Spatial distribution and hotspots of mammals in Canada

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Abstract

High-latitude countries often contain the polar range edge of species that are common farther south. The more peripherally a species occurs in a country, the smaller its national range will be and the more its national range will consist of range-edge populations, which are often predicted to be relatively small, isolated, and unproductive. Together, this may focus national conservation efforts toward peripheral species whose global conservation value is controversial. However, if range-edge taxa occur where overall diversity is also high, there would be fewer trade-offs in protecting them. Using 153 of the 158 terrestrial mammal species in Canada, we tested how species' distributions relate to their national conservation status and total mammal richness. Half of 'Canadian' mammals had <20% of their global range in Canada. Range area in Canada was strongly associated with national threat status; mammals considered 'at-risk' in Canada had 42% smaller Canadian ranges than mammals considered secure. However, after accounting for range area, being more peripheral (smaller proportion of global range in Canada) did not increase the likelihood that a taxon was considered at-risk. We overlaid the 153 maps to calculate mammal diversity across Canada, divided into 100x100 km grid cells. We found that hotspots of at-risk mammals (cells with >4 at-risk taxa) and hotspots of range-edge mammals (cells with >12 taxa with $\leq 20\%$ of their range in Canada) were about twice as species rich as non-hotspot cells, containing up to 44% of Canadian mammal diversity per grid-cell. Our results suggest that protecting areas with the most at-risk or range-edge mammals would simultaneously protect habitat for many species currently deemed secure.

Introduction

Large polar countries often contain the high-latitude range edge of many species that are more widely distributed beyond their borders (Cheffings et al. 2005; Gibson et al. 2009; Rassi et al. 2010; ArtDatabanken 2015). For a given species, the more peripherally it occurs in a country, the smaller its national range area will be. Thus range-edge taxa that occupy small areas in a country are more likely to be deemed nationally at-risk (Lesica & Allendorf 1995), especially if range-edge populations themselves are smaller, more isolated, or less productive than more central populations (Brown et al. 1996; Sagarin & Gaines 2002; Yakimowski & Eckert 2007; although this pattern is far from universal; Samis & Eckert 2009; Pironon et al. 2017; Hargreaves & Eckert 2019). Conservation in large polar countries may therefore be focused toward range-edge species even for taxa that are globally secure (Hunter & Hutchinson 1994).

The value and practicality of conserving range-edge populations are contentious. Ethically, some argue that countries have the greatest obligations to taxa with the largest percentage of their range in their borders, and that taxa are not truly at-risk if they are globally secure (Hunter & Hutchinson 1994). Practically, edge populations may be difficult to conserve if they are inherently unstable due to small numbers, low genetic diversity, or poor habitat (Hunter & Hutchinson 1994; although again these patterns do not hold for many taxa; Eckert et al. 2008). On the other hand, range-edge populations can be important for diversification if they occupy unique habitats (Van Rossum et al. 2003; Mimura & Aitken 2010), and natural range expansion following gradual local adaptation (Hargreaves & Eckert 2019). Polar edge populations are also geographically

poised to initiate range shifts in response to climate warming (Gibson et al. 2009). The geographic ‘head start’ edge populations offer is especially important when species’ dispersal ability is low compared to the rate of climate change, as is the case for many terrestrial mammals (Thomas et al. 2004; Schloss et al. 2012).

Evaluating the relative conservation merits of range-edge taxa would be less important if protecting edge populations involved few conservation trade-offs. One important conservation strategy is establishing protected areas (Myers et al. 2000; Le Saout et al. 2013). Protected areas will be most effective if multiple levels of biodiversity co-occur (Prendergast et al. 1993; Myers et al. 2000; Ricketts et al. 2005), e.g. if at-risk or range-edge species occur in areas with high species richness. Previous studies have not found significant co-occurrence of rare or threatened taxa and overall species richness, either at a global scale for vertebrates (Orme et al. 2005; Ceballos & Ehrlich 2006; Jenkins et al. 2013), or within the UK for invertebrates, plants and birds (Prendergast et al. 1993). However, co-occurrence may be more likely in large high-latitude countries if range-edge taxa are often considered nationally at-risk, since edge taxa and biodiversity will be concentrated toward the equatorward border of such countries (Buckley et al. 2010).

