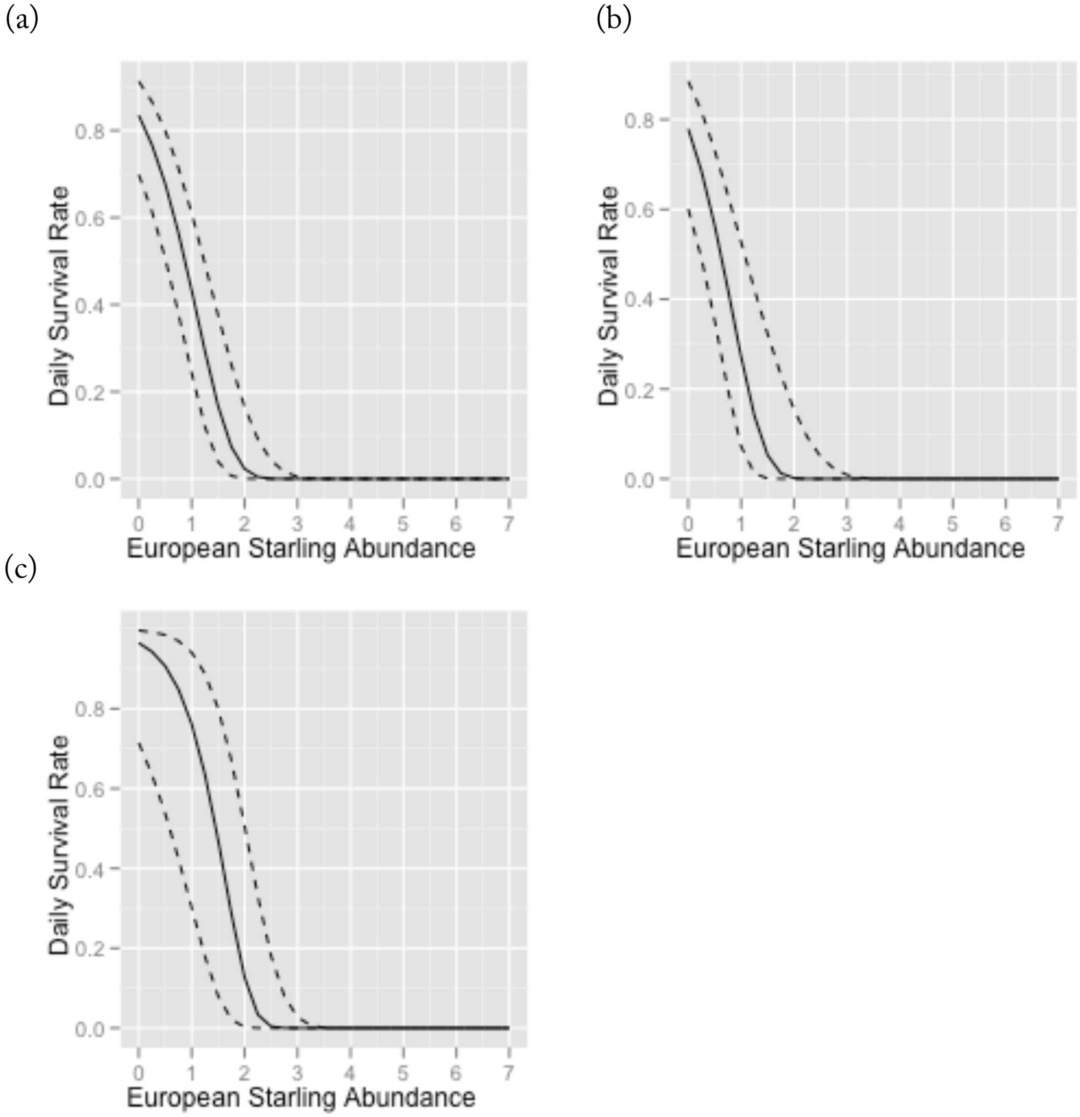

Figure 4.1 Average European Starling abundance near (~100 m) active woodpecker nest sites versus daily survival rate (DSR) and 95% CI for Red-headed Woodpeckers in (a) all sites, (b) woodlot sites only, and (c) open sites only, southern Ontario 2010 – 2011 using logistic-exposure nest survival modelling.

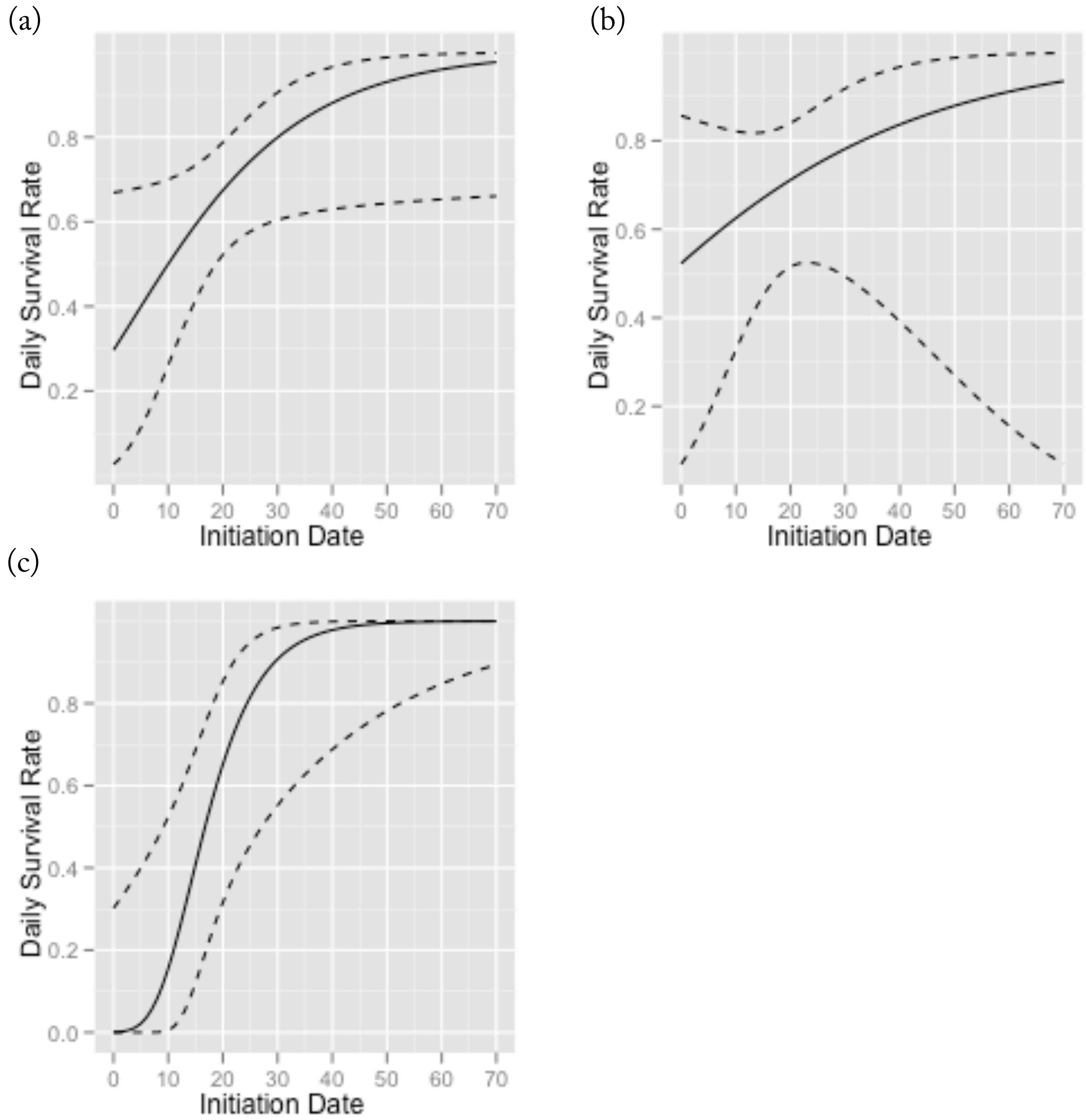

Figure 4.2 Nest initiation date versus daily survival rate (DSR) for Red-headed Woodpeckers in: (a) all sites, (b) woodlot sites only, and (c) open sites only, southern Ontario 2010 – 2011, using logistic-exposure nest survival modelling.

Table 4.1 Candidate models and supporting hypotheses comparing random, abiotic temporal, biotic, and habitat influences on nest survival of Red-headed Woodpecker nest in southern Ontario, 2010-2011.

Category and models	Alternative hypotheses
Null	Nest survival is random
Intercept	
Abiotic	Temperatures and precipitation may reduce survival of young nestlings and/or influence foraging and food availability (Newlon and Saab 2011; Saab et al. 2011; Charman et al. 2012).
Max_temp	
Min_temp	
Precip	
Max_temp + Min_temp + Precip	
Temporal	Earlier nesters have higher nest survival (Brown and Brown 1999; Blums et al. 2002; Bonnot et al. 2008; Newlon and Saab 2011). Adult and young behaviour, auditory and visual cues at various nest ages can influence nest survival (Tozer et al. 2009). Annual variation in food and predators can influence nest survival.
Initiation	
Initiation^2	
Age	
Age^2	
Year	
Initiation + Age + Year	
Biotic	European Starlings decrease Red-headed Woodpecker nest survival via nest-site competition (Ingold 1994). Higher feeding rates increase nest survival.
PEUST	
AEUST	
Feeding	
PEUST + AEUST + Feeding	
Habitat (small scale)	Higher cavities and those that lack bark may lower predation pressure (Li and Martin 1991; Fisher and Wiebe 2006). Dead limb on the nest tree may increase
CHEIGHT	
CBARK	
TLIMB	

CHEIGHT + CBARK + TLIMB	feeding potential, increasing nest survival.
Habitat (large scale)	Habitat characteristics found to be related to occupancy and/or nest success in a previous study (Frei et al. 2013); may be similar to those influencing nest survival.
PSMALL	
PSNAG	
PCWD	
POPEN	
WLIMB	
WOPEN	
PSMALL + PSNAG + PCWD + POPEN + WLIMB + WOPEN	
Global	A combination of all characteristics may provide the best nest site conditions, protection for predators and competitors, and feeding potential leading to high nest survival.
Global model	

Table 4.2 Covariates used for modelling nest survival of Red-headed Woodpeckers in southern Ontario 2010 – 2011.

Variable category/name	Variable description
Abiotic	
Max_temp	Daily temperature high (°C)
Min_temp	Daily temperature low (°C)
Precip	Daily precipitation (cm)
Temporal	
Initiation	Date when nest was initiation (1st egg laid)
Initiation^2	Quadratic effects of Initiation
Age	Daily nest age when Day 1 = Initiation date
Age^2	Quadratic effects of Age
Year	Year of study
Biotic	
PEUST	Presence of European Starling during nest Red-headed Woodpecker nest monitoring, binomial 1 = EUST present; 0 = EUST absent
AEUST	Average abundance of European Starlings during Red-headed Woodpecker nest monitoring
Feeding	Average number of feeding events
Habitat (small scale)	
CHEIGHT	Cavity height; measured with clinometer (m)
CBARK	Cavity exterior appearance (bark or no bark)
TLIMB	Visually estimated length in m of dead limbs ≥ 10 cm diameter on nest tree
Habitat (large scale)[a]	
PSMALL	No. of trees 3-23-cm dbh in a 0.04-ha circle around the nest tree
PSNAG	No. of dead trees (0.04-ha circle)
PCWD	Total volume of coarse woody debris on the ground > 3 cm in

	diameter and > 30 cm in length (0.04-ha circle)
POPEN	Percentage open sky from digital cover image taken at tree base
WLIMB	Average visually estimated length in m of dead limbs ≥ 10 cm diameter within woodlot
WOPEN	Average percentage open sky from digital cover image taken within woodlot
WBIG	Average no. of trees > 69-cm dbh within woodlot

[a] For woodlot sites only

Table 4.3 Nest outcomes and phenology for Red-headed Woodpeckers in southern Ontario.

