Assessing the risks to United States and Canadian mammals caused by climate change using a trait-mediated model

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A set of 182 populations of 76 mammal species in the United States and Canada, examined in natural conditions with minimized disturbances or management effects, shows that responses to climate change include negative responses, such as elevational range contractions, upward shifts and decreases in abundance, positive responses, such as range expansions, and no detectable responses. Responses vary among and within mammal species but many are correlated with species traits, particularly the responses linked to high extinction risks (= climate change risk: decreases in population sizes, range contractions, local extirpations). The traits showing the strongest links to differential responses to climate change are 1) body size—large mammals respond more often and most negatively to climate change, 2) activity times—few mammals with flexible active times respond to climate change, and 3) spatial distribution—high-latitude and high-elevation mammals responded more often to climate change. Using these traits and two approaches to trait weighting, I modeled the relative climate change risk for all 328 terrestrial, nonvolant mammal species in the United States and Canada across 10 levels of risk (low = 1–2, moderate = 3–4, moderate-high = 5–6, high = 7–8, very high = 9–10). The models predicted that 15% of these mammalian species are in the high- and very high-risk categories, including species from most orders. Many mammal populations and species listed as of conservation concern due to other human impacts by national or international agencies are also predicted by my models to be in the higher categories of climate change risk. My intention for these models is to clarify for managers and researchers which, where, and how mammals are responding to climate change relatively independent of other anthropogenic stressors (e.g., large-scale habitat change, overhunting) and to provide a preliminary assessment of species most in need of careful monitoring for climate change impacts.

Key words: activity times, body size, conservation, environmental change, global warming, predictive modeling, traits

Humans are causing a conservation crisis for mammals through habitat modification, encroachment on critical habitat, hunting, and other disturbances (Ceballos and Ehrlich 2002, 2006; Burns et al. 2003; Ceballos et al. 2005; Ricketts et al. 2005; Lawler et al. 2009; Rondinini et al. 2011; Crooks et al. 2017). Over 25% of mammalian species are estimated to be at imminent risk of extinction and many terrestrial mammal populations are decreasing worldwide (Ceballos and Ehrlich 2002, 2006; Ceballos et al. 2005; Ricketts et al. 2005; Lawler et al. 2009; Hoffmann et al. 2011; Rondinini et al. 2011; Ripple et al. 2014). Of the 328 native, terrestrial, nonvolant mammals in the United States and Canada (IUCN 2019), 53 are listed under some level of conservation concern by the International Union for Conservation of Nature

(IUCN 2019), the United States Endangered Species Act (ESA—FWS 2018), and Canada's Species at Risk Act (SARA 2018). Management plans for many species assume that areas protected at present will suffice to conserve the species living within them over long time periods (e.g., Burns et al. 2003), but those areas actually cannot accommodate potential, large-scale modifications due to anthropogenic climate change (e.g., IPCC 2014; Langdon and Lawler 2015). One way to be proactive about monitoring and management is to assess the potential for negative responses to climate change of the species of interest based on similar species that have already exhibited climate change responses (Parmesan and Galbraith 2004; Rowe 2007; Moritz et al. 2008; McCain and King 2014; Rowe et al. 2015).

Another, more common approach to predicting how organisms may respond to climate change is to construct individual species distributional models in present and future conditions (Lawler et al. 2009; Kearney et al. 2010; Langdon and Lawler 2015). These GIS-based, correlative models assume a similar and consistent response to temperature and precipitation for all species regardless of traits (e.g., the models assume upward latitudinal and elevational shifts). Evidence from climate change after the K-Pg asteroid impact and from the Pleistocene glacial cycles clearly demonstrates that not all mammal species responded to temperature change similarly in the directionality of range shifts and in extinctions (e.g., Lyons 2003; Barnosky et al. 2004b; Robertson et al. 2004; Blois et al. 2010; Elias 2015). Mammalian traits such as body size, fossoriality, hibernation, dispersal, food caching, and nocturnality have been suggested to have mediated species-specific responses (e.g., Barnosky et al. 2004a; Robertson et al. 2004; Liow et al. 2009; Sutton et al. 2016; Williams and Blois 2018). Accumulated evidence also suggests that not all mammalian species or populations currently are responding similarly to anthropogenic temperature changes (e.g., Rowe 2007; McCain and King 2014; Rowe et al. 2015 and references therein). For example, McCain and King (2014) showed that only 48% of 73 mammal species responded as generally predicted to increased temperatures (e.g., upward elevational and latitudinal shifts, declines in abundance). That study detected significant trait-mediated responses in which large-bodied (> 100 g) and obligate nocturnal or diurnal mammals responded more often and most negatively to anthropogenic climate change, with high impacts to species

with populations at high latitudes and high elevations (McCain and King 2014). Those results suggested that small-bodied mammals and mammals with flexible activity times may find shelter from climate change by using microhabitats and microclimates that are not available to larger mammals or to mammals that must be active in the warmest or coldest part of the day (McCain and King 2014; Leach et al. 2015; Fuller et al. 2016; Milling et al. 2018).