We explore the co-occurrence of at-risk and range-edge taxa with overall richness using terrestrial mammals in the world’s second largest country: Canada. Canadian mammals provide an excellent case study as distribution maps and national threat ranks are available for each taxon (usually species but sometimes subspecies or populations), and Canada’s conservation assessment body—the Committee on the Status of Wildlife in

Canada (COSEWIC)—uses IUCN criteria that emphasize local abundance and range area. Protection of edge populations in Canada is also of global conservation significance, as Canada contains the highest latitude refuges for species in the Americas. Many species designated ‘at-risk’ in Canada are range-edge populations of species largely distributed outside Canada (Gibson et al. 2009; Klemet-N’Guessan et al. 2019), but previous estimates have not compared at-risk to secure taxa or quantified range areas in Canada. It is therefore unclear whether so many at-risk taxa are peripheral simply because most taxa in Canada are peripheral, because edge populations have smaller range areas in Canada, or because edge populations are inherently more at risk.

Using IUCN range maps available for 153 of the 158 extant mammal species that occur in Canada, and categorizing each taxon as nationally at-risk or secure based on its COSEWIC status, we asked two questions. *Question 1*) How do range area in Canada and the proportion of a taxon’s global range in Canada (lower means more peripheral) relate to national conservation status? We predicted that: a) at-risk taxa will have smaller Canadian ranges given the link between range area and population size (Lawton 1993) and importance of both for conservation; b) at-risk taxa will have smaller percentages of their range in Canada given previous findings that many at-risk taxa are edge populations (Gibson et al. 2009; Klemet-N’Guessan et al. 2019); and c) that smaller range percentages would increase the probability that a taxon is at risk even after controlling for range area, if edge populations routinely suffer from factors that would increase their conservation risk (Coristine & Kerr 2011). We then divided Canada into 100x100 km grid-cells and asked *Question 2*) Do cells with the high richness of at-risk species or

range-edge species (hotspots) occur in regions of high overall mammal richness? If range-edge populations are over-represented among at-risk species, as predicted in Question 1, and since edge populations and species richness should both cluster toward Canada's low-latitude border, we predict that at-risk and range-edge hotspots will have higher total mammal richness than non-hotspot cells.

Methods

We recorded the Canadian conservation status for each mammal taxon from COSEWIC assessments; we used COSEWIC's recommendation rather than official status under the Species at Risk Act (SARA) as COSEWIC addresses only conservation risk whereas SARA also considers the economic impact of a given listing. Taxa per threat category: 10 Special concern, 5 Threatened, 7 Endangered, 8 assessed as Not at Risk. The remaining 123 mammal taxa had not been assessed. As COSEWIC assesses species in order of perceived risk, we assume that those that have not been assessed in the 41 years of COSEWIC assessments are relatively secure. Given the low sample sizes within at-risk categories, we binned taxa as either 'at-risk' (Special Concern, Threatened, or Endangered) or 'secure' (assessed as Not at Risk or not assessed).

We obtained distribution maps in the form of spatial polygons from the International Union for Conservation of Nature (IUCN 2018). We first selected the 158 terrestrial mammal species whose distribution polygon overlapped a polygon map of Canada (Natural Earth 2018). IUCN maps are by species, but COSEWIC sometimes assesses subspecies or populations. We retained subspecies and populations if the distribution map

provided in their COSEWIC assessment was similar to their IUCN distribution polygon (2 subspecies and 1 population), but discarded 5 at-risk taxa whose IUCN polygons did not match the geographic scale of their COSEWIC assessments. This yielded 153 taxa: 150 species, 2 subspecies, and 1 population (153 unique species in total; Fig. 1). Each map was cropped to land only by overlapping it with a world boundary map (Natural Earth 2018) using the “sf” package (version 0.7-3, Pebesma 2018) in the statistical platform R (version 3.5.1, R Core Team 2018). As we were interested in range area, polygons were projected into Albers equal area projection (Gibson et al. 2009).

Q1) How do range area in Canada and range percentage in Canada relate to national conservation status?