Nest outcome/Phenology	Northumberland	Elgin/Norfolk	All sites
Successful nests	23	23	46
Unsuccessful nests	8	6	14
Mean incubation date (± SE)	June 13 (± 2.0)	June 5 (± 3.4)	June 9 (± 2.2)
Mean nestling date (± SE)	June 29 (± 3.2)	June 22 (± 1.8)	June 25 (± 1.8)
Mean fledging date (± SE)	July 21 (± 1.9)	July 18 (± 1.7)	July 19 (± 1.9)

Table 4.4 Summary of rankings of candidate logistic-exposure models of nest success for Red-headed Woodpeckers in southern Ontario, 2010 – 2011. See Table 4.2 for model descriptions. *K* = number of parameters, w_i = Akaike weight, Cw_i = Cumulative Akaike weight.

Model	Deviance	K	ΔAICc	w_i	Cw_i
All sites (n = 440)					
AEUST	297.34	3	0.00	0.71	0.71
Biotic	299.56	5	1.85	0.28	0.99
Global	315.30	17	11.43	0.01	1.00
PEUST	232.46	3	64.87	0.00	0.00
Initiation	229.66	3	67.67	0.00	0.00
Woodlot sites (n= 311)					
AEUST	196.48	3	0.00	0.88	0.88
Biotic	196.56	5	4.04	0.12	1.00
Global	220.72	23	19.52	0.00	1.00
PEUST	175.42	3	21.06	0.00	1.00
WLIMB	173.40	3	23.08	0.00	1.00
Open sites (n= 129)					
AEUST	113.94	3	0.00	0.80	0.80
Biotic	115.42	5	2.83	0.20	1.00
Global	125.92	16	18.69	0.00	1.00
Temporal	77.48	7	45.20	0.00	1.00
Initiation	63.20	3	50.75	0.00	1.00

Table 4.5 Significant parameter estimates and standard error from logistic-exposure nest success models for Red-headed Woodpeckers in southern Ontario, 2010 – 2011. See Table 4.2 for model descriptions.

Model	Variable	Estimate	Standard Error	P-value
All sites	Initiation	0.00162	0.00083	0.0523
	Initiation^2	0.00002	0.00001	0.0977
	AEUST	-0.14558	0.01656	<0.0001
	PEUST	-0.04598	0.01789	0.0105
Woodlot sites	AEUST	-0.18250	0.03350	<0.0001
	PEUST	-0.06362	0.02321	0.0064
	PSNAG	0.01457	0.00835	0.0823
	WLIMB	0.03234	0.01384	0.0201
Open sites	Age^2	0.00004	0.00002	0.0851
	Initiation	0.00420	0.00189	0.0287
	Max_temp	0.00794	0.00387	0.0426
	AEUST	-0.15793	0.01909	<0.0001

Table 4.6 Summary of daily survival rates (DSR) and nest survival across the 47-day nesting period of Red-headed Woodpeckers for intercept only model and the top model, European Starling abundance (AEUST), with 95% confidence intervals.

Model	DSR	Nest Survival	Lower CI	Upper CI
Intercept only				
All sites	0.992	68.4	53.8	79.2
Woodlot only	0.992	69.1	51.3	81.5
Open only	0.990	63.6	38.9	80.6
Top model (AEUST)				
All sites	0.514	13.2	8.9	18.6
Woodlot only	0.451	10.1	5.9	16.9
Open only	0.478	19.2	10.7	25.8

Preface to Chapter 5

In Chapter 4 we identified the abundance of European Starlings at Red-headed Woodpeckers nest sites, a suggested proxy for interference competition, as a dominant driver of lower nest success. We propose this is evidence of an evolutionary trap wherein the native Red-headed Woodpecker's fitness is lowered by potential nest-cavity competition with the non-native starling.

Chapter 5 expands exploration of the relationship between Red-headed Woodpeckers and starlings to a macro-scale, by utilizing an existing database of avian surveys and geospatial analysis techniques. A previous large-scale analysis suggests that non-native starling have no adverse effect on native cavity-nesting species, contradicting our field-based findings in Chapter 4. By comparing non-spatial 'global' and spatially explicit 'local' regression models, we examine the relationship between Red-headed Woodpecker and two possible competitors across a 45-year period in southern Canada and east-central United States. Chapter 5 was co-authored by the candidate's supervisors, Drs. Joseph J. Nocera and James W. Fyles, and Dr. J.A. Cardille with planned submission to *Ecography.*

Frei, B., Fyles, J.W., Cardille, J.A., Nocera, J.J. Geographic-Dependency and Temporal Fluctuations in the Relationship Between a Threatened Species and Two Possible Competitors. To be submitted to: *Ecography.*

Chapter 5

5. Geographic-Dependency in the Relationship Between a Threatened Species and Two Possible Competitors

5.1 Abstract

Comparing geographical relationships of ecological variables may provide important findings for both theoretical ecology, and for conservation and management plans. Often, global (i.e., overall) comparisons are used for ecological data, whose values and/or relationship with other variables may differ over geographical space. This presents a problem, for although non-spatial global models are useful for their predictive abilities, their findings may be inappropriate when used with spatially structured data. We explore the use of non-spatial global, and spatial local modelling techniques in elucidating the potential interactions between the populations of a threatened species, the Red-headed Woodpeckers (*Melanerpes erythrocephalus*) and that of its two possible competitors, the European Starling (*Sturnus vulgaris*) and the Red-bellied Woodpecker (*M. carolinus*), over space and time. Using Breeding Bird Survey (BBS) data from 1966-2011 divided into 4 time periods we demonstrate high spatial autocorrelation, non-stationarity, and low model fit for species abundances relationships when non-spatial global models are used. Using geographically weighted regression, we greatly increased model fit, accounted for spatial variation, and demonstrated heterogeneity across time and space of the relationships between Red-headed Woodpeckers and its two possible competitors. Our study shows that accounting for

spatial variation using geographically weighted regression improves model fit, and provides better insight into the ecological relationships that influence species distributions relative to fitting global, non-spatial models. In addition, we suggest evidence for large-scale effects of interspecific competition between Red-headed Woodpecker and European Starlings, as well as niche differentiation between Red-headed Woodpecker and Red-bellied Woodpecker.

5.2 Introduction

Ecologists today employ powerful statistical techniques and geospatial techniques to explore various facets of environmental data. Geographical analysis is used to test specific hypotheses at a large spatial scale using 'global' models, or to explore 'local' variations in the data or relationships being tested (Jetz et al. 2005). Both global and local analyses may be useful in research, especially when used together. Non-spatial, global models such as linear or logistic regressions create a single coefficient estimate from the data. In doing so, global models assume average, uniform effects thus masking potentially important local variation (Fortheringham et al. 2002, Lieske and Bender 2009). The averaged parameters resulting from a global model may thus fail to reflect the true nature of the relationship at any individual point in the study area (Foody 2004).

The main shortcoming of non-spatially explicit global models when applied to spatial data, is that their use disregards two important features of a majority of ecological data: (1) spatial autocorrelation (i.e., the interaction or non-independence of neighbouring points), and (2) non-stationarity (i.e., model relationships that may vary depending on geographic location; Fortheringham et al. 2002). For predictive results or hypothesis testing using global models to meet the assumptions of statistical tests, the data used must be non-spatially autocorrelated and stationary. Models that consider local variation are better suited to spatially autocorrelated and non-stationary data. One example is geographically weighted regression (GWR; Fortheringham et al. 2002), which enhances data exploration by allowing parameter values to vary continuously across geographic space. The weakness of local models is that by creating spatially explicit coefficient estimates for specific locations, these models are then unable to test specific global hypotheses or be extrapolated to different geographic regions (Jetz et al. 2005). Although each type of model has its own strengths and weaknesses, the overall predominance of non-spatially explicit global models in ecology may be hazardous if inaccurate findings or predictive models are employed for conservation planning (Lieske and Bender 2009). Over the last decade, the use of GWR has slowly expanded beyond its social science roots to studies of vegetation patterns (Kupfer and Farris 2006), water quality (Tu and Xia 2008), species distribution (Osborne et al. 2007, Fortin and Melles 2009, Lieske and Bender 2009), and fisheries survey data (Windle et al. 2009).

Field-based research on the threatened Red-headed Woodpecker (*Melanerpes erythrocephalus*) in southern Ontario concluded that abundance of the invasive European Starling (*Sturnus vulgaris*), a known interference competitor, at Red-headed Woodpecker's nest sites was the dominant factor driving reduced nest survival for the species (Frei et al. in prep). Throughout most of its range, Red-headed Woodpeckers often inhabit areas that have been heavily influenced by human presence and activities (Smith et al. 2000). We found Red-headed Woodpecker habitat use at multiple-scales to be maladaptive in Ontario woodlots (Frei et al. 2013), and potentially driven or compounded by the evolutionary trap of losing nest cavities to the non-native starling. Therefore, we suggested that in order to conserve Red-headed Woodpeckers, areas that are less favorable to starlings should be targeted for management with the goal to enhance the habitat for Red-headed Woodpecker breeding potential (Frei et al. in prep).

European Starlings was introduced on the east coast in 1890 and swiftly established across most of the continent south of the tree line by 1970s (Feare 1984, Cabe 1993). The ecological impact of starlings was compounded by anthropogenic disturbances to habitat creating novel environments that benefited them, including habitat fragmentation, urban sprawl, and agricultural intensification (Feare 1984, Cabe 1993, Byers 2002). Starlings are aggressive interference competitors for nest cavities and will usurp nest cavities from primary (e.g., woodpeckers) and secondary (e.g., bluebirds) excavators in North America and Europe alike (Feare 1984, Ingold 1989, Kerpez and Smith 1990, Mazgajski 2000, Koch et al. 2012).

Our suggestion that the presence of starlings at nest-sites may negatively impact Red-headed Woodpecker fitness, as measured by nest survival, contradicts that of a previous large-scale, global analysis. Koenig (2003) compared the mean densities of 27 native cavity nesters before and after starling invasions using two continental surveys, the North American Breeding Bird Survey (BBS) and the Christmas Bird Count (CBC). He found no evidence to suggest that starlings negatively impact the native bird community, including Red-headed Woodpeckers. To further explore the demographic interactions between Red-headed Woodpeckers and starlings, as well as spatial variations in their comparison of abundances, we employed both global and local (GWR) modelling techniques. We also compared Red-headed Woodpecker abundance to that of its close congener, the Red-bellied Woodpecker (*M. carolinus*), as the three species occupy similar habitats and may compete for nest cavities (Ingold 1989, 1994a).

