Species Declines:

Examining patterns of species distribution, abundance, variability and conservation status in relation to anthropogenic activities

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Abstract

Humans are modifying the global landscape at an unprecedented scale and pace. As a result, species are declining and going extinct at an alarming rate. Here, I investigate two main aspects of species' declines: what factors are contributing to their declines and how effective our conservation efforts have been. I assessed one of the main mechanisms for protecting species by looking at the Endangered Species Act (ESA) in the United States. I examined three separate indicators of species declines for different groups of species: range contractions in Canadian imperilled species, declines in abundance in global amphibian populations and increases in temporal variability in abundance in North American breeding birds.

I found that change in recovery status of ESA listed species was only very weakly related to the number of years listed, number of years with a recovery plan, and funding. These tools combined explained very little of the variation in recovery status among species. Either these tools are not very effective in promoting species' recovery, or species recovery data are so poor that it is impossible to tell whether the tools are effective or not.

I examined patterns of species' declines in three different groups in relation to a number of anthropogenic variables. I found high losses of Canadian imperiled bird, mammal, amphibian and reptile species in regions with high proportions of agricultural land cover. However, losses of imperiled species are significantly more strongly related to the proportion of the region treated with agricultural pesticides. This is consistent with the hypothesis that agricultural pesticide use, or something strongly collinear with it (perhaps intensive agriculture more generally), has contributed significantly to the decline of imperiled species in Canada. Global increases in UV radiation do not appear to be a major cause of amphibian population declines. At individual sites, temporal changes in amphibian abundance are not predictably related to changes in UV intensity. Variability in species' abundance of North American breeding birds, after accounting for mean abundance, is not systematically higher in areas of high human-dominated land cover or climate change. Rather, it appears that areas with a high proportion of human-dominated cover come to have a higher proportion of highly abundant, and thus more variable, species.

Résumé

L’être humain modifie le paysage à un rythme et une échelle sans précédent. Conséquemment, le déclin et l’extinction des espèces augmentent à un rythme alarmant. Ici, j’étudie deux aspects importants du déclin des espèces : les facteurs qui contribuent à leur déclin ainsi que l’efficacité de nos efforts de conservation. J’ai d’abord évalué l’un des principaux mécanismes de protection des espèces, soit la loi sur la protection des espèces des États-Unis ; le « Endangered Species Act (ESA) ». De plus, j’ai examiné trois indicateurs distincts du déclin des espèces pour différents groupes d’espèces: la contraction de l’aire de répartition des espèces canadiennes en péril, le déclin en abondance des populations globales d’amphibiens et la variabilité temporelle en abondance des oiseaux nicheurs d’Amérique du Nord.

J’ai mis en évidence que le changement dans le statut de rétablissement des espèces listées par la loi ESA est seulement très faiblement lié au nombre d’années depuis que l’espèce fut listée, au nombre d’années depuis l’instauration d’un plan de rétablissement pour l’espèce ainsi qu’au financement accordé. Ceci démontre que ces outils sont très peu efficaces ou encore que les données disponibles sont de si piètre qualité qu’il est impossible de déterminer si ces outils sont efficaces pour le rétablissement des espèces.

J’ai examiné les patrons de déclin pour trois groupes d’espèces en fonction de différentes variables anthropiques. J’ai observé un haut taux de disparition d’oiseaux, de mammifères, d’amphibiens et de reptiles canadiens en péril dans les régions ayant une forte proportion de terres agricoles. Par contre, la perte de ces espèces en péril est davantage reliée à la proportion de la région traitée avec des pesticides agricoles. Ceci est conséquent avec l’hypothèse que l’utilisation de pesticides agricoles, ou quelque autres facteurs qui lui est fortement colinéaire (peut-être, plus généralement, l’intensité d’agriculture), a contribué de manière importante au déclin des espèces en péril au Canada. Par ailleurs, j’ai observé que l’augmentation globale du rayonnement UV n’apparait pas comme une cause majeure du déclin des populations d’amphibiens. Aux sites étudiés, les changements temporels dans l’abondance des amphibiens ne sont pas liés aux changements d’intensité du rayonnement UV. Finalement, la variabilité en abondance des espèces d’oiseaux nicheurs en Amérique du Nord, après avoir pris en compte leur abondance moyenne, n’est pas systématiquement plus élevée dans les régions où la couverture terrestre est fortement dominées par les êtres humains ni avec de grands changements climatiques. Plutôt, les régions avec de fortes proportions de terres dominées par l’activité humain ont une plus grande proportion d’espèces très abondantes qui, par conséquent, démontre plus de variabilité temporelle.

Table of Contents

List of Tables

List of Figures

INTRODUCTION

Humans are modifying the global landscape at an unprecedented scale and pace. Our need to provide food, fiber, water and shelter for an ever growing population has led to drastic changes of the Earth’s surface. We have transformed 40-50% of the Earth’s ice-free surface (Chapin et al. 2000) and now appropriate one-third to one-half of the planet’s resources (Foley et al. 2005).

It is clear that our actions are having a huge impact on the natural world; species are declining and going extinct at an alarming rate. Through over-harvesting, habitat loss, introduced species and climate change, species are being lost at numbers unprecedented in the Earth’s history. We have already seen extinctions of 5-20% of species in some groups (Chapin et al. 2000) and current extinction rates are thought to be 100-1000 times pre-human levels (Pimm et al. 1995). Rates of declines are expected to continue or even accelerate under future projections (Millennium Ecosystem Assessment 2005). There is growing evidence that this degree of human influence could be causing a planetary-scale state shift in the global ecosystem (Barnosky et al. 2012).

If left unaltered, the current rate of biodiversity loss that we are experiencing will drastically alter the world in which we live. In addition to the cultural, aesthetic and spiritual value of biodiversity, we also rely on it for the provision of ecosystem services such as: climate regulation, soil formation, nutrient cycling, natural pest control, direct harvesting of species for food, fibers, fuel and pharmaceuticals (Balmford et al. 2002, Millennium Ecosystem Assessment 2005). When a dollar value is put to these vital services it is clear that the benefits of conserving biodiversity and natural landscapes far outweighs the costs (Balmford et al. 2002, Cardinale et al. 2012).

Our actions are not all negative, we also have the ability to conserve and protect species. In addition to learning about the many threats facing species, we are learning more about how to protect them. Through direct management of species along with habitat protection, led by local groups, NGO's and governments, there are many examples of conservation initiatives that have been successful at protecting and recovering species (Millennium Ecosystem Assessment 2005). Currently, 12-13% of the Earth's terrestrial surface is classified as protected (Chape et al. 2005) and many countries now have legislation in place that aims to protect endangered species (Ray and Ginsberg 1999).

In this thesis, I applied a macroecological approach to conservation biology. The macroecological approach involves identifying general patterns and processes over broad-scales by combining observational data with correlative methods (Brown 1995, Gaston and Blackburn 2000, Kerr et al. 2007). The emphasis is on statistical pattern analysis rather than experimental manipulation (Brown 1995). These methods are highly applicable to conservation questions, as many of the most severe threats to species (e.g. habitat loss and climate change) are occurring at large spatial scales. In this thesis I investigated basic conservation questions, such as: what factors are leading to declines in species' abundances or causing range contractions? How effective are our conservation measures? However, instead of looking only at one or a few species, I am interested in the general patterns over large groups of species and vast spatial scales.

The increase in scale and applicability that comes with a macroecological approach often involves a trade off with respect to inference. Macroecological methods have been criticized for having lower inference; the correlative nature of macroecological studies can make it harder to show a clear causation (Gaston and Blackburn 1999, Kerr et al. 2007).

Smaller scale experimental studies do have stronger inference, but this comes at the expense of broad scale applicability. Results from studies at a broad scale are more immediately relevant to conservation than smaller scale manipulative studies (Kerr et al. 2007).

The aim of this thesis is to investigate two main aspects of species' declines: what factors are contributing to their declines, and how effective our conservation efforts have been. I assessed one of the main mechanisms for protecting species by looking at the Endangered Species Act in the United States. I examined three separate indictors of species decline: range contraction, decreases in abundance and increase in temporal variability in abundance, in relation to anthropogenic activities. I looked at the main anthropogenic activities that are threatening species, including: habitat loss, pesticide use, global increases in ultraviolet rays and climate change.

In the first chapter of this thesis, entitled *Assessing the effectiveness of the Endangered Species Act*, I investigated how effective various legislative tools under the Act have been at promoting species recovery. The Endangered Species Act in the U.S. is one of the oldest pieces of endangered species legislation and an example of one of the main mechanisms used for protecting species (Salzman 1990, Gosnell 2001). The tools available for species recovery include funding, recovery plan development, and critical habitat designation. Previous studies have examined some or all of these tools, but they have focused on whether or not statistically significant effects of the tools could be detected, not whether the effects are large enough to be biologically meaningful (Male and Bean 2005, Taylor et al. 2005, Kerkvliet and Langpap 2007). It is critical to assess how well our conservation measures are working, and to modify them accordingly (Pullin and Knight

2009). I asked how strongly changes in species status over time are positively related to the tools enabled under the act.

In the second chapter, entitled *Human land-use, agriculture, pesticides, and losses of imperiled species*, I investigated whether species' losses in Canada are more related to habitat loss or to other aspects of human activities. Habitat loss is generally regarded in the literature as being the main threat to species (Czech et al. 2000, Kerr and Deguise 2004, Venter et al. 2006) so I asked whether species losses are in fact more closely related to habitat loss than to any other human activities such as agricultural pesticides or human population density which reflects urbanization. Pesticide use has increased in recent years as part of agricultural intensification (Matson et al. 1997) and been implicated in the declines of individual species (Potts 1986, Ewins 1997, Chamberlain et al. 2000, Davidson et al. 2001, Sparling et al. 2001).

Previous broad-scale multi-species studies have looked at hot spots of endangered species richness (e.g. Dobson et al. 1997, Flather et al. 1998, Kerr and Deguise 2004), which could indicate places where some factor(s) is (are) causing species to become endangered (how most previous studies have interpreted them) or, they may be places where endangered species have avoided extinction, having been lost elsewhere (e.g. Channell and Lomolino 2000). Here, I aimed to determine how areas where imperiled species persist differ from areas where imperiled species have suffered serious range reductions by examining imperiled species losses in ecoregions across southern Canada.

In the third chapter, entitled *Do global amphibian declines correlate with increases in remotely sensed UV,* I investigated one of the main hypothesised causes of the global amphibian decline that is currently one of the most pressing conservation issues today.

Amphibians are currently more threatened than any other taxon (Stuart et al. 2004). Approximately 43% of amphibian species are experiencing some level of population decline and as a result, close to one third of species are considered threatened or endangered and as many as 159 species may have gone extinct in recent years (Stuart et al. 2004). These drastic global declines have caused some to speculate that amphibians are at the leading edge of the sixth mass extinction (Wake 2008).

There are a number of potential causes of the amphibian population declines, including: over-exploitation (Warkentin et al. 2009), land use change (Becker et al. 2007), climate change (e.g. Pounds et al. 2006), disease (e.g. Lips et al. 2008), predation (Boone et al. 2007), pollution (e.g. Davidson and Knapp 2007) and ultraviolet (UV) exposure (Bancroft et al. 2008). Of the proposed threats, UV radiation is possibly the most controversial (Bancroft et al. 2008). Many laboratory studies and field experiments have confirmed that UV-B can cause lethal and sub-lethal damage to amphibians at all life stages (Blaustein and Bancroft 2007, Croteau et al. 2008). Despite numerous studies showing that UV has the potential to be detrimental to individual amphibians at all life stages, it is not clear whether or not these effects translate into long-term population level declines or extinctions (Beebee and Griffiths 2005, Collins and Crump 2009). There have been few studies looking at the effect of UV on amphibian populations in the wild. The goal of this chapter is to test whether recent global amphibian population changes are correlated with broad scale increases in ambient UV radiation.

In the fourth chapter of this thesis, entitled *Do anthropogenic stressors affect temporal variability in abundance of North American breeding birds?*, I looked at how temporal variability in abundance is affected by anthropogenic activities. Many theoretical and empirical studies have shown that species extinction risk is related to population variability in addition to population size (Pimm 1991, Vucetich et al. 2000, Inchausti and Halley 2003). Most conservation research has focused on population size and trends in abundance; however, variability *per se* may be a useful indicator of population health and stability (Fraterrigo and Rusak 2008, Mellin et al. 2010). Here, I tested the hypothesis that temporal variability in abundance of North American breeding birds is affected by habitat conversion to human land cover as well as climatic changes and variability.

The goal of this thesis is to answer some important questions relating to conservation biology. How are our main conservation tools working? What are the main threats that are correlated with species range contractions, population declines and increases in population variability? I investigate these questions at a broad-scale, using a macroecological approach, in hopes that the patterns that emerge from this work will be directly applicable to conservation efforts.

CHAPTER 1: ASSESSING THE EFFECTIVENESS OF THE ENDANGERED SPECIES ACT

Abstract

It is critical to assess the effectiveness of the tools used to protect endangered species. The main tools enabled under the U.S. Endangered Species Act (ESA) to promote species recovery are funding, recovery plan development and critical habitat designation. Earlier studies sometimes found that statistically significant effects of these tools could be detected, but they have not answered the question of whether the effects were large enough to be biologically meaningful. Here, I ask: how much does the recovery status of ESA-listed species improve with the application of these tools? I used species' status reports to Congress from 1988 to 2006 to quantify two measures of recovery for 1179 species. I related these to the amount of federal funding, years with a recovery plan, years with critical habitat designation, the amount of peer-reviewed scientific information, and time listed. I found that change in recovery status of listed species was, at best, only very weakly related to any of these tools. Recovery was positively related to the number of years listed, years with a recovery plan, and funding, however, these tools combined explain <13% of the variation in recovery status among species. Earlier studies that reported significant effects of these tools did not focus on effect sizes; however, they are in fact similarly small. One must conclude either that these tools are not very effective in promoting species' recovery, or (as I suspect) that species recovery data are so poor that it is impossible to tell whether the tools are effective or not. It is critically important to assess the effectiveness of tools used to promote

species recovery; it is therefore also critically important to obtain population status data that are adequate to that task.

Introduction

For conservation efforts to succeed, it is critical to evaluate the effectiveness of available conservation tools and to adapt management accordingly (Pullin and Knight 2009). The U.S. Endangered Species Act (ESA) is one of the oldest and most comprehensive pieces of endangered species legislation and one of the main mechanisms for preventing species' extinction in the U.S. (Salzman 1990, Gosnell 2001). The main tools enabled under the act that are applicable to all species are protection from take, section 7 consultation, funding, recovery plan development and implementation, and critical habitat designation (Schwartz 2008). There are other tools such as Habitat Conservation Plans, Safe Harbor Agreements and Candidate Conservation Agreements that are used on a case by case basis (Thompson 2006).

However, even the main tools have not been applied equally to all species listed under the Act. This provides a quasi-experimental test of their efficacy: if the tools enabled under the ESA are effective, one would expect that, on average, recovery of species listed under the Act would be positively related to measures of the degree of implementation of those tools. Here, I ask: how strongly does the evidence support this prediction?

The question is not whether *any* species have benefitted from the ESA; this is undoubtedly true: e.g. Aleutian Canadian goose, Robbins' cinquefoil and Kirtland's Warbler (Solomon 1998, Scott et al. 2005). Rather, I ask whether, on average, recovery is improved materially in species that have benefitted from the tools enabled under the ESA. Previous studies have concluded that various tools under the Act are effective, based on significant statistical relationships (Male and Bean 2005, Taylor et al. 2005, Kerkvliet and Langpap 2007). However, whether tools implemented under the ESA have had *detectable* effects (i.e., statistically significant) is at least partly an issue of statistical power. Arguably, the more important question is how large or small those effects have been. Extant work has not addressed this question.

Consider these tools in more detail. Once listed, species are protected from take, which includes harassing, harming, or killing. Species also benefit from Section 7 consultation, which states that federal agencies must consult with the Fish and Wildlife Service (FWS) to ensure that their actions do not jeopardize the species (Schwartz 2008). The Fish and Wildlife Service and the National Oceanic Atmospheric Administration (NOAA) provide funding for a variety of purposes involving listed species (USFWS 1990a-2006a), including habitat acquisition, research, and enforcement. Further, the Act requires that a recovery plan be developed and implemented for every listed species, except when such a plan will not promote conservation of the species (Endangered Species Act 1973). The recovery plan details the conservation actions that are necessary for recovery. Critical habitat (CH), defined as the specific areas within the geographical area occupied by the species, at the time it is listed, essential to the conservation of the species, is designated at the time of listing when judged to be ‘prudent and determinable’(Endangered Species Act 1973).

Critical habitat designation is the most controversial aspect of the Act (Service 2007). Although required for all species, it is currently only in place for 43% of U.S. listed species (USFWS 2008). Critical habitat can be cited as ‘undeterminable’ or ‘not prudent’ to avoid designation (Hagen and Hodges 2006). In early 2000, only 10 % of species had CH designation. This prompted legal action, and a large number of designations were pushed through by court order (Hoekstra et al. 2002, Suckling and Taylor 2006). The Department of the Interior claimed that the flood of CH designations was undermining endangered species conservation by using up funds and that it "does not result in any benefit to the species that is not already afforded by the protections" in other aspects of the Act (U.S. Department of the Interior 2003). Federal agencies are already required under the Act to consult with FWS to ensure that their actions do not adversely modify species habitat to a point where it would jeopardize species (Bean 2009). However, this protection only applies to lands currently occupied by the species. Critical habitat designation can go a step further and designate areas that are currently unoccupied by the species but deemed necessary for their recovery (USFWS 2007). This controversy highlights the necessity of studying the effect of CH designation on species recovery (Schwartz 2008).

Earlier studies that have attempted to assess the effectiveness of the ESA yielded conflicting results. Kirkvliet and Langpap (2007) examined the recovery status of 225 listed species and concluded that spending reduced the probability of species doing poorly but was unrelated to the probability of doing well. They found that having a recovery plan (either in progress or completed) decreased the probability of species being reported as declining and increased the probability of species being stable or increasing. They did not find evidence that CH designation promotes species recovery. Taylor et al. (2005) considered a larger set of listed species (N=1095). Looking separately at single species and multi-species recovery plans, they found a positive effect of single species recovery plans but no effect of multi-species plans. They argued that species with CH designation were more likely to be increasing and less likely to be decreasing than species without CH designation. In contrast, Male and Bean (2005), using a similar data set that included federal funding, concluded that species status was positively related to funding but was not significantly related to CH designation. Miller et al. (2002) calculated funding as the amount of money received divided by the amount requested in the species recovery plan. They found that with increased funding, species status was more likely to be improving. Boersma et al. (2001) examined the effectiveness of recovery plans in detail and found that single species plans and those with a diversity of authors are related to increased likelihood of species doing well. In each case, the authors focus on whether statistical relationships are detectable, as opposed to how strong those relationships are.

In this study, I examine two measures of species recovery: population status trends (on which most earlier studies have focused) and the number of recovery objectives achieved (among those listed in the species' recovery plan). I test how much of the inter-specific variation in recovery of ESA-listed species can be statistically attributed to how long the species has been listed (i.e, the base protection from being listed), how long a recovery plan has been in place, whether and how long critical habitat has been designated, and federal funding. If such tools improve species' recovery, then change in species status over time and number of recovery objectives achieved should relate reasonably strongly to these variables. Since one of the main intentions of funding and recovery plan development is to support research and to increase what is known about a given species, I also look at the relationship between recovery status and the amount of published peer-reviewed scientific information available on each species. I look more closely at the effect of CH designation by comparing species' status before and after designation. I also test whether the effect of CH designation is stronger for species who are specifically threatened by habitat loss.

Not all species have a recovery status trend reported in each recovery report, presumably due to lack of information. I also test whether the availability of status information relates to the amount of peer-reviewed scientific information, funding, time listed, or taxonomic group.

Methods

Recovery status was assessed for all U.S. and joint U.S./foreign species listed under the ESA prior to 2003. Two measures of species recovery – change in population status over time, and the proportion of recovery objectives achieved by 2006, were extracted from biennial recovery reports to Congress from 1988-2006 (USFWS 1990b-2006b, 2008a). Population status reports rate each species as decreasing, stable, increasing or unknown, relative to the previous report based on population size estimates as well as perceived threats (USFWS 1990b-2006b, 2008a). These assessments are often based on qualitative information and can be based solely on the judgment of a species expert, but they are the best species status data available for all ESA listed species (Boersma et al. 2001).

Using the population status data, I calculated an index of change in status over the period 1988-2006 following Male and Bean (Bean 2009). For a given species, I first assigned a value of -1, 0 or 1 to each status report for declining, stable or increasing, respectively. These values were then summed, resulting in a final species score ranging from -9 to +9. Not all species had a status report for every biennial period in the data set. For these species, I calculated the proportion of reporting periods for which the population trend was known. I adjusted the final status score by dividing it by the proportion of known reports such that all population trend indices are based effectively on an 18 year period. This assumes that missing status information is equal to the average of the observed reports. The second metric of recovery status, the recovery objectives achieved, is reported on a scale from 1 to 4 representing the percent of recovery objectives that have been achieved, according to the most recent recovery report used in the analysis (2006). I excluded species with multiple listed populations where each population had a different status; otherwise they were included as one record. Species presumed extinct in the wild or found only in captivity were also excluded.

Yearly funding was obtained from annual expenditure reports to Congress covering 1989-2004 which include all reported federal and state funding (USFWS 1990a-2006a). For each species, I calculated mean yearly funding. Because different species require different amounts of funding, I also calculated mean yearly funding received as a proportion of the mean yearly estimated cost of recovery given in the recovery plan for each species (USFWS 2008). Analysis using the proportional funding data is therefore limited to species that have a recovery plan with recovery cost estimates (739 species).

For each species, I recorded the number of years since listing, CH designation and recovery plan completion using 2004 as the base year (USFWS 2008). Peer-reviewed scientific information was estimated as the number of studies found from a Web of Science search conducted in July 2007 of each species' scientific name. I also recorded whether habitat loss was a threat for each species, based on NatureServe (NatureServe 2009) and the FWS recovery plans (USFWS 2008). I separated threats into three categories: direct habitat loss (e.g. habitat destroyed for residential development), habitat related threats (e.g. habitat degradation, pollution) and non-habitat related threats (e.g. overharvest, predation or competition from introduced species). If any direct habitat loss threats were mentioned, then it was recorded as such regardless of whether other threats were also present. Species were grouped into seven taxonomic groups: amphibians, birds, fish, invertebrates, mammals, plants and reptiles.

Generalized linear models were used to test the relationships between measures of species recovery and the independent variables. General linear models were performed for the population status data and the proportion of periods for which a status estimate was available was used as a weighting factor. Proportional odds multinomial logistic models were performed for the recovery objective variable. I use McFadden’s pseudo R-square as a measure of explained variability (McFadden 1974, Mittlbock and Schemper 1999). I did these analyses for all species combined, and within taxonomic groups. Mean yearly funding and peer-reviewed information were log-transformed, and all variables were standardized (mean = 0, s.d. = 1).

I did two additional tests to focus more explicitly on the effect of CH designation. To determine whether the effect of CH designation on status depends on the degree to which species are jeopardized by habitat-related threats, I compared the effect of CH designation on status for each threat category separately. I did a second analysis using only species for which CH had been designated. This analysis included the 218 species with status information both before and after their CH designation. For these species, I calculated the difference between the average status before and after CH designation. To control for any positive effect of being listed, with or without CH, I also calculated the average change in status of species without CH designation.

Results

This study included 1179 species listed before 2003, of which plants made up 61%, invertebrates 14%, fish 9%, birds 6%, mammals 5%, reptiles 3% and amphibians 2%.

Population status data were available for 1146 species; 33 species were excluded because they had unknown status in every recovery report. I adjusted population status scores for a further 796 species that had at least one unknown status report. Considering all 1146 species, the trends in population status neither improved nor worsened from 1988-2006 (median slope = 0.0). The median status score for all species was -3: i.e., populations generally declined relative to earlier reports. Recovery objective data were available for 1169 species (all except 10 marine species under NOAA jurisdiction). Over all species, the median recovery objective value is a score of 1 which loosely corresponds to 0-25% of the recovery objectives achieved.

Recovery is detectably related to some of the factors expected to promote recovery, but the overall variation explained is small. In the strongest model, the proportion of recovery objectives achieved was significantly positively related to the number of years listed ($p<0.0001$; Fig.1.1a), amount of peer-reviewed scientific information ($p<0.0001$; Fig.1.1b), funding as a proportion of the amount required ($p=0.024$), and years with a recovery plan ($p=0.005$) (Table 1.1). A categorical variable distinguishing among taxonomic groups was also significant ($p=0.035$): birds, mammals and fish have recovered better, on average, than plants, amphibians and invertebrates. The overall model explained 13% of the variation in recovery objectives achieved (i.e., pseudo $R^2=0.129$).

I observed similar results for the change in population status over time. Status was significantly related to taxon ($p=0.017$), years listed ($p=0.029$) and proportional funding ($p<0.0001$; Fig.1.2; pseudo R^2 for full model=0.080). Population status was also related to mean yearly funding, but less strongly than to proportional funding (Table 1.1). Peer-reviewed scientific information and mean yearly funding were strongly collinear ($r=0.635$, $p<0.0001$; Fig. 1.3a); I therefore did not include both variables in my models.

Within taxonomic groups, significant relationships were found for birds, fish, mammals, invertebrates and plants; however, once again, the effect sizes were quite small. Overall, years listed was the most important variable for all groups and peer-reviewed scientific information and funding were important for most groups. The strongest relationships ($R^2 > 0.15$) were found for birds, mammals and plants. For birds, population status was significantly positively related to years listed ($N=69$; pseudo $R^2=0.213$). Population status for mammals was significantly positively related to proportional funding, but negatively related to critical habitat designation ($N=29$; pseudo $R^2 = 0.399$). The proportion of recovery objectives attained for plants was significantly positively related for years listed, peer-reviewed information and proportional funding ($N=519$; pseudo $R^2=0.193$).

Species' recovery scores were not significantly related to whether, or how long, CH had been designated. Species with CH designation were not doing better, on average, than those without. The effect size for CH designation remained small and insignificant when analyzed separately for each threat category (habitat loss versus other threats). There was no difference in the average status before and after CH designation (median difference = 0.0). This was also the case for the control group of species without CH designation (median difference = 0.0). These results were the same for both measures of recovery.

The proportion of reporting periods for which a species' status was known was positively related to peer-reviewed scientific information (Fig. 1.3b) and years listed , and it varied significantly among taxonomic groups ($p < 0.0001$ in all cases; $R^2= 0.127$). For all species, the average proportion of reporting periods for which a species' status was known was 0.68; birds and fish had the highest proportions while plants had the lowest.

Discussion

Earlier studies have reported statistically detectable associations between the recovery of species listed under the ESA and the main tools enabled under the act. In this study, I show that: 1) those effects have not been consistently detectable in earlier work, and 2) the effect sizes are very small. The variation among listed species in two measures of recovery – the number of recovery objectives achieved and the change in species status over time – is, at best, only weakly related to the main tools enabled under the Act. The present study considers more species, more indicators of recovery, and more variables that potentially influence recovery than any earlier study, and I still find only weak effects or none at all. Results in earlier studies were inconsistent (see Introduction above) probably because, when effect sizes are very small, small differences among data sets (and collinear variables) make parameters estimates highly unstable.