Herein, I take a new approach using what I term "trait-mediated prediction models" that seek to forecast responses to climate change for unassessed species through inference of similarity in key traits to those species that are already exhibiting responses to climate change. As of 2018, 182 populations of 76 mammal species have been studied for responses to current climate changes in the United States and Canada, including local extirpations, range contractions and shifts, population decreases or increases, phenological shifts, and genetic and morphological changes (Fig. 1; Supplementary Data SD1). Importantly, those studies were conducted in relatively natural areas where the measured responses were attributed statistically to climate change and not attributed largely to, or combined with, other human disturbances. Therefore, those studies, and the predictions based on them, assess climate change responses independently of human disturbance or management as much as is feasibly possible. Using a trait-mediated prediction framework for responses to climate change, I forecast the risk of negative responses to climate change—e.g., declining populations, contracting ranges, and local extirpation—for all previously unassessed terrestrial mammals of the United States and
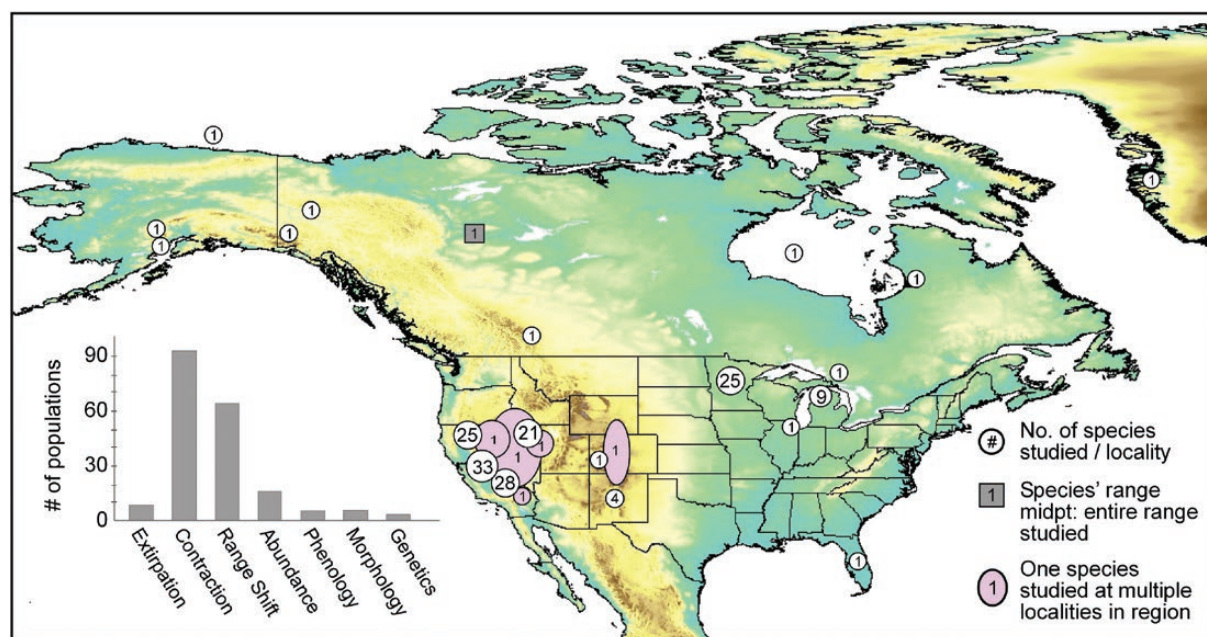

Fig. 1.—The distribution of terrestrial mammal studies that were tested for anthropogenic climate change impacts across the United States and Canada. Size-scaled white circles show localities of studies and the number of species included in each study. Gray ovals (pink online) show locations of studies of single species using multiple study sites for multiple populations in a region (e.g., extirpations of American pika, *Ochotona princeps*). The single gray square in northwest Canada is the midpoint of the geographic range of *Gulo gulo* (wolverine), as it was studied across its entire geographic range. The types of responses to climate change tested in these populations are shown in the inset histogram (local extirpations, range contractions, range shifts, abundance changes, phenology changes, morphological changes, and genetic changes). See the online article or pdf for a color version of this figure.

Canada. Of particular importance are the potential exacerbated risks from climate change for mammal species known already to be of conservation concern due to other human activities.

First, I reassess the validity of the model of McCain and King (2014) with the inclusion of data from additional studies. Then, I construct models of risk from climate change for each terrestrial mammal species in the United States and Canada based on the critical traits detected in the 2014 and the present analyses. Lastly, I provide a preliminary assessment of those species and clades of greatest predicted risk due to climate change with a proscription of future research and conservation efforts. Since these climate change predictions are constructed relatively independent of other human impacts, management and monitoring of individual populations and species will need to weigh these preliminary predictions in concert with local responses to other anthropogenic changes both negative and positive.