Red-bellied and Red-headed Woodpeckers are close congeners and share several nest-site habitat affinities (Jackson 1976, Stauffer and Best 1982, Ingold 1994b). Jackson (1976) hypothesized that three ecological differences between the species may drive co-existence despite their similar habitat and resource use, namely (1) Red-headed Woodpeckers favor more open areas than Red-bellied Woodpeckers, (2) foraging behavior for Red-headed Woodpeckers includes flycatching and stooping for insect prey while Red-bellied Woodpeckers glean insects from the bark, and (3) Red-headed Woodpeckers are migratory and initiate breeding later in the season than the non-migratory Red-bellied Woodpeckers that defend permanent territories. Currently, Red-headed Woodpeckers are undergoing long-term population declines across their range, especially in the northern part of their range (COSEWIC 2007, Sauer et al. 2012). Comparatively, Red-bellied Woodpecker populations are increasing and the species is expanding its range northwards (Sauer et al. 2012). Mechanisms that may be driving these demographic changes include direct competition between Red-headed and Red-bellied Woodpecker, or niche replacement by opportunistic Red-bellied Woodpecker as Red-headed Woodpecker decline due to other ecological drivers (e.g., climate or land-use changes).

In this paper we use GWR in a novel context, to investigate how the abundance of a threatened bird species may be related to the abundances of its two potential competitors across its range. The use of GWR in species predictive occurrence or richness models has grown in popularity over the last decade (Foody 2004, Osborne et al. 2007, Fortin and Melles 2009, Lieske and

Bender 2009, Hortal et al. 2011). Here we use GWR to explore potential geographic patterns in competing species' population demographics, recognizing that species distributions are inherently spatial, and thus rendering global-regression models results potentially inaccurate.

The aim of our research is to determine whether species abundances are related to one another (Red-headed Woodpecker vs. European Starling and Red-headed vs. Red-bellied Woodpecker), if these relationships vary spatially, and if so, to assess what impact this might have on the accuracy of global model prediction. We predict that spatially variable modelling using GWR will outperform the global model by capturing local variations in the species' abundances, thus producing more accurate comparisons. Our final objective is to use the power of GWR to show spatial structure in the species relationships that can provide insight into the population decline of Red-headed Woodpeckers, and inform future conservation and management initiatives.

5.3 Methods

5.3.1 Species Abundance and Distribution Data

We obtained abundance data for European Starlings, Red-headed, and Red-bellied Woodpeckers from 1966 - 2011 from the BBS. This monitoring project was initiated in 1966 to detect long-term trends in species abundances in Canada and the United States (Robbins et al. 1986). From May-July, skilled volunteers collect species abundance data along 39.5 km long roadside routes, using 50 3-minute point-counts stationed every 0.8 km. Currently all active BBS routes' start locations are georeferenced; efforts to georeference all 50 point-count locations per routes are increasing and considered a priority in (M.-A. Hudson, pers. comm.).

We chose routes from 36 states and 2 provinces corresponding with the common breeding ranges for all three focal species. All data were downloaded from the USGS Patuxent Wildlife Research Center website (https://www.pwrc.usgs.gov/bbs). As routes were not necessarily surveyed every year, the average abundance for each species was calculated based on the number active years of the route. We removed routes with missing data and with zero counts for both species (either Red-headed Woodpeckers vs. starlings or Red-headed vs. Red-bellied Woodpeckers). To visualize the three focal species population changes over the 45-year study period, we graphed annual indices from the BBS across (1) the entire survey area, (2) the eastern region, and (3) central regions (Sauer et al. 2012).

5.3.2 Study Area

The study area spanned the deciduous forests of the Eastern Avifaunal Biome, and the woodlands of the Prairie Avifaunal Biome (Rich et al. 2004). From north to south this includes southern Ontario, Manitoba, and regions of New England, and from Texas to Florida. Historically, this area was covered with deciduous forests to the east, southeastern longleaf pine (*Pinus palustris*) forests, and expansive grasslands and prairie-oak savannahs in the Midwest (Rich et al. 2004). Habitat loss and degradation due to extensive conversions from native habitats for agriculture, forestry, and urbanization are the basis for most conservation issues in this region (Rich et al. 2004).

5.3.3 Statistical and Geospatial Analysis

We ran a non-spatial, global model using an Ordinary Least Square (OLS) regression to compare abundances between Red-headed Woodpeckers vs. starlings, and Red-headed vs. Red-bellied Woodpeckers from 1966-2011. In a global model a single parameter is calculated from the regression, and assumed to apply universally across the study region (Foody 2004). A global regression model is described as:

$$(1) \qquad y_i = \beta_0 + \sum_{j=1}^{p} \beta_j x_{ij} + \varepsilon_i$$

where y_i is the value of the response variable y at the location i, β_0 is the intercept, β_j is the slope coefficient for the predictor variable j, x_{ij} is the value of predictor variable j at location i, and ε_I is the random error term (Kupfer and Farris 2006). Global model statistics include tests that assess model significance (Joint-F and Joint Wald statistics), stationarity (Koenker (BP)), and bias (Jarque-Bera).

Next we employed geographically weighted regression (GWR) to explore and document the spatial variation in the data. GWR allows regression parameter values to vary spatially, wherein local regressions and associated parameters are calculated by assigning greater weight to geographically neighboring points of influence than data points that are further away, via a distance decay function (Fortheringham et al. 2002). Thus a simple GWR is similar to a global regression:

(2) $$y_i = \beta_0(u_i,v_i) + \sum_{j=1}^{p} \beta_j(u_i,v_i)x_{ij} + \varepsilon_I$$

where (u_i, v_i) are coordinate locations for each location *i* and {β_0 (u_i, v_i), β_1 (u_i, v_i), …, β_p (u_i, v_i)} are p + 1 are continuous functions of the location (u_i, v_i) (Zhang et al. 2004).

The distance-decay function is regulated by spatial kernel (or bandwidth), which can either be fixed (measured as distance) or adaptive (measured as the number of samples). This results in a moving window of regression for each data point across the study area (Fortheringham et al. 2002). Smaller bandwidths, which are influenced by localized variations, are more variable across the global scale. Larger bandwidths however stray towards global regression estimate errors (Fortheringham et al. 2002). As our goal was to determine local patterns and variations in species abundances using local models, we were cautious to avoid using a larger bandwidth than necessary, as this would lead to a near replication of the results of the global model.

To assess model performance, we compared the corrected Akaike's Information Criterion for small sample sizes (AICc; Hurvich and Tsai 1989) and goodness-of-fit R^2 between the global and local models. A model with a lower AICc value suggested a better fit of the observed data and better model performance. The R^2 values are another goodness-of-fit measure between 0 (no fit) and 1 (perfect fit), where the numerator and denominator are normalized on the basis of the degrees of freedom. We determined the kernel bandwidth by minimizing the AICc for each of the fitted regression models. For each of the GWR models we mapped the slope or species coefficient (either starling or Red-bellied Woodpecker as the predictive variable) to illustrate geographic-dependencies in species' relationship across the study area, and the spatial distribution of the local R^2.

Lastly, we used Moran's *I* analysis of autocorrelation to assess spatial fit across a range of bandwidths. Autocorrelation occurs when there is a lack of independence between a pair of observations a given distance apart in both time and space (Legendre 1993). To compare the ability of both the global OLS and local GWR model to deal with spatial autocorrelation in the data, we computed Moran indexes of the model residuals. Models with either highly similar (clumped) or dissimilar (dispersed) neighboring values (i.e., autocorrelation of residuals) were considered spatially non-stationary. All maps and analysis were generated using ArcGIS (ESRI, version 10.1) software.

5.4 Results

5.4.1 Global Model Fit for Species Relationships

There was little, or a very slightly positive, correlation between Red-headed Woodpecker and European Starling abundances as measured by the BBS in the global model (Table 5.1). As well, the global model fit to the observed data was very low, as shown by R^2 values < 0.001. The model failed the Jarque Bera test for model bias, indicating non-normal model residuals distribution, and the model explanatory variable was found to be effective by the Joint Wald test (Table 5.1). We found similar results for the correlation between Red-headed and Red-bellied Woodpecker abundance, such as little or slightly positive correlations, very low goodness-of-fit, and non-normal model distributions (Table 5.1). Unlike the starling global model, the global model between Red-headed and Red-bellied Woodpeckers abundances failed both tests for model significance, suggesting that Red-bellied Woodpecker abundance is not an effective predictor of Red-headed Woodpecker abundances, as measured by the BBS from 1966-2011.

5.4.2 Predicting Species Relationships: Effects of Global and Local Models

The GWR model greatly increased the fit of the Red-headed Woodpecker vs. European Starling abundance data to the regression model, as compared to the non-spatially explicit global model. This is demonstrated by higher adjusted R^2 and lower AICc values (Table 5.1). To illustrate local variations in the species' abundance interactions, we mapped the starling coefficients resulting from the GWR model (Fig. 5.1). The resulting map illustrates areas where the starling abundance is negatively correlated with Red-headed Woodpecker abundance (blue areas), where it is positively correlated (yellow/red areas), and where the correlation values were close to zero the points were left blank (Fig. 5.1). The two species abundances appear negatively correlated in the southern part of the study area from Texas to South Carolina, as well as eastern part of the Midwestern United States (Fig. 5.1). These would be areas where starling abundance negatively predicts Red-headed Woodpecker abundances. The western part of the Midwest including Nebraska and the Dakotas the species are positively correlated, i.e., starling abundance negatively predicts Red-headed Woodpecker abundance. We also mapped the local R^2, ranging from 0 to 1, which indicates how well the local regression models fits the data, where local models with low values performing poorly and those with high values fitting the data well (Fig. 5.2). Spatial mapping of local R^2 values suggested that the GWR model for Red-headed Woodpecker vs.

European Starlings had greater explanatory power in certain parts of the study area, such as the western and northern edge (Fig. 5.2).

The local GWR model for Red-headed vs. Red-bellied Woodpecker had higher R^2 and lower AICc scores than the global model, indicating better model fit (Table 5.1). Similar to the previous model, we mapped the Red-bellied Woodpecker coefficients resulting from the GWR model (Fig. 5.3), as well as the local R^2 (Fig. 5.4). Across the range, Red-bellied Woodpecker abundances both positively and negatively predicted the abundance of its near congener, the Red-headed Woodpecker (Fig. 5.3).

Moran's I analysis of model residuals across a large range of bandwidths (500-1,400 km) confirmed improved performance of the GWR over the global methods. Strong spatial autocorrelation, namely significant clustering of residuals was found across the entire range of bandwidths for both species comparison global models (Moran's $I = 0.086 - 0.403$; $p < 0.001$). Comparatively, the GWR model residuals for both species comparisons had a random spatial pattern (Moran's $I = -0.0001 - -0.0035$; $p > 0.05$).

To visualize the pattern of Red-headed Woodpecker abundance, the dependent variable in both the global and GWR models, we mapped species abundance as measured by the BBS from 1966-2011 across the study area (Figure 5.5). Lastly, the graphing of the annual indices of the three focal species over the 45-year study period shows declines for Red-headed Woodpecker and European Starling, and increases for Red-bellied Woodpecker (Fig. 5.6).

5.5 Discussion

We found the correlation between Red-headed Woodpecker abundances and that of its two possible competitors to be highly spatially variable across the 45 years of BBS survey data. Regressions using GWR produced models between Red-headed Woodpeckers and both European Starlings and Red-bellied Woodpeckers, separately, produced far better goodness-of-fit compared to global OLS models, as indicated by R^2 and AICc statistics (Table 1). Therefore, although it is possible to analyze community data over large spatial scales, often interactions between species and their community and/or environment occur at smaller spatial scales. The result of conflicts between findings on local scales is a cloudy overall global image, whose findings are thus inaccurate. Although GWR lacks the predictive qualities of the global model, its 'moving window' of local regressions allowed us to identify several regions where the European Starlings and Red-bellied Woodpecker abundances positively or negatively predicated Red-headed Woodpecker abundances (Figs. 1,3). It was also apparent that the explanatory power of the models varied spatially, with local estimates of R^2 differing across the study area for both the starling predictive model (Fig. 2), and the Red-bellied Woodpecker predictive model (Fig. 4).