There are two possible interpretations of these data. One must conclude either that the tools provided by the ESA have had only modest impacts on the recovery of ESA-listed species over 18 years (at best), or that data used to assess recovery are too imprecise to show whether the tools have had a substantial effect or not. Either way, strong evidence that the tools provided by ESA are working is lacking. To manage recovery of imperiled species, it is essential to assess the effectiveness of management actions, and to modify them to improve outcomes.

The aggregate evidence regarding the beneficial effects of being listed under the ESA is mixed. The best among the weak predictors of recovery is the number of years a species has been listed (Table 1.1) which implies some benefit from protection from take and section 7 consultations. Other studies have reported a significant correlation between number of years listed and species status (Rachlinski 1997, Male and Bean 2005). Taylor et al. (2005) found a positive effect of years listed, after accounting for CH designation and recovery plans. In contrast, Ferraro et al. (2007) found a *negative* effect of being listed on species status. They compared ESA-listed species to a control group of species from the Nature Serve data base and their study was limited to 135 vertebrate species. They found that listing was only beneficial when combined with high levels of funding. Inconsistent effects probably reflect small absolute effect size and imprecise data.

The aggregate evidence about the effects of recovery plans is also mixed. I observed a positive effect on recovery objectives achieved, but not on species status trends (Table 1.1). Other studies have observed positive effects of recovery plans when those plans focused on single species and/or had a diversity of authors, but not for multi-species recovery plans (Boersma et al. 2001, Taylor et al. 2005, Kerkvliet and Langpap 2007). Perhaps the reason I only see an effect of recovery plans in two out of four models is that I did not distinguish between single- and multi-species plans.

The effect of funding on ESA-listed species has been examined in many other studies, but this study it the first to examine both absolute funding and funding as a proportion of the estimated amount required for species recovery. I found that recovery was more strongly related to proportional funding than to absolute funding, but the effect was still modest (Table 1.1). Male and Bean (2005) found that recovery was significantly related to annual FWS+NOAA funding. They do not quantify the strength of this relationship; however, all of the variables included in their study explained only 13% of the variation in species’ status, including variables such as “risk of extinction” and “recovery potential”, so necessarily the effect of funding was small. Kerkvliet and Langpap (2007) found that an additional million dollars in funding decreased the likelihood of a species being listed as extinct by less than 1% and declining by 1.3-1.7%, but that it did not increase the probability of being stable or increasing. Kerkvliet and Langpap’s (2007) study was limited to vertebrate species with no unknown status reports (i.e., 19% of all listed species), which generally had high funding levels, so their results cannot be applied to listed species in general. Miller et al. (2002) looked at funding as a proportion of the amount requested in the species recovery plan that had been received and found that species with higher funding were more likely to be stable or increasing (although, again, they did not specify effect size).

While the detectable effects of funding on recovery may be modest, the amount of information available on ESA-listed species relates more strongly to funding, both in terms of peer-reviewed scientific publications and availability of assessments of recovery status. Mean yearly funding and numbers of publications are strongly correlated (Fig. 1.3a), and there is a positive relationship between the proportion of known status reports and mean yearly funding (Fig. 1.3b) and peer-reviewed information (Fig.1.3c). This is consistent with the notion that a portion of species funding goes towards research which provides more information on species status. However, even this relationship accounted for only 12% of the variability in available reports.

The aggregate evidence regarding critical habitat suggests that there is no detectable effect. I found that species with CH designation are not doing better than those without it. I tested this both with a general linear model and by looking the difference in average status before and after designation. The studies of Male and Bean (2005) and Kerkvliet and

Langpap (2007) were also consistent with this conclusion. In contrast, Taylor et al. (2005), who reported a positive effect of CH designation, looked at two time periods, 1990-1994 and 1997-2002, and tested whether or not species with CH in each period were more likely to be increasing and less likely to be decreasing than those without it. Only two of their four tests were significant. One explained less than 1% of the variation in status, the other explaining less than 10%. I conclude that the relationship between species status and CH is, at best, very weak.

Given that habitat loss is cited as the main threat to imperiled species in the U.S. (Wilcove et al. 1998) one would expect CH designation to have a strong positive effect on species status. However, legal designation of CH does not necessarily mean that habitat is protected on the ground, since CH designation applies only to situations involving federal agencies (USFWS 2007). Suckling and Taylor (2006) provide a number of case studies where CH designation was used to provide effective habitat protection. However, for endangered species generally, CH designation that is limited to the actions of federal agencies is apparently insufficient to promote recovery appreciably.

I suspect that the ESA tools I studied may be more effective than the study suggests, but that the species recovery data are grossly inadequate. Species population status data are published in biennial recovery reports to Congress as mandated by the Act. If species status data are available at all, they are qualitative and are relative to a previous recovery report. There are no standards on how status decisions are made, nor are the reports peer reviewed in any way. Many of the status assessments are based on the opinion of FWS staff (Boersma et al. 2001). Despite this, species status reports have been used in most of the previous assessments of the effectiveness of the ESA (Male and Bean 2005, Taylor et al. 2005). Due to these limitations I used a second measure of species recovery – the number of recovery objectives achieved. But this measure also has severe limitations. The recovery objectives outlined in the recovery reports have been criticized as being arbitrary and not based on science (Tear et al. 1995, Boersma et al. 2001).

I have no independent verification of the quality of species status and recovery objective data. The two recovery metrics that I studied are positively correlated (r= 0.49; see also Abbitt and Scott (2001) and Kerkvliet and Langpap (2007)) but for a given recovery objectives achieved score, there is a large amount of variation in species population status, especially for the lower scores (Fig. 1.4). This suggests that the FWS population status scores are indeed very imprecise indicators of species' recovery status (Schwartz 2008). Accurate, quantitative information on species status is necessary for assessing the ESA and subsequently improving and strengthening it.

Another criticism of the ESA is that delays in listing at-risk species results in species not being listed until their situation is already critical (Greenwald et al. 2006, Schwartz 2008). Greenwald et al. (2006) found that the average time to list a candidate species was 11 years. They note that these delays make recovery very difficult, and in some cases, impossible. Perhaps tools would be more effective if species were listed more quickly.

Despite including more species and more variables than previous studies, I find that species recovery is, at best, only weakly related to the main tools enabled under the Act. I am not suggesting that the Act should be abandoned; there is no way to know what would have been the fate of listed species in the absence of protections offered by the Act. I have no direct evidence to assess whether the Act *per se* is flawed, or the implementation of the Act is flawed (perhaps because of lack of funding), or the data available to assess the implementation are flawed. It is critically important to assess the effectiveness of tools used to promote species recovery; it is therefore also critically important to obtain population status data that are adequate to that task.

Acknowledgments

I thank T. Male and M. Bean for providing species funding and critical habitat data from 1989-2002. I also thank Mark Schwartz and anonymous reviewers for useful comments on this work.

Tables

Table 1.1: Regression results for models relating ESA tools to species recovery. General linear models were performed for the population status data and the proportion of periods for which a status estimate was available was used as a weighting factor. Proportional odds multinomial logistic models were performed for the recovery objective variable. I use McFadden’s pseudo R-square for the multinomial models.

Model	Dependent Variable	Independent Variable	Parameter estimate	P	Odds ratio	N	R^2
Model 1	Proportion of recovery objectives achieved	Taxon	-*	0.035	-*	752	0.129
		Recovery plan	0.463	0.005	1.59		
		Critical habitat	0.063	0.476	1.07		
		Years listed	0.840	<0.0001	2.32		
		Scientific information	0.561	<0.0001	1.75		
		Proportional funding	0.249	0.024	1.28		
Model 2	Proportion of recovery objectives achieved	Taxon	-*	0.083	-*	1169	0.115
		Recovery plan	0.340	<0.0001	1.10		
		Critical habitat	0.075	0.227	1.08		
		Years listed	0.39	<0.0001	1.89		
		Mean yearly funding	0.431	<0.0001	1.54		
Model 3	Population status	Taxon	-*	0.017	-*	739	0.080
		Recovery plan	0.069	0.283	-		
		Critical habitat	0.038	0.302	-		
		Years listed	0.119	0.029	-		
		Scientific information	-0.016	0.724			
		Proportional funding	0.162	<0.0001	-		
Model 4	Population status	Taxon	-*	<0.0001	-*	1146	0.057
		Recovery plan	0.027	0.414	-		
		Critical habitat	0.025	0.394	-		
		Years listed	0.078	0.047	-		
		Mean yearly funding	-0.027	0.465	-		

[*] Taxon is a categorical variable and therefore the parameter estimates and odds ratios are given for each level and are not reported here.

Figures

Figure 1.1: Recovery objectives achieved as a function of years listed and scientific information. Scatter plots of recovery objectives achieved and (a) number of years listed and (b) amount of peer-reviewed scientific information. Peer-reviewed scientific information is calculated as the number of Web of Science search conducted in July of 2007 of each species' scientific name and is natural logarithm transformed. Lines on the graphs show LOWESS smoothing functions with tension=0.7, N=1169.

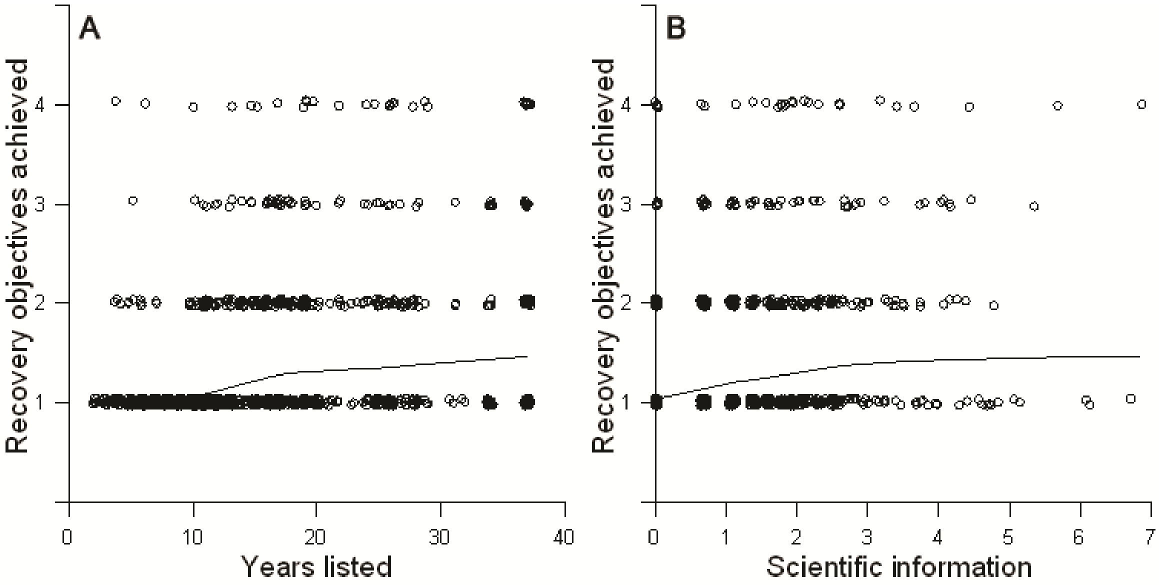


Figure 1.2: Relationship between population status and funding. Scatter plot of species population status score and the proportion of funding requested in species recovery plan that has been received. Proportion of funding received is natural logarithm transformed. Line shows LOWESS smoothing function with tension = 0.7, N=752.

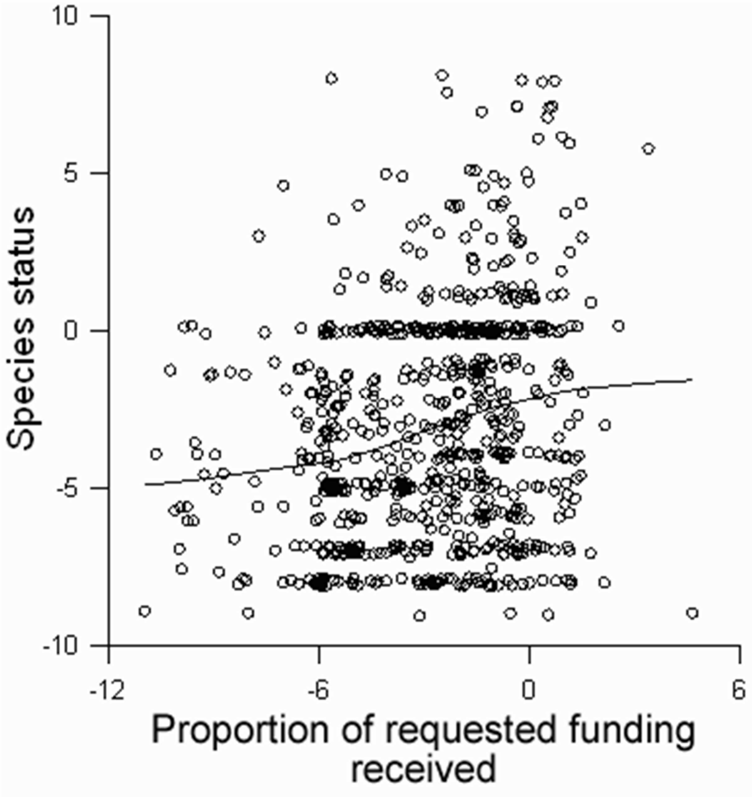


Figure 1.3: Relationships between funding, scientific information and the proportion of known reports. Scatter plots showing the relationship between (a) mean yearly funding and the amount of peer-reviewed scientific information available on a species, (b) mean yearly funding and the proportion of known reports and (c) amount of peer-reviewed scientific information and the proportion of known reports. Peer-reviewed scientific information is calculated as the number of Web of Science search conducted in July of 2007 of each species' scientific name. Mean yearly funding and peer-reviewed scientific information are natural logarithm transformed. Lines on the graphs show LOWESS smoothing functions with tension=0.7, N=1169.

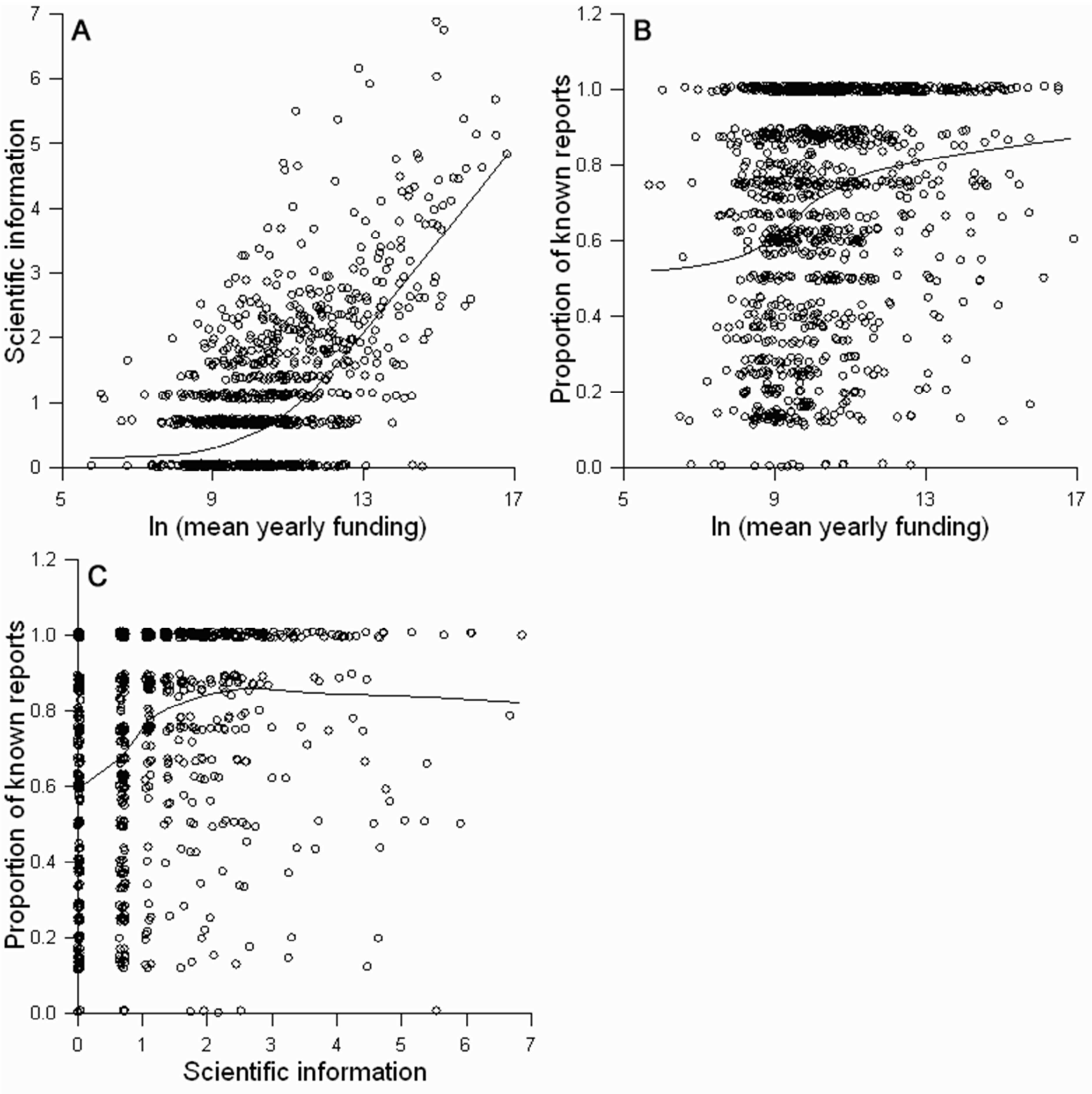
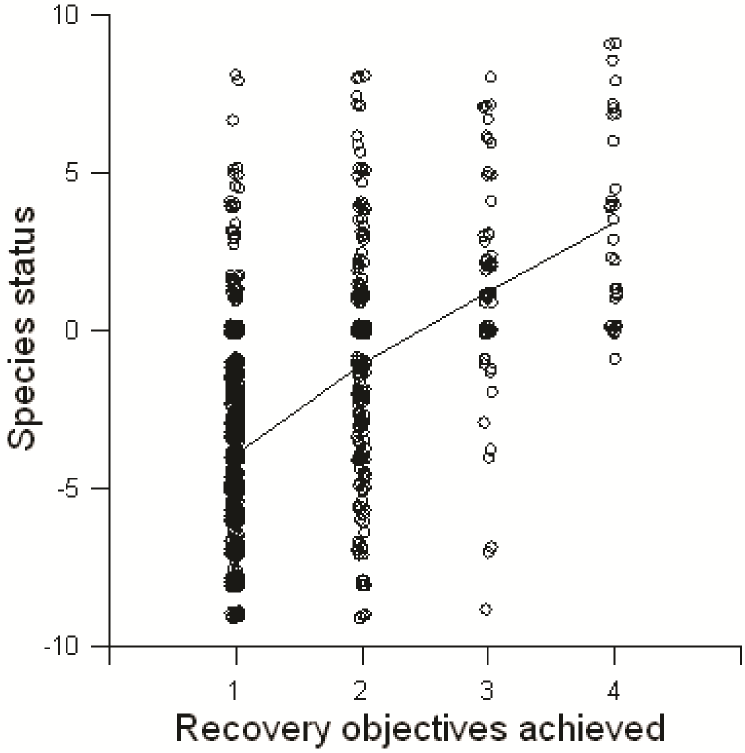

A
Scientific information
0
1
2
3
4
5
6
7
5
9
13
17
ln (mean yearly funding)
B
Proportion of known reports
0.0
0.2
0.4
0.6
0.8
1.0
1.2
5
9
13
17
ln (mean yearly funding)
C
Proportion of known reports
0.0
0.2
0.4
0.6
0.8
1.0
1.2
0
1
2
3
4
5
6
7
Scientific information

Figure 1.4: Relationship between population status and recovery objectives achieved. Scatter plot showing the relationship between change in population status over time and recovery objectives achieved for ESA listed species. Data come from biennial FWS recovery reports to Congress. Line shows LOWESS smoothing functions with tension=0.7, N=1179.



CHAPTER 2: HUMAN LAND-USE, AGRICULTURE, PESTICIDES, AND LOSSESS OF IMPERILED SPECIES

Preface

The work in Chapter 2, *Human land-use, agriculture, pesticides, and losses of imperiled species,* builds on work done by Robin Mackey that was presented in her thesis from 2001 titled *Disturbance and Biodiversity,* but that was never published. I began with the original question in her thesis. I updated the literature review, updated the data, ran new analyses and substantially re-wrote the work. This chapter was ultimately published as: Gibbs, K. E., R. L. Mackey, and D. J. Currie. (2009). "Human land use, agriculture, pesticides and losses of imperiled species." Diversity and Distributions **15**(2): 242-253.

Abstract

Anthropogenic habitat loss is usually cited as the most important cause of recent species' extinctions. I ask whether species losses are in fact more closely related to habitat loss than to any other aspect of human activity such as use of agricultural pesticides, or human population density (which reflects urbanization). I statistically compared areas in Canada where imperiled species currently occur, versus areas where they have been lost. Using multiple regressions, I relate the numbers of species that had suffered range reductions in an ecoregion to variables that represent present habitat loss, pesticide use and human population density. I find high losses of imperiled species in regions with high proportions of agricultural land cover. However, losses of imperiled species are significantly more strongly related to the proportion of the region treated with agricultural pesticides. These results are consistent with the hypothesis that agricultural pesticide use, or something strongly collinear with it (perhaps intensive agriculture more generally), has contributed significantly to the decline of imperiled species in Canada. Habitat conversion *per se* may be a less important cause of species declines than how that converted habitat is used.

Introduction

The ecological literature holds that, "In general terms, the loss of biodiversity is caused by habitat loss.... Therefore, general policies that prevent habitat destruction will, on the whole, ameliorate the decline of biodiversity" (Roughgarden 1995). This idea is echoed in the economics literature (Swanson 1995) and it is prominent in the Global Biodiversity Outlook 2 (Secretariat of the Convention on Biological Diversity 2006).

Much of the evidence supporting this generalization has been based on studies of individual endangered species. Such studies typically identify multiple contributing factors to a species' decline. These virtually always include some aspect of anthropogenic habitat loss among those threats (Primack 1995, Wilcove et al. 1998). For example, Czech *et al.* (2000) reviewed the accounts of the threats to 877 U.S. endangered species, and they concluded "Collectively, the studies have shown that habitat loss is the most prevalent cause of species endangerment." A similar study in Canada concluded that habitat loss affected 84% of endangered species and was the greatest overall cause of endangerment based on the threats given when the species were listed as being endangered (Venter et al. 2006). Kerr & DeGuise (2004) found that the numbers of endangered species that occurred in 15 Canadian ecozones was related to the extent of broad-scale habitat conversion. Certainly, it is a truism that elimination of a species' habitat leads to extirpation of the species in the wild. Based on this logic, both governmental and private efforts to preserve imperiled species typically target habitat preservation (e.g., the Endangered Species Act in the United States and the Species at Risk Act in Canada; The Nature Conservancy, Wildlife Habitat Canada).

Are species losses in fact more closely related to habitat loss than to any other aspect of human activity? One such possibility is pesticide use. Habitat loss is very often the result of conversion of natural habitat to agricultural land, where pesticide use can be extensive. Over forty years ago, Carson (1962) hypothesized that pesticides could lead to dramatic declines in bird species. Since then, ample evidence has accumulated that agricultural pesticides can be directly toxic to wildlife species and can reduce their food supply (for reviews, see Freemark and Boutin 1995, McLaughlin and Mineau 1995, Fleischli et al. 2004, Devine and Furlong 2007, McKinlay et al. 2008). Pesticides have been implicated in the decline of particular species of amphibians (Davidson et al. 2001, Sparling et al. 2001) and birds (Potts 1986, Ewins 1997, Chamberlain et al. 2000). The link between pesticide exposure and the resulting physiological effects causing population declines has been well studied in the case of the American alligator in Southern Florida (Rauschenberger et al. 2007).

Curiously, although agriculture is often cited as one of the main threats to endangered species, there is rarely specific mention of pesticides. Czech et al. (2000) list agriculture as the third most frequent contributor to species declines in the U.S. (after non-native species and urbanization), but they do not mention pesticides. Venter *et al*. (2006) list habitat lost as the most prevalent threat to endangered species, with agriculture and urbanization as the most common human activities contributing to habitat loss. Again, they do not mention pesticides.

Hypotheses regarding which human modifications of the environment pose the greatest threat to imperiled species have been examined by relating broad-scales patterns of endangerment to habitat characteristics. Broad-scale multi-species studies to date have focused on identifying hot spots of endangered species (e.g. Dobson et al. 1997, Flather et al. 1998, Kerr and Deguise 2004). However, hot spots of endangered species could result from several processes. They may be places where some factor(s) is (are) causing species to become endangered. Alternatively, they may be places where endangered species have avoided extinction, having been lost elsewhere (e.g. Channell and Lomolino 2000). Knowing where the most endangered species remain may be relevant to the establishment of reserves. Knowing what distinguishes places where species persist from places where they do not persist is relevant to establishing what causes species losses in the first place.

The objective of this study is to determine how areas where imperiled species persist differ from areas where imperiled species have suffered serious range reductions. I examine this question by comparing imperiled species losses in ecoregions across southern Canada. More specifically, are there hot spots of species losses? Are species losses most closely related to habitat loss (to urban and agricultural development), use of agricultural pesticides, or human population density (which reflects urbanization)? It is unquestionable that many factors contribute to the loss of particular species (e.g. Czech et al. 2000); in this study I am looking for the strongest effects that are most consistent among imperiled species in general. This study is the first, to my knowledge, that quantifies the spatial variation in numbers of species losses (versus the number of extant imperiled species) and that statistically examines correlates of those losses.

Methods

Species Distribution Data

Species distribution data were obtained from reports prepared for the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), the body that officially designates the conservation status (e.g., threatened, endangered) of species in Canada. To determine where species have been lost, both historic and current distribution data are required. Unfortunately, the historic, and sometimes current, distributions of most COSEWIC-listed plants and aquatic taxa are unknown. This study was therefore limited to terrestrial mammals, birds (breeding distribution only), amphibians and reptiles whose historic and current range distributions have been confidently described or mapped. The most recently reported distribution of a species in the COSEWIC reports was defined as the current distribution (generally between the 1980s and the late 1990s). The historic distribution of a species was acquired from the earliest known or recorded range distribution and dated anywhere from the early 1800s to the early 1900s.

Within the four major taxa examined, those species listed as extinct, extirpated, endangered, threatened, or vulnerable/rare were included in this study. Subspecies or specific populations of species were not included in the analysis unless only one subspecies or population of a species had ever existed in Canada, or if Canadian distribution data for the remainder of the species were included in the subspecies or population report. The study only considered the Canadian portions of species' distributions. Consequently, in any ecoregion that straddles the US-Canadian border, I consider imperiled species declines, agriculture and pesticide use only in the Canadian area (mainly since US and Canadian ecoregions are not coordinated). See Appendix 1 for a list of all species included in this analysis.

The spatial resolution of the study was the terrestrial ecoregion, a subunit of the coarser ecozones that delineate areas of reasonably homogeneous physical and biotic characteristics (Ecological Stratification Working Group 1995; Fig. 2.1). Although fine-scale information on species distributions is often lacking, presence/ absence and range reduction data at the ecoregion scale are reliable. For each ecoregion, I tallied the number of imperiled species currently extant, the number historically present, and the number that have suffered significant range losses.