We determined each taxon’s range area and range percentage in Canada using the “sf” package. We determined range area in Canada (km²) by overlapping each species’ map with a boundary map of Canada (Natural Earth 2018), then measuring the area of the overlap. Canadian range area varied from 2 km² (*Lontra canadensis*) to >9 million km² (*Nycticeius humeralis*), with mean = 1 678 850 km² and median = 460 130 km². Due to the large spread of range areas, we ln-transformed Canadian range area for analyses (see below). We quantified each taxon’s global range area by measuring the area of overlap between its range map and a global land map. Global range area varied from 2075 km² (*Marmota vancouverensis*) to >22 million km² (*Puma concolor*), with mean = 4 449 710 km² and median = 3 263 110 km². We calculated the percentage of each taxon’s global range that occurs in Canada (i.e. the inverse of peripherality in Canada) as Canadian

range area/Global range area x 100; this varied from <0.001% (*Nycticeius humeralis*) to 100% (*Dicrostonyx nunatakensis* & *Marmota vancouverensis*).

We tested the relationships between range area in Canada, range percentage in Canada, and conservation status in Canada using three models. We tested whether range area (ln(range area), gaussian response; *model a*) or percentage (proportion response; *model b*) in Canada differed between taxa deemed at-risk or secure (conservation status = binomial predictor), using generalized linear models (GLMs) with a gaussian and binomial error structure, respectively (*glm* command, base R; ln(range area) or percentage ~ conservation status). Next, using a binomial GLM we tested whether the probability of a taxa being at-risk (conservation status = binomial response) varied with range percentage in Canada (proportion predictor) even after accounting for range size (continuous predictor; *model c*): conservation status ~ ln(range area) + range percentage (Venables & Ripley 2002). We assessed the significance of predictors using likelihood ratio Chisquare tests (*Anova* type=III command, *car* package).

Q2) Do hotspots of at-risk or range-edge taxa coincide with high overall diversity?

To quantify the spatial distribution of mammal diversity, we overlaid a grid of 100x100 km cells on the Canadian equal area map. This produced a map of Canada divided into 1285 cells (not all equal in area as the Canadian border bisected some cells; Supporting Information). We overlaid the range map polygons of all terrestrial mammals on the grid map, then counted the total mammal species, at-risk species, and range-edge species in each cell. We defined ‘range-edge species’ as taxa with ≤20% of their global range in

Canada (as per Klemet-N'Guessan et al. 2019); using a threshold of 10% reduced the number of range-edge taxa from 76 to 53 but did not alter conclusions to Questions 1 and 2 (Supporting Information). Following Prendergast et al. (1993) and Reid (1998), we identified cells with the highest richness ('hotspots') of at-risk and of range-edge taxa up to a maximum of 5% of the total grid cells. We use 'hotspot' *sensu* Prendergast et al. (1993) to refer to areas with high biodiversity, rather than *sensu* Myers (1988) as areas of high diversity *and* high extrinsic threat. This yielded 47 hotspot cells for at-risk taxa (5 to 6 at-risk taxa/cell; 3.6% of total grid cells; Fig. 2a), and 47 hotspot cells for range-edge taxa (17 to 29 range-edge taxa/cell; Fig. 2b). Cells containing 4 at-risk or 16 range-edge taxa were not counted as the number of hotspot cells would have exceeded 5% of total cells. This method of identifying cells of high richness creates richness indices that are reasonably independent of total species richness (Reid 1998).

Whereas regression models assume data points are independent, we detected significant spatial autocorrelation; i.e. hotspot cells for at-risk taxa occurred closer to each other than expected by chance (Moran's $I \pm SD = 0.0628 \pm 0.00137$, $P < 0.001$), as did range-edge hotspots (Moran's $I \pm SD = 0.116 \pm 0.00137$, $P < 0.001$). We accounted for this spatial autocorrelation by incorporating the spatial configuration of data via a fixed effect covariate (*s*), using the Spatial Eigenvector Mapping method (Griffith & Peres-Neto 2006; Dormann et al. 2007; Thayn & Simanis 2013). We selected the neighborhood size of the spatial configuration covariate using the value that maximized model fit based on its Akaike Information Criterion (AIC) value (Supporting Information, Augustin et al.

1996; Dormann et al. 2007). Including s as a fixed effect corrected the autocorrelation in residuals and improved model fit (Supporting Information).