The global model statistics showed starling abundance to be an effective predictor of Red-headed Woodpecker abundance, as measured over a 45-year period by the BBS. Our GWR mapping revealed both positive and negative correlations in abundance between the species, with the positive correlations occurring in the western part of the species core, and the negative correlations spread across the eastern core and southern part of the range (Fig. 1). Positive correlations between the species abundance occurs when, within the local regression, higher abundances of starlings are associated with higher abundances of Red-headed Woodpecker, and vice versa for low abundances. The parallel flux of the species' abundances may thus be driven by an external variable, such as habitat or availability of dead wood and cavities for nesting that affects starlings and Red-headed Woodpeckers in tandem. Negative correlations between the species occurs when within local regressions higher abundances of starlings is associated with low Red-headed Woodpecker numbers, and vice versa. This pattern could also be driven by an external factor that affects the two species differently, or competition between the two species. This can occur in one of two ways: (1) starlings increasing in abundance as they outcompete Red-headed Woodpeckers, thus driving the latter to decline, or (2) starlings decreasing in abundance, 'releasing' Red-headed Woodpeckers from competition, leading to their increase.

Areas that showed negative starling coefficient trends included (1) the south (portions of Texas, Oklahoma, and Louisiana), the Midwest south of the Great Lakes (portions of Wisconsin, Illinois, and Indiana), and the East Coast (portions of Virginia, North and South Carolina; Fig. 1). In the south and Midwest, all states show significant Red-headed Woodpecker declines ranging from -5.2 for Wisconsin to -1.3 for Texas. In comparison, the East Coast states had non-significant, positive (Virginia; 1.1) or slightly negative (South Carolina, -0.1) Red-headed Woodpecker trends with correspondingly significant negative starling (-1.5, Virginia; -2.9, South Carolina) trends (Fig. 1.; Sauer et al. 2012).

According to our competition hypothesis, these findings suggest that European Starlings may be outcompeting Red-headed Woodpecker in the south and Midwest while starling declines in the east are releasing Red-headed Woodpecker from competition, resulting in the latter's slight increase or stabilization in these areas. In contrast, areas with consistently positive correlations such as Kansas, Nebraska, Colorado, and New Mexico, are typified by either slightly negative significant declines by one or the other species (e.g., -1.0 for RHWO in Kansas and -1.5 for EUST in Colorado; Sauer et al. 2012), or in most cases non-significant trends for both species. According to interspecific competition and the competitive exclusion theory, this suggests that in these areas there are either enough resources (e.g., dead wood and naturally occurring or excavated cavities) for both species to co-exist, or there are small-scale differences in habitat use that create therefore specific habitat niches for each species (Wiens 1993). Lastly, areas little to no correlation between the two species (i.e., slope near zero), are those where within the local regression, Red-headed Woodpecker abundances remained unchanging. A majority of these areas, such as Ontario, western New England, and the northern Midwest, are areas at the periphery of the species core range (Fig.1, 5). Therefore these areas have baseline low numbers of Red-headed Woodpeckers and thus population fluctuations are minimal. The constancy of the lower Red-headed Woodpecker abundances also explains the high model fit in parts of the range periphery (Fig. 2). As the only variables used in these models were species abundances, we do not suggest that these species relationship patterns are especially robust support for interspecific competition between Red-headed Woodpeckers and starlings in these geographic areas, but instead suggest that mapping local regressions and local model fit using GWR is a useful tool for research and conservation planning.

The GWR model between the Red-headed and Red-bellied Woodpecker abundances increased model fit (Table 1) and reduced effects of autocorrelation, when compared to the global OLS model. But, global model statistics suggests that Red-bellied Woodpecker abundance is not an effective predictor of Red-headed Woodpecker abundance, as measured over a 45-year period by the BBS. We speculate this may, in part, be due to the demographic changes that have occurred for both species. In the 45-year study period, the Red-headed Woodpecker population diminished by as much as 80% in some areas, while Red-bellied Woodpecker increased by nearly 50% (Fig. 6). In fact, the increase in Red-bellied Woodpeckers, especially at the northern edge the species' range, mirrors the decrease in the Red-headed Woodpeckers population in these areas (Sauer et al. 2012). Whether the demographic changes are due to land use changes that favor Red-bellied Woodpecker at the cost of Red-headed Woodpecker, or to the filling of the habitat niche by the Red-bellied Woodpecker due to Red-headed Woodpecker disappearances, is unknown. Given these population fluxes, we may have expected to see a strong negative correlation between the species at the northern edge of the range, a pattern not supported by the mapping of Red-bellied Woodpecker coefficients in GWR (Fig. 4). The lack of this pattern could be explained by the failure of Red-bellied Woodpeckers to be a strong predictor variable in the model, or that the pattern is not evident at the scale of the sample point of a 39.5 km BBS route. Future research between the species can still benefit from the findings of this study, where hypotheses of external drivers can be derived from the patterns of abundance patterns (Fig. 4), and research comparing habitat use or other ecology between the species can be targeted in areas where local model fit between the two species abundance was the highest (Fig. 5).

Our research demonstrates the risk of using non-spatial global models, and the usefulness of local modelling techniques such as GWR for ecological data at a large scales. Despite significant correlation and model prediction for the starling model, both global model fits were very low, suggesting the absence of one or more critical variables or the inability of the model to represent the spatial structure in the data (ESRI 2013). The use of GWR greatly increased model fit, and removed the effects of spatial autocorrelation, as demonstrated by Moran's *I* test for autocorrelation across a range of bandwidths. Understanding the drivers of the Red-headed Woodpecker population trends and interspecies patterns with the possible interference competitor, European Starlings, are key to Red-headed Woodpecker conservation efforts across its range. This study illustrates how GWR can be used to further our understanding of community dynamics and how it may be applied to conservation planning. We suggest additional research to further examine the species abundance patterns and underlying ties to competition exclusion theory and interspecific competition. For example, areas where starlings are negative correlated with Red-headed Woodpeckers, and the Red-headed Woodpecker populations are decreasing, would be expected to have high rates of interspecific competition for nest cavities between the two species. Other areas with were the two species abundances are negatively correlated and Red-headed Woodpecker populations are increasing and starling populations are decreasing, Red-headed Woodpeckers would be expected to show niche expansion as part of the 'ecological release' from starlings (Bolnick et al. 2010). Our attempts to model Red-headed Woodpecker abundances as predicted by the abundance of its near congener, the Red-bellied Woodpecker was less successful, with little support for Red-bellied Woodpecker abundance as an explanatory variable, and difficult to interpret patterns of species abundance relationships mapped from the GWR model. This may suggest that the mirrored decline of Red-headed Woodpeckers and increases of Red-bellied Woodpeckers in the northern part of the study area is the result of an external, unmeasured driver, and not competition between the species.

As technology continues to advance creating powerful statistical and geospatial techniques, care must be taken to ensure that the right variety of tools is utilized to obtain comprehensive results. Incorporating spatial and temporal variability in ecological data is key to ensuring the highest quality of results using modelling techniques. Both global and local models have strengths and weaknesses that must be evaluated in the context of the project goals and desired outcome. As shown in this study, local modelling techniques are both an integral and useful tool for understanding spatially variable ecological data.

5.6 Acknowledgments

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5.7 Literature Cited

Bolnick, D.I., Ingram, T., Stutz, W.E., Snowberg, L.K., Lau, O.L. and Paull, J.S. 2010. Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. — Proceedings of the Royal Society B 277: 1789-1797.

Byers, J. 2002. Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. — Oikos 97: 449–458.

Cabe, P.R. 1993. European Starling (*Sturnus vulgaris*). In: Poole A (ed) The Birds of North America. — Cornell Lab of Ornithology, Retrieved from the Birds of North America Online, Ithaca. doi:10.2173/bna.518

COSEWIC. 2007. COSEWIC assessment and update status report on the Red-headed Woodpecker *Melanerpes erythrocephalus* in Canada. — Committee on the Status of Endangered Wildlife in Canada, Ottawa.

ESRI 2013. ArcGIS Desktop Help 10.1 – Interpreting OLS results. — Available online:http://resources.arcgis.com/en/help/main/10.1/index.html#/Interpreting_OLS_results/005p00000030000000

Feare 1984. The Starling. — Oxford Press, Oxford, U.K.

Foody, G.M. 2004. Spatial nonstationarity and scale-dependency in the relationship between species richness and environmental determinants for the sub-Saharan endemic avifauna. — Global Ecology and Biogeography 13: 315–320.

Fotheringham, A.S., Brundson, C. and Charlton, M.E. 2002. Geographically Weighted Regression: the Analysis of Spatially Varying Relationships. — Wiley, Chichester, UK. 269 pp.

Fortin, M.-J. and Melles, S.J. 2009. Avian spatial responses to forest spatial heterogeneity at the landscape level: conceptual and statistical challenges, in: Miao, S., Carstenn, S., Nungesser, M. (Eds.), Real World Ecology: Large-Scale and Long-Term Case Studies and Methods. — Springer New York, New York, NY, pp. 137–160.

Frei, B., Fyles, J.W. and Nocera, J.J. 2013. Maladaptive Habitat Use of a North American Woodpecker in Population Decline. — Ethology 119: 377–388.

Frei, B., Nocera, J.J. and Fyles, J.W. Invasive Species Interference Competition as an Evolutionary Trap for a Threatened North American Woodpecker. — In prep.

Hortal, J., Diniz-Filho, J.A.F., Bini, L.M., Rodríguez, M.Á., Baselga, A., Nogués-Bravo, D., Rangel, T.F., Hawkins, B.A. and Lobo, J.M. 2011. Ice age climate, evolutionary constraints and diversity patterns of European dung beetles. — Ecology Letters 14: 741–8.

Hurvich, C. and Tsai, C.-L. 1989. Regression and time series model selection in small samples. — Biometrika 76: 297.

Ingold, D.J. 1994a. Influence of nest-site competition between European Starlings and woodpeckers. — Wilson's Bulletin 106: 227–241.

Ingold, D.J. 1994b. Nest-site characteristics of Red-bellied and Red-headed Woodpeckers and Northern Flickers in east-central Ohio. — Ohio Journal of Science 94: 2–7.

Ingold, D.J. 1989. Nesting phenology and competition for nest sites among Red-headed and Red-bellied Woodpeckesr and European Starlings. — Auk 106: 209–217.

Jackson, J.A. 1976. A comparison of some aspects of the breeding ecology of Red-headed and Red-bellied Woodpeckers in Kansas. — Condor 78: 67–76.

Jetz, W., Rahbek, C. and Lichstein, J. 2005. Local and global approaches to spatial data analysis in ecology. — Global Ecology and Biogeography 14: 97–98.

Kerpez, T.A and Smith, N.S. 1990. Competition between European Starlings and Native Woodpeckers for Nest Cavities in Saguaros. Auk 107, 367–375.

Koch, A., Martin, K. and Aitken, K. 2012. The relationship between introduced European Starlings and the reproductive activities of Mountain Bluebirds and Tree Swallows in British Columbia, Canada. — Ibis 154, 590–600.