Ecoregion Attributes and Land-cover Data

Ecoregion attributes and land-cover data were obtained from several sources. Land cover data for Canada were compiled and classified by Marshall *et al*. (1999) in pixels of 1.1 km^2. They distinguished natural cover, versus land dominated by built-up areas (e.g., towns, roads, industrial), croplands, or domestic livestock rangelands. Habitat loss was measured as the area of human dominated land cover, which includes all land cover classifications other than natural cover. Human dominated land cover is an imperfect surrogate for habitat loss but at broad scales and for broad taxa, it is the best approximation available. I also obtained estimates from E-Stat 1999 (Statistics Canada 1999) of the areas of croplands, the area treated with insecticide, and the area treated with herbicide in each ecoregion. These estimates were based upon the 1999 release of the 1996 Census of Agriculture. The Census of Agriculture was carried out simultaneously with the national Census of Population. Any household that responded positively to the question, “Is anyone in this household a farm operator?" was asked to complete the Census of Agriculture form.

Following Mineau & Whiteside (2006), I use area treated with pesticide as the primary independent variable in this study. In principle, an estimate of the total toxicity of pesticides applied per ecoregion would have been preferable to the area treated with pesticide. Toxicity may vary according to the quantity of pesticide applied, the formulation of the pesticide (aqueous, dry powder, granular, etc.), or carriers applied with the pesticide. Toxicity will also vary among the imperiled species in question. To combine amounts of pesticide used, beyond area treated with pesticides, would have required much more information than was available for a very broad-scale study.

The landscape data used here are recent (1990s), and they therefore do not directly measure historic landscape characteristics. However, historic land use data are rare. Because colonial settlement and wide-scale human land use are relatively recent in Canada (population in 1760 was less than 100 000; Wynn 1991), I assume that the differences in current landscape characteristics among ecoregions are proportional to those that existed while species’ declines occurred. This assumption argues that, to a first approximation, the ranking of agricultural intensity among ecoregions has remained fairly constant: only a small proportion of natural areas and agricultural areas have traded places. Where this assumption is not true, it will tend to add noise to the data, obscuring statistical relationships.

Statistical Analyses

Using multiple regressions, I tested the hypothesis that the numbers of species that had suffered range reductions in an ecoregion is related to variables that represent present habitat loss, pesticide use and human population density. I carried out these regressions using the number of bird, mammal, amphibian, and reptile species combined, as well as for birds and mammals separately. The numbers of species of amphibians and reptiles were too small for independent statistical analysis.

As my main hypothesis dealt with effects of pesticides versus habitat loss, I related numbers of species lost to one variable describing land cover conversion, one pesticide variable, and total regional species richness. Land cover was described by either land in agriculture, or by total human-dominated cover (agriculture plus urban). Pesticides variables were area treated with herbicides, area treated with insecticides, or total area treated with pesticides (herbicide + insecticides + fungicides). I did not include other combinations of variables because these variables are strongly collinear (see Appendix 2 for a complete correlation matrix). Tolerance values of the independent variables in these regressions (i.e., the proportion of their variance that is uncorrelated with other independent variables) were reasonably high (>0.6). I excluded the 131 ecoregions in northern Canada in which neither habitat loss nor pesticide use was detectable, because habitat loss and pesticide use are perfectly collinear in those samples. This left 86 southern ecoregions with a total area of 3.6 x 10^6 km^2. Note that collinearity between pesticide use and habitat loss in the remaining data reduces the probability of detecting effects of pesticides after controlling for area in agriculture. Thus, the tests of the pesticide hypothesis are conservative.

Total regional species richness was included in the regression models since the number of species lost from an ecoregion seemed likely to depend upon the number of species originally present in that region. Bird species richness per ecoregion was compiled from feral distributions and was provided by Parks Canada. Mammal, amphibian, and reptile species richness per mainland ecoregion were estimated from feral regional distribution data compiled by Currie (1991). Richness in island ecoregions was estimated from feral distributions in Banfield (1974, mammals) and Cook (1984, amphibians and reptiles). Using species richness as a covariate in regression models serves the same function as expressing the number of species losses as a proportion of total richness, but it avoids using a ratio as the dependent variable.

Many of the variables in this study were strongly positively skewed. I therefore used power transformations to make the distributions of both dependent and independent variables as close to Gaussian as possible: $X'=(X+0.5\ X_{min})^a$, where X_{min} is the limit of detection of X (e.g., for species counts, $X_{min}=1$ species). The coefficient *a* was iteratively varied from 0 to 1, and agreement with the Gaussian distribution was assessed with a Komolgorov-Smirnov test.

A further statistical complication is that ecoregions do not necessarily accrue or lose species independently. This may produce spatial autocorrelation in the data (i.e., ecoregions may not be independent data points). The predictor variables in this study are also spatially structured. Since I hypothesize that environment is driving species losses, I first carried out ordinary least squares regression, and I then tested for residual autocorrelation in the residuals (Legendre 1993). I carried out conditional autoregressive regressions using SAM

(Rangel et al. 2006) on the final models to test whether any contributing variables become non-significant when the spatial structure of the data is taken into account.

Statistical analyses were performed using Systat v. 10. and SAM.

Results

A total of 62 COSEWIC-listed species of birds (n = 37), mammals (n = 12), amphibians (n = 6), and reptiles (n = 7) whose historic and current range distributions are known were identified for this study. Of these, approximately 9% were listed as extinct or extirpated, 31% listed as endangered, 24% listed as threatened, and 36% listed as vulnerable/rare (COSEWIC 2004). These numbers represent approximately 60% of the species in these groups listed by COSEWIC. Birds are the best represented with over 80% of COSEWIC-listed species included in this dataset, and amphibians are the least with approximately 40% of the listed species represented here. Excluded species were those for which historic distributions could not be accurately determined.

COSEWIC status reports do not explicitly mention pesticides as a major threat. Among the COSEWIC-listed terrestrial vertebrate species, land conversion to agriculture was listed as a threat for 64% of species. “Agricultural pollutants” were cited as a threat for only 21% of species.

Distributions and losses of COSEWIC–listed species

The geographic locations of hot and cold spots of species’ losses, with several of their respective and agriculture attributes are presented in Table 2.1. Hot spots are areas where many imperiled species have suffered historic range losses. Cold spots of losses are ecoregions in which many imperiled species currently persist and few have experienced historic range losses.

All four classes combined

High concentrations of imperiled species were apparent in several southern ecoregions of Canada (Fig. 2.2a). The most prominent hot spot of listed species is in the Mixedwood Plains ecoregion of southern Ontario and an adjacent ecoregion of the Boreal Shield ecozone. High numbers of imperiled species were also found in the Prairies and Boreal Plains ecozones, in the southern portion of the Montane Cordillera, and in the far southwest corner of the Pacific Maritime ecozone.

The greatest number of losses of imperiled species occurred in the two southernmost ecoregions of the Mixedwood Plains ecozone; 30 of the 62 species included in this study suffered significant range losses in the southernmost ecoregion (Fig. 2.2b). A much larger but less intense (up to 20 losses in a single ecoregion) hot spot of species' losses is located in the Prairies ecozone and bordering ecoregions of the Boreal Plains ecozone. Smaller hot spots were found in the southwest corner of the Pacific Maritime ecozone (which contains the city of Vancouver, 12 species losses), and ecoregions of the Atlantic Maritime ecozone (generally 7 - 9 losses per ecoregion). These regions of Canada include the most heavily agricultural parts of the country, but not the most urbanized areas (with the exception of Vancouver).

Equally interesting are the ecoregions containing many imperiled species that have suffered no known or detectable range losses in those ecoregions (i.e., 'cold spots' of species' losses) (Fig. 2.2c). The most notable cold spot is found in the southern Montane Cordillera ecozone.

Individual classes

Patterns of imperiled bird species richness and species' losses resemble those for all species combined (Fig. 2.3a, 2.3b): species richness and species' losses are greatest in the Mixedwood Plains and Prairies ecozones where land is dominated by extensive agriculture and human settlement. The southern Montane Cordillera is also the most noteworthy cold spot for losses of imperiled bird species (Fig. 2.3c). In contrast, richness of imperiled mammal species is greatest in a large area of mountainous and taiga habitat encompassing much of northwestern mainland Canada (Fig. 2.4a); this region is also a cold spot of losses for imperiled mammals (Fig. 2.4c). Listed mammal species have experienced their greatest losses in the Prairies ecozone and bordering ecoregions of the Boreal Plains ecozone (Fig. 2.4b). As with imperiled birds, hot spots of imperiled amphibians and reptiles are found in the southernmost part of Canada. Low sample sizes obscure patterns of declines for amphibians and reptiles, but the southernmost Mixedwood Plains experienced the most extirpations.

Correlates of Losses of COSEWIC–Listed Species

The number of imperiled species lost per ecoregion was strongly correlated with habitat loss and with rates of use of pesticides, but only weakly correlated with human population density (Table 2.2). The number of species lost is also strongly correlated with the total regional species richness. These correlations reflect, in part, the strong climatic gradients in Canada, which have concentrated both agriculture and total species richness in southern Canada (Rivard et al. 2000).

After controlling for the geographic gradient in total richness, the relationship between species losses and herbicide use (transformed to be bivariate normal), is approximately linear (Figure 2.5). There is no evidence of a threshold effect. The relationship between species losses and area in agriculture, after controlling for regional species richness, is similar but noisier (Table 2.3). Models that related imperiled species losses to area treated with herbicides account for 56% – 70% of the variance, compared to models relating losses to area in agriculture (46% - 57%). The statistical effect of herbicides was significant above and beyond the amount of agriculture. Herbicides account for additional variability after accounting for agriculture, whereas the inverse is not true (Table 2.3).

Discussion

These results indicate that the most prominent driver of species losses in Canada is more than simply habitat conversion to agriculture and urbanization. Collectively, the hot spots of species losses in Canada contain 12% of Canada's area, 61% of the human population, 84% of farmland, 87% of lost habitat, and 90% of herbicide-treated croplands. The southernmost ecoregions of the Mixedwood Plains ecozone, where bird, amphibian, and reptile losses are greatest, are densely populated (112 persons/km^2) and 71% of the landscape has human-dominated land-cover (mostly farmland). With more horticultural crops (e.g., fruits and vegetables) than any other ecozone in Canada, agriculture is very chemically–intensive in the Mixedwood Plains (Agriculture and Agri-Food Canada 1998). The Prairies and southern Boreal Plains constitute a large hot spot of losses that, in comparison to the Mixedwood Plains, is less intense for birds but more so for mammals. This area has low human population density (5.2 persons/km^2), but high agricultural intensity. A total of 63% of agricultural pesticide expenditures in Canada are from this area due to vast field crops (e.g. wheat, canola, barley), but the areal rate of use is less intense than in the Mixedwood Plains hot spots.

Although Venter *et al.* (2006) list urbanization and agriculture as the main human activities contributing to habitat loss, and habitat loss as the main cause of species loss, I found that the relationship between species losses and urbanization is weak. Many ecoregions with large population centers (e.g. Montreal, Halifax) or with the longest history of human alteration of the environment (e.g. the St. Lawrence River lowlands and areas surrounding the Bay of Fundy, settled beginning in the 17th century) have had relatively few species losses. Some losses may have occurred in these areas before systematic species inventories occurred. If this is the case, then species' losses will have been underestimated in these regions. While accounts of historic bird distributions appear to be relatively thorough, those of mammals and, particularly, both amphibians and reptiles, appear less so.

Cold spots of losses of listed species were characterized by high amounts of natural area and little use of agricultural pesticides. For mammals, these were typically found in mountainous and northern taiga habitats. However, cold spots of losses of birds and amphibians are located in southern regions with greater human population density and habitat loss, but where neither agriculture land-cover (0.7-14.5% is cropland) nor agricultural pesticide coverage is extensive.

Species losses were more strongly related to herbicide use than to use of other pesticides. Herbicides are by far the most widely used agricultural pesticides in Canada (Agriculture and Agri-Food Canada 1998, Crop Protection Institute of Canada 2000). Agricultural herbicides may lead to species mortality through direct chemical toxicity (e.g.

Raimondo et al. 2007), or through indirect effects on prey species (Freemark and Boutin 1995, Wilson et al. 1999).

The observation that species losses are significantly more strongly related to pesticide use than to agricultural area indicates that something related to agriculture beyond habitat conversion affects imperiled species persistence. However, this study cannot exclude the hypothesis that species declines result from some other characteristic of agriculture that is correlated with pesticide use, rather than from pesticide use *per se*. Areas with high pesticide use are also likely to have very large farms (and consequent habitat homogenization), frequent habitat disturbance (e.g., through use of heavy machinery), low plant diversity, etc. It is possible, therefore, that pesticide use is a surrogate for agricultural intensity in general. Moreover, the marginal effect of herbicides, after controlling for agricultural area, was only moderate. A data set that disentangles this collinearity would be necessary to distinguish between these two competing hypotheses. In practice, such data would be difficult to obtain over large spatial scales.

These results are consistent with the hypothesis that agriculture, irrespective of pesticide use, is a significant contributor to species losses (Krebs et al. 1999, Kerr and Cihlar 2004). There is growing evidence that many aspects of the increasing intensification of agriculture, e.g. monocultures, changes in crop type and harvest methods, etc. (Krebs et al. 1999), can all have negative effects on species.

Two main ideas regarding how to lessen the negative impacts of agriculture on wildlife have been put forth by Green *et al.* (2005). The “wildlife-friendly” option involves reducing the amount of pesticides and fertilizers applied to crops and incorporating more semi-natural land within agricultural areas. The other approach is built around the idea of "land sparing" and involves increasing the yield of current agricultural land in order to spare new land from being converted for agriculture. Current literature suggests that conservationists look at the land sparing approach as a viable option (Balmford et al. 2005, Mattison and Norris 2005). The increase in yield that is recommended by this approach would need to be met through the increased use of pesticides, fertilizers and possibly genetically modified crops (Cassman et al. 2003, Balmford et al. 2005, Green et al. 2005). These results suggest that further research needs to be done into the effects of pesticides on wildlife populations before choosing the land sparing approach as a solution.

The range of variability of factors that potentially influence the persistence of imperiled species may determine the extent to which these results can be generalized beyond the situation in southern Canada. In West Africa, for example, mammal declines have been linked to bushmeat hunting (Brashares et al. 2004). In Canada, the human population is relatively small, agricultural intensity varies greatly, there is relatively little subsistence hunting, and there are only limited areas of severe industrial pollution. In parts of the world where these other factors are more variable, or agricultural use of pesticides is less variable, spatial variation in the persistence of imperiled species may correlate more strongly with other variables. A further test of the hypothesis that declines are specifically related to pesticides would be to examine this relationship in such regions.

This study indicates that hot spots of imperiled species richness can comprise two classes of areas: areas where many imperiled species have suffered range losses (hot spots of species' losses; e.g. birds) and areas where many imperiled species persist with their historic ranges intact (cold spots of species' losses; e.g. mammals). If one examined only the current distribution of imperiled mammal species richness in Canada (Fig. 2.4a), it may appear that, because relatively few imperiled mammals exist in the Prairies ecozone, the survival of mammals is generally not at risk in this region. And, it may appear that mammals are at great risk in the mountainous and taiga regions of western Canada because many imperiled mammals are found in these areas. In contrast, it is clear that imperiled mammals have undergone extensive losses throughout the prairies, but have suffered little loss throughout the western mountain ranges and taiga (Fig 2.4b and c). Identifying and examining hot and cold spots of losses of species, compared with studying only hot spots of imperiled species richness, provides a clearer picture of where species are most threatened and what factors pose a risk to the survival of imperiled species.

In conclusion, my results are consistent with the hypothesis that conversion of natural habitat to human-dominated land cover is a contributor to species losses. However, losses have occurred not simply in areas where native vegetation has been converted to agriculture or human settlement; rather, losses are concentrated in areas where agriculture is chemically-intensive (i.e. widespread areal coverage of pesticides). Either pesticides *per se*, or something correlated with their use (other characteristics of intensive agriculture) apparently contributes to species losses. Conservation strategies to protect endangered species that focus mainly on habitat losses, rather than on patterns of surrounding habitat use, may be inadequate to prevent species losses. In particular, more research is needed on the role that pesticide use plays in species losses and on the possibility of reducing pesticide use as a means to help conserve species.

Acknowledgments

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Chapleau, David Green, Frances Pick, and Anthony Francis provided helpful suggestions and comments.

Tables

Table 2.1: Location, landcover, and agricultural pesticide data for hot and cold spots of losses of COSEWIC–listed species. Hot spots are areas where many imperiled species have suffered historic range losses. Cold spots of losses are areas where many imperiled species currently persist and have not experienced historic range losses. Landcover, pesticide, and population data are from 1991 Statistics Canada census (Statistics Canada 1999).

Hot or Cold Spot	Location	Taxa	Area (10^3 km^2)	% Human Landuse	% Cropland	% Treated with Herbicides	% Treated with Insecticides	Population Density (persons/km^2)
Hot	Mixedwood Plains (2 southern ecoregions)	Total Birds Reptiles	72.2	70.7	39.4	22.5	6.0	112.1
Hot	Mixedwood Plains (southernmost ecoregion)	Amphibians	25.1	89.9	52.0	35.4	10.2	236.6
Hot	Prairies/southern Boreal Plains	Total Mammals Birds	812.5	62.0	31.0	21.9	2.4	5.2
Hot	Atlantic Maritime	Total	201.1	12.0	3.7	0.9	0.4	12.5
Hot	Pacific Maritime (southwestern tip)	Total	4.4	38.8	11.1	3.9	2.5	406.9

Hot or Cold Spot	Location	Taxa	Area (10^3 km^2)	% Human Landuse	% Cropland	% Treated with Herbicides	% Treated with Insecticides	Population Density ($persons/km^2$)
Hot	Pacific Maritime (southern coast and ranges of mainland)	Amphibians	58.3	0.2	0.06	<0.01	<0.01	0.6
Cold	Montane Cordillera (southern)	Total Birds	129.4	5.0	0.7	0.2	0.09	3.3
Cold	Cordillera and Taiga of northwest Canada	Mammals	1352.9	0.05	0.01	<0.01	<0.01	0.05
Cold	Eastern Mixedwood Plains/southern Boreal Shield	Total Birds	111.5	27.3	13.2	5.7	1.0	57.4

Hot or Cold Spot	Location	Taxa	Area (10^3 km^2)	% Human Landuse	% Cropland	% Treated with Herbicides	% Treated with Insecticides	Population Density (persons/km^2)
Cold	Eastern Mixedwood Plains/western Atlantic Maritime	Amphibians	123.1	31.8	14.5	5.6	1.1	55.4

Table 2.2: Simple Pearson correlations between the numbers per ecoregion of imperiled species lost during approximately the last century, extant imperiled species richness (SR), regional species richness (SR), and measures of: agricultural pesticide use, landscape fragmentation, and human population. “Combined” refers to the combination of birds, mammals, amphibians, and reptiles. Correlation coefficients ≥ 0.133, ≥ 0.174, ≥0.190, and ≥0.222 are significant at $P < 0.05$, $P < 0.01$, $P < 0.005$, and $P < 0.001$, respectively.

	Combined Losses $^{0.33}$	Combined SR $^{0.33}$	Imperiled Combined SR$^{0.33}$
Combined Losses $^{0.33}$	--		
Combined SR $^{0.33}$	0.456	--	
Imperiled Combined SR$^{0.33}$	0.775	0.552	--
Habitat loss*, $\log_{10}$	0.736	0.443	0.685
Builtup area, $\log_{10}$	0.502	0.153	0.485
Cropland area, $\log_{10}$	0.737	0.431	0.635
Herbicide-treated area, $\log_{10}$	0.815	0.402	0.675
Insecticide-treated area, $\log_{10}$	0.791	0.337	0.653
Natural area, $\log_{10}$	-0.061	0.034	0.036
Human population, $\log_{10}$	0.492	0.159	0.486
Human population density, $\log_{10}$	0.290	0.062	0.236
Ecoregion area, $\log_{10}$	0.285	0.156	0.384

* measured as the area of human dominated land cover

Table 2.3: Multiple regressions relating the number of losses of imperiled species (birds, mammals, amphibians, and reptiles combined; birds; and mammals) to habitat characteristics in the 86 ecozones across southern Canada that have experienced some habitat loss. Variables were transformed as necessary to improve normality (superscripts indicate power transformations). ΔAIC is the difference in Akaike's Information Criterion between the best model for a given dependent variable and competing models. ΔAIC>10 indicates a significantly inferior model. In all cases, the best model includes total species richness and the area treated with herbicides. Area in crops and human-dominated land cover were significantly poorer predictors of the numbers of species lost per ecozone. All the individual terms in the models reported here were significant at $p<10^{-5}$, except log(area in crops) when log(area treated with herbicides) was already in the model. In those cases, log(area in crops) was not significant ($p>0.05$) , n=86.

Dependent Variable	Independent Variables	Model R^2	ΔAIC
Combined losses$^{0.33}$	Combined species richness$^{0.33}$, log (area treated with herbicides), log (area of cropland)	0.695	--
	Combined species richness$^{0.33}$, log (area treated with herbicides)	0.684	0.8
	Combined species richness$^{0.33}$, log (area of cropland)	0.566	28.2
	Combined species richness$^{0.33}$, log (habitat loss*)	0.563	28.9
	Combined species richness$^{0.33}$	0.230	75.0
Bird losses$^{0.25}$	Bird species richness$^{0.25}$, log (area treated with herbicides)	0.562	--
	Bird species richness$^{0.25}$, log (area treated with herbicides) , log (area of cropland)	0.569	0.7
	Bird species richness$^{0.25}$, log (area of cropland)	0.464	17.4
	Bird species richness$^{0.25}$, log (habitat loss*),	0.444	20.5

	Bird species richness$^{0.25}$	0.132	55.9
Mammal losses	Mammal species richness, log (area treated with herbicides), log (area of cropland)	0.616	--
	Mammal species richness, log (area treated with herbicides)	0.597	2.0
	Mammal species richness, log (area of cropland)	0.469	25.8
	Mammal species richness, log (habitat loss*)	0.490	22.3
	Mammal species richness	0.094	66.2

* measured as the area of human dominated land cover

Figures

Figure 2.1: The terrestrial ecozones (n=15) and ecoregions (n=217; delineated by black lines within ecozones) of Canada.

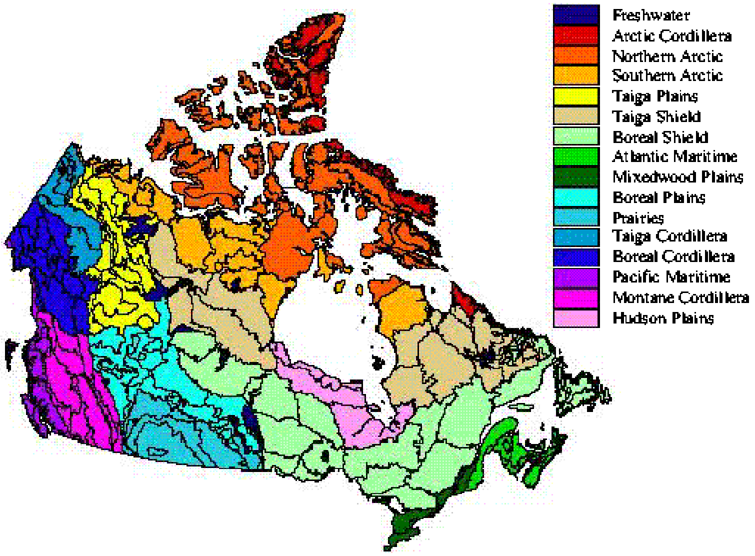


Figure 2.2: Maps of the numbers of extant imperiled species (i.e. species officially designated as endangered, threatened, or vulnerable) per ecoregion in Canada, and of the numbers of imperiled species that have been lost per ecoregion, for birds, mammals, amphibians, and reptiles combined. (a) extant imperiled species; (b) imperiled species lost; (c) extant imperiled species that have suffered no historic range losses in the ecoregion in question, but have undergone losses in other ecoregions (an indicator of cold spots of losses).

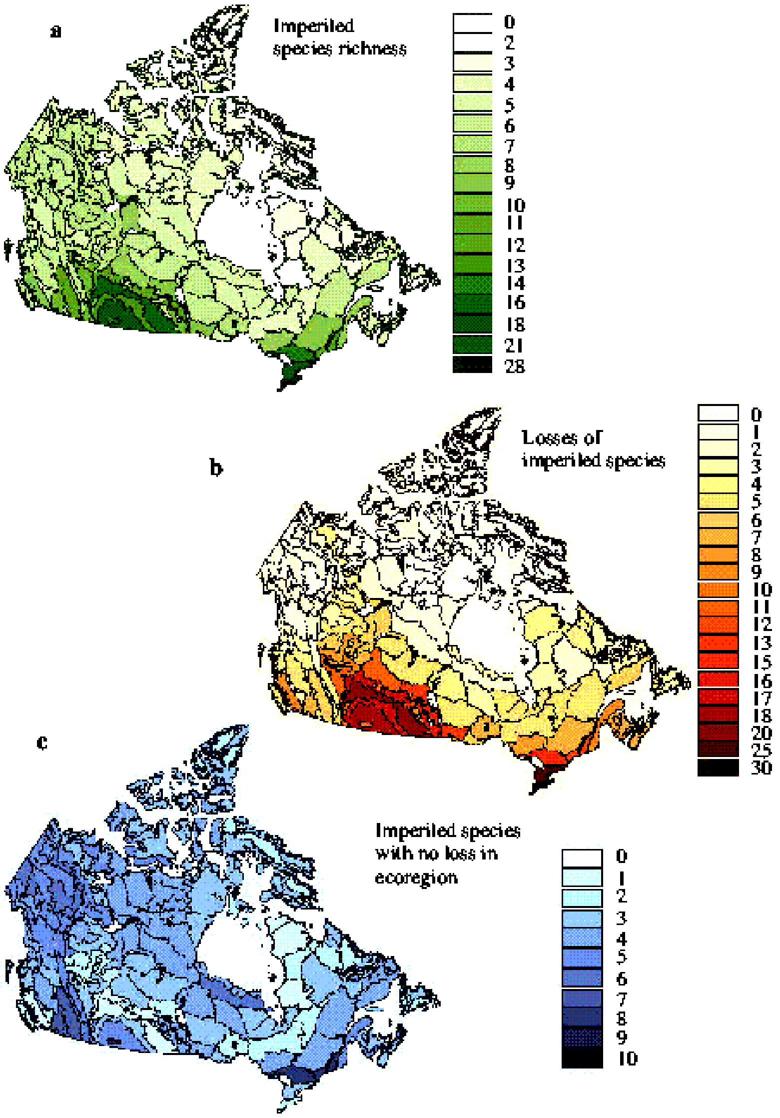

a
Imperiled species richness
0
2
3
4
5
6
7
8
9
10
11
12
13
14
16
18
21
28
b
Losses of imperiled species
0
1
2
3
4
5
6
7
8
9
10
11
12
13
15
16
17
18
20
25
30
c
Imperiled species with no loss in ecoregion
0
1
2
3
4
5
6
7
8
9
10

Figure 2.3: Maps of the numbers of extant imperiled bird species (i.e. species officially designated as endangered, threatened, or vulnerable) per ecoregion in Canada, and of the numbers of imperiled species that have been lost per ecoregion. (a) extant imperiled species; (b) imperiled species lost; (c) extant imperiled species that have suffered no historic range losses in the ecoregion in question, but have undergone losses in other ecoregions (an indicator of cold spots of losses).