Materials and Methods

Reassessment of traits.—To apply the new approach of trait-mediated predictions to forecast responses to climate change for unassessed species of terrestrial mammals in the United States and Canada, I used and updated the database of mammalian responses to climate change from McCain and King (2014). The original database was compiled from standardized literature searches (*ISI Web of Science*, *Google Scholar*, and *Scirus*) using various combinations of keywords (climate change, global warming, mammals, USA, Canada). To augment the previous database, I used the same search engines and keywords to look for additional studies for inclusion from the end of the previous search in 2013 through 2018. Of the 1,050 (up to 2013) and 20 (2014–2018) relevant journal articles reviewed, I only included studies that empirically examined and statistically tested pre- and post-anthropogenic climate change resurvey data or long-term monitoring data on native mammal species across a time period of documented anthropogenic climatic change. Overall, the critical elements for inclusion were to use studies that empirically measured and statistically inferred a response to anthropogenically increased temperature or a change in precipitation that were largely independent of other human disturbance or management. Therefore, I did not include studies that could not exclude anthropogenic habitat change as the main driver of the change, those that did not have strong similarities in data collection methodology between the pre- and post-climate change periods, and those that only examined shifts in response to current climate and extended their results to predictions in the future (see McCain and King 2014 for more detail). Data quality and statistical inferences still varied among the included studies; therefore, I also analyzed a best data subset that included only those studies with greater than 5 years of sampling, with the least amount of potential anthropogenic habitat change, and with the strongest statistical inference and sampling methodology. As an estimate of detrimental impacts of climate change, an extinction risk subset was analyzed, which only included studies testing for local extirpations, decreases in abundance, and range contractions.

Lastly, I compared mammal species that had contracted their elevational ranges to those that had expanded their elevational ranges using only the best elevational subset.

Using the original database supplemented with the additional studies, I re-analyzed if mammalian traits mediated which species responded negatively, positively, or did not respond to climate change following the methodology in McCain and King (2014). The mammalian traits (independent variables) included 1) body size, 2) activity times (diurnal, nocturnal, flexible), 3) maximum latitudinal limit for the species, 4) elevational range of the species (nonmontane, mid-montane, high montane; only used in elevational analyses), 5) latitudinal position of studied population within the species' geographic range (north, middle, south), and ability 6) to burrow or nest, 7) to hibernate, and 8) to exhibit heterothermy. These traits were chosen to represent species traits and geographic trends predicted in the literature to be important in determining responses to climate change. Body size has been theorized to be important in past and present climatic responses of mammals for its influence on sheltering, microclimate use, and movement patterns, for example, during the K-T extinction event (e.g., Robertson et al. 2004), the Pleistocene (e.g., Lyons 2003; Barnosky et al. 2004b; Blois et al. 2010), and currently (e.g., Schloss et al. 2012; McCain and King 2014; Fuller et al. 2016), as well as during the current anthropogenic extinction crisis (e.g., Cardillo et al. 2005; Liow et al. 2009). Other traits that modify the climatic conditions experienced by a mammal species include activity times, hibernation, heterothermy, burrowing, and nesting, which are also predicted to be important in the past and present responses to climate and anthropogenic change (e.g., Robertson et al. 2004; Cardillo et al. 2005; Liow et al. 2009; Schloss et al. 2012; McCain and King 2014). Responses to climate change are predicted to be concentrated geographically, particularly at high latitudes and elevations, and at range edges (Grabherr et al. 1994; Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003; Hickling et al. 2006). Thus, variation in response rate among mammals may be related to the severity of the climate change in the study location (e.g., Grabherr et al. 1994; Parmesan and Yohe 2003; Chen et al. 2009; Beever et al. 2011). Clearly, an innumerable array of species traits could be assessed that are not included here, such as life history traits, diet, metabolic measurements, and food web dynamics. But these analyses are limited by sample sizes as well as availability and completeness of data for each trait across all species. Nonetheless, many of additional traits are correlated with either mammalian body size (e.g., metabolic rates, number of offspring, life span, and time at weaning) or clade (e.g., diet), which are both included in the analyses. Additions of more traits to modeling efforts would be a fruitful future direction once more species responses to climate change accumulate.

All analyses were conducted at the species level, because traits are a property of the species and not populations, and because the statistical analyses were conducted using multivariate nominal logistic regressions that necessitated data independence and could accommodate species-level phylogenies. The mammalian responses to anthropogenic climate change

included local population extirpations, range contractions and range shifts, abundance changes, phenological shifts, morphological changes, and genetic changes (Fig. 1 inset; Supplementary Data SD1). To simplify these varied responses for a logistic regression analysis, I condensed these to "predicted" and "unpredicted" responses to climate change as the dependent variable in the models. The authors of each study stated their a priori predictions of how each species should respond to climate change, which was almost always the expected detrimental responses: local extirpations, range contractions or upward range shifts, decreases in abundance, advancement of phenological trends, reduction in body size, and directional genetic change. If the measured response matched the author's predictions, it was denoted as "predicted." If the measured response was opposite of the author's predictions (e.g., range expansion, increase in abundance) or if no response was detected, it was denoted as "unpredicted."

Because multiple populations of the same species were tested across the published studies (e.g., 23+ populations of *Ochotona princeps*), a single, composite response for each species was necessary. This was denoted as "predicted" if ANY of the populations detected the expected response, otherwise as "not predicted" if a combination of opposite or no response was detected among populations (e.g., Fig. 2). I calculated the percent consistency in responses within a species (e.g., 100% = all populations with same response; 0% = one population with a predicted response and another a not-predicted response) and the range in percent consistency within mammal clades (Supplementary Data SD2). For data quality in the latter, I only used the best subset of studies.