Koenig, W.D. 2003. European starlings and their effect on native cavity-nesting birds. — Conservation Biology 17: 1134–1140.

Kupfer, J.A and Farris, C.A. 2006. Incorporating spatial non-stationarity of regression coefficients into predictive vegetation models. — Landscape Ecology 22: 837–852.

Legendre, P. 1993. Spatial Autocorrelation : Trouble or New Paradigm. — Ecology 74: 1659–1673.

Lieske, D.J. and Bender, D.J. 2009. Accounting for the Influence of Geographic Location and Spatial Autocorrelation in Environmental Models: A Comparative Analysis Using North American Songbirds. — Journal of Environmental Informatics 13: 12–32.

Mazgajski, T. 2000. Competition for nest sites between Starling Sturnus vulgaris and other cavity nesters - study in a forest park. — Acta Ornithologica 35: 103 35, 103–107.

Osborne, P.E., Foody, G.M. and Suárez-Seoane, S. 2007. Non-stationarity and local approaches to modelling the distributions of wildlife. — Diversity and Distributions 13: 313–323.

Rich, T.D., Beardmore, C.J., Berlanga, H., Blancher, P.J., Bradstreet, M.S.W., Butcher, G.S., Demarest, D.W., Dunn, E.H., Hunter, W.C., Iñigo-Elias, E.E., Kennedy, J.A., Martell, A.M., Panjabi, A., Pashley, D.N., Rosenberg, K.V., Rustay, C.M., Wendt, J.S. and Will, T.C. 2004. Partners in Flight North American Landbird Conservation Plan, Partners in Flight, Ithaca, NY. — Partners in Flight website. http://www.partnersinflight.org/cont_plan/ (VERSION: March 2005).

Robbins, C.S., Bystrak, D., Geissler and P.H. 1986. The Breeding Bird Survey: Its First Fifteen Years, 1965-1979. —USGS Patuxent Wildlife Research Center, Laurel, MD, U.S.A.

Smith, K.G., Withgott, J.H. and Rodewald, P.G. 2000. Red-headed Woodpecker (*Melanerpes erythrocephalus*). In: (Poole A, Ed) The Birds of North America. — Cornell Lab of Ornithology, Retrieved from the Birds of North America Online, Ithaca.

Stauffer, D. and Best, L. 1982. Nest-site selection by cavity-nesting birds of riparian habitats in Iowa. —Wilson's Bulletin 94: 329–337.

Sauer, J. R., Hines, J.E., Fallon, J.E., Pardieck, K.L., Ziolkowski, D.J. Jr. and Link, W.A. 2012. The North American Breeding Bird Survey, Results and Analysis 1966 - 2011. Version 12.13.2011 — USGS Patuxent Wildlife Research Center, Laurel, MD, U.S.A.

Tu, J., Xia and Z.-G. 2008. Examining spatially varying relationships between land use and water quality using geographically weighted regression I: model design and evaluation. — The Science of the Total Environment 407: 358–78.

Wiens, J. 1993. Fat times, lean times and competition among predators. — Trends in Ecology & Evolution 8: 348-349.

Windle, M.J.S., Rose, G. a., Devillers, R. and Fortin, M.-J. 2009. Exploring spatial non-stationarity of fisheries survey data using geographically weighted regression (GWR): an example from the Northwest Atlantic. — ICES Journal of Marine Science 67: 145–154.

Zhang, L., Bi, H., Cheng, P. and Davis, C.J. 2004. Modeling spatial variation in tree diameter–height relationships. — Forest Ecology and Management 189: 317–329.

5.8 Tables and Figures

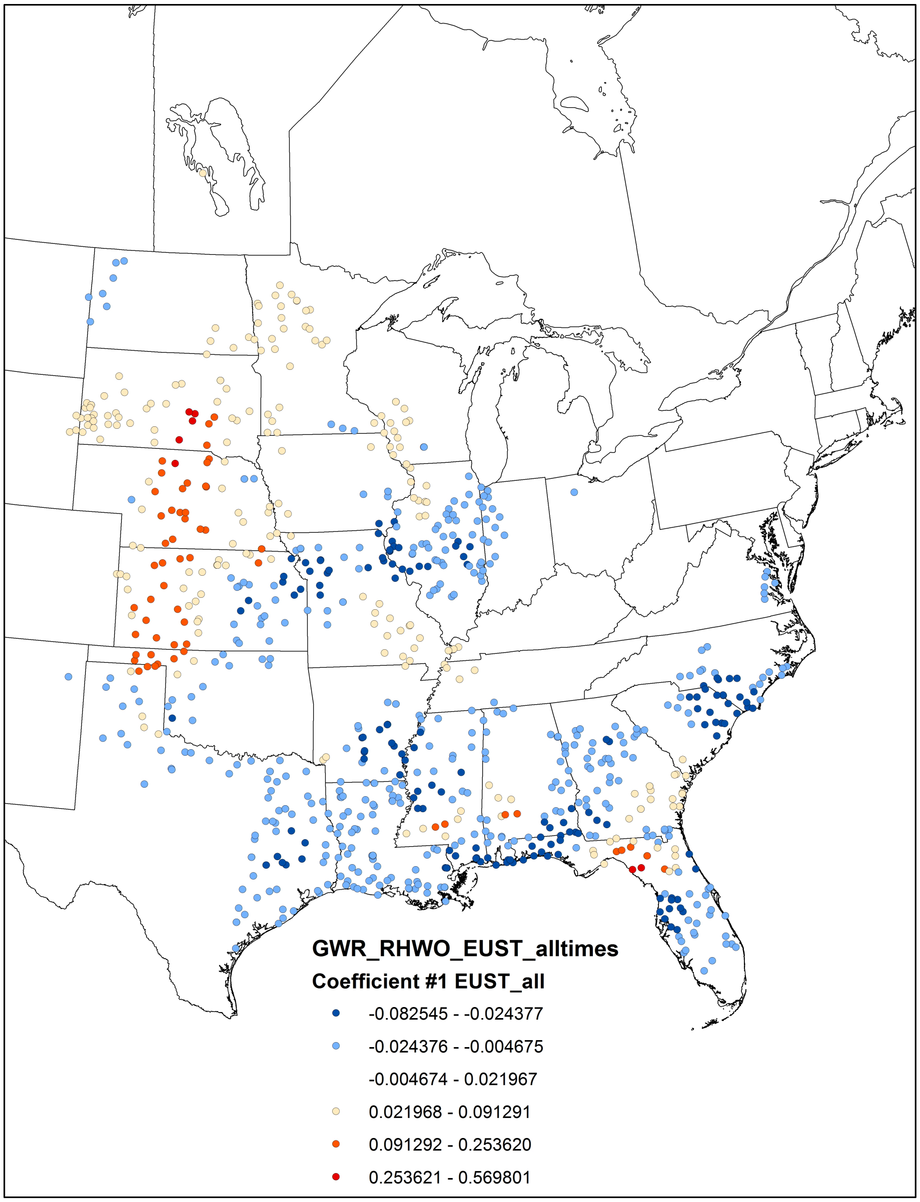

Figure 5.1 GWR-derived local coefficient estimates for European Starling abundance as a predictor for Red-headed Woodpecker abundance from the Breeding Bird Survey from 1966-2011 mapped in ArcGIS 10.1.

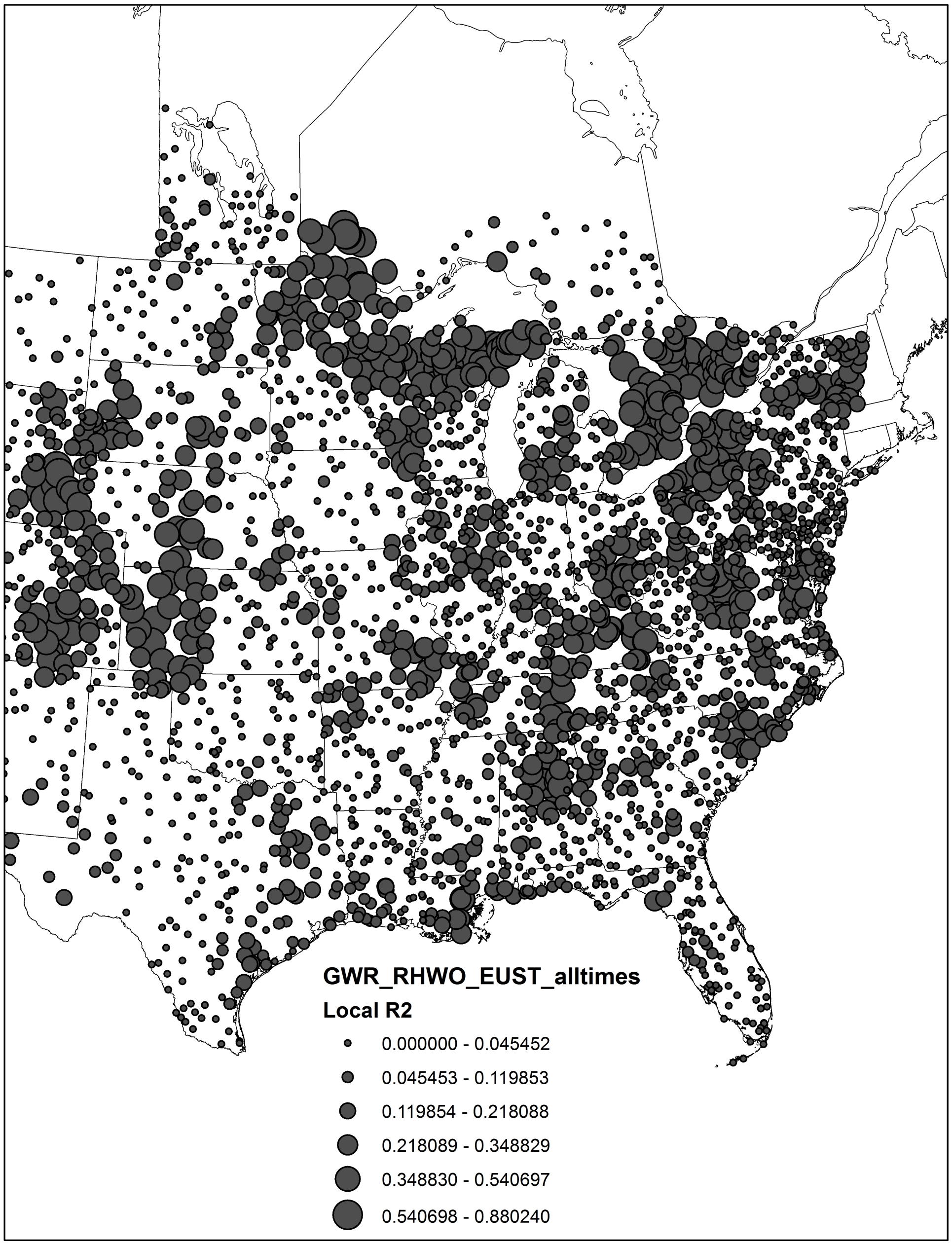

Figure 5.2 Mapped local R^2 values from the GWR model of Red-headed Woodpecker vs. European Starling abundances from the Breeding Bird Survey from 1966-2011 mapped in ArcGIS 10.1.