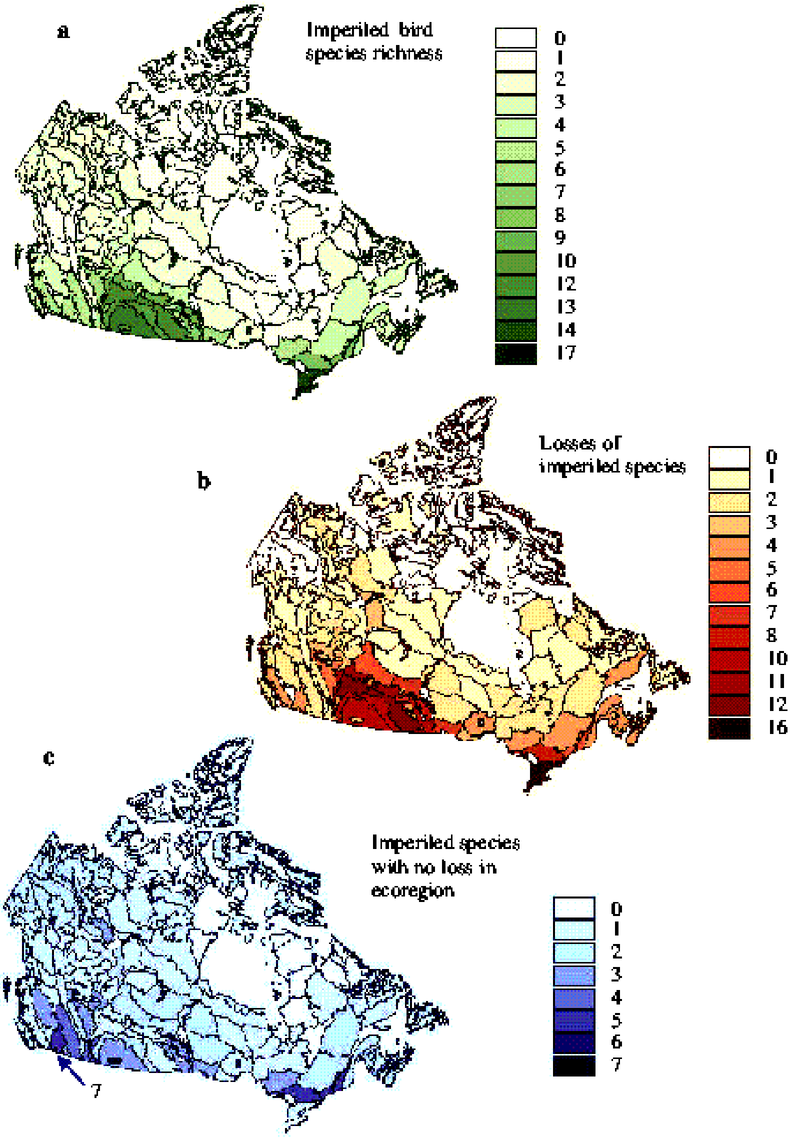

a
Imperiled bird species richness
0
1
2
3
4
5
6
7
8
9
10
12
13
14
17
b
Losses of imperiled species
0
1
2
3
4
5
6
7
8
10
11
12
16
c
Imperiled species with no loss in ecoregion
0
1
2
3
4
5
6
7
7

Figure 2.4: Maps of the numbers of extant imperiled mammal species (i.e. species officially designated as endangered, threatened, or vulnerable) per ecoregion in Canada, and of the numbers of imperiled species that have been lost per ecoregion. (a) extant imperiled species; (b) imperiled species lost; (c) extant imperiled species that have suffered no historic range losses in the ecoregion in question, but have undergone losses in other ecoregions (an indicator of cold spots of losses).

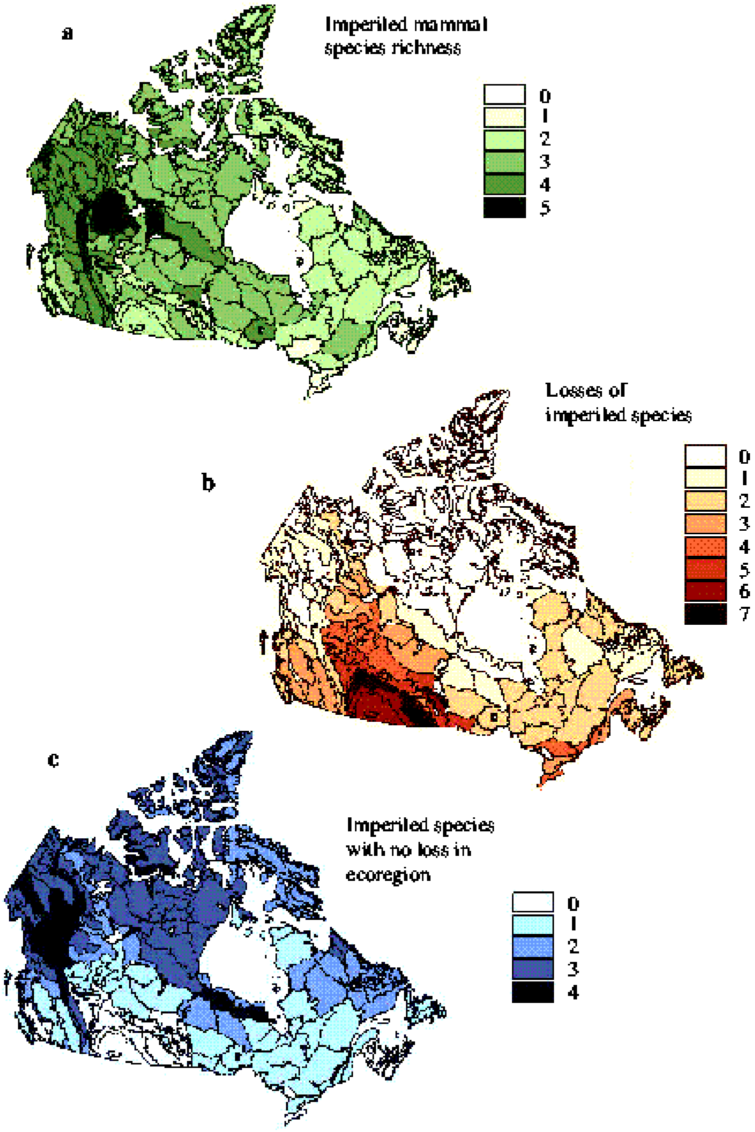
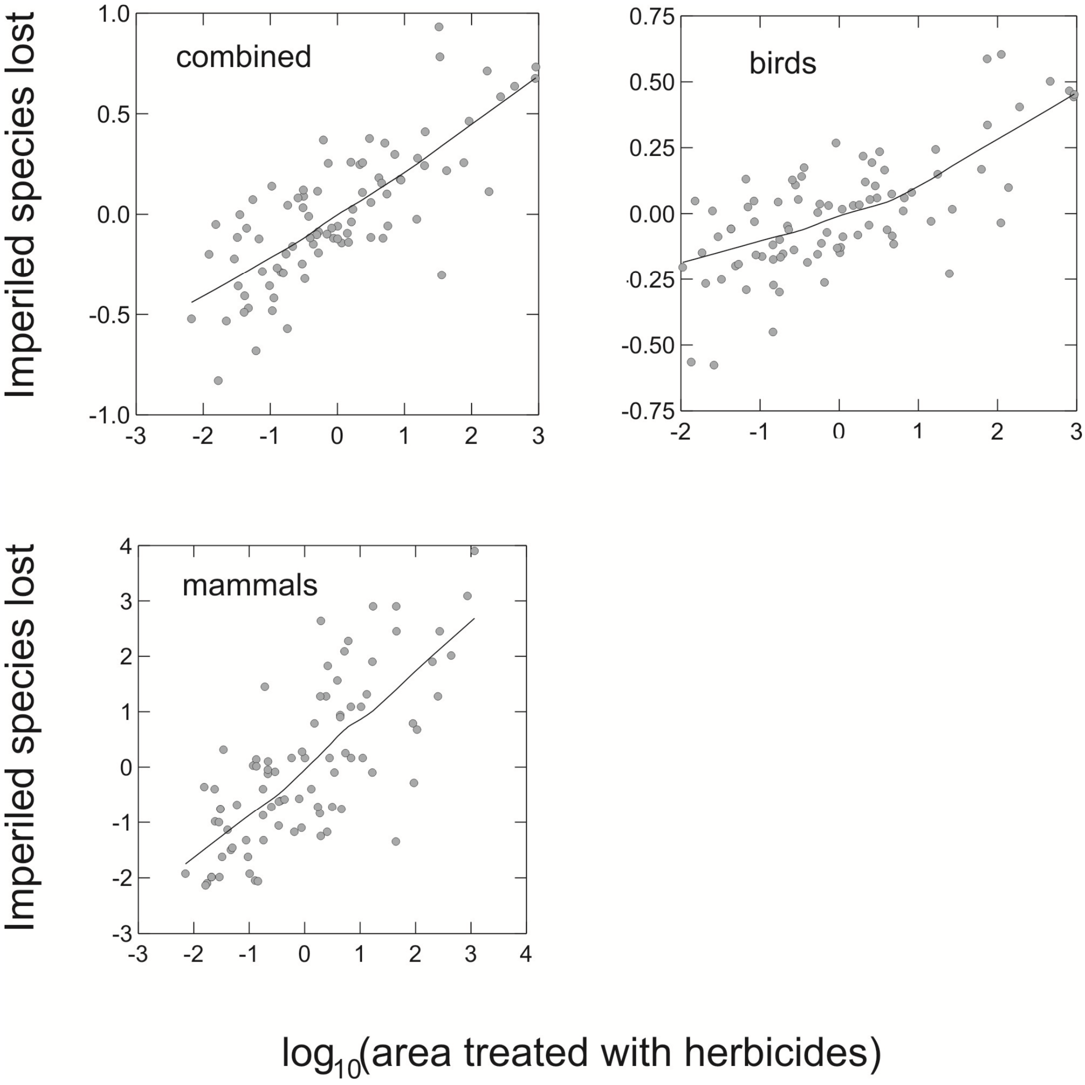

a
Imperiled mammal species richness
0
1
2
3
4
5
b
Losses of imperiled species
0
1
2
3
4
5
6
7
c
Imperiled species with no loss in ecoregion
0
1
2
3
4

Figure 2.5: Residual plots of the numbers of imperiled (a) combined species (bird, mammal, amphibian, and reptile), (b) bird species and (c) mammal species lost per ecoregion in Canada versus area treated with agricultural herbicides, after controlling for regional species richness (see Table 2.2). The statistical effect of regional species richness was removed from the species loss and herbicide variables by performing regression analyses and then using the residuals from these analyses. Variables were transformed to stabilize their variance (combined loss $^{0.33}$, bird loss $^{0.25}$, $\log_{10}$(area treated with herbicides)). Lines on the graphs show LOWESS smoothing functions with tension=0.7.


Imperiled species lost
combined
1.0
0.5
0.0
-0.5
-1.0
-3
-2
-1
0
1
2
3
birds
0.75
0.50
0.25
0.00
-0.25
-0.50
-0.75
-2
-1
0
1
2
3
Imperiled species lost
mammals
4
3
2
1
0
-1
-2
-3
-3
-2
-1
0
1
2
3
4
log10(area treated with herbicides)

CHAPTER 3: DO GLOBAL AMPHIBIAN DECLINES CORRELATE WITH INCREASES IN REMOTELY SENSED UV?

Abstract

The global decline in amphibian populations is one of the most pressing issues in conservation biology yet there is no clear consensus on which factors are driving these declines. Ultraviolet (UV) radiation has been suggested as a cause because radiation has been increasing since the 1970's and amphibians are particularly susceptible to UV damage. Many studies have confirmed that UV can cause serious damage to amphibians. Here, I use a global amphibian population dataset and remotely sensed global UV radiation to examine whether there is a correlation between amphibian population changes and increases in UV radiation at a global spatial scale for numerous amphibian species. The dataset includes 513 amphibian population time series varying from 5-21 years over 1979-1999 from 37 countries (Houlahan 2000). Amphibian populations declined in abundance on average. At individual sites, temporal changes in amphibian abundance are not predictably related to changes in UV intensity. Nor is the global spatial variation in amphibian population trends predictably related to variation in UV temporal trends. It could be that negative effects of UV on individual amphibians do not result in changes at the population level or that factors that affect UV at a local scale are more important to amphibian populations than broad scale UV. However, global increases in UV radiation do not appear to be a major cause of amphibian declines.

Introduction

The global decline in amphibian populations is one of the most pressing issues in conservation biology (Wake 2008). Starting in the 1980's, many studies from geographically diverse locations were reporting local amphibian population declines. By 2000, it was clear that amphibian populations were declining on a global scale (Alford and Richards 1999, Houlahan et al. 2000, Collins and Crump 2009). Houlahan et al. (2000) combined global data on close to 1000 amphibian populations to assess whether the declines were indeed occurring globally. They concluded that populations had undergone sharp declines from the late 1950's to late 1960's followed by a reduced rate of decline into the late 1990's. Amphibians are currently more threatened than any other taxon (Stuart et al. 2004). Approximately 43% of amphibian species are experiencing some level of population decline and as a result, close to one third of species are considered threatened or endangered and as many as 159 species may have gone extinct in recent years (Stuart et al. 2004). These drastic global declines have caused some to speculate that amphibians are at the leading edge of the sixth mass extinction (Wake 2008).

There is consensus that amphibian populations are declining, but it is still not clear which factors are causing the declines. Potential causes of amphibian population declines include: over-exploitation (Warkentin et al. 2009), land use change (Becker et al. 2007), climate change (e.g. Pounds et al. 2006), disease (e.g. Lips et al. 2008), predation (Boone et al. 2007), pollution (e.g. Davidson and Knapp 2007) and ultraviolet (UV) exposure (Bancroft et al. 2008). For reviews of threats, see Collins and Storfer (2003). The amount of evidence varies among the different threats but it is clear that no single factor is responsible for the declines (Blaustein and Kiesecker 2002, Sodhi et al. 2008). The importance of these threats likely varies taxonomically and spatially (Hof et al. 2011) and there are synergistic interactions taking place (e.g. Pounds et al. 2006, Bancroft et al. 2008, Hof et al. 2011).

Of the proposed threats, UV radiation is possibly the most controversial (Bancroft et al. 2008). Ultraviolet radiation first garnered attention as a potential threat to amphibians when a number of amphibian population declines were reported from relatively pristine high elevation areas (Middleton et al. 2001). Ultraviolet radiation is broken into UV-A, UV-B and UV-C based on wavelength. Most UV radiation is absorbed by the atmosphere but some UV-A and UV-B reaches the earth’s surface and has the potential to be damaging to life. UV-B radiation in particular has been increasing since the 1970’s due to stratospheric ozone depletion (Eck et al. 1995) and is the most biologically damaging wavelength due to its ability to damage DNA (Middleton et al. 2001).

Amphibians are particularly susceptible to UV-B damage due to their permeable skin, unshelled eggs and the fact that they seek sunlight to thermoregulate (Croteau et al. 2008). Many laboratory studies and field experiments have confirmed that UV-B can cause lethal and sub-lethal damage to amphibians at all life stages (Blaustein and Bancroft 2007, Croteau et al. 2008). Effects include reduced survivorship of embryos and larva, disruptions in growth and development, developmental malformations and abnormalities, increased susceptibility to disease and behavioural changes (Croteau et al. 2008). A meta-analysis on the effects of UV-B on amphibians (Bancroft et al. 2008) found that UV-B reduced survival 1.9 fold when compared to shielded conditions. However; not all studies have found a negative effect of UV (e.g. Corn 1998, Starnes et al. 2000, Vredenburg et al. 2010).

There is conflicting evidence regarding the role of increasing UV radiation in amphibian population declines. Despite numerous studies showing that UV has the potential to be detrimental to individual amphibians at all life stages, it is not clear whether these effects result in long-term population level declines or extinctions (Beebee and Griffiths 2005, Collins and Crump 2009). Most studies that have shown a deleterious effect of UV have focused on the amphibian egg and larval stages (Schmidt et al. 2005). Yet demographic studies have shown that juvenile and adult survival are the most influential parameters on amphibian population dynamics (Vonesh and De la Cruz 2002, Schmidt et al. 2005).

Even juvenile or adult mortality does not necessarily translate into population declines. If UV is a major contributor to amphibian declines, one would expect that area where UV increased in recent decades would have experienced high rates of population decline. There have been few studies looking at the effect of UV on amphibian populations in the wild. Middleton et al. (2001) looked at 20 sites in Central and South America and found that most sites that were experiencing amphibian declines had experienced increases in UV-B and that UV-B had not increased at sites where amphibian populations were not declining. Davidson et al. (2002) looked at the spatial pattern of decline of four amphibian species in California in relation to pesticide use, habitat loss, UV and climate change. They found that the spatial variation in rates of declines were not consistent with UV increases. Adams et al. (2005) looked at the spatial distribution of eight amphibian species in relation to UV and found moderate evidence for a negative relationship for two species and no relationship for 6 species. A study of boreal toads found that their distribution was not limited by UV-B (Hossack et al. 2006). So while it is clear that UV radiation is harmful to amphibians, evidence that the negative effects of increasing UV radiation translate into long-term population level declines in the wild is lacking.

The goal of this study is to test whether recent global amphibian population changes were correlated with broad scale increases in ambient UV radiation. I use the global amphibian population dataset collected by Houlahan et al. (2000) and remotely sensed global UV radiation to examine whether temporal changes in amphibian abundance were related to changes in UV intensity at a global spatial scale for numerous amphibian species. Because I am primarily interested in whether amphibian population declines occurred in response to increases in UV, I focused the analysis on sites where UV has increased; however, I also include the analysis for all sites for comparison. I investigated whether there is a time lag in the effect of increasing UV radiation on amphibian population trends. It is possible that the negative effects of UV exposure do not show up immediately and will have a stronger effect on amphibian populations in subsequent years. I investigate whether this relationship is stronger for species that are more susceptible to the negative effects of UV. I also look to see if there is spatial autocorrelation in the relationship between abundance and UV as this could indicate that UV is interacting with other threats and/or environmental variables. Additionally, I test if the spatial variation in amphibian population trends is related to the trends in mean UV. Previous studies of the effect of UV on amphibian populations have all been regional in their spatial extent; this is the first global analysis.

Methods

To assess amphibian population trends, I used the global dataset of relative abundance time series assembled by Houlahan et al. (2000). They collected time series data on global amphibian population sizes from journal publications, technical reports and unpublished datasets. The original dataset included 936 amphibian populations from 37 countries. The time series varied in duration from 2-31 years over the period 1940 to 1998.

For this analysis, the dataset was limited to include only those populations with at least three years of data between 1979 and 1999 to correspond with the years for which UV data were available. I further restricted the data to populations with at least one year where population size was greater than 5 individuals.

Ultraviolet irradiances for each site were estimated from the Total Ozone Mapping Spectrometer (TOMS) aboard NASA’s Nimbus 7 and Earth Probe satellites. The TOMS sensor measured backscattered radiation in six wavelength channels, which was used to calculate ozone and aerosol amounts, SO_2 concentration, elevation and cloud cover. These estimates were then used to produce a data product called daily erythemal local noon irradiance, which provides daily estimates of the incoming UV irradiance (W/m^2) at local noon (NASA 2009). The data are weighted for different wavelengths according to the susceptibility of Caucasian skin to sun burn at that wavelength. The result can be interpreted as the potential for biological damage due to solar UV radiation. Many other amphibian studies have looked specifically at UV-B radiation. The erythemal irradiance includes all wavelengths; however, because it is weighted for shorter wavelengths (i.e. UV-B), it is highly correlated with UV-B estimates. The spatial resolution of the data is 1.00 degree latitude by 1.25 degrees longitude. The erythemal UV irradiances for 1979-2000 were downloaded from the public NASA Mirador FTP server. There are missing values in the UV data; most notably there are no data for 1993 - 1995.

Remotely sensed UV data have been show to correlate closely with ground based estimates. Daily estimates will differ from ground values due to changing cloud and aerosol conditions, but values averaged or integrated over a longer time period (at least a week) are very comparable to ground based estimates (Herman et al. 1999). Eck et al. (1995) compared

TOMS UV estimates with ground based Brewer UV measurements and found that the differences were similar to the amount of variation found in simultaneous ground based instruments. The differences decreased significantly when the values were averaged over longer time periods.

Yearly UV values were calculated from the daily data for each amphibian site to investigate both a linear and threshold effect of UV. For each site in the amphibian population data set, the yearly maximum, mean and standard deviation for the daily erythemal irradiance were calculated. For the threshold analysis, I calculated the number of days per year where UV irradiance was over a number of threshold values. I used various percentiles between the 50th and 90th percentile as different threshold values as no obvious value exists in the literature. For each site, I correlated mean yearly UV with time over the time period corresponding to the population data to determine at which sites UV has increased over time and included sites where the slope was greater than zero.

To test for a relationship between amphibian declines and increases in UV irradiance I calculated the non-parametric Spearman's rank correlation coefficient between amphibian relative abundance and each of the UV variables for each population. I did this for both all sites, and restricting the data to sites where UV irradiance increased over the time period.

I looked at the distribution of correlation coefficients to see if there were more negative correlations between abundance and UV than positive correlations. The Wilcoxon signed rank test was used to test the hypothesis that the median correlation coefficient was less than zero. I account for the different time series length by calculating the weighted mean using the number of years of data as a weighting variable. I repeated the analysis including only populations with at least 10 years of data; it is possible that studies of shorter duration may not be long enough to show a trend in abundance and may mask an overall effect. To investigate whether populations that are geographically close to one another have similar trends in abundance, I calculated a global Moran’s I on the distribution of correlation coefficients.

A randomization test was calculated to test whether there were more negative correlations than would be expected by chance. Given the *a priori* information that amphibian populations in general have been declining, and UV radiation has been increasing over time, there may be more negative relationships than positive relationships even if there is no effect of UV radiation on amphibian populations. I therefore created a null expectation by pairing a randomly selected amphibian population time series with a UV time series from a randomly selected site. I then reduced the UV data to the same years that the amphibian time series covered, and I calculated the Spearman’s rank correlation coefficient. I repeated this process 10,000 times to get a null model distribution of correlation coefficients. I used the Mann Whitney test to see if the observed distribution of Spearman rank correlations was significantly different from the randomly sampled distribution.

I repeated these methods for a number of subsequent analyses. I included a one year and two year time lag between UV irradiation and amphibian abundance, and only included susceptible species. Susceptible species were defined as species that breed aquatically and lay uncovered, shallow eggs. Species that breed terrestrially generally have rocks or canopy protecting their eggs from UV exposure while aquatic breeders are more likely to be susceptible to UV damage. The dissolved organic matter (DOM) in water bodies affects the rate at which UV is attenuated, but generally, the amount of UV will decrease with water depth, so species that oviposit in shallow water may be more susceptible. I define shallow as less than 10 cm from the surface. Breeding behaviours for each species were taken from various books and web resources (see Appendix 3 for details).

I also looked at the spatial variation in amphibian population trends and tested if they are related to spatial variation in UV trends. In other words, are places where amphibians are declining places where UV is increasing? I ask this because it is possible that short term temporal variation in amphibian abundance and/or UV irradiance could mask a relationship between the two at individual sites. Both amphibian population time series and UV irradiance have been shown to have large annual variation (Marsh 2001; Collins & Halliday 2005). In order to assess this, I looked at the spatial relationship between amphibian population trends and change in UV. I estimated the amphibian population trend and the change in UV over time by calculating the Spearman's correlation between time and amphibian relative abundance and time and UV irradiance. I then calculated the correlation coefficient between change in relative abundance over time and change in UV over time.

Results

The final dataset included 513 amphibian populations and 99 species. The mean duration of the amphibian population time series was 7 years with studies ranging from 3 to 17 years. Amphibian populations were declining on average with more populations decreasing over time than increasing.

There was no consistent relationship between amphibian relative abundance and UV irradiance. Correlations between relative abundance and mean UV, maximum UV and UV standard deviation were consistent. Relationships were slightly stronger for mean yearly UV irradiance so I present these results. In no case did the randomization test yield different results than the Wilcoxon test, so only the Wilcoxon p-value is shown. At sites where UV has increased, the median correlation coefficient between relative abundance and UV irradiance is -0.11 and not significantly different from zero (p=0.07). For all populations, the median correlation coefficient is -0.05 (Fig 3.1a). The median is not significantly different from zero (p=0.37). Limiting the analysis to populations with at least 10 years of abundance and UV data did not change the results (Fig 3.1b; median Spearman's Rank correlation coefficient = -0.068, p=0.524). The correlations were not spatially autocorrelated (Fig. 3.2; Moran's I = 0.11).

The threshold UV variable was slightly more strongly related to amphibian population declines than to mean UV, but the relationship is still quite weak. For the various percentiles between 50 and 95 that I investigated as possible UV thresholds, the 60th percentile had the strongest relationship with abundance. All UV threshold results presented from this point use the number of days per year where UV irradiance is greater than the 60th percentile. For all populations, the median correlation coefficient between relative abundance and threshold UV is -0.14 which is significantly different from zero (p=0.017; Table 3.1).

There is not a strong time lag effect of UV on amphibian abundance. Including all populations, there is significant but very small negative relationship between amphibian abundance and a one year lag effect of UV irradiance (Fig 3.3a, median correlation coefficient = -0.09, p=0.026). This relationship is no longer significant when looking at only the longer time series (median =-0.07, p=0.64). Analysis including a two-year lag produced similar results (Fig. 3.3b, Table 3.1). Neither the one nor two year time lags where significant when using the threshold UV variable.

Susceptible species were not more strongly affected by UV. Limiting the analysis to species that breed in aquatic environments and lay shallow, uncovered eggs results in a median correlation coefficient of -0.07 that is not significantly different from zero (p=0.38). When using the threshold UV variable, the median correlation coefficient was -0.064 which is significantly different from zero (p=0.014).

The spatial variation in amphibian abundance trends was not correlated with trends in UV irradiation. Over all sites, the average change in amphibian relative abundance over time is -0.11. The average change in UV over time is 0.4. The spatial variation in abundance trends was not correlated with trends in UV (rho=0.068, p=0.15).

Discussion

I did not find evidence to support the hypothesis that global increases in UV during the 1940's to 1990's were a main driver in global amphibian population declines. There was no consistent relationship between amphibian relative abundance and UV irradiance. The relationship does not get materially stronger by including time lags, by pooling over all species, by limiting analysis to the species that should be most sensitive to UV, or otherwise manipulating the data. Additionally, the spatial variation in abundance trends was not correlated with trends in UV.

These results corroborate other studies that have shown little effect of UV at the population level for amphibians. Davidson et al. (2002) found that the spatial pattern of declines of four amphibian species in California was not consistent with UV increases. Adams et al. (2005) found little evidence that the distribution patterns of 8 amphibian species in western North America were negatively related to UV. A study of boreal toads found that their distribution was not limited by UV-B (Hossack et al. 2006).

It is possible that aspects of the local environment and amphibian breeding behaviour mitigate the harmful effects of UV. The amount of UV radiation that is able to penetrate freshwater depends on the dissolved organic matter (DOM), which can vary dramatically both spatially and temporally (Brooks et al. 2005). Some studies have shown that the DOM in amphibian breeding habitats can be high enough to reduce UV exposure to a level that is not harmful (Palen et al. 2002, Palen and Schindler 2010). There is also evidence that amphibians may modify breeding phenology, oviposition depth and behaviour (e.g. covering eggs with leaves) to avoid UV exposure (Corn and Muths 2002, Calfee et al. 2010, Palen and Schindler 2010). However; Searle et al. (2010) looked at the effects of UV along with other stressors in a laboratory environment and found that larva did not modify their behaviour to avoid exposure. These factors mostly afford protection to embryos while still leaving later life stages open to the damaging effects of UV (Blaustein et al. 2004) but there are some laboratory and field evidence for behavioural avoidance of UV in adult frogs (Han et al. 2007).