To detect the best-fit models and the strongest predictor variables for each of the four data sets (all data, best subset, extinction risk, elevational ranges), I used multivariate, nominal logistic regressions. Initial models included all predictor variables, and variables were removed stepwise by lowest individual significance value until the best model was detected with the lowest AICc value and all variables individually significant ($P < 0.05$) using JMP Pro. In 2014, a multivariate phylogenetic logistic regression was also included, but did not detect any phylogenetic signal (McCain and King 2014). Thus, for simplicity and because only a few new species were added, I only present the nonphylogenetic analyses.

Trait-mediated prediction models.—For each terrestrial mammal in the United States and Canada (*n* = 328—IUCN 2019), I tabulated the traits statistically linked to climate change response based on McCain and King's (2014) results and the current re-analyses (Supplementary Data SD3). Because no bats— hence their trait combinations—met our criteria for empirical climate change responses in the United States and Canada, no climate change risks are predicted for bats. Mammalian trait data were compiled from various sources, including body sizes from the MOM database (Smith et al. 2003); body sizes, activity patterns, and latitudinal ranges from the PanTHERIA database (Jones et al. 2009); and supplemented with additional resources as needed (e.g., Hall 1981; Nowak 1991; Baker et al. 2003; Matocq and Murphy 2007; Armstrong et al. 2011; and
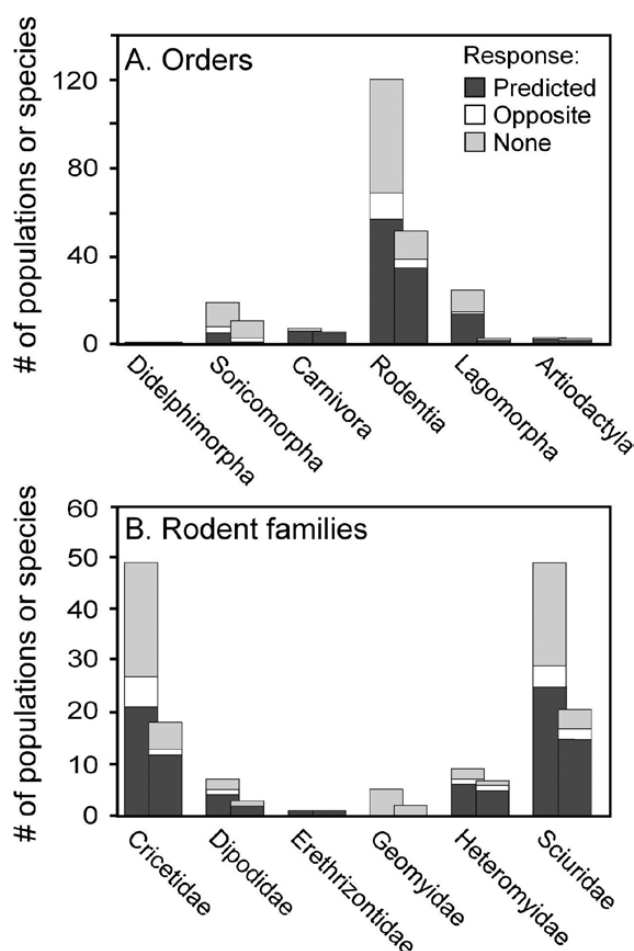

Fig. 2.—The documented responses to anthropogenic climate change, including predicted responses (dark gray), opposite responses (white), and no response (light gray) among populations (left bar) and species (right bar) within the mammal orders (A) and rodent families (B).

Mammalian Species accounts). Elevational distributions can be highly variable across the geographic range of a species, often higher in the southern portion of the range. Thus, for a species trait, elevational range was simplified into broad categories constructed specifically to emphasize its montane populations where they do exist: 1) low elevation or nonmontane; 2) mid-elevations (middle third of mountain or middle elevations in southern part of its geographic range); and 3) montane (upper third of mountain, or upper elevations in the southern part of range). Both McCain and King (2014) and the re-analyses detected the same four species traits (body size, activity times, latitudinal range maximum, and elevational range) as linked to differential responses to climate change. But the two analyses and the subsets differed slightly in the magnitude of effect among traits. Thus, to contrast the two results, I conducted the trait-mediated predictive ranking based on each analysis through differential weighting schemes.

For the "weighted model," McCain and King (2014) detected body size as of the largest importance, followed by activity times, then smaller effects of latitude and elevational distributions. Thus, for this predictive model, the variables