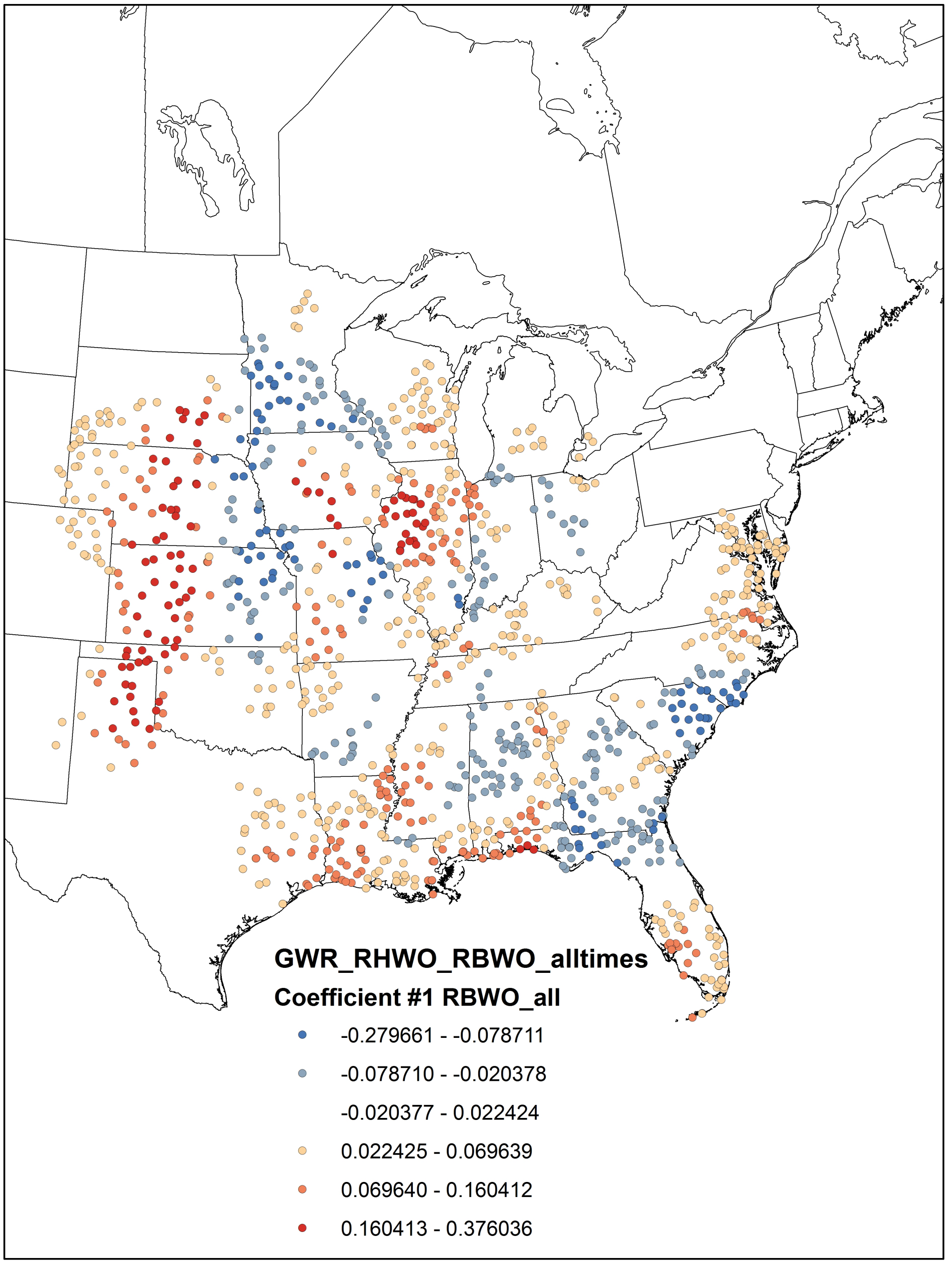

Figure 5.3 GWR-derived local coefficient estimates for Red-bellied Woodpecker abundance as a predictor for Red-headed Woodpecker abundance from the Breeding Bird Survey from 1966-2011 mapped in ArcGIS 10.1.

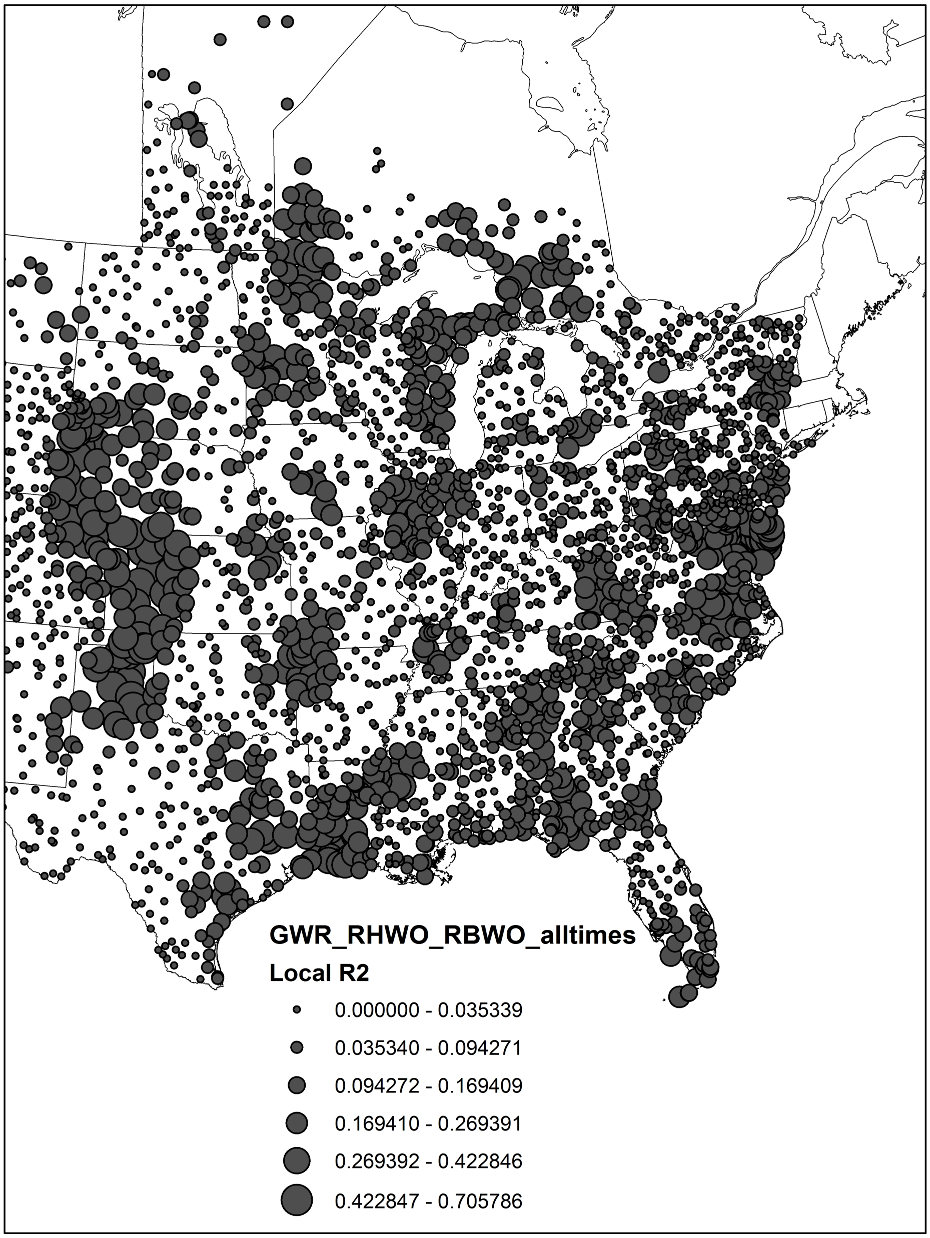

Figure 5.4. Mapped local R^2 values from the GWR model of Red-headed vs. Red-bellied Woodpecker abundances from the Breeding Bird Survey from 1966-2011 mapped in ArcGIS 10.1.

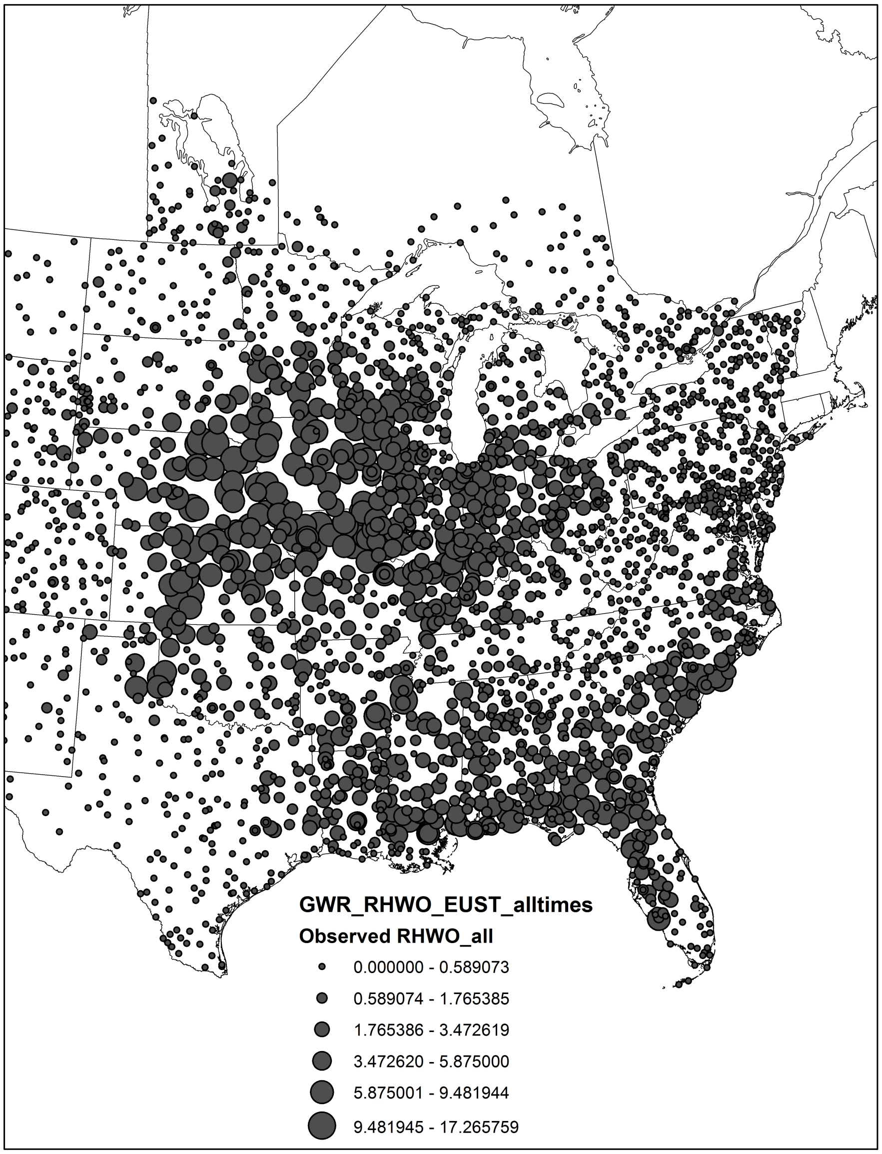

Figure 5.5. Mapped Red-headed Woodpecker average abundance per route from 1966-2011 using data from the Breeding Bird Survey mapped in ArcGIS 10.1.