It is also likely that increased exposure to UV radiation is interacting with other threats including predation, disease and exposure to toxins. This could make it harder to find a strong direct effect of UV radiation. Cues that simulate predation have been shown to amplify the lethal effects of UV-B on tadpoles (Alton et al. 2010). Amphibians are susceptible to a number of infectious diseases, but chytridiomycosis caused by the chytrid fungus *Batrachochytrium dendrobatidis,* is one of the most concerning as it can spread quickly and lead to high mortality (Lips et al. 2006). There is speculation that there could be an interaction between UV-B and chytrid, where UV-B exposure can interfere with the amphibian's normal immune response and lead to increases susceptibility to the disease (Blaustein and Kiesecker 2002). This interaction could be due in part to changes in climate (Kiesecker et al. 2001). However, not all studies have found a synergistic effect between chytrid and UV (Searle et al. 2010). UV can also affect the toxicity of pesticides (Puglis and Boone 2011) and interact synergistically with various other stressors (Bancroft et al. 2008).

The amphibian population dataset I use is one the largest available for time series data, but it does have taxonomic and biogeographic limitations. It is likely that the effect of UV varies among regions, species and even populations (Bancroft et al. 2008). The data come primarily from North America and Europe with large areas unrepresented. The dataset includes only 99 amphibian species, of which most are widespread common species (e.g. *R. temporaria, B. bufo,* and *R. arvalis*). Species have different degrees of susceptibility to the effects of UV (Blaustein and Belden 2003) so these results may not be applicable for all species (Schiesari et al. 2007). So while I cannot rule out that UV may be contributing factor to declines for some amphibians, it does not appear to be a general pattern.

There are limitations to using remotely sensed data to assess the effect of UV on amphibian populations (Middleton et al. 2001, Blaustein et al. 2004). The large spatial scale of the remotely sensed UV data and the fact that it is calculated using average elevation over the entire area means that UV irradiance is underestimated for high elevation areas. There are few high elevation sites in the dataset so this is unlikely to be a problem. Remotely sensed measures of UV radiation are going to differ from the amount of UV radiation amphibians are exposed to during their lifetime as that is affected by numerous other factors of the local environment and amphibian behaviour. But here I am interested in whether the broad scale increases in ambient UV radiation are related to amphibian declines. Remotely sensed UV data are the only estimates available that cover the spatial and temporal periods of the dataset.

UV radiation is one of the most controversial threats to global amphibian populations. While it is clear that high levels of UV radiation are harmful to amphibians at all life cycles, I fail to find evidence that increasing global UV radiation is a main cause of global amphibian population declines. It could be that negative effects of UV on individual amphibians do not result in changes at the population level or that factors that affect UV at a local scale are more important to amphibian populations than broad scale UV. However, global increases in UV radiation do not appear to be a major cause of amphibian declines. While it is not difficult to postulate possible ways that UV could affect amphibians, the fact remains that regional UV changes contributes very little to the ability to predict their population declines.

Acknowledgements

I would like to thank Jeff Houlahan for advice and feedback on this study as well as access to the amphibian population dataset. C.S. Findlay, B.R. Schmidt, A.H. Meyer and S.L. Kuzmin who put together the dataset and Mona’a Malik for her preliminary study on UV and amphibian populations.

Tables

Table 3.1: Median and weighted mean correlation coefficient from the Spearman's Rank correlation coefficient between amphibian population and UV for various subsets of the data. P-Value is for a Wilcoxon test to see if the median is less than zero.

Analysis	**UV Variable**	**Median**	**Weighted mean**	**p-value (Wilcoxon)**	**N**
All data	Mean	-0.05	-0.022	0.371	464
1 year lag	Mean	-0.088	-0.046	0.026**	308
2 year lag	Mean	-0.08	-0.06	0.001**	234
UV increasing	Mean	-0.11	-0.047	0.07	294
UV increasing, 1 yr lag	Mean	-0.061	-0.026	0.38	186
UV increasing, 2 yr lag	Mean	-0.028	-0.027	0.41	141
>10 years data	Mean	-0.068	-0.036	0.524	60
>10 years, 1 yr lag	Mean	-0.07	-0.017	0.64	60

>10 years, 2 yr lag	Mean	-0.01	-0.006	0.71	60
All data	Threshold	-0.14	-0.055	0.017**	459
1 year lag	Threshold	-0.11	-0.042	0.084	307
2 year lag	Threshold	0	-0.011	0.68	232
Aquatic species	Mean	-0.05	-0.023	0.43	379
Aquatic, shallow, uncovered species	Mean	-0.07	-0.018	0.38	321
Aquatic species	Threshold	-0.14	-0.052	0.035**	379
Aquatic, shallow, uncovered species	Threshold	-0.15	-0.064	0.014**	321

Figures

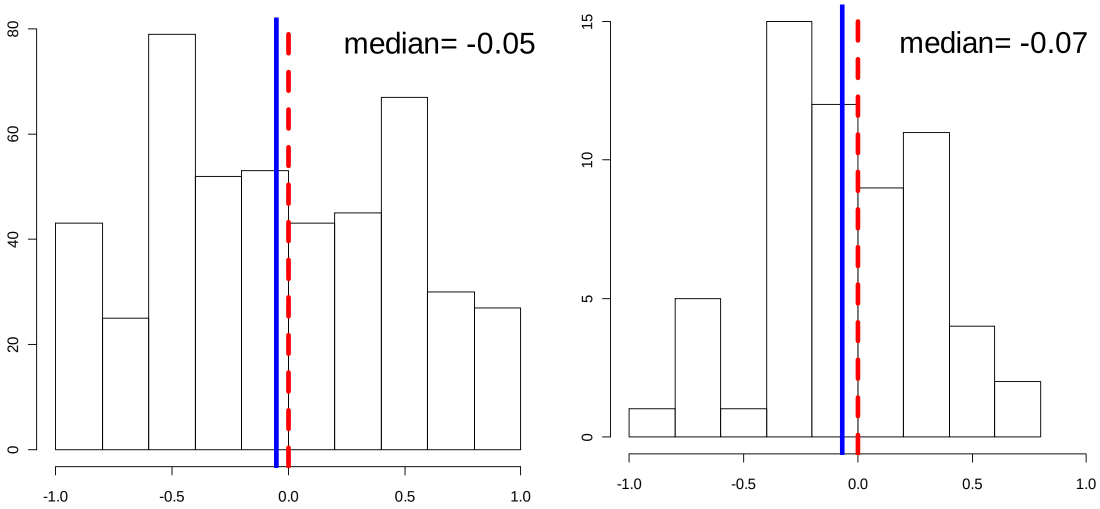


Figure 3.1: Distribution of correlations coefficients between amphibian relative abundance and mean yearly UV for a) all populations and b) populations with over 10 years of data. The dotted line represents zero and the solid line represents the median.

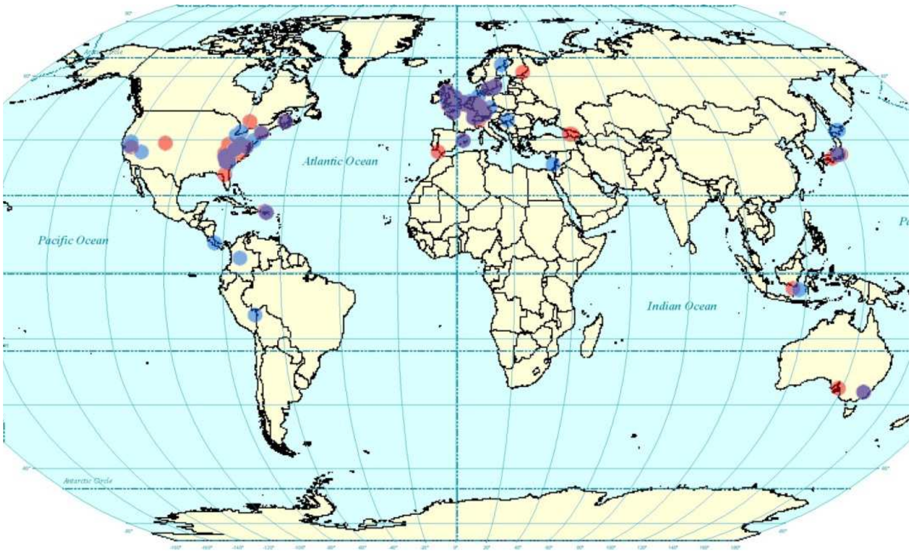


Figure 3.2: Map of the distribution of correlation coefficients between amphibian relative abundance and mean yearly UV. Red points represent negative correlation and blue points represent positive correlations.

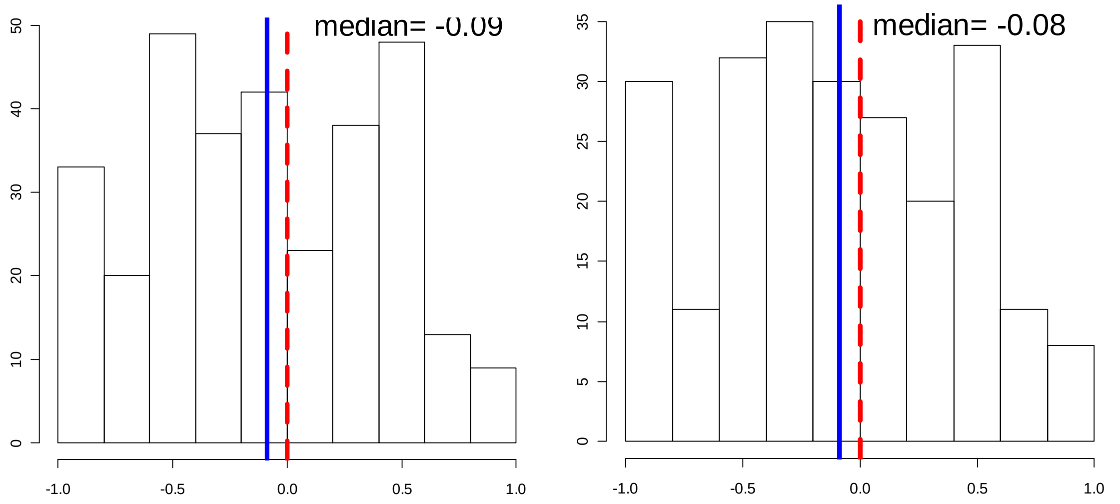


Figure 3.3: Distribution of correlation coefficients between amphibian relative abundance and mean yearly UV for a) one year UV time lag and b) two year UV time lag. The dotted line represents zero and the solid line represents the median.

CHAPTER 4: DO ANTHROPOGENIC STRESSORS AFFECT TEMPORAL VARIABILITY IN ABUNDANCE OF NORTH AMERICAN BREEDING BIRDS?

Abstract

The question of what drives variability in species abundance through time is central to ecology and conservation biology. Many theoretical and empirical studies have shown that species' extinction risk is related not only to mean population size, but also to temporal variability around that mean. Most conservation research has focused on population size and trends in abundance; however, variability *per se* may be a useful indicator of population health and persistence. Here, I tested the hypothesis that variability in abundance of North American breeding birds is affected by: a) habitat conversion to human land cover, and b) climatic changes and variability. Measuring population variability can be challenging; variability is closely related to mean abundance following Taylor's power law. I used residuals from a Taylor power law regression calculated for each species as measure of variability that is independent of mean abundance. Residuals were averaged for all species on each Breeding Bird Survey route and related to: a) the proportion of human-dominated land cover surrounding the route, b) inter-annual variability in minimum annual temperature on each route, and c) the slope of temperature as a function of year since 1966. Variability in species' abundance, after accounting for mean abundance, is not systematically greater in areas of high human-dominated land cover or climate change. Rather, it appears that areas with a high proportion of human-dominated cover come to have a greater proportion of highly abundant, and thus more variable, species. This is a small piece of good news for bird conservation, as other studies have suggested that increased variability can be an indicator of population stress even before changes in trends in abundance are detected.

Introduction

What drives variability in species abundance through time? Many theoretical and empirical studies have shown that species' extinction risk is related to population size and to temporal variability in population size (Pimm 1991, Vucetich et al. 2000, Inchausti and Halley 2003). Most conservation research has focused on population size and trends in abundance; however, variability *per se* may be a useful indicator of population health and stability (Fraterrigo and Rusak 2008, Mellin et al. 2010). High variability can lead to bottlenecks and increase the likelihood of the population falling below its minimum viable population density (Melbourne and Hastings 2008). When all other factors are equal, populations that are more variable will have a higher probability of extinction. In order to conserve species, it is essential to understand what factors drive temporal variability of species population abundance.

The most consistent predictor of temporal variability is population size. Taylor's power law (TPL) predicts that (temporal or spatial) variability (σ^2) is positively related to mean abundance (μ) according to the power law $\sigma^2 = \alpha\mu^\beta$ (Taylor 1961), where α and β are empirical constants. The relationship between σ^2 and μ is usually plotted on a log-log plot where the slope equals β. The value of β is population specific; it usually ranges between values of one and two but it is not constrained within this range (Samaniego et al. 2012). Taylor's power law has been demonstrated for over 400 species in various environments (e.g. Taylor and Woiwod 1982). This pattern is thought to arise from species aggregation in space and time, but there is still debate around the relative contribution of density dependent processes (Murdoch 1994), stochasticity and mathematical artifacts associated with populations (Samaniego et al. 2012). Variability can also be driven by changes in demographic parameters in response to environmental variation (Grenfell et al. 1998).

Anthropogenic disturbances can result in increased variability, even when there are no detectable trends in mean abundance. For example, Warwick and Clark (1993) found that increased variability was a symptom of stress in marine communities. Hsieh et al. (2006) demonstrated that fishing elevated the variability of exploited species, even when these species did not appear to be declining. Mellin et al. (2010) observed that temporal variability of fish populations in the Great Barrier Reef was greater on small and isolated reefs. From this, they inferred that those populations were at greater risk from perturbations, although they did not actually observe the effects of any perturbations. Fraterrigo and Rusak (2008) proposed a conceptual model for how disturbance can affect both spatial and temporal variability of ecological responses. Yet, is it generally true that populations subjected to prominent anthropogenic stressors have increased variability?

In the present study, I examine two of the anthropogenic stressors most discussed in recent literature: conversion of natural habitat to human-dominated land cover, and climate change. I test whether the temporal variability in the abundance of North American breeding birds is greater in areas more affected by these stressors. I use data from the North American Breeding Bird Survey (BBS) to test this hypothesis. The BBS is one of the longest running surveys of species abundances available, making it suitable for studying population variability over time. I predict that species abundance will be more variable at routes that have greater levels of anthropogenic stress.

Habitat conversion/loss is considered to be one of the main causes of species declines (Wilcove et al. 1998) and there are many examples of human land use affecting bird populations. Abundance appears to be negatively related to human land use for most species (Lepczyk et al. 2008). In the present study, I look at the proportion of human-dominated land cover surrounding each BBS route as a measure of human land use.

I include two climate variables as possible stressors: directional climate change in recent decades, and variance in climatic variables. There is evidence that North American breeding bird populations track weather variability (Sillett et al. 2000). Climate change, both in terms of magnitude of change and increasing frequency of climatic events, is suspected of being a main stressor for species (Walther et al. 2002). To my knowledge, this is the first study of how these factors affect variability in BBS species.

Quantifying variability in a way that is independent from mean abundance and comparable over populations is surprisingly difficult (Gaston and McArdle 1994). In order to account for the relationship between mean abundance and variability, I use residuals from a Taylor's Power law (TPL) regression as a measure of variability, where positive residuals represent populations or routes with higher than expected variability. I predict that temporal variability in abundance will be higher on BBS routes that have a higher proportion of human-dominated land cover, higher climate change and/or greater climate variability.

Methods

I used data from the North American BBS from 1966-2010 (Sauer et al. 2011). The BBS is one of the longest running and most extensive datasets available for species' abundances. Each year, skilled observers collect species abundance information along roadside survey routes during the breeding season (June for most of the U.S.). Close to 4000 routes have been surveyed since the start of the BBS in 1966, generating data for more than 400 species. The routes are 39.4 km long and are broken up into 50 stops at 0.8 km intervals.

At each stop, all the birds seen or heard during a three minute period are recorded. The species counts are an index of relative abundance, not a complete population count. However, it is frequently assumed that changes in these counts are representative of population abundance (Sauer et al. 1997). I only included passerine species in the analysis because they are more easily detected from the roadside and thus are best suited for the BBS methodology (Howe et al. 1989). I only included routes in years where the BBS quality standards were met; this excludes routs that were not surveyed during the appropriate time of year, routes that were not started at the appropriate time and routes where the weather conditions were not appropriate for observing birds.

Estimates of species abundance from the BBS data are influenced by a number of methodological factors including: observer bias (Sauer et al. 1994), within observer bias (first time effects, age)(Kendall et al. 1996) and interference from changing traffic frequency (Griffith et al. 2010). A number of corrections and modifications for dealing with the BBS data have been proposed, but they are mostly for correcting long term trends in abundance. I have not applied any such corrections, as it is unclear how they would affect variance estimates. Rather, I assume that any biases in estimates of species' abundances are not systematically related to either human land cover or climate change. I assume that they simply add random noise to the relationships I report.

I used residuals from Taylor Power Law (TPL) regressions calculated for each species, and for all species combined, as measures of variability after accounting for mean abundance. To do this, I first calculated mean abundance and variance for each species on each route over the time period of available data. I then regressed natural log variance on natural log abundance for a given species using all routes on which the species was present. I also calculated a combined TPL regression for all species. I then extracted the residuals from each TPL regression to use as a measure of variability, standardized for mean abundance, on each route (Leps 1993). Routes with positive residuals indicate higher than expected variability. I also calculated the variance in natural log abundance for each species as an additional measure of variability for comparison.

There are a number of statistical issues with calculating variability and the TPL relationship. Gaston and McArdle (1994) identified three data requirements for calculating mean-variance relationships: more than 15 samples from which variance is calculated (years in this case), more than five variance-mean pairs (routes per species), and abundance values that encompass at least two orders of magnitude. Further, variance estimates may be biased when mean abundance is low (Leps 1993). I therefore excluded cases that failed to meet all of the above criteria.

Shape files for each BBS route were obtained from the National Atlas of the United States (USGS-PWRC 2006). Using ArcGIS 10 (ESRI 2011), I created a 1 km buffer around each 39.4 km route, resulting in an average total area of 90 km^2. Studies have looked at how birds are affected by landscape characteristics using 0.1 km, 1 km and 10 km buffers and have found that the buffer size that performs best is both species and variable specific (Thogmartin et al. 2004, Fearer et al. 2007).Variation of habitat characteristics over broad spatial extents is strongly collinear at the three different buffer sizes (r values range from 0.86 to 0.94). Below, I only present results using the intermediate buffer of 1 km. Albers conic equal area projection was used for all spatial analysis.

The proportion of human-dominated land cover was calculated for each buffered route. Land cover data for 2011 were obtained from the National Land Cover Database

(NLCD 2011) derived from Landsat Thematic Mapper satellite data (Vogelmann et al. 2001). The data have a spatial resolution of 30 metres and have 16 land cover classifications (excluding those only found in Alaska). I reclassified the original classifications into human-dominated and natural land covers. Low-, medium- and high-intensity developed land, open-space developed, pasture/hay, cultivated crops, and barren land were classified as human-dominated land covers. Deciduous, evergreen and mixed forest, shrub/scrub, grassland, woody wetlands and emergent herbaceous wetlands were classified as natural land covers. Open water and perennial ice/snow cover were omitted. I also analyzed population variability as a function of four separate human-dominated land cover categories: developed, pasture/hay, cropland and barren rather than the aggregated human-dominated cover. The results of the two sets of analyses were qualitatively quite similar. I therefore present only the simpler, aggregated human-dominated land cover analysis below.

I estimated both climate change and climate variability in each BBS route buffer. Annual minimum temperatures from 1966 to 2010 were obtained from the PRISM Climate Group. The PRISM models use weather station data with a digital elevation model to interpolate climate data (Daly et al. 1994). The spatial resolution of the data is 4 km. I calculated the variance in minimum temperature over the time period for each route. I quantified directional temperature change by the slope of a regression of annual minimum temperature as a function of year.

I modeled the mean TPL residual (over all species) for each route as a function of the land use and climate variables. The mean TPL residual for each route was used as the dependent variable in the models, where positive values indicate higher than expected variability.

Finally, I tested whether species with different habitat preferences related differently to human land use and climate changes. Species were classified based on their main habitat preference. Terrestrial species were classified as preferring open habitat, edge, or forest. Wetland species were classified as open-water, coastal or wetland. I used the same classifications as Valiela and Martinetto (2007). For species not classified there, I used the habitat descriptions from Pool (2005). See Appendix 4 for the list of species habitat classifications.

Results

Variance in natural log abundance was significantly related to land cover and climate change ($p<0.001$, $R^2=0.22$). Population abundance is significantly more variable in areas of high human-dominated land cover (Fig. 4.1a). Population variance is also significantly related to both directional temperature change and to inter-annual temperature variability. However, these two variables are collinear ($r=0.59$). A multiple regression including temperature change had a lower AIC value than the model including climate variability, so I present those results here. Population abundance is actually *less* variable in areas where temperature increased most; however, the effect is quite weak ($R^2 = 0.03$ Fig 4.1b).

After controlling for differences in mean abundance by using TPL, there is considerable variation in the mean TPL residual over all species on each route. The mean TPL residual for all species on a route varies from -1.65 (i.e., species' abundances are less variable, by a factor of 5, than on an average route) to +1.88 (i.e., species' abundances are >6 times more variable than on the typical route). There is no obvious spatial pattern across the United States in where species' abundances are variable and where they are not.

The TPL residuals were not strongly related to any of the independent variables. The residuals were significantly related to the proportion of human-dominated land cover ($p=0.01$), but land cover only explained 0.3% of the variation (Fig. 4.2a). TPL residuals were not significantly related to either temperature variability or directional change in temperature (Fig. 4.2b). The analysis using residuals from the TPL regression for all species combined also showed similar results, as did the results that included only forest species.

The fact that population variability relates to human-dominated land cover, but the TPL residuals do not, means that the relationship between population variability and human land cover is entirely driven by the close relationship between mean abundance and land cover. In other words, bird populations are larger, on average, in areas with more human-dominated cover ($p<0.001$, $R^2=0.19$, Fig. 4.3b). Because populations are larger, they are also more variable, as expected from the TPL ($R^2=0.94$, Fig. 4.3a). Human land cover explains no additional variance when abundance is included in the model ($p=0.20$).

I investigated two possible hypotheses for the somewhat counterintuitive positive relationship between abundance and human-dominated land cover. The productivity hypothesis proposes that areas that are more productive can support more individuals and species, and that they are also places where humans settle, causing a positive relationship between abundance (and often richness) and human development (Evans and Gaston 2005). A second hypothesis is that the relationship is driven by a few open habitat/edge species that have a positive relationship with human land use and/or are present on more routes at high abundance. These species could thus have a disproportionate influence on the overall relationship. I investigated this by looking at the relationship between abundance and human land use for each species.

I did not find any evidence for the productivity hypothesis, using actual evapotransporation (AET) data as a measure of productivity. AET data were derived from a water balance model estimated using a uniform 0.5 m vegetation root depth at 0.5 degree grid cells for the United States (Vorosmarty et al. 1998). Mean abundance per route was not related to AET ($p = 0.08$, Fig 4.4). Human-dominated land cover was significantly related to AET; however, the relationship was very weak ($p<0.001$, $R^2=0.05$).

Neither did I find that abundance of individual species was consistently related to human land cover. Out of 146 species, only 12 species had significant positive relationships with human land cover, as might be expected from the overall positive relationship. In contrast, 22 species had negative relationships. The 12 species that exhibit a positive relationship are present on a greater number of routes than species in general (355 vs 110), but there is no difference in mean abundance between species with positive relationships (90 individuals per route) vs species with negative relationships (99 individuals per route). Almost all species that have positive abundance-human land cover relationships are open-habitat or edge species (10/12 or 83%). However, these species are not driving the overall pattern; the positive relationship between abundance and human land cover holds even when these species are removed.

Rather, the positive relationship between abundance and human land use appears to be driven by a more general pattern: that the most abundant species are present over a larger range of human land uses, while species that prefer lower levels of human land use are generally present at lower abundances. Species described by Valiela and Martinetto (2007) as preferring open/edge habitats generally have much higher abundance (Fig. 4.5a) and (as expected) are found in areas with higher proportions of human land use (Fig. 4.5b). This results in a positive overall relationship between abundance (or variability) and human land cover. The northern cardinal (high abundance) and warbling vireo (lower abundance) illustrate this pattern (Fig.4. 6).

Discussion

To recapitulate, I find that geographic variation in the among-year variability in population density of U.S. breeding birds cannot be related to either the amount of human-dominated land cover or to climate change. I find no relationship when using residuals from species-specific Taylor's Power Law (TPL) regressions or from a single, all-species-combined TPL regression. Perhaps surprisingly, not even forest-interior species are more variable in landscapes with more human-dominated cover. I do find a positive relationship between human land cover and variance in abundance, but this is entirely due to the close relationships between variability and mean abundance, and between mean abundance and human land cover.

It appears that areas with a high proportion of human-dominated cover come to have a greater proportion of highly abundant, and thus more variable, species. Plots of mean abundance and human land cover for individual species show two main patterns. There is a set of cosmopolitan species that are present across the entire spectrum of human land cover and that are abundant everywhere within their range, irrespective of land cover (Fig 4.6a). There is also a set of habitat specialists: species that are present at much lower abundances and only on routes with less human-dominated land cover (Fig 4.6b). However, variability in individual species' abundance, after accounting for mean abundance, is not systematically greater in areas of high human-dominated land cover or climate change. When I analyzed variation in abundance as a function of human-dominated land cover for each species individually, I found nine significantly positive ($p<0.05$) relationships out of 147 species, and seven significantly negative relationships (results not shown). This is only slightly more significant results than would be expected by chance, and not in a consistent direction. Further, there are no obvious geographic patterns in variability: no geographic regions where species are more variable overall. Individual species' abundance is not predictably more variable in areas with a high proportion of human-dominated land cover.

This is a small piece of good news for bird conservation, as other studies (Mellin et al. 2010) have suggested that increased variability can be an indicator of population stress even before changes in trends in abundance are detected. So, while it may be possible to identify some species and some disturbances for which this is true, North American breeding bird species overall are not more variable in areas with high human land conversion or with greater climate change and variability.

Despite the strong effect that weather conditions can have on birds (Crick 2004), I find that U.S. breeding bird species are not more variable in areas with greater climate change or inter-annual climate variability. Previous studies have shown that North American breeding bird populations track weather variability (Sillett et al. 2000), and that changes in breeding phenology (Dunn and Winkler 1999) and migrant arrival times (Butler 2003) in recent years are correlated with climate changes. These effects have been shown to vary greatly spatially and among and within species, with many species not showing a relationship (Butler 2003, Torti and Dunn 2005). Other studies have found that changes in species' abundances are not correlated with climate (Valiela and Martinetto 2007). I conclude that climate change is responsible for little, if any, additional variability in species' abundances.

Is it possible that bird variability is not related to land cover or to climate change for methodological reasons? It may be that variability depends upon species-specific land use variables instead of just natural versus human-dominated land cover. Some semi-natural land classes (pasture and hay for example) may be better predictors of the dynamics of some species (Lepczyk et al. 2008). Similarly, while urban centers are inhabitable for some species, they are potentially beneficial to others. Shochat et al. (2006) suggests that urban environments can lead to reduced temporal variability in environmental variables (e.g. dampened seasonality). This may benefit some species and potentially reduce their temporal variability. However, the analyses using more detailed land cover classes suggest that this is not the explanation.