were unequally weighted based on their combined strength in the original models: A) body size in log grams (weighed from 1 to 27): 1 = 0–0.99; 5 = 1–1.99; 13 = 2–2.99; 22 = 3–3.99; 27 = ≥ 4; B) activity times (weighted from 0 to 15): 0 = flexible; 10 = nocturnal; 15 = diurnal; C) maximum latitude (weighted from 0 to 10): 0 = < 40°N; 5 = 40–50°N; 10 = > 50°N; and D) elevational range (weighted from 0 to 5): 0 = low; 2 = mid-elevation; 5 = montane. For this weighted model, the sum of weights ranged from 1 to 57, which were rescaled to ranks of 1 to 10. The re-analyses detected a more equal importance of body size and activity times followed by latitude and elevation. Given its contrast to the earlier model, this variation suggests that the four variables are all important but their relative importance is less clear. Thus, in the "equal model", the variables were equally weighted stressing the general importance of each variable with less emphasis on relative strengths: A) body size in grams (weighted 0 to 2): 0 = < 100 g; 1 = 100–999 g; 2 = >1,000 g; B) activity times (weighted −1 to 2): −1 = flexible; 1 = nocturnal; 2 = diurnal; C) maximum latitude (weighted 0 to 2): 0 = < 40°N; 1 = 40–50°N; 2 = > 50°N; and D) elevational range (weighted 0 to 2): 0 = low; 1 = mid-elevation; 2 = montane. For this equal model, the sum of weights ranged from −1 to 8, which were rescaled to ranks of 1 to 10. Most rankings (83%) were the same or differed by only one rank between the two models, but bigger differences of 2–3 ranks existed among the mammal species with the largest body sizes. Both rankings are presented in the Supplementary Data SD3, whereas the average of the two rankings is used as a composite in the text according to low risk (1–2), moderate risk (3–4), moderate-high risk (5–6), high risk (7–8), and very high risk (9–10), because likely both contain important predictive value. I chose this wording to emphasize the higher-risk categories because there were species in each group, even the low and moderate groups, which have already responded negatively to current climate change. Additionally, it may be the case that these analyses are highlighting the fast responders, and with greater and more sustained change into the future, even the moderate risk species may show greater negative responses.

Next, I highlight the climate change risk among those species already of conservation concern based on global (The International Union for Conservation of Nature Red List—IUCN 2019) and regional (United States Endangered Species—FWS 2018; Canadian Species at Risk—SARA 2018) conservation assessments (Supplementary Data SD3). Lastly, to validate the trait-mediated models, at least in a preliminary way, I calculated the average percentage of "predicted" responses to climate change for the risk categories of the seven newly added species using the data and analyses of 2014.

RESULTS

A total of 182 mammal populations of 76 species have been tested for climate change responses in the United States and Canada according to my inclusion criteria, including the newly added 59 populations of 36 species, seven of which species are new to the data set (Supplementary Data SD1 and SD2; Brodie

and Post 2010; Smiley 2010; Rowe et al. 2015; Baltensperger et al. 2017). The studied species and populations are distributed across the region (Fig. 1) with a skew toward California and Nevada, with 59% of species and 70% of populations. Most responses to climate change were assessed for range contractions, range shifts, and abundance changes (Fig. 1 inset). Six mammalian orders were represented (Fig. 2A), including marsupials (Didelphimorpha), shrews (Soricomorpha), carnivores (Carnivora), rodents (Rodentia), rabbits and pikas (Lagomorpha), and even-toed, hoofed mammals (Artiodactyla). The largest representation of populations and species was among rodents, particularly the New World voles, mice, and rats (Cricetidae) and squirrels (Sciuridae; Fig. 2B). All three types of climate change responses—predicted, opposite, and no response—were detected in the populations and species in each mammal clade except those with only one or two populations tested. Overall, 46 mammal species displayed the responses predicted from climate change, 24 species did not respond, and another six species displayed opposite responses. Consistency of responses varied within the populations tested for a species and within the species tested for a mammal clade (Supplementary Data SD2). Most populations within a species and species within clades (except several rodent families) had relatively high consistency among responses, and 20 of the 40 species with multiple-tested populations had identical responses.

Re-analyses of trait influences on differential responses to climate change were similar to those calculated by McCain and King (2014). The best-fit models, evaluated using stepwise, multivariate, nominal logistic regression for all data (χ^2 = 17.85, P = 0.0005, n = 76) and extinction risk data (χ^2 = 14.75, P = 0.002, n = 42), included body size and activity times. Models using the best subset included only body size (χ^2 = 6.078, P = 0.0137, n = 52; Fig. 3). The best subset of elevational data included body size, activity times, and latitudinal range (χ^2 = 14.97, P = 0.0048, n = 23) with more high-elevation species responding as predicted. The main difference between these analyses and those of McCain and King (2014) was the magnitude of effects among the traits. Body size had the strongest effect in McCain and King's (2014) models, whereas, in my new models, body size and activity times were closer in the magnitude of their effects using all data and extinction risk data. For example, comparing variable strength using the logWorth of the logistic regressions, variable strength of body size compared to that of activity times was 2.9 to 2.2 in 2014 versus 1.55 to 1.4 in 2018 in the extinction risk models.

