

1 **Agency plans are inadequate to conserve US endangered species under climate change**

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19 **Abstract**

20 **Despite widespread evidence of climate change as a threat to biodiversity, it is unclear**
21 **whether government policies and agencies are adequately addressing this threat to species¹⁻**
22 **⁴. We evaluate species sensitivity, a component of climate change vulnerability, and whether**
23 **climate change is discussed as a threat in planning for climate-related management action**
24 **in official documents from 1973-2018 for all 459 US animals listed as endangered under the**
25 **Endangered Species Act. We find that 99.8% of species are sensitive to one or more of eight**
26 **sensitivity factors, but agencies consider climate change as a threat to only 64% of species**
27 **and plan management actions for only 18% of species. Agencies are more likely to plan**
28 **actions for species sensitive to more factors, but such planning has declined since 2016.**
29 **Results highlight the gap between climate change sensitivity and the attention from**
30 **agencies charged with conserving endangered species.**

31

32 **Introduction**

33 Climate change is a threat to ecosystems and biodiversity globally^{5,6}, and has emerged as a driver of
34 observed and potential species decline and extinction⁷⁻⁹. Government laws and policies should play a
35 vital role in supporting climate change adaptation for imperiled species, yet imperiled species
36 protections have been critiqued as insufficient in Australia^{10,11}, Canada¹², and Europe¹³. Funding
37 shortfalls for environmental programs mean that governments may not be adequately addressing
38 baseline threats to species, let alone more complex emerging threats from climate change^{14,15}.
39 Furthermore, the politicization of climate change in many countries, including the US, has led to
40 different levels of concern and action on the topic among political parties^{16,17}. Understanding
41 whether and to what extent government authorities are supporting climate change adaptation,

42 especially for imperiled species, is critical for improving tools and processes to reduce climate
43 change impacts on biodiversity^{18,19}.

44 The primary law directing the conservation of imperiled species in the US is the Endangered
45 Species Act²⁰ (hereafter, ESA). Central to the listing and recovery processes under the ESA is the
46 enumeration and abatement of threats to species. The law directs the Secretaries of the Interior and
47 Commerce to use the “best available scientific and commercial data” to make listing determinations
48 on the basis of five threat factors: 1) habitat destruction and degradation, 2) overutilization, 3)
49 disease or predation, 4) inadequacy of existing protections, or 5) other factors. While each factor
50 may result from or be exacerbated by climate change, this threat is not explicitly described among
51 the five factors. This is likely because the ESA was most recently amended legislatively in 1988²¹, the
52 same year as the formation of the Intergovernmental Panel on Climate Change and four years before
53 the first detailed discussion the consequences of climate change for biological diversity in the US²².

54 Nonetheless, the two agencies responsible for implementing the ESA, the US Fish and Wildlife
55 Service (FWS) and the National Marine Fisheries Service (NMFS), have explicitly recognized the
56 threat that climate change poses to species and the need to manage for its impacts. The FWS first
57 described climate change as a threat in its January 2007 proposal to list the polar bear (*Ursus*
58 *maritimus*) as threatened. Later that year, discussion of climate change appeared in recovery plans for
59 the Indiana bat (*Myotis sodalis*) and Hawaiian monk seal (*Monachus schauinslandi*) and in five-year
60 reviews for the red wolf (*Canis rufus*) and five sea turtle species (for references to species ESA
61 documents, see archived data). The only assessment of climate change in ESA documents to date (to
62 our knowledge) found that by the end of 2008, 87% of species recovery plans still did not address
63 whether or not climate change was a threat¹⁸. The scientific community has identified climate change
64 as the “primary threat” to nearly 40% of ESA-listed animals and over 50% of ESA-listed plants in
65 the US¹⁴, and agency options for climate-related management action under the ESA have been

66 available for over a decade²³. Thus, it is vital to understand whether the lead agencies responsible for
67 endangered species conservation have improved the use of their authority to help species adapt to
68 the threat of climate change.