We tested whether total mammal richness was higher in at-risk hotspots than other cells using a GLM with binomial error structure. Each cell contributed one data point. The cells' at-risk hotspot status (at-risk hotspot or not) was a binomial response, and total mammal richness and the spatial covariate s were fixed effects (at-risk hotspot $\sim$ total richness + s). Significance of predictors was determined using likelihood ratio Chisquare tests as for Question 1. This approach is consistent with previous studies comparing at-risk vs. total richness (Prendergast et al. 1993; Orme et al. 2005; Ceballos & Ehrlich 2006), but we recognize two complicating issues: first, that the response and predictors are not fully independent as an increase in at-risk richness automatically increases total richness; second that smaller cells (bisected by the Canadian border) may contain fewer species due to sampling error. We ran two alternate GLMs to test whether our results were sensitive to either issue, one with richness of secure mammals as the predictor (at-risk hotspot $\sim$ secure mammal richness + s ; Supporting Information), and one including cell area as a fixed effect (Supporting Information). Both models reached the same conclusions as our original model, so we present analyses using total richness and not including cell size to facilitate comparison with previous studies.

Similarly, we tested whether total mammal richness was higher in hotspots of range-edge taxa richness than other cells (range-edge hotspot $\sim$ total richness + s). Results using

richness of secure mammals instead of total richness were again similar (Supporting Information).

Results

In Canada, mammal richness is highest toward the south and along the western mountains (Fig. 1a, Fig 2. grey scale maps), although this pattern was not apparent for the 22 taxa deemed at-risk (Fig. 1b). Half (50%) of all ‘Canadian’ mammals had less than 20% of their global range in Canada.

Q1) How do range area in Canada and range percentage in Canada relate to national conservation status?

Range area in Canada differed significantly between nationally at-risk and nationally secure mammals, but peripherality did not (Fig. 1). As predicted, mammals at-risk of extinction in Canada had smaller Canadian ranges than mammals considered secure (model a: $X^2_{df=1} = 6.28$, $P = 0.012$; Fig. 1c). Contrary to our predictions, at-risk mammals did not have smaller fractions of their global ranges in Canada (model b: $X^2_{df=1} = 0.39$, $P = 0.53$; Fig. 1d). Probability of being at-risk in Canada increased as Canadian range area decreased (area: $X^2_{df=1} = 4.54$, $P = 0.033$), but was not affected by range percentage in Canada after controlling for range area (percentage: $X^2_{df=1} = 0.06$, $P = 0.85$, model c).

Q2) Do hotspots of at-risk or range-edge taxa coincide with high overall diversity?

Of the 1285 100x100 km grid cells in Canada, cells with the highest richness of at-risk and range-edge mammals (‘hotspots’) coincided with areas of high total richness (Fig. 2).

Hotspots of at-risk mammals had significantly higher total mammal richness than other cells ($X^2_{df=1} = 140.3$, $P < 0.0001$; Fig. 2c). At-risk hotspot cells each contained 37 to 67 mammal species (24–44% of Canada’s mammal richness; Fig. 2c), and together were home to 80% of the 153 Canadian mammals in our data. Similarly, hotspots of range-edge species, i.e. species only present in Canada in $\leq 20\%$ of their range, also had significantly higher mammal richness than other cells ($X^2_{df=1} = 266.8$, $P < 0.0001$; Fig. 2d). Range-edge hotspot cells each contained 41 to 67 mammal species (27–44% of Canada’s mammal richness), and together were home to 81% of the 153 Canadian mammals in our data. The two types of hotspot partially coincided with each other: almost a third of at-risk hotspot cells were also range-edge hotspots and vice versa (15 of 79 hotspot cells overlapped; Fig. 2).

Discussion

Our quantitative analyses of how mammals are spatially distributed in Canada revealed three main findings. First, our results confirmed earlier qualitative assessments (Yakimowski & Eckert 2007; Gibson et al. 2009) that Canada is a land of edge populations; half the mammals that live in Canada only do so at the northernmost 20% or less of their global range. Second, by quantifying range area we showed that species with smaller Canadian ranges are more likely to be nationally at-risk (Fig. 1a), but that species with smaller fractions of their range in Canada were not (Fig. 1d and model c). Thus we found no evidence that range-edge populations are inherently more vulnerable due to their demography (e.g. putatively small or isolated populations) or coincidence with areas of high human population density. Third, we found significant spatial overlap between

high mammal diversity and hotspots of both at-risk mammals and range-edge mammals (Fig. 2). This result is particularly exciting, as it suggests that protecting habitat for at-risk mammals could have significant co-benefits to mammals considered secure, and that protecting range-edge populations need not involve a trade-off with protecting Canada's overall mammal diversity.