It is also possible that I failed to detect a relationship between population variability and land cover because BBS data are too noisy to detect an effect. Bird counts on individual BBS routes may not reflect population abundance well. A phenomenon called ‘sloshing’ can occur where there are local migrations from sampled routes to un-sampled sites which can interfere with the abundance estimates (Keitt et al. 2002). There is, unfortunately, no way to control for this in the BBS data. There are also a number of observer biases that affect the quality of the abundance data (see methods for more details). Yet, BBS data have been used successfully in many earlier studies.

It may also be that route level variability is more affected by the local population dynamics occurring in the species range. Other studies have examined patterns of variability in North American breeding birds in relation to species’ characteristics and population dynamics. Curnutt et al. (1996) found that sites closer to the edge of a species range generally had smaller abundances and were relatively more variable for 6 species of grassland sparrows. Samaniego et al. (2012) attributed differences in the TPL between two bird species to differences in their social structure and behaviour.

This analysis highlights the problems with using the variance to examine variability in abundance. Much has been written about the challenges of quantifying temporal variability (Gaston and McArdle 1994). This study demonstrates that you can get very misleading results from looking only at the variance in log abundance and that these patterns can be driven entirely by patterns in abundance. I suggest that residuals from a TPL regression can be used as a measure of population variability that is independent from mean abundance.

Acknowledgements

I would like to thank the thousands of U.S. and Canadian BBS participants who survey routes every year as well as the work of dedicated USGS and CWS scientists and managers who make these data possible.

Figures

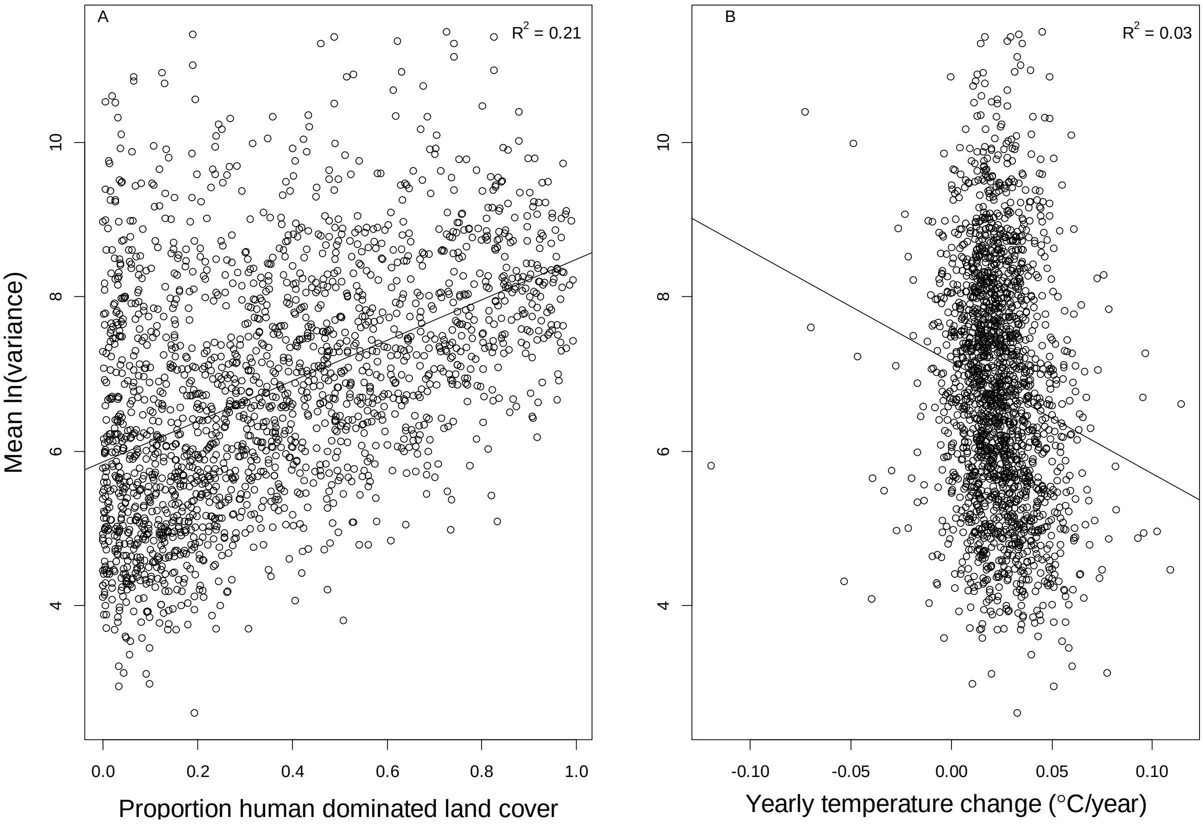


Figure 4.1: Natural log variance in abundance averaged over all species on each route as function of a) proportion of human-dominated land cover and b) directional temperature change in a 1 km buffer around each route. Directional climate change was calculated as the slope of a regression of annual minimum temperature as a function of year and has been natural log transformed to improve normality.

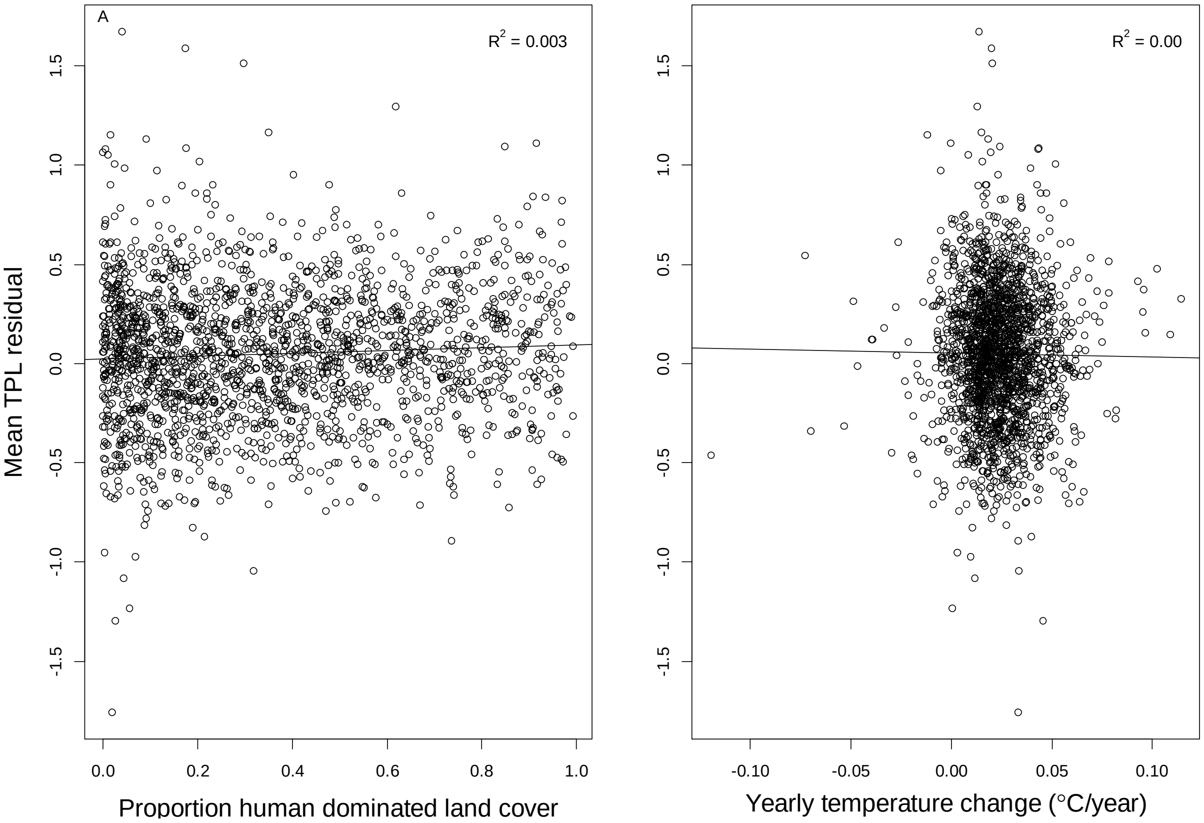


Figure 4.2: For each Breeding Bird Survey route, the Taylor power law residuals averaged over for all species on the route as a function of a) the proportion of human-dominated land cover and b) directional temperature change in a 1 km buffer around each route. Temperature change was calculated as the slope of a regression of annual minimum temperature as a function of year.

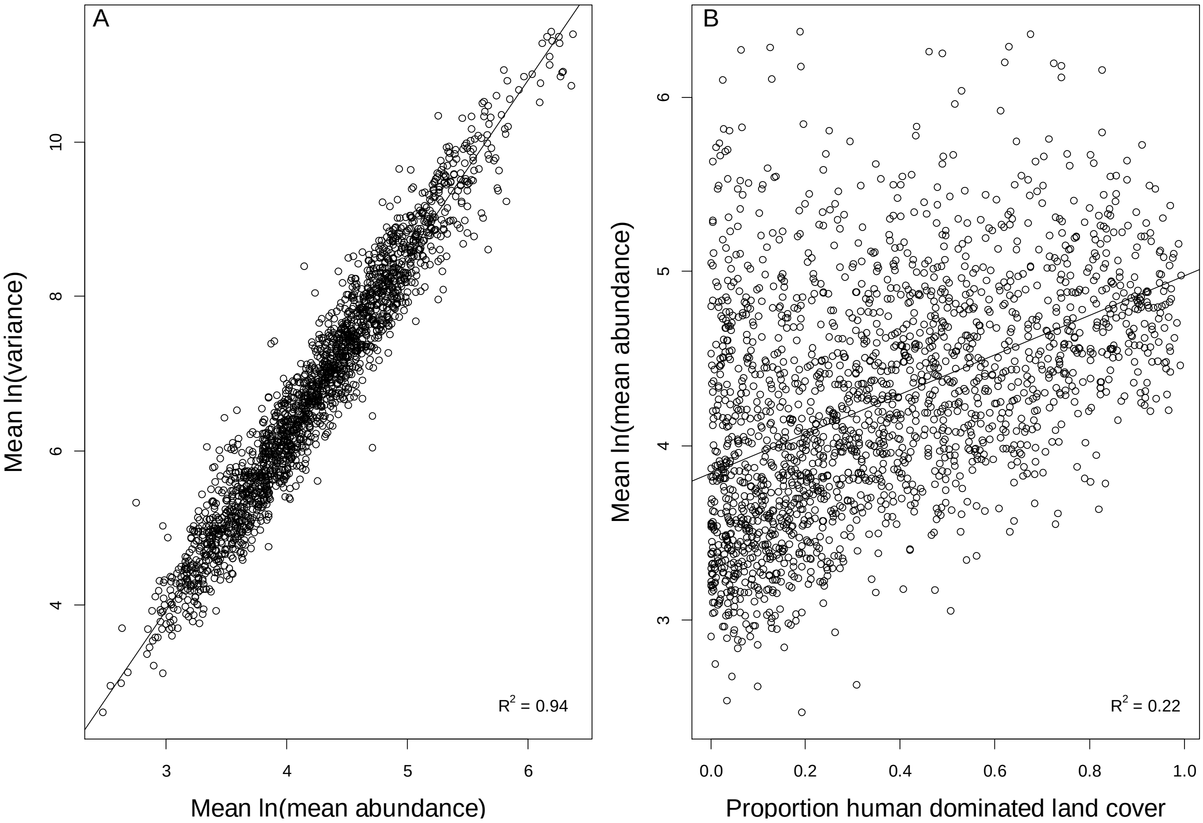


Figure 4.3: a) Variance as a function of mean abundance for all species on a ln-ln scale. b) Ln (mean abundance) as a function of the proportion of human-dominated land cover in a 1 km buffer around each route.

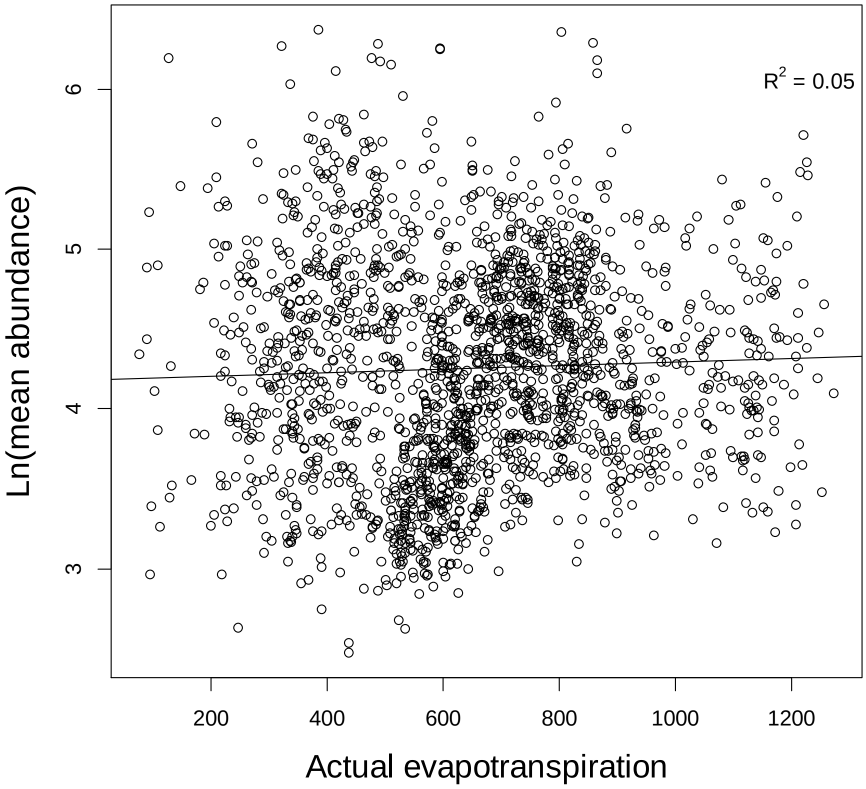


Figure 4.4: On each Breed Bird Survey route, the natural logarithm transformed mean abundance of all species on the route, as a function of estimated actual evapotranspiration.

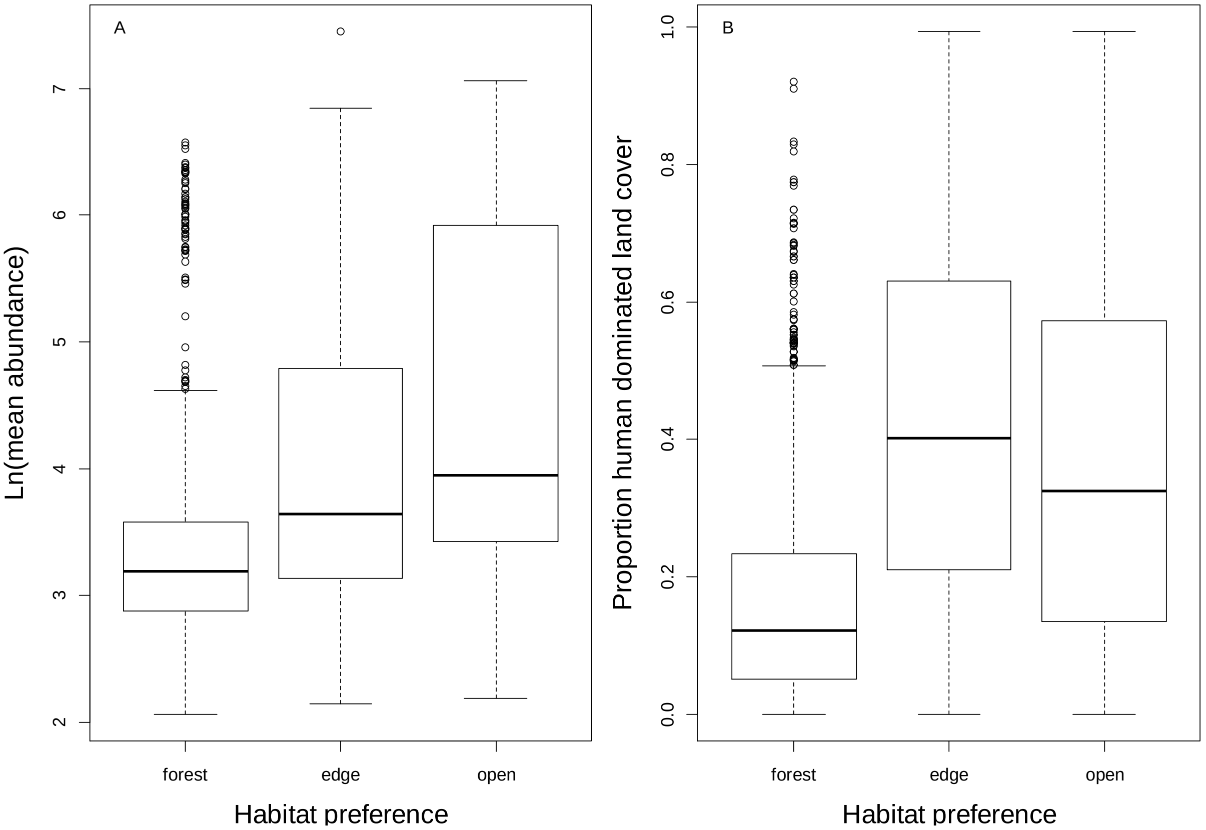


Figure 4.5: Box plots showing a) the distribution of ln (mean abundance) and b) proportion of human-dominated land cover on BBS routes occupied by species that are described by Valiela and Martinetto (2007) as preferring forest, edge and open habitats.

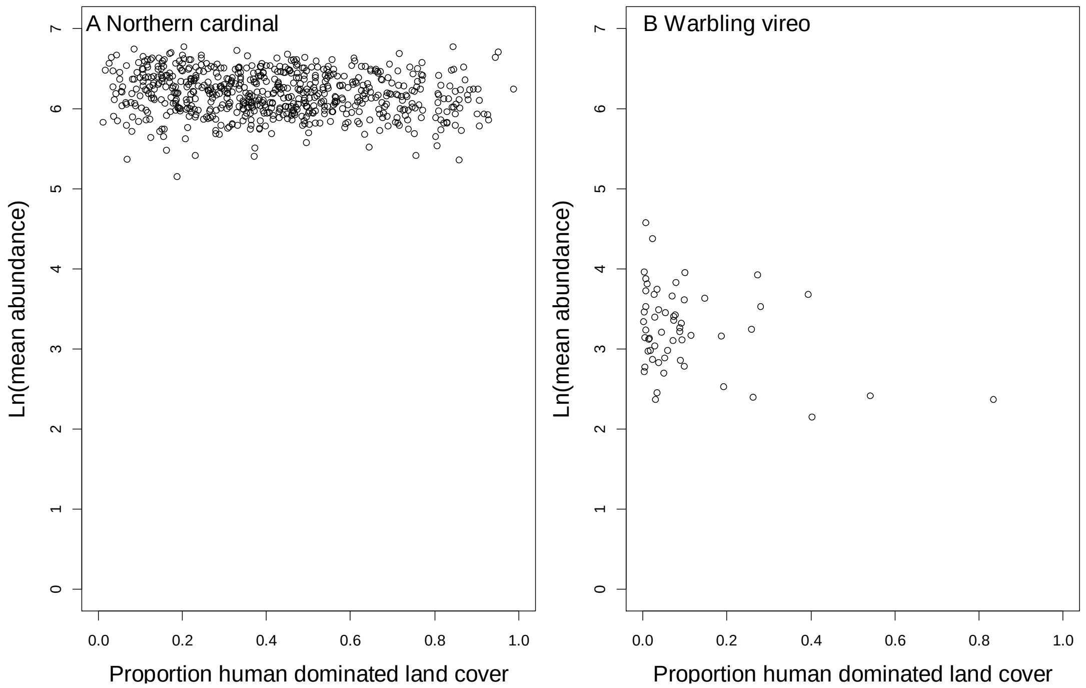


Figure 4.6: Relationship between ln (mean abundance) and proportion of human-dominated land use for a) a typical edge species, the northern cardinal (*Cardinalis cardinalis*) and b) a typical forest species, the warbling vireo (*Vireo gilvus*).

CONCLUSION

In this thesis, I set out to investigate patterns of species distributions, abundance, variability and conservation status in relation to anthropogenic activities. I used a macroecological approach to examine these patterns at a broad scale in hopes that this work will be applicable to conservation. I investigated two main aspects of species' declines: what factors are contributing to their declines, and how effective our conservation efforts have been. I assessed one of the main mechanisms for protecting species by looking at the Endangered Species Act in the United States. I examined three separate indictors of species' declines: range contractions, decreases in abundance and increases in temporal variability in abundance, in relation to anthropogenic activities. I looked at many of the main anthropogenic activities that are thought to be threatening species, including: habitat loss (Wilcove et al. 1998, Czech et al. 2000, Venter et al. 2006), pesticide use (McLaughlin and Mineau 1995), global increases in ultraviolet rays (Bancroft et al. 2007) and climate change (Walther et al. 2002).

In my first chapter, I asked whether or not the Endangered Species Act in the U.S. has been effective in improving species' recovery statuses. Previous studies have concluded that various tools under the Act are effective, based on significant statistical relationships (Male and Bean 2005, Taylor et al. 2005, Kerkvliet and Langpap 2007). However, whether tools implemented under the ESA have had *detectable* effects (i.e., statistically significant) is at least partly an issue of statistical power. Arguably, the more important question is how large or small those effects have been. Extant work has not addressed this question. I found that change in recovery status of listed species was, at best, only very weakly related to any of these tools. Recovery was positively related to the number of years listed, years with a recovery plan, and funding, however, these tools combined explain <13% of the variation in recovery status among species. Earlier studies that reported significant effects of these tools did not focus on effect sizes; however, they are in fact similarly small. Either these tools are not very effective in promoting species' recovery, or species recovery data are so poor that it is impossible to tell whether the tools are effective or not. It is critically important to assess the effectiveness of tools used to promote species recovery; it is therefore also critically important to obtain population status data that are adequate to that task.

In chapter 2, I looked at where imperilled species in Canada have been lost and correlated these areas with human population density, agricultural intensity and pesticide use. Broad-scale multi-species studies to date have focused on identifying hot spots of endangered species (e.g. Dobson et al. 1997, Flather et al. 1998, Kerr and Deguise 2004). However, hot spots of endangered species could result from several processes. They may be places where some factor(s) is (are) causing species to become endangered. Alternatively, they may be places where endangered species have avoided extinction, having been lost elsewhere (e.g. Channell and Lomolino 2000). Knowing what distinguishes places where species persist from places where they do not persist is relevant to establishing what causes species losses in the first place. I found high losses of imperiled species in regions with high proportions of agricultural land cover. However, losses of imperiled species are significantly more strongly related to the proportion of the region treated with agricultural pesticides. My results are consistent with the hypothesis that agricultural pesticide use, or something strongly collinear with it (perhaps intensive agriculture more generally), has contributed significantly to the decline of imperiled species in Canada. Habitat conversion *per se* may be a less important cause of species declines than how that converted habitat is used.

The decline of global amphibian populations is one of most pressing issues in conservation biology today (Wake 2008). Global increases in UV radiation due to reductions in the ozone layer have been suggested as a cause (Middleton et al. 2001). It is clear that high levels of UV radiation are harmful to amphibians at all life cycles (Croteau et al. 2008); however, evidence that the negative effects of increasing UV radiation translate into long-term population level declines in the wild is lacking (Collins and Crump 2009). In chapter 3, I used a global database of amphibian populations to relate population changes to global changes in UV. This was the first global-scale multi species study to examine changes in amphibian populations in relation to increases in UV.

I failed to find evidence that increasing global UV radiation is a main cause of global amphibian population declines. While it is not difficult to postulate possible ways that UV could affect amphibians, the fact remains that regional UV changes contributes very little to the ability to predict their population declines. At individual sites, temporal changes in amphibian abundance are not predictably related to changes in UV intensity. Nor is the global spatial variation in amphibian population trends predictably related to variation in UV temporal trends. It could be that negative effects of UV on individual amphibians do not result in changes at the population level or that factors that affect UV at a local scale are more important to amphibian populations than broad scale UV. However, global increases in UV radiation do not appear to be a major cause of amphibian declines.

In Chapter 4, I used temporal variability in abundance as an indicator of population stability. Previous studies have shown that anthropogenic disturbances can result in increased variability, even when there are no detectable trends in mean abundance (Warwick and

Clarke 1993, Fraterrigo and Rusak 2008, Mellin et al. 2010). There are examples that this can happen, but is it a general pattern? I investigated this in North American breeding birds.

It appears that areas with high human-dominated cover come to have a greater proportion of highly abundant, and thus more variable, species. Individual species plots of mean abundance and human land cover show two main patterns: highly abundant species that are present across the entire spectrum of human land cover and species that are present at much lower abundances and only on routes with less human-dominated land cover. However, species variability, after accounting for mean abundance, is not greater in areas of high human-dominated land cover or climate change. There are not geographic areas where species are more variable overall. This is a small piece of good news for bird conservation as other studies (Mellin et al. 2010) have found that increased variability can be an indicator of population stress even before changes in trends in abundance are detected. So, while some species are likely affected, North American breeding bird species overall are not more variable in areas with high human land conversion and greater climate change and variability.

I choose to use a macroecological approach throughout the thesis so that the results would be at a scale immediately relevant to conservation. However, this increase in scale does come at a cost. Critics of the macroecological approach would point out that it can be hard to distinguish between multiple competing hypotheses (as in Chapter 2) or that one may see non-significant results simply because the data at large scales are often noisy (as in Chapters 1, 3 and 4)(Gaston and Blackburn 1999). It is true that correlation does not mean causation; but we can use correlations to test whether or not the expected patterns from a given hypothesis are in fact seen. In chapter 2 I am able to use correlations to distinguish between habitat loss and pesticide hypotheses; however, I am not able to distinguish between pesticides and other aspects of intense agriculture.

Large scale datasets are often collected for other purposes and from secondary sources which can cause them to have a higher level of random noise. If the data are particularly noisy, this can obscure the patterns we are interested in. I have used the best available data throughout the thesis and there is no reason to expect that the data are noisy enough to be obscuring the interesting patterns. Additionally, I am interested in characterizing the main threats to species, not simply which factors *can* be a threat, so it is not unreasonable to expect to see a pattern despite data that may be noisy.

The macroecological approach is not perfect, but neither is the alternative. Smaller scale studies often have greater inference to make strong conclusions, but it is unclear how the results extrapolate to the larger scale that is necessary for management and conservation decisions. It has often been shown that ecological patterns seen at one scale do not extrapolate to different scales (Gaston and Blackburn 1999). Despite its limitations, the macroecological approach can be very useful if the goal is to be able to say something about conservation at a realistic scale.

The results from this thesis have many potential conservation applications. My findings indicate the importance of assessing our conservation tools. It is not enough to implement them, we must also monitor and assess them to see if they are affective and modify them accordingly. This work demonstrated that factors that may negatively affect species in the laboratory may not necessarily scale up to have population effects, as is the case for UV and amphibian populations. Additionally, my findings indicate that the effects of habitat loss on species are quite complicated. It appears that for imperiled species in Canada, how the land is used, particularly for intense agriculture, may be more important than the direct habitat loss. For breeding birds in North America, many species appear at high abundances even in areas with high human land conversion. And human land conversion and climate change to do not appear to increase variability in abundance, which can be an indicator or stress even before changes to trends in abundance.