69 To determine if threats from climate change are being addressed by US agencies, we compared
70 the climate change sensitivity of species to agencies' discussion of climate change and plans for
71 managing climate change threats for the 459 ESA-listed endangered animals found within US lands
72 and waters. Because climate change sensitivity had not been systematically assessed for many of
73 these species, we developed a trait-based climate change sensitivity assessment²⁴. This assessment is
74 a simplified version of existing tools (see Methods) and provides a preliminary evaluation of whether
75 and which species' life history and biological characteristics contribute to sensitivity to climate
76 change (see Table 1). We focused on sensitivity (and related traits sometimes characterized as
77 measures of adaptive capacity) because these, rather than exposure, are the elements of vulnerability
78 that management plans can address¹⁰. Furthermore, because of the small populations and range sizes
79 of many of the species we evaluated, available exposure tools may not accurately capture granular
80 scale and stochastic effects in a meaningful way²⁵. Focusing on sensitivity greatly reduced the time
81 required to assess each species, allowing the assessment to be applicable to large groups of species,
82 such as the >2,300 US and foreign species listed under the ESA. Our assessment relies on
83 affirmative statements about relevant aspects of biology and life history; certain traits had to be
84 identified in the literature for a species to be determined sensitive, and a species was considered not
85 sensitive by default. Therefore, the assessment represents a conservative estimate of sensitivity and
86 likely underestimated the actual sensitivity for some poorly-studied species or those for which that
87 information was not described in publicly available sources.

88 After assessing species sensitivity, we determined whether climate change was described as a
89 threat for species by reviewing official ESA documents published by FWS and NMFS. All

90 endangered species have listing determinations, and most have either critical habitat designations,
91 five-year reviews, recovery plans, or recovery outlines. We focused on the most recently published
92 one or two of these types of documents to determine if climate change was described as a threat. We
93 then determined whether these agencies planned management action to address climate change
94 threats as part of species recovery by evaluating the same ESA documents (excluding species whose
95 only ESA document was a listing decision, as these are not management-oriented). We tested if
96 species sensitivity was a significant predictor of whether species ESA documents contained
97 discussion of climate change as a threat and to what extent federal agencies planned to respond to
98 climate change impacts. Data and results of the study are available in a free, interactive web
99 application at https://defenders-cci.org/app/ESA_climate/.

100

101 **Results and Discussion**

102 We found that nearly all endangered animals are sensitive to climate change impacts. All but one
103 (Hawaiian goose [*Branta sandvicensis*]) of the 459 species (99.8%) are sensitive to at least one of the
104 eight sensitivity factors (Table 1), and three-fourths (74%) are sensitive to three or more factors (Fig.
105 1a). However, agencies describe climate change threats in documents for only slightly more than half
106 of species we assessed (64%; Fig. 1b) and plan management actions to address those threats for only
107 a small fraction of species (18%; Fig. 1c). Logistic regression indicated that the number of sensitivity
108 factors is a strong predictor of whether ESA documents discussed management action
109 ($F(1,419)=6.57$, $\beta=-0.31$, $p<0.01$; Fig. 1a). Agencies are more likely to plan climate adaptation
110 management actions for species that are sensitive to more climate factors than for species that are
111 sensitive to fewer factors; for example, documents for species sensitive to one vs seven factors are
112 10% vs 41% likely to contain management actions. Likewise, species sensitivity is marginally related
113 to whether climate change is considered as a threat ($F(1,458)=0.33$, $\beta=0.15$, $p=0.07$; Fig. 1a). These

114 results indicate some prioritization of species based on potential climate threat and sensitivity,
115 though this may be unintentional. However, overall, there is a significant gap between the sensitivity
116 of endangered animals to climate change and the attention that climate change receives from the
117 agencies charged with recovery of these species.

118 The prevalence of sensitivity factors varied considerably. The highest proportion of species
119 across taxa was sensitive to isolation (mean across taxa=0.71, all taxa ≥ 0.50), whereas the lowest
120 proportion was sensitive to phenology (mean=0.09, all taxa ≤ 0.21 ; Fig. 2a). Hydrology and
121 chemistry showed the highest variation in sensitivity across taxa (mean=0.60, sd=0.25, cv=0.95;
122 mean=0.25, sd=0.22, cv=0.89, respectively); disturbance showed the least (mean=0.61, sd=0.11,
123 cv=0.17; Fig. 2a). Of the taxa assessed, mammals were sensitive to the fewest number of factors
124 (Fig. 2b). Amphibians, mollusks, and arthropods were sensitive to the greatest number of factors;
125 many of these species exhibit an aquatic life cycle phase and are thus subject to hydrological and
126 chemical sensitivities. Furthermore, mollusks and arthropods also commonly depend on obligate
127 species relationships, although reproductive host species are not known for some mollusks.
128 Agencies appear to be prioritizing at least some of these high-sensitivity taxa for climate change-
129 related management. Arthropods and reptiles had the greatest proportion of species for which
130 climate change was evaluated as a threat (80% and 75%, respectively) and management action was
131 described (29% and 28%, respectively), whereas mollusks had the least (50% and 31%, respectively;
132 Fig. 3a-b).