Our finding of high spatial overlap between total mammal richness and at-risk mammal richness (Fig. 2c) contrasts results from other areas and taxa. Globally, hotspots of at-risk mammals do not strongly overlap areas of high total mammal richness (Ceballos & Ehrlich 2006), nor do hotspots of at-risk birds strongly overlap with hotspots of total bird richness (Orme et al. 2005). Diversity is driven largely by energy availability and biogeographic history (Gaston 2000), whereas threats to wildlife are driven by human impacts (Schipper et al. 2008; Szabo et al. 2012). Poor global congruence between at-risk and total diversity suggests these drivers have different global distributions (Orme et al. 2005). In Canada however, mammal richness concentrates in the south and west (Fig. 1), as does the intensity of human land conversion (Kerr & Cihlar 2004; Kerr & Deguise 2004). To the extent that diversity and human impacts co-occur in other high-latitude countries, high overlap between at-risk and total diversity may be more common at regional than global scales.

Of course, habitat protection generally happens on a much smaller scale than our 100x100 km grid cells, and species rarely occupy all land area within their occurrence polygon at fine scales. Protecting habitat within a hotspot may not capture all the species

whose ranges overlap with the larger grid cell. Nevertheless, identifying hotspots at a coarse scale is still useful for conservation planning; the hotspots identified here should now be priorities for finer scale assessments (Rodrigues et al. 2004). Further, we are in an era of species on the move, as species shift their geographic distributions in response to anthropogenic change (Chen et al. 2011; Freeman et al. 2018). Protecting habitat in high diversity areas provides habitat options that nearby species may well use in the future, even if they don't use them currently.

Cells that were hotspots for both at-risk and range-edge taxa are particularly interesting for long term conservation. Since the highest densities of mammals deemed at-risk in Canada occur in the United States (Fig. 1b), one effective conservation strategy for many at-risk taxa in Canada may be to maintain habitat connections to US populations. This would both enable natural immigration and population replenishment, and provide bridges if or when species begin to shift northward in response to warming, both of which could bolster Canadian populations. Indeed, given worldwide range shifts to higher latitudes (Chen 2011), Canada's current range-edge species may become much less peripheral in the coming decades, and much of Canada's future biodiversity may be on our doorstep. Protecting habitat in the 'double hotspots' is a win-win-win, protecting high numbers of mammals overall, protecting the at-risk species to whom Canada deems it has a national responsibility, and protecting Canada's future biodiversity in terms of currently peripheral species and the wildlife refugees from climate change coming our way.

Supporting Information

SI is available online. Appendix S1 = distributions of species assessed by COSEWIC grouped by COSEWIC threat status. Appendix S2 = grid map of Canada. Appendix S3 = results from analyses exploring sensitivity of hotspot models and from alternate analytical decisions described in Methods. Appendix S4 = AICs of spatial GLMs according to different neighborhood distances. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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427

428 **Figures**

Fig. 1: Geographic distributions of terrestrial mammals deemed secure (purple) and at risk (teal) in Canada. (a & b) Each polygon shows one taxon's distribution, areas of darker colour contain more taxa (colour scale bars indicate species richness). Although only taxa that occur in Canada are mapped, areas of high richness occur south of the Canadian border. At-risk and secure mammals differ in Canadian range size (c; * indicates statistical difference from model considering ln-transformed data), but not the percentage of their global range that occurs in Canada (d). c and d show raw data, centre lines and box boundaries represent the median, 25th and 75th percentiles respectively, whiskers extend to 1.5x the distance between the 25th and 75th percentiles, dots are outliers.

Fig. 2: High spatial overlap between hotspots and total mammal richness. Maps of Canada are divided into 1284 100x100 km grid cells, shaded in greyscale to show total species richness of terrestrial mammals. Coloured cells show locations of hotspot cells, i.e. those with the highest richness of a) mammals deemed at-risk in Canada (teal), and b) mammals that only occur in Canada in the northernmost 20% or less of their global distribution (red). (c & d) Relative diversity of hotspot (coloured) vs. non-hotspot (grey) cells. Middle plots show raw data, where each point represents one grid cell. Bottom: Hotspots have higher total mammal richness than non-hotspot cells (* indicates a significant difference within panel). Boxes summarize raw data, showing the median and quartiles, formatting as per Fig. 1.