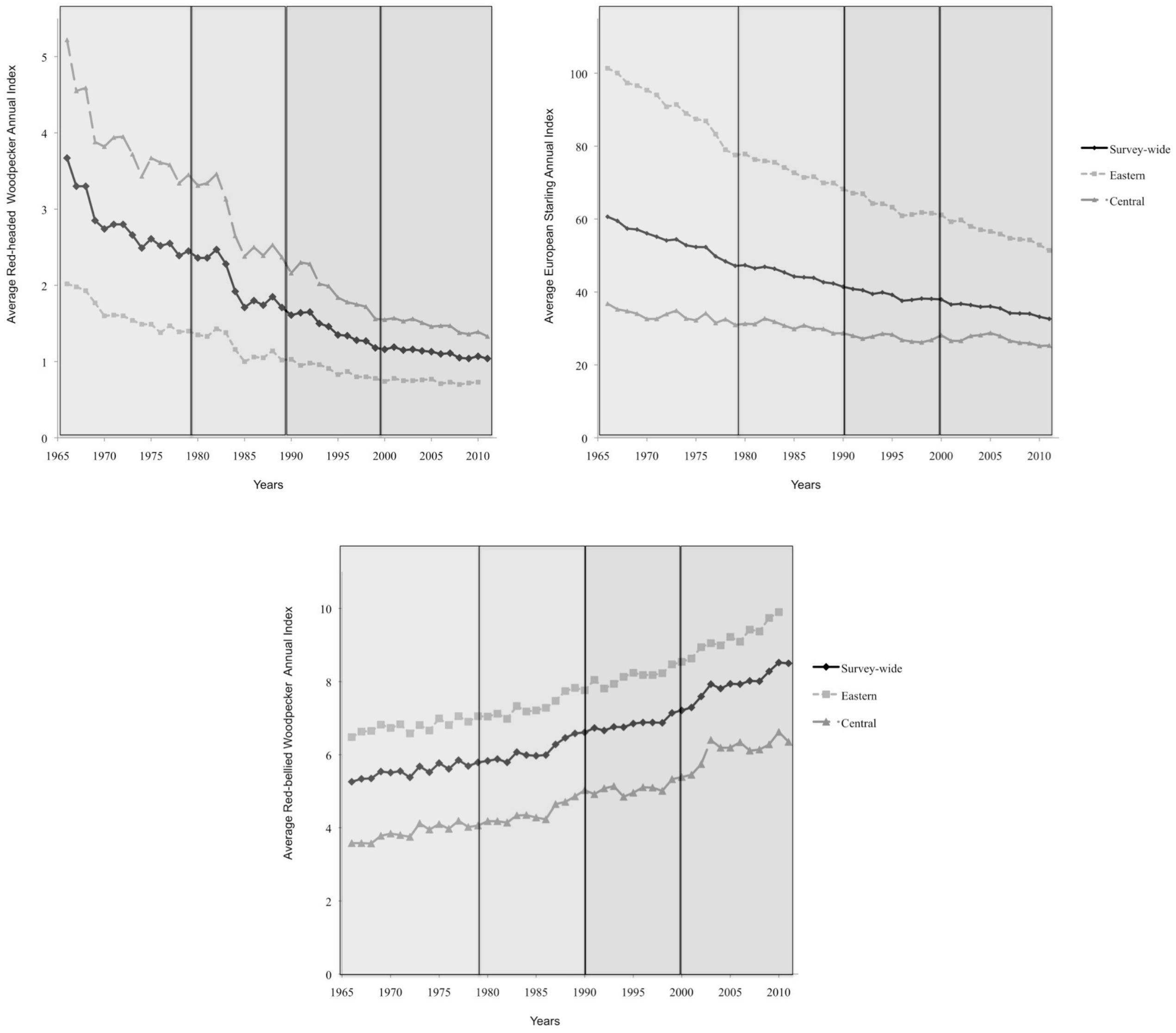

Figure 5.6 Red-headed Woodpecker, European Starling, and Red-bellied Woodpecker annual indices from the Breeding Bird Survey from 1966 – 2011 for survey-wide, eastern, and central areas.

Table 5.1 Global and local GWR model statistics related to Red-headed Woodpecker vs. European Starling, and Red-headed vs. Red-bellied Woodpecker abundances for 1966 – 2011 from the North American Breeding Bird Survey. Asterisks denote statistics significant at $p < 0.05$.

Model statistics	Red-headed Woodpecker vs. European Starling	Red-headed vs. Red-bellied Woodpecker
Observations (*N*)	3016	3213
Global model		
Joint F-statistic	2.76	1.97
Joint Wald	4.32*	2.89
Koenker (BP)	0.0085	0.9260
Jarque-Bera	22700.8*	27525.8*
Coefficient / slope	0.001*	0.004
R^2	0.0009	0.0006
AICc	13003.42	13705.06
Local model		
R^2	0.70	0.69
AICc		

Preface to Chapters 6 and 7

In the previous chapters I reviewed the literature on the focal species, the Red-headed Woodpecker, described the theories of animal-habitat associations and possible disjoints between habitat use and fitness benefits due to ecological novelties, and the mechanisms of evolutionary traps. This was followed by chapters presenting the rationale of the study, along with the research questions and overall hypothesis, and chapters now being prepped, revised, or published in peer-reviewed scientific literature and therefore disseminating the results of my efforts to address existing knowledge gaps (Chapter 3-5). In Chapter 6 I revisit the rationale for the study by describing key findings and other elements that highlight the interest and novelty of the research. I summarize key findings and synthesize information across the three data chapters, present final conclusions and challenges, and identify priorities for future research. In the final Chapter 7 I describe the contributions of knowledge of my work.

Chapter 6

6. Summary, Conclusions and Challenges, and Future Research

Despite their threatened status and ongoing declines, Red-headed Woodpeckers have been the focus of few studies and little to no conservation action in Canada and in the United States. As a species occupying a predominantly human-modified, novel landscape Red-headed Woodpeckers recovery and conservation is unlikely without a clear understanding of the species' threats and their mitigation. This doctoral thesis evolved as a response to the immediate and critical need for further understanding of the drivers of Red-headed Woodpecker population declines, as well as to contribute to the increasing evidence of the new field of behavioural conservation within an ecological novel world.

As a once widespread, and apparently flexible generalist species, Red-headed Woodpecker population declines are both unexpected and poorly understood. Within a theoretical ecology framework, I hypothesized that population declines are driven by maladaptive behaviour, where an animal's choices result in lower fitness. Maladaptive behaviour is often a consequence of an evolutionary trap driven by human-induced rapid environmental changes (HIREC) including habitat loss/degradation and the introduction of non-native species (Palumbi 2001, Sih et al. 2011).

To explore this hypothesis, four underlying questions were considered:

1. Is Red-headed Woodpecker habitat use adaptive (habitat occupancy = increased fitness) or non-adaptive (habitat occupancy ≠ increased fitness)?
2. Are European Starlings a potential evolutionary trap for Red-headed Woodpeckers and influencing their fitness in ecologically novel landscapes?
3. As previous research using large-scale population demographics suggests that European Starling abundances do not have adverse effects on Red-headed Woodpeckers, is a global model analysis effective, or do local variations in the interspecies relationships exist over space and time?
4. Can Red-headed Woodpeckers persist despite the challenges of rapid anthropogenic changes and ecological novelties?

6.1 Summary of Results

In Chapter 3 (Maladaptive Habitat Use of a North American Woodpecker in Population Decline), we investigated multi-scale habitat use and nesting success of Red-headed Woodpeckers in southern Ontario to assess their vulnerability to mismatches between use and fitness as a result of non-ideal habitat use across multiple scales. Over two summers (2010-2011) we located and monitored 60 Red-headed Woodpecker nests, 42 of which were in woodlots. We undertook habitat sampling following nest completion (either successful with ≥ 1 young fledged, or failed), including cavity scale for all 60 nests and addition tree, patch, woodlot, and landscape scale measurements for the woodlot nests as well as random comparison random sites. By comparing habitat use/occupancy (occupied vs. unoccupied) and breeding success (successful vs. unsuccessful) within each scale, we found Red-headed Woodpecker to exhibit maladaptive habitat use (use = lower success) across tree, patch, and woodlot scales. As several of the habitat characteristics we found to be maladaptive were those associated with promoting feeding potential (i.e., greater canopy openness and dead limb length), we speculated that food might be a limiting resources for the species. Due to logistic constraints, we were unable to determine the causes of nest failures and thus could not differentiate if failed nests were predated, usurped, or abandoned. We suggested two possible causes of nest failure associated with the maladaptive habitat traits: (1) increased predation of adult woodpeckers, (2) increased aggressive interactions with, and/or nest cavity usurpation by, interspecific competitors including European Starlings. These findings illustrated the variability of habitat associations between animals and their environment at different scales, and increased our interested in further understanding drivers of Red-headed Woodpecker nest survival.

In Chapter 4 (Invasive Species Interference Competition as an Evolutionary Trap for a Threatened North American Woodpecker), we explored the relative importance of abiotic, temporal, biotic, and habitat variables as drivers of Red-headed Woodpecker nest survival in southern Ontario. Given our findings from Chapter 3, of particular interest was the role of the non-native European Starlings, whose known interference competition for nest cavities may act as an evolutionary trap for Red-headed Woodpeckers. We monitored all 60 woodpecker nest every 3-5 days during the breeding season collecting data on woodpecker feeding rates (as a proxy for food availability), presence and abundance of starlings at active woodpecker nests, temperature, precipitation, nest initiation timing, cavity height, and habitat structure. The results presented in this chapter show overwhelming evidence that the abundance of European Starlings are the strongest predictor by far of Red-headed Woodpecker nest survival in a variety of habitats in southern Ontario. Starling abundance, used as a proxy measurement of interference competition pressure for nest cavities, drastically lowered estimates of nest success from 68% (assuming constant survival) to a mere 13%. Additional findings included earlier initiated woodpecker nests being less successful than those initiated later on, and the number of snags in a nest patch and total dead limbs in the woodlot both being associated with higher daily nest success. Both these additional findings may be associated with starlings as well. A higher likelihood of nest failure earlier in the nesting season may be a result of increased nest usurpation and interference competition in this period, as starlings and Red-headed Woodpecker breeding period's overlap. In contrast, increased standing dead wood at or near the nest site may increase Red-headed foraging opportunities and parental attentiveness, decreasing the likelihood/success of usurpation attempts by starlings. We surmise that previous research on the impact of non-native starlings on Red-headed Woodpeckers may have failed to capture the dynamics of woodpecker and starling species interaction, and/or that competition pressure may vary from one geographic area to another. This study concludes that successful Red-headed Woodpecker management needs to focus on managing habitat to increase woodpecker fitness (i.e. increasing standing dead wood), in areas with lower starling abundance or those made less attractive to starlings.