REFERENCES

Abbitt, R. J. F. and J. M. Scott. 2001. Examining differences between recovered and declining endangered species. Conservation Biology 15:1274-1284.

Adams, M. J., B. R. Hossack, R. A. Knapp, P. S. Corn, S. A. Diamond, P. C. Trenham, and D. B. Fagre. 2005. Distribution patterns of lentic-breeding amphibians in relation to ultraviolet radiation exposure in western North America. Ecosystems 8:488-500.

Agriculture and Agri-Food Canada. 1998. Manure, fertilizer and pesticide management in Canada: Results of the 1995 farm inputs management survey. Agriculture and Agri-Food Canada, Ottawa, Canada.

Alford, R. A. and S. J. Richards. 1999. Global amphibian declines: A problem in applied ecology. Annual Review of Ecology and Systematics 30:133-165.

Alton, L. A., R. S. Wilson, and C. E. Franklin. 2010. Risk of predation enhances the lethal effects of UV-B in amphibians. Global Change Biology 16:538-545.

Balmford, A., A. Bruner, P. Cooper, R. Costanza, S. Farber, R. E. Green, M. Jenkins, P. Jefferiss, V. Jessamy, J. Madden, K. Munro, N. Myers, S. Naeem, J. Paavola, M. Rayment, S. Rosendo, J. Roughgarden, K. Trumper, and R. K. Turner. 2002. Ecology - Economic reasons for conserving wild nature. Science 297:950-953.

Balmford, A., R. E. Green, and J. P. W. Scharlemann. 2005. Sparing land for nature: exploring the potential impact of changes in agricultural yield on the area needed for crop production. Global Change Biology 11:1594-1605.

Bancroft, B. A., N. J. Baker, and A. R. Blaustein. 2007. Effects of UVB radiation on marine and freshwater organisms: a synthesis through meta-analysis. Ecology Letters 10:332-345.

Bancroft, B. A., N. J. Baker, and A. R. Blaustein. 2008. A meta-analysis of the effects of ultraviolet B radiation and its synergistic interactions with pH, contaminants, and disease on amphibian survival. Conservation Biology 22:987-996.

Banfield, A. W. F. 1974. The mammals of Canada. University of Toronto Press, Toronto, Canada.

Barnosky, A. D., E. A. Hadly, J. Bascompte, E. L. Berlow, J. H. Brown, M. Fortelius, W. M. Getz, J. Harte, A. Hastings, P. A. Marquet, N. D. Martinez, A. Mooers, P. Roopnarine, G. Vermeij, J. W. Williams, R. Gillespie, J. Kitzes, C. Marshall, N. Matzke, D. P. Mindell, E. Revilla, and A. B. Smith. 2012. Approaching a state shift in Earth's biosphere. Nature 486:52-58.

Bean, M. J. 2009. The Endangered Species Act Science, Policy, and Politics. Pages 369-391. Year in Ecology and Conservation Biology. Blackwell Publishing, Oxford.

Becker, C. G., C. R. Fonseca, C. F. B. Haddad, R. F. Batista, and P. I. Prado. 2007. Habitat split and the global decline of amphibians. Science 318:1775-1777.

Beebee, T. J. C. and R. A. Griffiths. 2005. The amphibian decline crisis: A watershed for conservation biology? Biological Conservation 125:271-285.

Blaustein, A. R. and B. A. Bancroft. 2007. Amphibian population declines: Evolutionary considerations. Bioscience 57:437-444.

Blaustein, A. R. and L. K. Belden. 2003. Amphibian defenses against ultraviolet-B radiation. Evolution & Development 5:89-97.

Blaustein, A. R., B. Han, B. Fasy, J. Romansic, E. A. Scheessele, R. G. Anthony, A. Marco, D. P. Chivers, L. K. Belden, J. M. Kiesecker, T. Garcia, M. Lizana, and L. B. Kats. 2004. Variable breeding phenology affects the exposure of amphibian embryos to ultraviolet radiation and optical characteristics of natural waters protect amphibians from UV-B in the US Pacific Northwest: Comment. Ecology 85:1747-1754.

Blaustein, A. R. and J. M. Kiesecker. 2002. Complexity in conservation: lessons from the global decline of amphibian populations. Ecology Letters 5:597-608.

Boersma, P. D., P. Kareiva, W. F. Fagan, J. A. Clark, and J. M. Hoekstra. 2001. How good are endangered species recovery plans? Bioscience 51:643-649.

Boone, M. D., R. D. Semlitsch, E. E. Little, and M. C. Doyle. 2007. Multiple stressors in amphibian communities: Effects of chemical contamination, bullfrogs, and fish. Ecological Applications 17:291-301.

Brashares, J. S., P. Arcese, M. K. Sam, P. B. Coppolillo, A. R. E. Sinclair, and A. Balmford. 2004. Bushmeat hunting, wildlife declines, and fish supply in West Africa. Science 306:1180-1183.

Brooks, P. D., C. M. O'Reilly, S. A. Diamond, D. H. Campbell, R. Knapp, D. Bradford, P. S. Corn, B. Hossack, and K. Tonnessen. 2005. Spatial and temporal variability in the amount and source of dissolved organic carbon: Implications for ultraviolet exposure in amphibian habitats. Ecosystems 8:478-487.

Brown, J. H. 1995. Macroecology. The University of Chicago Press, Chicago.

Butler, C. J. 2003. The disproportionate effect of global warming on the arrival dates of short-distance migratory birds in North America. Ibis 145:484-495.

Calfee, R. D., E. E. Little, C. A. Pearl, and R. L. Hoffman. 2010. Effects of Simulated Solar UVB Radiation on Early Developmental Stages of the Northwestern Salamander (*Ambystoma gracile*) from Three Lakes. Journal of Herpetology 44:572-580.

Cardinale, B. J., J. E. Duffy, A. Gonzalez, D. U. Hooper, C. Perrings, P. Venail, A. Narwani, G. M. Mace, D. Tilman, D. A. Wardle, A. P. Kinzig, G. C. Daily, M. Loreau, J. B. Grace, A. Larigauderie, D. S. Srivastava, and S. Naeem. 2012. Biodiversity loss and its impact on humanity. Nature 486:59-67.

Carson, R. 1962. Silent spring. Houghton Mifflin, Boston, MA.

Cassman, K. G., A. Dobermann, D. T. Walters, and H. Yang. 2003. Meeting cereal demand while protecting natural resources and improving environmental quality. Annual Review of Environment and Resources 28:315-358.

Chamberlain, D. E., R. J. Fuller, R. G. H. Bunce, J. C. Duckworth, and M. Shrubb. 2000. Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. Journal of Applied Ecology 37:771-788.

Channell, R. and M. V. Lomolino. 2000. Dynamic biogeography and conservation of endangered species. Nature 403:84-86.

Chape, S., J. Harrison, M. Spalding, and I. Lysenko. 2005. Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. Philosophical Transactions of the Royal Society B-Biological Sciences 360:443-455.

Chapin, F. S., E. S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S. Lavorel, O. E. Sala, S. E. Hobbie, M. C. Mack, and S. Diaz. 2000. Consequences of changing biodiversity. Nature 405:234-242.

Collins, J. P. and M. L. Crump. 2009. Extinction in Our Time. Oxford University Press, New York, NY.

Collins, J. P. and A. Storfer. 2003. Global amphibian declines: sorting the hypotheses. Diversity and Distributions 9:89-98.

Cook, F. R. 1984. Introduction to Canadian amphibians and reptiles. National Museums of Canada, Ottawa, Canada.

Corn, P. S. 1998. Effects of ultraviolet radiation on boreal toads in Colorado. Ecological Applications 8:18-26.

Corn, P. S. and E. Muths. 2002. Variable breeding phenology affects the exposure of amphibian embryos to ultraviolet radiation. Ecology 83:2958-2963.

COSEWIC. 2004. Canadian Species at Risk, November 2004. Committee on the status of endangered wildlife in Canada, Ottawa, Canada.

Crick, H. Q. P. 2004. The impact of climate change on birds. Ibis 146:48-56.

Crop Protection Institute of Canada. 2000. Survey of sales of pest control products for the year ending December 31, 1998. Crop Protection Institute, Etobicoke, Canada.

Croteau, M. C., M. A. Davidson, D. R. S. Lean, and V. L. Trudeau. 2008. Global Increases in Ultraviolet B Radiation: Potential Impacts on Amphibian Development and Metamorphosis. Physiological and Biochemical Zoology 81:743-761.

Curnutt, J. L., S. L. Pimm, and B. A. Maurer. 1996. Population variability of sparrows in space and time. Oikos 76:131-144.

Currie, D. J. 1991. Energy and large-scale patterns of animal species and plant species richness. American Naturalist 137:27-49.

Czech, B., P. R. Krausman, and P. K. Devers. 2000. Economic associations among causes of species endangerment in the United States. Bioscience 50:593-601.

Daly, C., R. P. Neilson, and D. L. Phillips. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. Journal of Applied Meteorology 33:140-158.

Davidson, C. and R. A. Knapp. 2007. Multiple stressors and amphibian declines: Dual impacts of pesticides and fish on yellow-legged frogs. Ecological Applications 17:587-597.

Davidson, C., H. B. Shaffer, and M. R. Jennings. 2001. Declines of the California red-legged frog: Climate, UV-B, habitat, and pesticides hypotheses. Ecological Applications 11:464-479.

Davidson, C., H. B. Shaffer, and M. R. Jennings. 2002. Spatial tests of the pesticide drift, habitat destruction, UV-B, and climate-change hypotheses for California amphibian declines. Conservation Biology 16:1588-1601.

Devine, G. J. and M. J. Furlong. 2007. Insecticide use: Contexts and ecological consequences. Agriculture and Human Values 24:281-306.

Dobson, A. P., J. P. Rodriguez, W. M. Roberts, and D. S. Wilcove. 1997. Geographic distribution of endangered species in the United States. Science 275:550-553.

Dunn, P. O. and D. W. Winkler. 1999. Climate change has affected the breeding date of tree swallows throughout North America. Proceedings of the Royal Society of London Series B-Biological Sciences 266:2487-2490.

Eck, T. F., P. K. Bhartia, and J. B. Kerr. 1995. Satellite Estimation of Spectral Uvb Irradiance Using Toms Derived Total Ozone and Uv Reflectivity. Geophysical Research Letters 22:611-614.

Ecological Stratification Working Group. 1995. A national ecological framework for Canada. Agriculture and Agri-Food Canada, Ottawa, Canada.

Endangered Species Act. 1973. Endangered Species Act. US Statutes at Large 884.

ESRI. 2011. ArcGIS Version 10. Environmental Systems Research Institute, Redlands, California.

Evans, K. L. and K. J. Gaston. 2005. People, energy and avian species richness. Global Ecology and Biogeography 14:187-196.

Ewins, P. J. 1997. Osprey (*Pandion haliaetus*) populations in forested areas of North America: Changes, their causes and management recommendations. Journal of Raptor Research 31:138-150.

Fearer, T. M., S. P. Prisley, D. F. Stauffer, and P. D. Keyser. 2007. A method for integrating the Breeding Bird Survey and Forest Inventory and Analysis databases to evaluate forest bird-habitat relationships at multiple spatial scales. Forest Ecology and Management 243:128-143.

Ferraro, P. J., C. McIntosh, and M. Ospina. 2007. The effectiveness of the US endangered species act: An econometric analysis using matching methods. Journal of Environmental Economics and Management 54:245-261.

Flather, C. H., M. S. Knowles, and I. A. Kendall. 1998. Threatened and endangered species geography. Bioscience 48:365-376.

Fleischli, M. A., J. C. Franson, N. J. Thomas, D. L. Finley, and W. Riley. 2004. Avian mortality events in the United States caused by anticholinesterase pesticides: A retrospective summary of National Wildlife Health Center records from 1980 to 2000. Archives of Environmental Contamination and Toxicology 46:542-550.

Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, J. H. Helkowski, T. Holloway, E. A. Howard, C. J.

Kucharik, C. Monfreda, J. A. Patz, I. C. Prentice, N. Ramankutty, and P. K. Snyder. 2005. Global Consequences of Land Use. Science 309:570-574.

Fraterrigo, J. M. and J. A. Rusak. 2008. Disturbance-driven changes in the variability of ecological patterns and processes. Ecology Letters 11:756-770.

Freemark, K. and C. Boutin. 1995. Impacts of agricultural herbicide use on terrestrial wildlife in temperate landscapes – a review with special reference to North America. Agriculture Ecosystems & Environment 52:67-91.

Gaston, K. J. and T. M. Blackburn. 1999. A critique for macroecology. Oikos 84:353-368.

Gaston, K. J. and T. M. Blackburn. 2000. Pattern and Process in Macroecology. Blackwell Science Ltd., Oxford.

Gaston, K. J. and B. H. McArdle. 1994. The temporal variability of animal abundances - measures, methods and patterns. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 345:335-358.

Gosnell, H. 2001. Section 7 of the endangered species act and the art of compromise: The evolution of a reasonable and prudent alternative for the Animas-La Plata Project. Natural Resources Journal 41:561-626.

Green, R. E., S. J. Cornell, J. P. W. Scharlemann, and A. Balmford. 2005. Farming and the fate of wild nature. Science 307:550-555.

Greenwald, D. N., K. F. Suckling, and M. Taylor. 2006. The listing record. Pages 51-67 in J. M. Scott., F.W. Davis and D.D. Globe, editor. The Endangered Species Act at Thirty: Renewing the Conservation Promise. Island Press, Washington, DC.

Grenfell, B. T., K. Wilson, B. F. Finkenstadt, T. N. Coulson, S. Murray, S. D. Albon, J. M. Pemberton, T. H. Clutton-Brock, and M. J. Crawley. 1998. Noise and determinism in synchronized sheep dynamics. Nature 394:674-677.

Griffith, E. H., J. R. Sauer, and J. A. Royle. 2010. Traffic effects on bird counts on North American breeding bird survey routes. Auk 127:387-393.

Hagen, A. N. and K. E. Hodges. 2006. Resolving critical habitat designation failures: Reconciling law, policy, and biology. Conservation Biology 20:399-407.

Han, B. A., L. B. Kats, R. C. Pommerening, R. P. Ferrer, M. Murry-Ewers, and A. R. Blaustein. 2007. Behavioral avoidance of ultraviolet-B radiation by two species of neotropical poison-dart frogs. Biotropica 39:433-435.

Herman, J. R., N. Krotkov, E. Celarier, D. Larko, and G. Labow. 1999. Distribution of UV radiation at the Earth's surface from TOMS-measured UV-backscattered radiances. Journal of Geophysical Research-Atmospheres 104:12059-12076.

Hoekstra, J. M., W. F. Fagan, and J. E. Bradley. 2002. A critical role for critical habitat in the recovery planning process? Not yet. Ecological Applications 12:701-707.

Hof, C., M. B. Araujo, W. Jetz, and C. Rahbek. 2011. Additive threats from pathogens, climate and land-use change for global amphibian diversity. Nature 480:516-U137.

Hossack, B. R., S. A. Diamond, and P. S. Corn. 2006. Distribution of boreal toad populations in relation to estimated UV-B dose in Glacier National Park, Montana, USA. Canadian Journal of Zoology-Revue Canadienne De Zoologie 84:98-107.

Houlahan, J. E., C. S. Findlay, B. R. Schmidt, A. H. Meyer, and S. L. Kuzmin. 2000. Quantitative evidence for global amphibian population declines. Nature 404:752-755.

Howe, M. A., P. H. Geissler, and B. A. Harrington. 1989. Population trends of North American shorebirds based on the International Shorebird Survey. Biological Conservation 49:185-199.

Hsieh, C. H., C. S. Reiss, J. R. Hunter, J. R. Beddington, R. M. May, and G. Sugihara. 2006. Fishing elevates variability in the abundance of exploited species. Nature 443:859-862.

Inchausti, P. and J. Halley. 2003. On the relation between temporal variability and persistence time in animal populations. Journal of Animal Ecology 72:899-908.

U.S. Department of the Interior. 2003. Endangered Species Act “Broken”. U.S. Department of the Interior. Washington, DC.

Keitt, T. H., L. A. N. Amaral, S. V. Buldyrev, and H. E. Stanley. 2002. Scaling in the growth of geographically subdivided populations: invariant patterns from a continent-wide biological survey. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 357:627-633.

Kendall, W. L., B. G. Peterjohn, and J. R. Sauer. 1996. First-time observer effects in the North American Breeding Bird Survey. Auk 113:823-829.

Kerkvliet, J. and C. Langpap. 2007. Learning from endangered and threatened species recovery programs: A case study using US Endangered Species Act recovery scores. Ecological Economics 63:499-510.

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

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

Kerr, J. T., H. M. Kharouba, and D. J. Currie. 2007. The macroecological contribution to global change solutions. Science 316:1581-1584.

Kiesecker, J. M., A. R. Blaustein, and L. K. Belden. 2001. Complex causes of amphibian population declines. Nature 410:681-684.

Krebs, J. R., J. D. Wilson, R. B. Bradbury, and G. M. Siriwardena. 1999. The second silent spring? Nature 400:611-612.

Legendre, P. 1993. Spatial autocorrelation - trouble or new paradigm. Ecology 74:1659-1673.

Lepczyk, C. A., C. H. Flather, V. C. Radeloff, A. M. Pidgeon, R. B. Hammer, and J. G. Liu. 2008. Human impacts on regional avian diversity and abundance. Conservation Biology 22:405-416.

Leps, J. 1993. Taylor power-law and the measurement of variation in the size of populations in space and time. Oikos 68:349-356.

Lips, K. R., F. Brem, R. Brenes, J. D. Reeve, R. A. Alford, J. Voyles, C. Carey, L. Livo, A. P. Pessier, and J. P. Collins. 2006. Emerging infectious disease and the loss of biodiversity in a Neotropical amphibian community. Proceedings of the National Academy of Sciences of the United States of America 103:3165-3170.

Lips, K. R., J. Diffendorfer, J. R. Mendelson, and M. W. Sears. 2008. Riding the wave: Reconciling the roles of disease and climate change in amphibian declines. Plos Biology 6:441-454.

Male, T. D. and M. J. Bean. 2005. Measuring progress in US endangered species conservation. Ecology Letters 8:986-992.

Marshall, I. B., P. Schut, and M. A. Ballard. 1999. A national ecological framework for Canada: Attribute data. Agriculture and Agri-Food Canada, Ottawa, Canada.

Matson, P. A., W. J. Parton, A. G. Power, and M. J. Swift. 1997. Agricultural intensification and ecosystem properties. Science 277:504-509.

Mattison, E. H. A. and K. Norris. 2005. Bridging the gaps between agricultural policy, land-use and biodiversity. Trends in Ecology & Evolution 20:610-616.

McFadden, D. 1974. Analysis of qualitative choice behavior. Pages 105-142 in P. Zarembka, editor. Frontiers in Econometrics. Academic Press, New York, New York.

McKinlay, R., J. A. Plant, J. N. B. Bell, and N. Voulvoulis. 2008. Endocrine disrupting pesticides: implications for risk assessment. Environment International 34:168-183.

McLaughlin, A. and P. Mineau. 1995. The impact of agricultural practices on biodiversity. Agriculture Ecosystems & Environment 55:201-212.

Melbourne, B. A. and A. Hastings. 2008. Extinction risk depends strongly on factors contributing to stochasticity. Nature 454:100-103.

Mellin, C., C. Huchery, M. J. Caley, M. G. Meekan, and C. J. A. Bradshaw. 2010. Reef size and isolation determine the temporal stability of coral reef fish populations. Ecology 91:3138-3145.

Middleton, E. M., J. R. Herman, E. A. Celarier, J. W. Wilkinson, C. Carey, and R. J. Rusin. 2001. Evaluating ultraviolet radiation exposure with satellite data at sites of amphibian declines in Central and South America. Conservation Biology 15:914-929.

Millennium Ecosystem Assessment. 2005. Ecosystems and Human Well-Being: Biodiversity Synthesis Island Press, Washington, DC.

Miller, J. K., J. M. Scott, C. R. Miller, and L. P. Waits. 2002. The Endangered Species Act: Dollars and sense? Bioscience 52:163-168.

Mineau, P. and M. Whiteside. 2006. Lethal risk to birds from insecticide use in the United States - A spatial and temporal analysis. Environmental Toxicology and Chemistry 25:1214-1222.

Mittlbock, M. and M. Schemper. 1999. Computing measures of explained variation for logistic regression models. Computer Methods and Programs in Biomedicine 58:17-24.

Murdoch, W. W. 1994. Population regulation in theory and practice - The Robert H MacArthur award lection presented August 1991 in San Antonio, Texas, USA. Ecology 75:271-287.

NASA. 2009. TOMS Erythemal UV data. NASA.

NatureServe. 2009. NatureServe Explorer: An online encyclopedia of life [web application] Version 7.1. NatureServe, Arlington, Virginia.

NLCD. 2011. National Land Cover Database 2006 Land Cover. U.S. Geological Survey, Sioux Falls, SD.

Palen, W. J. and D. E. Schindler. 2010. Water clarity, maternal behavior, and physiology combine to eliminate UV radiation risk to amphibians in a montane landscape. Proceedings of the National Academy of Sciences of the United States of America 107:9701-9706.

Palen, W. J., D. E. Schindler, M. J. Adams, C. A. Pearl, R. B. Bury, and S. A. Diamonds. 2002. Optical characteristics of natural waters protect amphibians from UV-B in the US Pacific Northwest. Ecology 83:2951-2957.

Pimm, S. L. 1991. The Balance of Nature? Ecological issues in the conservation of species and communities. University of Chicago Press, Chicago.

Pimm, S. L., G. J. Russell, J. L. Gittleman, and T. M. Brooks. 1995. The Future of Biodiversity. Science 269:347-350.

Poole, A. 2005. in A. Poole, editor. The Birds of North America Online: http://bna.birds.cornell.edu/BNA/. Cornell Laboratory of Ornithology, Ithaca, NY.

Potts, G. R. 1986. The Partridge: Pesticides, Predation and Conservation, London, Collins.

Pounds, J. A., M. R. Bustamante, L. A. Coloma, J. A. Consuegra, M. P. L. Fogden, P. N. Foster, E. La Marca, K. L. Masters, A. Merino-Viteri, R. Puschendorf, S. R. Ron, G. A. Sanchez-Azofeifa, C. J. Still, and B. E. Young. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. Nature 439:161-167.

Primack, R. B. 1995. A primer of conservation ecology. Sinauer, Sunderland, USA.

Puglis, H. J. and M. D. Boone. 2011. Effects of Technical-Grade Active Ingredient vs. Commercial Formulation of Seven Pesticides in the Presence or Absence of UV Radiation on Survival of Green Frog Tadpoles. Archives of Environmental Contamination and Toxicology 60:145-155.

Pullin, A. S. and T. M. Knight. 2009. Doing more good than harm - Building an evidence-base for conservation and environmental management. Biological Conservation 142:931-934.

Rachlinski, J. J. 1997. Noah's choice: The future of endangered species. Cornell Law Review 82:356-389.

Raimondo, S., P. Mineau, and M. G. Barron. 2007. Estimation of chemical toxicity to wildlife species using interspecies correlation models. Environmental Science & Technology 41:5888-5894.

Rangel, T., J. A. F. Diniz-Filho, and L. M. Bini. 2006. Towards an integrated computational tool for spatial analysis in macroecology and biogeography. Global Ecology and Biogeography 15:321-327.

Rauschenberger, R. H., J. J. Wiebe, M. S. Sepulveda, J. E. Scarborough, and T. S. Gross. 2007. Parental exposure to pesticides and poor clutch viability in American alligators. Environmental Science & Technology 41:5559-5563.

Ray, J. C. and J. R. Ginsberg. 1999. Endangered species legislation beyond the borders of the United States. Conservation Biology 13:956-958.

Rivard, D. H., J. Poitevin, D. Plasse, M. Carleton, and D. J. Currie. 2000. Changing species richness and composition in Canadian national parks. Conservation Biology 14:1099-1109.

Roughgarden, J. 1995. Can economics protect biodiversity? Pages 149-155 in T. M. Swanson, editor. The economics and ecology of biodiversity decline: The forces driving global change Cambridge University Press, Cambridge.

Salzman, J. 1990. Evolution and Application of Critical Habitat under the Endangered Species Act. Harvard Environmental Law Review 14:311-342.

Samaniego, H., G. Serandour, and B. T. Milne. 2012. Analyzing Taylor's Scaling Law: qualitative differences of social and territorial behavior on colonization/extinction dynamics. Population Ecology 54:213-223.

Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Z. Jr., and W. A. Link. 2011. The North American Breeding Bird Survey, Results and Analysis 1966 - 2010. Version 12.07.2011. USGS Patuxent Wildlife Research Center, Laurel, MD.

Sauer, J. R., J. E. Hines, G. Gough, I. Thomas, and B. G. Peterjohn. 1997. The North American Breeding Bird Survey Results and Analysis. Version 96.4. Patuxent Wildlife Research Center, Laurel, MD.

Sauer, J. R., B. G. Peterjohn, and W. A. Link. 1994. Observer differences in the North American breeding bird survey. Auk 111:50-62.

Schiesari, L., B. Grillitsch, and H. Grillitsch. 2007. Biogeographic biases in research and their consequences for linking amphibian declines to pollution. Conservation Biology 21:465-471.

Schmidt, B. R., R. Feldmann, and M. Schaub. 2005. Demographic processes underlying population growth and decline in Salamandra salamandra. Conservation Biology 19:1149-1156.

Schwartz, M. W. 2008. The Performance of the Endangered Species Act. Annual Review of Ecology Evolution and Systematics 39:279-299.

Scott, J. M., D. D. Goble, J. A. Wiens, D. S. Wilcove, M. Bean, and T. Male. 2005. Recovery of imperiled species under the Endangered Species Act: the need for a new approach. Frontiers in Ecology and the Environment 3:383-389.

Searle, C. L., L. K. Belden, B. A. Bancroft, B. A. Han, L. M. Biga, and A. R. Blaustein. 2010. Experimental examination of the effects of ultraviolet-B radiation in combination with other stressors on frog larvae. Oecologia 162:237-245.

Secretariat of the Convention on Biological Diversity. 2006. Global Biodiversity Outlook 2. United Nations Environment Program, Montreal, Canada.

Shochat, E., P. S. Warren, and S. H. Faeth. 2006. Future directions in urban ecology. Trends in Ecology & Evolution 21:661-662.

Sillett, T. S., R. T. Holmes, and T. W. Sherry. 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. Science 288:2040-2042.

Sodhi, N. S., D. Bickford, A. C. Diesmos, T. M. Lee, L. P. Koh, B. W. Brook, C. H. Sekercioglu, and C. J. A. Bradshaw. 2008. Measuring the meltdown: Drivers of global amphibian extinction and decline. Plos One 3:e1636.

Solomon, B. D. 1998. Impending recovery of Kirtland's warbler: Case study in the effectiveness of the Endangered Species Act. Environmental Management 22:9-17.

Sparling, D. W., G. M. Fellers, and L. L. McConnell. 2001. Pesticides and amphibian population declines in California, USA. Environmental Toxicology and Chemistry 20:1591-1595.

Starnes, S. M., C. A. Kennedy, and J. W. Petranka. 2000. Sensitivity of embryos of southern Appalachian amphibians to ambient solar UV-B radiation. Conservation Biology 14:277-282.

Statistics Canada. 1999. E-Stat. Statistics Canada, Ottawa, Canada.

Stuart, S. N., J. S. Chanson, N. A. Cox, B. E. Young, A. S. L. Rodrigues, D. L. Fischman, and R. W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306:1783-1786.