452 Appendix S1

453

454

455 **Appendix S1:** Spatial distribution of the Canadian terrestrial mammals that have been
 456 assessed by COSEWIC, separated by their COSEWIC status: Not-at-risk of extinction
 457 (n=8), Special concern (n=10), Threatened (n=6), and Endangered (n=8).

458

459 **Appendix S2**

460

461 **Appendix S2:** Grid map of Canada. The grid is a 100 x 100 km cell grid overlapped on
 462 the map of Canada projected in an Albers equal area projection. Mammal diversity
 463 metrics were calculated for each grid cell for analyses in *Question 2* (hotspots).

Appendix S3

Results from additional models exploring the sensitivity of hotspot analyses. All models compared a binary response (a cell was or was not a hotspot) to a measure of overall richness (fixed effect). Results show the analysis of deviance of each model. Models presented in the main text are in bold. *Spatial covariate*: Including a term to capture the spatial covariance in the data (*s*: Spatial Eigenvector Mapping) improved model fit compared to equivalent models without *s* (models 1 vs 2, models 5 vs 6). Including *s* also corrected the autocorrelation in residuals for the at-risk hotspot model (model 2 without *s*: Moran's $I \pm SD = 0.046 \pm 0.0014$, $P < 0.001$; model 1 with *s*: Moran's $I \pm SD = -0.00060 \pm 0.0014$, $P = 0.90$) and the range-edge hotspot model (model 7 without *s*: Moran's $I \pm SD = 0.063 \pm 0.0014$, $P < 0.001$; model 6 with *s*: Moran's $I \pm SD = -0.0023 \pm 0.0013$, $P = 0.020$). *Richness of secure mammals vs. all mammals*: Comparing richness of secure mammals between hotspots vs. non-hotspots yielded similar results to comparing total mammal richness (at-risk + secure) between hotspots vs. non-hotspots for analyses of at-risk hotspots (model 1 vs 3) and range-edge hotspots (models 5 vs 7). *Cell area*: Accounting for cell area in models did not change conclusions (models 1 vs 4, 5 vs 8). *Threshold for being considered a range-edge taxon*: Reducing the threshold for 'range-edge' taxa from $\leq 20\%$ of their global range in Canada to $\leq 10\%$ of their range in Canada did not qualitatively change results (model 5 vs 9).

<i>Hotspot type</i>	Fixed effects			Model
Model)	Effect	$X^2_{df=1}$	<i>P</i>	AIC
<i>At-risk hotspots vs non-hotspots</i>				
1)	Total richness <i>s</i> (170)¹	140.3	<.0001	94.0
2)	Total richness	141.2	<.0001	266.1
3)	Secure richness <i>s</i> (170) ¹	163.7	<.0001	116.9
4)	Total richness	201.6	<.0001	100.9
	Cell area <i>s</i> (170) ¹	16.8	<.0001	
<i>Range-edge hotspots vs non-hotspots</i>				
5) 20% threshold	Total richness <i>s</i> (380)¹	266.8	<.0001	70.3
6) 20% threshold	Total richness	203.4	<.0001	203.9
7) 20% threshold	Secure richness <i>s</i> (350) ¹	281.6	<.0001	69.9
8) 20% threshold	Total richness	269.6	<.0001	69.4
	Cell area <i>s</i> (380) ¹	2.9	.089	
9) 10% threshold	Total richness <i>s</i> (380) ¹	307.9	<.0001	75.8

1. Number in brackets is the neighbourhood of *s* in km²

486 Appendix S4

487
488 **Appendix S4:** Akaike information criterion (AIC) values for different distances of
489 neighborhood within the spatial extra covariate integrated to GLMs. Neighborhood
490 distances were used to obtain the spatial covariate using Spatial Eigenvector Mapping
491 (SEVM). Absent values indicate distances for which the eigenvector filtering could not
492 yield results. AICs for different distances are presented for all three GLM models
493 presented in the methods. The distance resulting in the lowest AIC was selected for the
494 given model.