The two trait-mediated prediction models applied to the entirety of the 328 native, terrestrial, nonvolant mammals in the United States and Canada based on the differential weighting of the four key traits (body size, activity time, latitudinal maximum, and elevational range) predicted about 15% of mammal species at high or very high risk from climate change (Fig. 4A; Supplementary Data SD3). Most species were given similar ranks by the weighted and the equal weights models. In all, 83% were given equal ranks or ranks that differed by only one rank while the other 17% differed by two or three ranks,
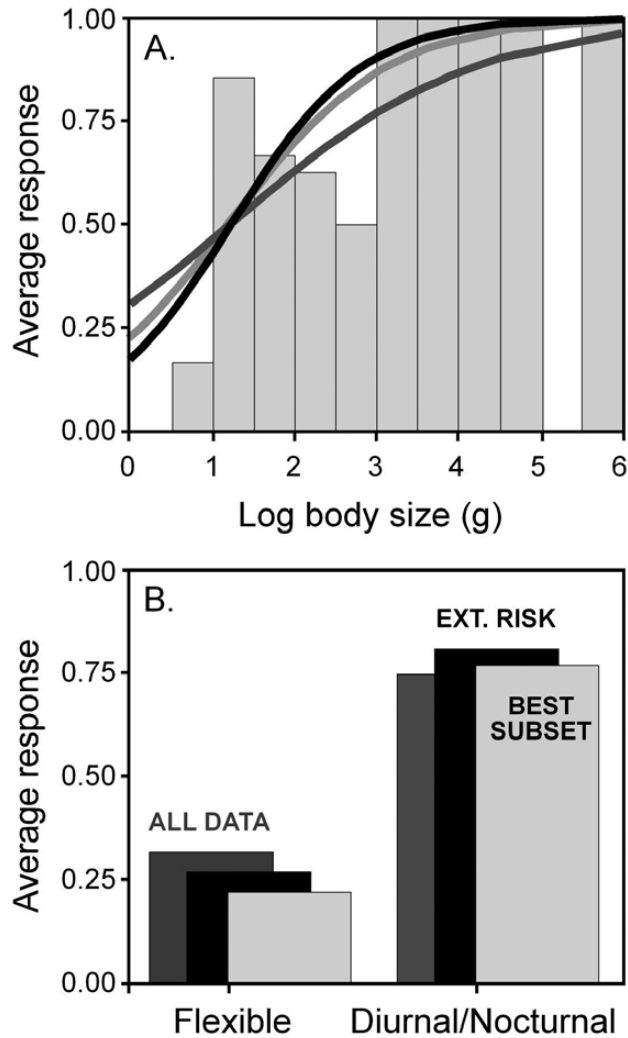
Fig. 3.—Multivariate nominal logistic regressions detected both body size and activity times as critical traits in determining mammalian responses to climate change. Individual logistic regressions for body size (A) and activity times (B) show that predicted, negative responses to climate change increase with body size and diurnal and nocturnal activity times. Predicted response is 1.00 and nonpredicted response is 0.00 on the y-axis. The logistic regression curves and the bar colors indicate all data (dark gray), extinction risk data (black), and the best subset (light gray).

Fig. 4.—The trait-mediated model predictions for negative responses to climate change in United States and Canadian mammals based on four mammalian traits: body size, activity times, latitudinal maximum, and elevational range. (A) Comparison of the number of mammals within each risk category for the weighted model with more emphasis on body size (left bars), the equal model (middle bars), and the composite, averaged model (right bars). (B) The percent of predicted responses for the newly tested species (dotted line and circles; $n = 7$) compared to the trait-mediated prediction ranks (x-axis) for the model built solely using the 2014 database. This is contrasted to the expected increasing trends in the model data from 2014. (C) The number of species in the various risk categories for the diverse mammal orders. The risk for the monotypic orders and families include Didelphimorpha = 7; Cingulata = 5; Aplodontiidae = 6; Erethizontidae = 8; and the low diversity Dipodidae = 2–6.5.

mainly due to weighting of body size. For figures, I averaged the ranks of the two models but results of both models and the averages are presented online for each of the 328 species (Supplementary Data SD3). The United States and Canadian mammals most at risk due to climate change according to these models (very high: model ranks 9–10) include iconic carnivores (e.g., *Lynx canadensis*, *Ursus maritimus*), medium to large-sized, cold-adapted mammals (e.g., *Lepus americanus*, *Ovibos moschatus*, both pika species), and most marmot species and several other squirrel species (e.g., *Callospermophilus lateralis*, *C. saturatus*, *Tamiasciurus hudsonicus*). Additionally, many of the species predicted to respond negatively to climate change are already of conservation concern due to other human impacts (Fig. 5) and are on the IUCN Red List (IUCN 2019),
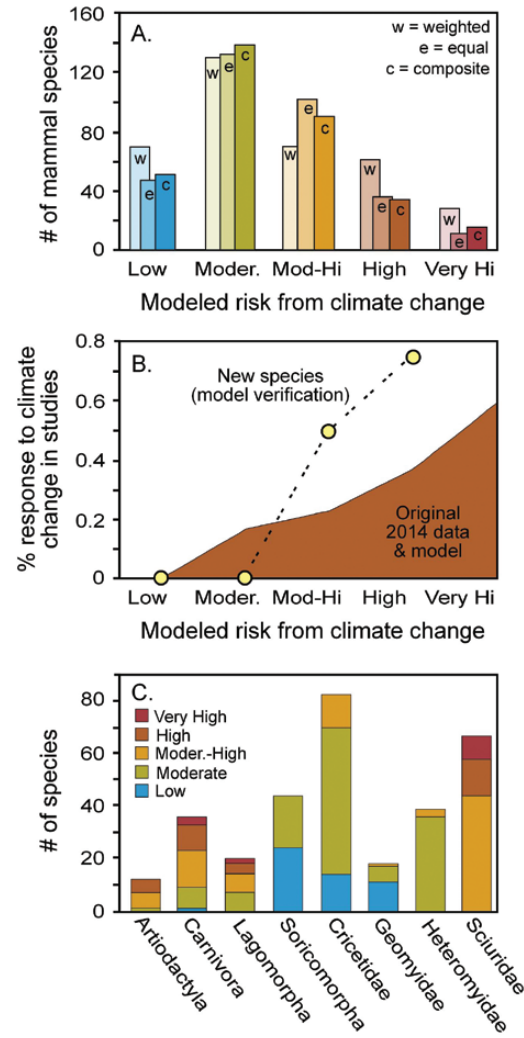
listed by the United States Endangered Species Act (FWS 2018), and the Canadian Species of Concern Act (SARA 2018; Supplementary Data SD3).