In Chapter 5 (Geographic-Dependency and Temporal Fluctuations in the Relationship Between a Threatened Species and Two Possible Competitors), we explored the use of non-spatial global, and spatial local modelling techniques to elucidate the interspecies relationships between the Red-headed Woodpeckers and its two possible competitors, the European Starling and Red-bellied Woodpecker over space and time. Using 45 years of Breeding Bird Survey data for 38 states and provinces, we used global and local (geographically weighted regression; GWR) models to compare the abundances of Red-headed Woodpecker vs. European Starlings and Red-bellied Woodpeckers. The results presented in this chapter demonstrated the risk of using non-spatial global, and the usefulness of local modelling techniques for ecological data at a large scale. Global model had very low goodness-of-fit, suggesting the absence of one or more critical variables or the inability of the model to represent spatial structure in the data. The use of local modelling techniques, GWR enhance data exploration by allowing parameter values to vary continuously across geographic space, and as a result greatly increased model fit, and removed the effects of spatial autocorrelation. Based on data exploration via mapping of local species relationship trends with GWR we suggest that European Starling abundances are associated with driving Red-headed Woodpecker declines in certain areas of North America, while starling declines in other areas may be 'releasing' Red-headed Woodpeckers from competition, leading to population increases. Comparatively, the relationship between Red-headed Woodpecker abundances and that of its close congener Red-bellied Woodpeckers are less spatially variable, and we suspected this is due to habitat use associations and niche differentiation at various scales. The conclusions presented in this chapter illustrate the usefulness of GWR in understanding spatially variable ecological data, and in mapping spatial variations in interspecies relationships.

6.2 Conclusions and Challenges

The results of this thesis provide a deeper understanding of why Red-headed Woodpeckers are declining in southern Ontario and, potentially, across their range in North America. However, as some conclusions are reached, current and future challenges are also evident. A discussion of both the conclusions found and the challenges that remain are equally important for future researchers and the evolution of the theoretical ecology in which this thesis is framed. Specifically outlined are the conclusions and challenges found for multi-scale research, animal-habitat associations, and evolutionary traps and maladaptive behaviour.

6.2.1 Multi-scale Research: Conclusions and Challenges

It is increasingly evident, both in the scientific literature and the findings of this thesis that including multiple scales in ecological research provides a more comprehensive understanding of the questions asked and the answers found. Our finding that Red-headed Woodpecker exhibit maladaptive selection across multiple scales strengthens our conclusions that the species may be 'caught' in an ecological trap. Single scale studies risk missing the fitness trade-offs that may be occurring between scales, thus leading to false assumption of animal's behaviour. Likewise, despite the overall positive correlation between Red-headed Woodpeckers and European Starlings abundances in southern Canada and east-central United States derived from global models, local regression techniques show distinct areas where species' abundances are negatively correlated as well as areas with positive correlations. Without examining the interspecies relationship at multiple scales, very different conclusion can be reached on the relationships between the threatened woodpecker and its non-native competitor.

Planning research, collecting data, and interpretation of results for studies done on multiple scales is an additional challenge for researchers. The most prominent challenge is the delineation of pertinent scales for the study, which are often partially dictated by logistical constraints. Knowledge of the ecosystem studied or species' natural history is key in choosing biologically relevant scales. Field observations, such as Red-headed Woodpecker's tendencies to cache food in or near the nest tree (i.e., importance of the nest tree and nest patch), and watching an individual consistently travel a 1-km distance for feeding (i.e., importance of landscape-level) are invaluable. Lastly, the scale at which management is likely to occur is an important consideration for information dissemination beyond academia. Our research on Red-headed Woodpeckers, a species-at-risk found predominately on private land, made it imperative to include scales pertinent to landowners and land managers, such as a the nest tree or woodlot scales.

6.2.2 Animal-Habitat Associations: Conclusions and Challenges

Understanding how a species uses or occupies its habitat is a central focus of ecology overall and especially recovery and management of threatened species. The findings of our research on Red-headed Woodpeckers demonstrates the species' ability to breed in a variety of habitats, from woodlots, to urban parks, golf courses, and treed pastures. In Chapter 3, we demonstrate Red-headed Woodpecker's affinity for standing dead wood and canopy openness both at the nest cavity and at larger scales, despite these affinities appearing maladaptive. In Chapter 4, we found two measures of standing dead wood to be associated with higher nest success for the species, the number of snags directly surrounding the nest tree (nest patch), and the overall dead limb length in the 3-5 ha woodlot.

The main challenge in researching animal-habitat associations is that findings are correlations, which may not represent causation. Thus the underlying drivers of the associations may be related to the physical structure of the habitat, or more likely, a response to additional ecological drivers associated with habitat structure including resource availability, and predator/competitor community. Red-headed Woodpeckers preferentially nest in habitats that lower their fitness in southern Ontario. Yet, is this due to a fitness tradeoff that we have not measured, or due to higher affinities of starlings, thus increased competition pressure, in the same habitats? We cannot be certain. Thus we suggest managing habitat to increase Red-headed Woodpecker attraction and fitness (i.e., increasing standing dead wood and canopy openness) in areas with lower starling abundance or those made less attractive to starlings.

6.2.3 Evolutionary Traps and Maladaptive Behaviour: Conclusions and Challenges

Human-induced rapid environmental changes (HIREC) are challenges facing a majority of animals in today's changing world, for which the Red-headed Woodpecker may serve as a perfect example. We found that the species has a tendency to occupy habitats in which their nests are more likely to fail (Chapter 3), have far lower nest success when European Starlings are in the vicinity of the nest (Chapter 4), and appear to suffer population declines as a result of starlings abundance in different locations across their range (Chapter 5). Given these findings, we can conclude the species' is susceptible to maladaptive behaviour and is 'trapped' by its poor choices and/or inability to adapt to competition with a non-native species.

Behavioural ecology is a relatively new addition to conservation biology, and as such, most management and recovery plans for species-at-risk do not integrate species' behaviour into the planning processes. This omission may have unfortunate consequences, for example certain restoration projects have been demonstrated to serve as ecological traps, thus lowering species survival in these sites (Robertson et al. 2013). As demonstrated by our results in Chapter 3, correlation studies can pinpoint cases of maladaptive behaviour, in this case habitat use by Red-headed Woodpeckers in southern Ontario, exhibited by a species but understanding the causation of the behaviour is a far greater challenge. For example, whether its the interspecific competition pressure of European Starlings shown to decrease Red-headed Woodpecker nest success in Chapter 4 that is the ultimate driver of maladaptive habitat use of the species in southern Ontario, or any number of other possible factors, is difficult to state with certainty.

6.2.4 Red-headed Woodpecker Persistence

Red-headed Woodpeckers appear unable to deal with the ecological novelties of human-driven changes to the habitat and/or competition for nest sites with non-native European Starlings. Given that starling abundance is correlated with decreased Red-headed Woodpecker nest success on a small-scale, and with Red-headed Woodpecker population declines in specific areas on a large scale, we suggest managing nesting habitat to increase woodpecker fitness in areas with lower starling abundance or those made less attractive to starlings. Allowing for patches of standing dead wood (i.e., snags or trees with dead branches) to persist woodlots, urban parks, golf courses, and treed pastures where Red-headed Woodpeckers are present are shown to both be associated with habitat use on multiple scales, and increased nest success.

6.3 Recommendations for Future Research

The objective of this research was to determine possible drivers of Red-headed Woodpecker population declines. We found evidence the species' exhibiting maladaptive habitat use and depressed nest success correlated with abundance of European Starlings near its nest site. We also demonstrated large scale, spatially and temporally variable correlation between Red-headed Woodpeckers and European Starling. To strengthen these findings and improve the understanding of possible drivers of population declines for Red-headed Woodpecker as well as the species' behavioural ecology, our recommendations for future studies include:

1. Animal-habitat associations:
    - Determine if Red-headed Woodpecker habitat use in other geographical areas of the species' range is adaptive or maladaptive, to provide further understanding of the mechanisms driving maladaptive habitat use.
    - Investigate the habitat niche of Red-headed Woodpeckers in areas of population increase as delineated by local model maps in Chapter 5, and compare this to habitat niche in areas of population decline (e.g, southern Ontario) for evidence supporting the suggesting of ecological release from competitors in areas of Red-headed Woodpecker population increase.
    - Investigate habitat use for European Starlings and Red-bellied Woodpeckers in areas with and without Red-headed Woodpeckers for evidence supporting predictions of the competitive exclusion theory.

2. Interspecific competition

- Utilizing nest cameras, determine whether the competition pressure with European Starlings, as measured by number or length of aggressive interactions, is related to the abundance of starlings observed a the nest site and/or the abundance of starlings recorded on the nearest Breeding Bird Survey route.
- Investigate if the European Starling abundance near active Red-headed Woodpecker nest sites and/or the number or length of aggressive interspecies interactions is associated with other measures of fitness, including the number of fledglings, and fledgling weight.

3. Landscape-level research:

- Explore the relationship between Red-headed Woodpeckers, European Starlings, and Red-bellied Woodpecker at more regional scales (e.g. using survey results from Breeding Bird Atlas) including land use changes using both global and local models.

Chapter 7

7. Contributions to Knowledge

Despite consistent, long-term population declines and being listed as a threatened species both in Canada and the United States, there are remarkable few studies on Red-headed Woodpecker or potential drivers of the species' population decline. In addition, there are no multi-scale studies, research on Red-headed Woodpecker's at the northern edge of their range in Canada, or detailed nest survival models for the species. The few studies that have focused on Red-headed Woodpeckers detail habitat associations often at a single scale and/or habitat type, and accounts of aggressive interactions at nest cavities with other species. My research has bridged some of the existing knowledge gaps. It has identified several avenues for future research, and has generated knowledge that will inform future management and recovery of the species. Thus, the research and analyses conducted to answer the questions and objectives of this work provide the following contributions to knowledge.

This study was the first to:

1. Explore Red-headed Woodpecker habitat use and nest survival in at the northern edge of the species range in Canada, specifically southern Ontario, where the species' population declines are among the highest in its range.
2. Demonstrate that Red-headed Woodpecker habitat use/associations are maladaptive across multiple scales, suggesting an ecological trap. The results presented in Chapter 3 show maladaptive habitat use by the species across three scales, including habitat features

that have been reported as in other studies to be related to Red-headed Woodpecker occupancy, such as standing dead wood and canopy openness.

3. Examine abiotic, biotic, temporal, and habitat drivers of Red-headed Woodpecker nest survival using logistic-exposure models. In Chapter 4 we found European Starling abundance near active woodpecker nest sites was the strongest factor influencing Red-headed Woodpecker nest survival, suggesting the species may be acting as an evolutionary trap. The results of the chapter are the first to quantify the effects of starling abundance on nest survival of an North American cavity nesters, and the most comprehensive evidence on the detrimental impact of starlings on Red-headed Woodpecker fitness.
4. Compare the use of global and local techniques to model the interspecies relationships between Red-headed Woodpecker and its two possible competitors, European Starlings and Red-bellied Woodpeckers. In Chapter 5 we demonstrated the failure of global models to account for spatial variation, and introduced geographically weighted regression (GWR) as a novel tool for conservation biology.

Advancement in knowledge:

1. I have undertaken, as of today, the most comprehensive and statistically advanced study on Red-headed Woodpeckers and the possible drivers of the species' declines in their breeding grounds. I explored facets of the species' habitat associations, nest survival, and relationship with non-native starlings on multiple scales and over time.
2. I have contributed quantitative evidences of maladaptive behaviour, habitat-based ecological traps, and non-native species driven evolutionary traps to the scientific literature. These elements of theoretical ecology are still evolving and are critical

components to the future of the conservation and management of ecosystems and the species within them in changing world. Thus, my research allows for advancements in knowledge not only the focal species, but may also serve as an example for future studies with species susceptible to evolutionary traps and maladaptive behaviour in human-altered landscapes.

3. This study outlines the disadvantages of global modelling techniques on spatially variable ecological data, and showcases a geostatistical technique (GWR) currently underused by ecologists.