Suckling, K. F. and M. Taylor. 2006. Critical habitat and recovery. Pages 75-89 in D. D. Globe, J. M. Scott, and F. W. Davis, editors. The Endangered Species Act at Thirty: Renewing the Conservation Promise. Island Press Washington, DC.

Swanson, T. M. 1995. Uniformity in development and the decline of biological diversity. Pages 41-54 in T. M. Swanson, editor. The Economics and Ecology of Biodiversity Decline: The Forces Driving Global Change. Cambridge Univ. Press, Cambridge, UK.

Taylor, L. R. 1961. Aggregation, variance and mean. Nature 189:732-735.

Taylor, L. R. and I. P. Woiwod. 1982. Comparative synoptic dynamics. 1. Relationships between interspecific and intraspecific spatial and temporal variance mean population parameters. Journal of Animal Ecology 51:879-906.

Taylor, M. F. J., K. F. Suckling, and J. J. Rachlinski. 2005. The effectiveness of the endangered species act: A quantitative analysis. Bioscience 55:360-367.

Tear, T. H., J. M. Scott, P. H. Hayward, and B. Griffith. 1995. Recovery Plans and the Endangered-Species-Act - Are Criticisms Supported by Data. Conservation Biology 9:182-195.

Thogmartin, W. E., J. R. Sauer, and M. G. Knutson. 2004. A hierarchical spatial model of avian abundance with application to Cerulean Warblers. Ecological Applications 14:1766-1779.

Thompson, B. H., Jr. 2006. Managing the working landscape. Pages 101-126 in D. D. Globe, Scott, J. M. and Davis, F. W., editor. The Endangered Species Act at Thirty: Renewing the Conservation Promise. Island Press, Washington, DC.

Torti, V. M. and P. O. Dunn. 2005. Variable effects of climate change on six species of North American birds. Oecologia 145:486-495.

USFWS. 1990a-2006a. Federal and state endangered and threatened species expenditure: fiscal years: 1989-2004. USFWS, Washington, DC.

USFWS. 1990b-2006b, 2008a. Report to Congress on the recovery of threatened and endangered species: fiscal years 1990, 1992, 1994, 1996, 1997-1998, 1999-2000, 2001-2002, 2003-2004, 2005-2006. USFWS, Washington, DC.

USFWS. 2007. Critical habitat. What is it? USFWS, Washington, DC.

USFWS. 2008. Threatened and endangered species system. USFWS, Washington, DC.

USGS-PWRC. 2006. Breeding Bird Survey Route Locations for Lower 48 States. National Atlas of the United States, Reston, VA.

Valiela, I. and P. Martinetto. 2007. Changes in bird abundance in eastern North America: Urban sprawl and global footprint? Bioscience 57:360-370.

Venter, O., N. N. Brodeur, L. Nemiroff, B. Belland, I. J. Dolinsek, and J. W. A. Grant. 2006. Threats to endangered species in Canada. Bioscience 56:903-910.

Vogelmann, J. E., S. M. Howard, L. M. Yang, C. R. Larson, B. K. Wylie, and N. Van Driel. 2001. Completion of the 1990s National Land Cover Data set for the conterminous United States from Landsat Thematic Mapper data and Ancillary data sources. Photogrammetric Engineering and Remote Sensing 67:650-662.

Vonesh, J. R. and O. De la Cruz. 2002. Complex life cycles and density dependence: assessing the contribution of egg mortality to amphibian declines. Oecologia 133:325-333.

Vorosmarty, C. J., C. A. Federer, and A. L. Schloss. 1998. Evaporation functions compared on US watersheds: Possible implications for global-scale water balance and terrestrial ecosystem modeling. Journal of Hydrology 207:147-169.

Vredenburg, V. T., J. M. Romansic, L. M. Chan, and T. Tunstall. 2010. Does UV-B Radiation Affect Embryos of Three High Elevation Amphibian Species in California? Copeia:502-512.

Vucetich, J. A., T. A. Waite, L. Qvarnemark, and S. Ibarguen. 2000. Population variability and extinction risk. Conservation Biology 14:1704-1714.

Wake, D. B. V., V. T. 2008. Are we in the midst of the sixth mass extinction? A view from the world of amphibians. Proceedings of the National Academy of Sciences of the United States of America 105:11466-11473.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389-395.

Warkentin, I. G., D. Bickford, N. S. Sodhi, and C. J. A. Bradshaw. 2009. Eating Frogs to Extinction. Conservation Biology 23:1056-1059.

Warwick, R. M. and K. R. Clarke. 1993. Increased variability as a symptom of stress in marine communities Journal of Experimental Marine Biology and Ecology 172:215-226.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. Bioscience 48:607-615.

Wilson, J. D., A. J. Morris, B. E. Arroyo, S. C. Clark, and R. B. Bradbury. 1999. A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. Agriculture Ecosystems & Environment 75:13-30.

Wynn, G. 1991. On the margins of the Empire (1760-1840). Pages 189-278 in C. Brown, editor. The Illustrated History of Canada. Lester Publishing Ltd, Toronto, Canada.

APPENDIX 1: COSEWIC-LISTED SPECIES INCLUDED IN THE ANALYSIS FOR CHAPTER 2.

	Common Name	Scientific Name
Birds	Acadian flycatcher	*Empidonax virescens*
	American white pelican	*Pelecanus erythrorhynchus*
	Ancient murrelet	*Synthiliboramphus antiquus*
	Bald eagle	*Haliaeetus leucocephalus*
	Bicknell's thrush	*Catharus bicknelli*
	Burrowing owl	*Speotyto cunicularia*
	Caspian tern	*Sterna caspia*
	Eskimo curlew	*Numenius borealis*
	Ferruginous hawk	*Buteo regalis*
	Forester's tern	*Sterna forsteri*
	Great auk	*Pinguinus impennis*
	Great blue heron	*Ardea herodias*
	Greater Prairie-chicken	*Tympanuchus cupido*
	Henslow's sparrow	*Ammodramus henslowii*
	Hooded warbler	*Wilsonia citrina*
	Ivory gull	*Pagophila eburnea*
	King rail	*Rallus elegans*
	Labrador duck	*Camptorhynchus labradorius*
	Least bittern	*Ixobrychus exilis*

Lewis' woodpecker	*Melanerpes lewis*
Loggerhead shrike	*Lanius ludovicianus*
Long-billed curlew	*Numenius americanus*
Louisiana waterthrush	*Seiurus motacilla*
Northern bobwhite	*Colinus virginianus*
Passenger pigeon	*Ectopistes migratorius*
Peregrine falcon	*Falco peregrinus*
Piping plover	*Charadrius melodus*
Prairie warbler	*Dendroica discolor*
Prothonotary warbler	*Prothonotaria citrea*
Red-headed woodpecker	*Melanerpes erythrocephalus*
Red-shouldered hawk	*Buteo lineatus*
Roseate tern	*Sterna dougallii*
Sage grouse	*Centrocercus urophasianus*
Sage thrasher	*Oreoscoptes montanus*
Spotted owl	*Strix occidentalis*
Sprague's pipit	*Anthus spragueii*
Yellow-breasted chat	*Icteria virens*

Mammals	Bison	*Bison bison*
	Caribou	*Rangifer tarandus*
	Gray wolf	*Canis lupus*
	Grey fox	*Urocyon cinereoargenteus*
	Grizzly bear	*Ursus arctos*
	Mountain beaver	*Aplodontia rufa*
	Pacific water shrew	*Sorex bendirii*
	Southern flying squirrel	*Glaucomys volans*
	Swift fox	*Vulpes velox*
	Townsend's mole	*Scapanus townsendii*
	Vancouver Island marmot	*Marmota vancouverensis*
	Wolverine	*Gulo gulo*
Amphibians	Fowler's toad	*Bufo fowleri*
	Northern cricket frog	*Acris crepitans*
	Northern dusky salamander	*Desmognathus fuscus*
	Northern leopard frog	*Rana pipiens*
	Northern red-legged frog	*Rana aurora*
	Pacific giant salamander	*Dicamptodon tenebrosus*
Reptiles	Black rat snake	*Elaphe obsoleta obsoleta*
	Eastern hognose snake	*Heterodon platyrhinos*

Eastern Massasauga rattlesnake	*Sistrurus catenatus catenatus*
Five-lined skink	*Eumeces fasciatus*
Queen snake	*Regina septemvittata*
Racer	*Columber constrictor*
Short-horned lizard	*Phrynosoma douglassii*

APPENDIX 2: COMPLETE CORRELATION MATRIX FOR IMPERILED SPECIES LOST, SPECIES RICHNESS, IMPERILED SPECIES RICHNESS AND MEASURES OF HUMAN-DOMINATED LAND-COVER.

Table A2: Simple Pearson correlations between the numbers per ecoregion of imperiled species lost from the ecoregion during approximately the last century, extant imperiled species richness (SR), regional species richness (SR), area treated with agricultural pesticides, and human population. “Combined” refers to the combination of birds, mammals, amphibians, and reptiles. Correlation coefficients ≥ 0.133, ≥ 0.174, ≥0.190, and ≥0.222 are significant at $P < 0.05$, $P < 0.01$, $P < 0.005$, and $P < 0.001$, respectively.

	Combined Losses $^{0.33}$	Bird Losses	Mammal Losses	Combined SR $^{0.33}$	Bird SR $^{0.25}$	Mammal SR	Imperiled Combined	Imperiled Bird SR	Imperiled Mammal SR
Combined Losses $^{0.33}$	--								
Bird Losses $^{0.25}$	0.943	--							
Mammal Losses	0.798	0.648	--						
Combined SR $^{0.33}$	0.456	0.403	0.364	--					
Bird SR $^{0.25}$	0.399	0.363	0.374	0.930	--				
Mammal SR	0.293	0.216	0.310	0.848	0.668	--			
Imperiled Combined SR $^{0.33}$	0.775	0.689	0.618	0.552	0.435	0.499	--		
Imperiled Bird SR $^{0.25}$	0.836	0.761	0.708	0.467	0.350	0.369	0.877	--	
Imperiled Mammal SR	-0.188	-0.211	-0.021	0.143	0.212	0.268	0.200	-0.223	--
Habitat loss*, $\log_{10}$	0.736	0.654	0.696	0.443	0.375	0.342	0.685	0.774	-0.122
Builtup area, $\log_{10}$	0.502	0.494	0.254	0.153	0.063	0.041	0.485	0.484	-0.119
Cropland area, $\log_{10}$	0.737	0.672	0.672	0.431	0.383	0.278	0.635	0.729	-0.165
Herbicide-treated area, $\log_{10}$	0.815	0.744	0.764	0.402	0.370	0.257	0.675	0.784	-0.181

Insecticide-treated area, $\log_{10}$	0.791	0.738	0.695	0.337	0.281	0.207	0.653	0.770	-0.223
Natural area, $\log_{10}$	-0.061	-0.051	-0.145	0.034	0.171	-0.085	0.036	-0.210	0.488
Human population, $\log_{10}$	0.492	0.495	0.236	0.159	0.094	-0.006	0.486	0.481	-0.069
Human population density, $\log_{10}$	0.290	0.309	0.048	0.062	-0.089	-0.043	0.236	0.366	-0.369
Ecoregion area, $\log_{10}$	0.285	0.257	0.228	0.156	0.262	0.042	0.384	0.159	0.449

	Habitat loss*, $\log_{10}$	Builtup area, $\log_{10}$	Cropland area, $\log_{10}$	Herbicide-treated area, $\log_{10}$	Insecticide-treated area, $\log_{10}$	Natural area, $\log_{10}$	Human population, $\log_{10}$	Human population density, $\log_{10}$
Habitat loss*, $\log_{10}$	--							
Builtup area, $\log_{10}$	0.552	--						
Cropland area, $\log_{10}$	0.966	0.531	--					
Herbicide-treated area, $\log_{10}$	0.917	0.470	0.936	--				
Insecticide-treated area, $\log_{10}$	0.883	0.545	0.889	0.954	--			
Natural area, $\log_{10}$	-0.080	0.157	-0.088	-0.156	-0.216	--		
Human population, $\log_{10}$	0.577	0.889	0.561	0.470	0.537	0.212	--	
Human population density, $\log_{10}$	0.341	0.642	0.355	0.291	0.424	0.386	0.694	--
Ecoregion area, $\log_{10}$	0.295	0.383	0.272	0.248	0.184	0.821	0.420	0.311

APPENDIX 3: AMPHIBIAN BREEDING DATA FOR CHAPTER 3

Appendix 3.1: Amphibian breeding data table

Table A3.1: Main breeding habitat (1=aquatic, 2=terrestrial), deposition depth (1=shallow, 2=deep) and whether or not eggs are covered (1=yes, 0=no) for 80 amphibian species. Sources are given in Appendix 3.2.

Scientific name	**Habitat**	**Deposition Depth**	**Cover**
Rana arvalis	1	1	0
Rana dalmatina	1	1	0
Bufo calamita	1	1	0
Ambystoma talpoideum	1	1	0
Ambystoma tigrin	1	1	0
Scaphiopus holbrook	1	1	0
Bufo terrestris	1	1	0
Pseudacris crucifer	1	1	0
Pseudacris nigrita	1	1	0
Pseudacris ornata	1	1	0
Rana clamitans	1	1	1
Rana utricularia	1	1	0
Ambystoma opacum	2	na	1
Eurycea quadridigitata	1	1	1
Ambystoma maculatum	1	1	0
Ambystoma californiense	1	1	0
Bufo bufo	1	1	0
Rana boylii	1	1	1
Pseudacris regilla	1	1	0
Eleutherodactylus coqui	2	na	1
Alytes muletensis	2	na	1
Desmognathus monticola	1	2	1
Rana temporaria	1	1	0
Triturus cristatus	1	2	1
Bufo fowleri	1	1	0
Taricha torosa	1	1	0
Notophthalmus perstriatus	1	1	1
Acris gryllus	1	2	1
Bufo quercicus	1	1	0
Rana capito	1	1	0
Triturus dobrogicus	1	2	1

Scientific name	**Habitat**	**Deposition Depth**	**Cover**
Bombina bombina	1	1	0
Bufo viridis	1	1	0
Pelobates fuscus	1	2	0
Rana lessonae	1	2	1
Triturus alpestris	1	2	1
Triturus helveticus	1	2	1
Triturus vulgaris	1	2	1
Hynobius tokyoensis	1	1	1
Rana sakuraii	1	2	1
Cynops pyrrhogaster	1	1	1
Rana japonica	1	2	1
Agalychnis callidrya	1	1	0
Rana catesbeiana	1	1	0
Rana septentrionalis	1	2	0
Plethodon jordani	2	na	1
Ambystoma jeffersonianum	1	1	0
Rana sylvatica	1	1	0
Desmognathus fuscus	2	na	1
Hyla versicolor	1	1	0
Philoria frosti	2	na	1
Triturus marmoratus	1	2	1
Leptodactylus fuscus	2	na	1
Buergeria buergeri	1	2	1
Pelodytes caucasicus	1		
Salamandra salamandra	2	na	1
Salamandrella keyserlingii	1	1	0
Triturus vulgaris	1	1	0
Bombina variegata	1	1	0
Alytes obstetricans	2	na	0
Rana onca	1	1	0
Rana subaquavocalis	1	1	0
Desmognathus quadramaculatus	1	2	1
Desmognathus ochrophaeus	1	2	1
Desmognathus aeneus	2	na	1
Eleutherodactylus cooki	2	na	1
Bufo canorus	1	1	0
Atelopus chiriquiensis	1	1	0
Hyla rivularis	1	2	1
Dendropsophus labialis	1	1	0
Ambystoma macrodactylum	1	1	0
Hynobius retardatus	1	1	0

Scientific name	**Habitat**	**Deposition Depth**	**Cover**
Mertensiella caucasica	1	2	0
Bufo torrenticola	1	1	0
Rana pipiens	1	2	0
Pseudacris triseriata	1	1	0
Bufo americanus	1	1	0
Aneides aeneus	2	na	1
Eurycea lucifuga	1	2	1
Plethodon cinereus	2	na	1
Plethodon glutinosus	2	na	1

Appendix 3.2: References for Appendix 3.1

1. AmphibiaWeb. (2011) Information on amphibian biology and conservation. Berkeley, California: AmphibiaWeb. Available: http://amphibiaweb.org/. (Accessed: July, 2011).

2. Tsuju, H. and Kawamichi, T. (1998) Field Observations of the Spawning Behavior of Stream Toads, *Bufo torrenticola*. *Journal of Herpetology*, **32**, 34-40.

3. Hakansson, P, and Loman, J. (2004) Communal spawning in the common frog *Rana temporaria* – Egg Temperature and Predation Consequences. *Ethology*, **110**, 665-680.

4. Hartel, T. (2008) Long-term within pond variation of egg deposition sites in the agile frog, *Rana dalmatina*. *Biologia*, **63**, 1-4.

5. Rafinska A. (1991) Reproductive biology of the fire-bellied toads, *Bombina bombina* and *B. variegata* (Anura: Discoglossidae): egg size, clutch size and larval period length differences. *Biological Journal of the Linnaean Society*, **43**, 197-210.

6. Sjögren, P., Elmberg, J. and Berglind, S. (1988) Thermal Preference in the pool frog *Rana lessonae*: Impact on the reproductive behaviour of a Northern fringe population. *Holarctic Ecology*, **11**, 178-184.

7. Maragna, F.P. and Cechin, S.Z. (2009) Reproductive biology of *Leptodactylus fuscus* (Anura, Leptodactylidae) in the suptropical climate, Rio Grande do Sul, Brazil. *Iheringia Série Zoologia*, **99**, 237-241.

8. Rogowitz, G.L., Candelaria, C.L., Denizard, L.E. and Melendez, L.J. (2001) Seasonal Reproduction of a neotropical frog, the cave coqui (*Eleutherodactylus cooki*). *Copeia*, **2,** 542-547.

9. Lips, K.R. (1998) Decline of a tropical montane amphibian fauna. *Conservation Biology*, **12**, 106-117.

10. Livezey, R.L. (1952) Some observations on *Pseudacris nigrita triseriata* in Texas. *American Midland Naturalist*, **47**, 372-381.

11. Banks, B. and Beebee, T.J.C. (1988) Reproductive success of natterjack toads *Bufo calamita* in two contrasting habitats. *Journal of Animal Ecology*, **57**, 475-492.

APPENDIX 4: BREEDING BIRD HABITAT PREFERENCES FOR CHAPTER 4

Table A4.1: Main habitat preference for North American breeding birds included in Chapter 4. Terrestrial species were classified as preferring open habitat, edge, or forest. Wetland species were classified as open-water, coastal or wetland. I used the same classifications as Valiela and Martinetto (2007). For species not classified there, I used the habitat descriptions from Pool (Poole 2005).

Common Name	**Scientific Name**	**Habitat**
Scissor-tailed Flycatcher	*Tyrannus forficatus*	edge
Eastern Kingbird	*Tyrannus tyrannus*	edge
Western Kingbird	*Tyrannus verticalis*	edge
Great Crested Flycatcher	*Myiarchus crinitus*	edge
Ash-throated Flycatcher	*Myiarchus cinerascens*	forest
Eastern Wood-Pewee	*Contopus virens*	forest
Western Wood-Pewee	*Contopus sordidulus*	forest
Pacific-slope Flycatcher	*Empidonax difficilis*	forest
Acadian Flycatcher	*Empidonax virescens*	forest
Willow Flycatcher	*Empidonax t. extimus*	edge
Alder Flycatcher	*Empidonax alnorum*	forest
Least Flycatcher	*Empidonax minimus*	forest
Horned Lark	*Eremophila alpestris*	open
Black-billed Magpie	*Pica hudsonia*	edge
Blue Jay	*Cyanocitta cristata*	edge
Steller's Jay	*Cyanocitta stelleri*	forest
Western Scrub-Jay	*Aphelocoma californica*	forest
Common Raven	*Corvus corax*	open
American Crow	*Corvus brachyrhynchos*	open
Fish Crow	*Corvus ossifragus*	coastal
European Starling	*Sturnus vulgaris*	edge
Bobolink	*Dolichonyx oryzivorus*	open
Brown-headed Cowbird	*Molothrus ater*	edge
Yellow-headed Blackbird	*Xanthocephalus xanthocephalus*	wetland
Red-winged Blackbird	*Agelaius phoeniceus*	wetland
Eastern Meadowlark	*Sturnella magna*	open
Western Meadowlark	*Sturnella neglecta*	open
Orchard Oriole	*Icterus spurius*	edge
Baltimore Oriole	*Icterus galbula*	edge

Bullock's Oriole	*Icterus bullockii*	open
Brewer's Blackbird	*Euphagus cyanocephalus*	open
Common Grackle	*Quiscalus quiscula*	edge
Great-tailed Grackle	*Quiscalus mexicanus*	edge
Boat-tailed Grackle	*Quiscalus major*	edge
House Finch	*Carpodacus mexicanus*	edge
American Goldfinch	*Spinus tristis*	open
Pine Siskin	*Spinus pinus*	edge
Vesper Sparrow	*Pooecetes gramineus*	edge
Savannah Sparrow	*Passerculus sandwichensis*	wetland
Grasshopper Sparrow	*Ammodramus savannarum*	open
Lark Sparrow	*Chondestes grammacus*	open
White-crowned Sparrow	*Zonotrichia leucophrys*	open
White-throated Sparrow	*Zonotrichia albicollis*	edge
Chipping Sparrow	*Spizella passerina*	edge
Clay-colored Sparrow	*Spizella pallida*	edge
Brewer's Sparrow	*Spizella breweri*	open
Field Sparrow	*Spizella pusilla*	edge
Dark-eyed Junco (Slate-colored Junco)	*Junco hyemalis*	forest
Dark-eyed Junco (Oregon Junco)	*Junco hyemalis*	forest
Black-throated Sparrow	*Amphispiza bilineata*	open
Cassin's Sparrow	*Peucaea cassinii*	open
Song Sparrow	*Melospiza melodia*	edge
Lincoln's Sparrow	*Melospiza lincolnii*	open
Fox Sparrow	*Passerella iliaca*	edge
Eastern Towhee	*Pipilo erythrophthalmus*	edge
Spotted Towhee	*Pipilo maculatus*	forest
Green-tailed Towhee	*Pipilo chlorurus*	open
California Towhee	*Melozone crissalis*	edge
Northern Cardinal	*Cardinalis cardinalis*	edge
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	forest
Black-headed Grosbeak	*Pheucticus melanocephalus*	open
Blue Grosbeak	*Passerina caerulea*	forest
Indigo Bunting	*Passerina cyanea*	edge
Painted Bunting	*Passerina ciris*	edge
Dickcissel	*Spiza americana*	edge
Lark Bunting	*Calamospiza melanocorys*	open
Western Tanager	*Piranga ludoviciana*	forest
Scarlet Tanager	*Piranga olivacea*	forest
Summer Tanager	*Piranga rubra*	forest
Purple Martin	*Progne subis*	open
Cliff Swallow	*Petrochelidon pyrrhonota*	open
Barn Swallow	*Hirundo rustica*	edge

Tree Swallow	*Tachycineta bicolor*	open
Violet-green Swallow	*Tachycineta thalassina*	edge
Cedar Waxwing	*Bombycilla cedrorum*	edge
Red-eyed Vireo	*Vireo olivaceus*	forest
Warbling Vireo	*Vireo gilvus*	forest
White-eyed Vireo	*Vireo griseus*	forest
Nashville Warbler	*Oreothlypis ruficapilla*	forest
Orange-crowned Warbler	*Oreothlypis celata*	forest
Northern Parula	*Setophaga americana*	edge
Yellow Warbler	*Setophaga petechia*	edge
Yellow-rumped Warbler (Myrtle Warbler)	*Setophaga coronata*	forest
Yellow-rumped Warbler (Audubon's Warbler)	*Setophaga coronata*	forest
Magnolia Warbler	*Setophaga magnolia*	edge
Chestnut-sided Warbler	*Setophaga pensylvanica*	open
Pine Warbler	*Setophaga pinus*	forest
Ovenbird	*Seiurus aurocapilla*	forest
Mourning Warbler	*Geothlypis philadelphia*	edge
MacGillivray's Warbler	*Geothlypis tolmiei*	edge
Common Yellowthroat	*Geothlypis trichas*	edge
Yellow-breasted Chat	*Icteria virens*	edge
Wilson's Warbler	*Cardellina pusilla*	edge
American Redstart	*Setophaga ruticilla*	forest
House Sparrow	*Passer domesticus*	edge
Sage Thrasher	*Oreoscoptes montanus*	open
Northern Mockingbird	*Mimus polyglottos*	edge
Gray Catbird	*Dumetella carolinensis*	edge
Brown Thrasher	*Toxostoma rufum*	edge
Cactus Wren	*Campylorhynchus brunneicapillus*	open
Carolina Wren	*Thryothorus ludovicianus*	edge
Bewick's Wren	*Thryomanes bewickii*	edge
House Wren	*Troglodytes aedon*	edge
Winter Wren	*Troglodytes hiemalis*	forest
Red-breasted Nuthatch	*Sitta canadensis*	forest
Tufted Titmouse	*Baeolophus bicolor*	edge
Black-capped Chickadee	*Poecile atricapillus*	edge
Carolina Chickadee	*Poecile carolinensis*	edge
Mountain Chickadee	*Poecile gambeli*	forest
Chestnut-backed Chickadee	*Poecile rufescens*	open
Ruby-crowned Kinglet	*Regulus calendula*	forest
Blue-gray Gnatcatcher	*Polioptila caerulea*	edge
Wood Thrush	*Hylocichla mustelina*	forest

Veery	*Catharus fuscescens*	forest
Swainson's Thrush	*Catharus ustulatus*	forest
Hermit Thrush	*Catharus guttatus*	forest
American Robin	*Turdus migratorius*	edge
Varied Thrush	*Ixoreus naevius*	forest
Eastern Bluebird	*Sialia sialis*	edge
Cassin's Kingbird	*Tyrannus vociferans*	edge
Eastern Phoebe	*Sayornis phoebe*	edge
Olive-sided Flycatcher	*Contopus cooperi*	edge
Dusky Flycatcher	*Empidonax oberholseri*	edge
Yellow-billed Magpie	*Pica nuttalli*	edge
Lesser Goldfinch	*Spinus psaltria*	edge
Chestnut-collared Longspur	*Calcarius ornatus*	open
Dark-eyed Junco (Gray-headed Junco)	*Junco hyemalis*	forest
Sage Sparrow	*Amphispiza belli*	open
Pyrrhuloxia	*Cardinalis sinuatus*	open
Lazuli Bunting	*Passerina amoena*	open
Bank Swallow	*Riparia riparia*	open
Plumbeous Vireo	*Vireo plumbeus*	forest
Bell's Vireo	*Vireo bellii*	forest
Black-and-white Warbler	*Mniotilta varia*	forest
Prothonotary Warbler	*Protonotaria citrea*	forest
Black-throated Green Warbler	*Setophaga virens*	forest
Townsend's Warbler	*Setophaga townsendi*	forest
Hermit Warbler	*Setophaga occidentalis*	forest
Hooded Warbler	*Setophaga citrina*	edge
Rock Wren	*Salpinctes obsoletus*	open
Pygmy Nuthatch	*Sitta pygmaea*	forest
Oak Titmouse	*Baeolophus inornatus*	forest
Wrentit	*Chamaea fasciata*	coastal
Verdin	*Auriparus flaviceps*	open
Golden-crowned Kinglet	*Regulus satrapa*	forest
Western Bluebird	*Sialia mexicana*	edge
Mountain Bluebird	*Sialia currucoides*	edge