Among the included studies, each mammal clade had species that responded as predicted to climate change and species that did not. Nonetheless, some groups of mammal species responded as predicted more often than others. In particular, scuirids and carnivores responded the most often and negatively (i.e., higher extinction risk responses; Fig. 2); therefore, the trait-mediated predictions for unassessed species were of
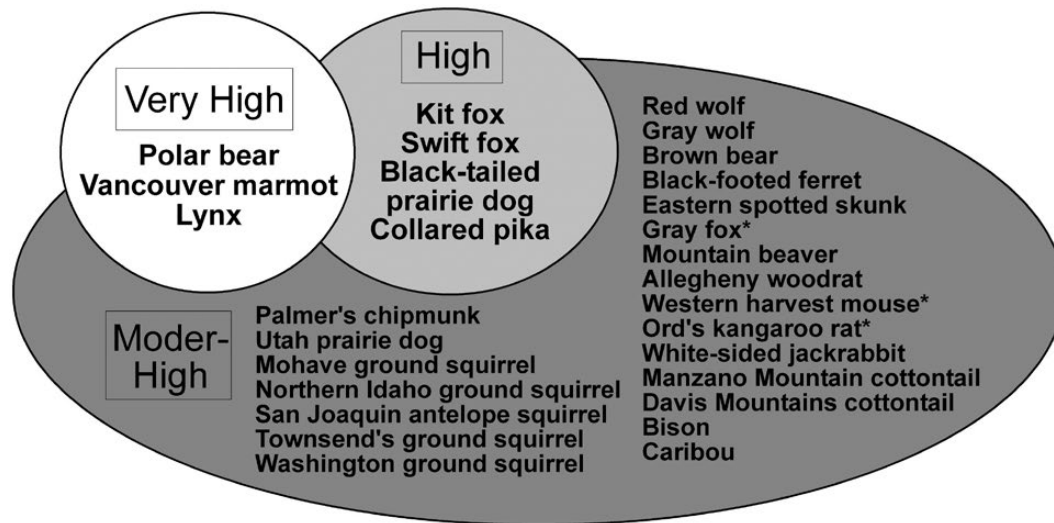
Fig. 5.—North American mammals already listed as of conservation concern in the United States and Canada by the IUCN, ESA, or SARA with their calculated risk from anthropogenic climate change as very high potential responses (white: 9–10 ranks), high (light gray: 7–8 ranks), and moderate–high risk (dark gray: 5–6 ranks). The starred species are only of conservation concern at their northern range limit in southern Canada.

higher risk (Fig. 4C). Similarly, artiodactlys and lagomorphs also had more species responding and therefore more species in the higher-risk rankings. In contrast, populations of New World voles, mice, and rats (Cricetids) and shrews (Soricomorpha) were tested the most often for climate change responses (Fig. 2), but both clades responded less often to climate change and thus have overall lower predicted risks for unassessed species (Fig. 4C). As a preliminary confirmation of the validity of the trait-mediated predictions, the predictions based only on the 2014 database for the seven new species confirmed the expections of the model: those with higher-risk rankings responded as predicted, whereas those with lower-risk rankings did not respond as predicted (Fig. 4B).

DISCUSSION

My results confirmed McCain and King's (2014) original findings suggesting that predictive models of climate change risk for mammals should include the traits of body size, activity times, maximum latitude in a species' geographic range, and elevational ranges. Herein, I developed such trait-mediated models to forecast the potential risks of climate change on unassessed populations of mammal species in the United States and Canada. The aim of these models was to aid researchers and managers with species-based conservation plans beyond the simplistic assumption that all species will respond and respond similarly to climate change at some point in the future. But these predictions should be treated as hypotheses. Their accuracy will undoubtedly be tested in the coming decades by accumulating studies on species responses, new model developments with additional traits, and the sustained intensification of changes to the global climate. Improvements to this framework for trait-mediated models can be accomplished by individual researchers or conservation managers by adding or changing traits and their weighting through modifications to the online appendices of traits and model data. Realistically,

since we are only starting to measure climate change responses, the response trends in mammals may worsen if climate change conditions intensify, which would shift the potential risks for unassessed species higher. In contrast and optimistically, if humans can reduce the quantity of greenhouse gases emitted and circulating in the atmosphere, and thus dampen climate change conditions, then the potential risks for unassessed species could shift lower. Nonetheless, these results from the trait-mediated models are a data-informed starting point for researchers and managers facing immediate decisions on monitoring.

Critically, researchers and managers need to keep in mind that model results are based on studies that tried to identify climate change impacts independent of other anthropogenic changes to habitats and populations. Thus, for individual populations, responses to climate change may be compounded by responses to other stressors. If a species is expanding its range or increasing population sizes into disturbed or human-modified habitats, or is actively managed to increase population sizes for hunting, but is predicted to respond negatively to climate change, then the net outcome will depend on which impact is stronger. Thus, the outcomes will vary among populations across the species' geographic range. Assessing the impacts of climate change plus all other human effects for each of the 328 mammalian species is beyond the scope of this study.

The trait-mediated predictions and analyses are based on data from 76 mammal species and 182 populations across the United States and Canada (Fig. 1), most of which reflect the ideal approach to such analyses—robust historical and contemporary sampling, detected change in climate, and clear statistical inference of a climate change effect. Even with new data from additional populations (59) and species (36, including seven new to the data set), the same four traits predict which species are responding negatively to climate change and which are not. The responses of those additional seven species were predicted by the risk model based solely on the 2014 data set: only those in the higher-risk classes responded as expected

($n = 3$) and the others did not ($n = 4$). Thus preliminarily, these risk predictions seem robust at least for the investigated species and climate change levels experienced so far.

Another preliminary examination of the accuracy of these predictions are comparisons to the literature for climate change responses of mammal species outside of the United States and Canada. Fewer mammal species have been tested in Europe and globally, mainly due to a lack of quality historical data for comparison that is relatively free of other anthropogenic influences (McCain and King 2014). There was also more of a publication bias toward climate change responders than in the United States–Canada data. Nonetheless, more studies are accumulating, particularly in Europe (Hansen et al. 2013; Tafani et al. 2013; Elmhagen et al. 2015; Vetter et al. 2015; Rézouki et al. 2016; Hamilton et al. 2017). In those studies, large, high-latitude, as well as diurnal and montane species are also responding as expected in Europe (e.g., *Marmota marmota*, *Lynx lynx*, *Lepus timidus*, *Capreolus capreolus*). Additionally, many of the responding species are in Scandinavia and have circumpolar distributions, thus also occur in the United States–Canada region (trait-mediated risk rankings: moderate-high to high; $n = 7$).

Despite the preliminary evidence supporting these trait-mediated predictions, they may be indicative of faster and slower responders rather than responders and nonresponders due to time lags in climate change response (e.g., IPCC 2014; Savage and Vellend 2015). Currently, this option remains untestable until more species responses accumulate over time. Another issue may be that current methods and sampling windows are better at detecting climate change responses in larger mammal species due to their lower population variability year to year (e.g., McCain et al. 2016). But if that was the case, I would expect 1) uniformly strong responses only for the largest mammal species with low interannual population variability; and 2) mixed responses for all other mammal species with about one-half predicted responses and one-half nonresponders or opposite responders. Neither is supported with these data. Although population variability can reduce our ability to detect a response to climate change, there are clear trends in the data that are not random: some groups are almost uniformly nonresponders (e.g., shrews, gophers, many small rodents), and responders vary in traits other than body size (i.e., montane, activity times). Understanding the role population variability may play in detecting climate change responses is a critical component of future research, but is not entirely masking mammalian response trends so far. Other potential reasons for not detecting climate change responses in specific species or populations include incomplete survey data, stronger anthropogenic habitat impacts than assumed, nonclimatically determined range limits or abundance trends, strong phenotypic plasticity, or larger tolerance limits than currently expressed (Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003; Lenoir et al. 2008; Rowe et al. 2010). Most of these potential reasons for not detecting a species' response were untested in the primary studies, so their prevalence is currently not measureable, but they remain as alternative hypotheses to test in the future as more climate change responses accumulate.

Clearly some United States and Canadian mammals are responding to current anthropogenic climate change ($n = 46$),

and some quite negatively, whereas others are not responding ($n = 24$), or, in a few cases, are expanding their ranges in the face of climate impacts ($n = 6$). Based on identified trait combinations and their associated risks (Figs. 3 and 4), my analyses indicate that our large, high-latitude, and high-elevation carnivores and artiodactyls, most of the larger squirrels—in particular marmots, ground squirrels, and prairie dogs—and montane hares, pikas, and cottontails should be of highest concern to the mammal research and conservation community (Fig. 5; Supplementary Data SD3). I urge managers, conservation practitioners, and researchers to use these hypotheses of climate change risk as an additional tool for planning and management of the mammal species in their purview and to monitor species of highest risk as well as to further test the validity of these results.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Data and citations for mammal species and populations that have been studied for responses to anthropogenic climate change in the United States and Canada through 2018.

Supplementary Data SD2.—Species-level composite responses to climate change with the percent consistency of responses among tested populations, and the traits used in the trait-mediated prediction models.

Supplementary Data SD3.— Trait-mediated predictions of climate change risk for each of the 328 United States and Canadian terrestrial mammals using the weighting schemes of the three models (weighted, equal, composite) as well as the traits used in the risk models and the species of conservation concern.

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