133 Agencies have increasingly considered climate change as a potential threat to species in ESA
134 documents over time, mirroring rising concern about climate change over the past few decades²⁶.
135 However, they have not yet widely translated this concern into articulated management actions to
136 help species adapt to climate change. After the agencies first described climate change as an
137 influence on habitat loss (listing factor 1) in 2007, the proportion of species with climate change

138 mentioned in their ESA documents rose and thereafter stabilized at around 87% of species in 2015-
139 2016 (Fig. 4a). In 2017-2018 however, this trend reversed, with declines in both the proportion of
140 species where climate change was listed as a threat, and in the absolute number of newly published
141 ESA-related documents for endangered animals. With regard to management planning, climate
142 change was first identified as a topic for future study for the Indiana bat (*Myotis sodalis*) and
143 Choctawhatchee beach mouse (*Peromyscus polionotus allophrys*) in 2007, and the first discussion of
144 management action occurred in a 2008 recovery plan for the stellar sea lion (*Eumetopias jubatus*; Fig.
145 4b). The proportion of species with planned climate change-related action each year generally
146 increased until peaking in 2014. Since then, discussion of action has steadily declined; of documents
147 published in 2017, one species' five-year review (Kaua'i cave amphipod [*Spelaeorchestia koloana*])
148 described a management response to climate change, and no 2018 documents mentioned actions to
149 address climate impacts. In summary, although the number of ESA documents mentioning climate
150 change has increased over time, most species' documents either describe climate change as a
151 potential problem without including any actions to specifically address the issue, or the documents
152 do not discuss climate change at all. Across time(2007-2018), the proportion of species with planned
153 climate change-related action has been low on average (mean=0.23, range=0.03-0.39; Fig. 4b),
154 indicating a shortfall in planning of on-the-ground management for climate change that to date
155 shows no sign of improving.

156 In short, across time and taxa, management agencies are inadequately assessing climate change
157 threats, or planning action to manage those threats, to imperiled species. In terms of baseline
158 assessment, this inadequacy affects species regardless of their climate sensitivity, as we found no
159 relationship between the number of sensitivity factors and the consideration of climate change as a
160 potential threat. Agencies may be inadvertently prioritizing species for management planning based
161 on their degree of sensitivity to climate factors, however we caution that the mere presence of

162 management action in documents does not assure the adequacy of plans or, more importantly, the
163 enactment of those plans¹⁰. Even for species with planned actions, we observed substantial variation
164 in the content: several five-year reviews merely recommended updating recovery plans to include
165 climate change. More robust discussions for action entailed protecting refugia (e.g., Chinook salmon
166 [*Oncorhynchus tshawytscha*] and white abalone [*Haliotis sorenseni*] recovery plans) and diverse microsites
167 (e.g., Karner blue butterfly [*Lycia melissa samuelis*] five-year review), improving connectivity (e.g.,
168 jaguar [*Panthera onca*] recovery plan), establishing additional populations for redundancy in case of
169 stochastic climate events (e.g., Sonoran pronghorn [*Antilocapra americana sonoriensis*] recovery plan),
170 reducing non-climate-related threats (e.g., water allocations in spikedace [*Meda fulgida*] five-year
171 review), and designating critical habitat in areas likely to persist or become important areas in the
172 future (e.g., tidewater goby [*Eucyclogobius newberryi*] and Bartram's scrub-hairstreak butterfly [*Strymon*
173 *acis bartrami*] critical habitat designations). Our results offer insights for how agencies, including
174 different management jurisdictions (see Supplemental Information), might prioritize the types of
175 climate change adaptation options to target susceptible taxa and sensitivity factors.

176 Three main issues may explain why the relevant US agencies have yet to address climate change
177 threats as part of their imperiled species conservation programs. First, the politicization of climate
178 change has caused its prioritization to shift every 4 or 8 years with changes in Presidential
179 administration. In 2017, the Trump administration revoked many policies and commitments on
180 climate change established by the Obama Administration, such as Executive Order 13653 on
181 adaptation²⁷ and the Paris Global Climate Agreement.^{27,28} This has disrupted progress on both
182 mitigation and adaptation nationally and internationally³. Imperiled species conservation in the face
183 of climate change urgently requires the return of a bipartisan and durable commitment to both
184 mitigation of and adaptation to climate change. For example, legislative bodies, such as the US

185 Congress and central governments in other countries, could integrate climate change adaptation and
186 mitigation into law rather than leaving these important processes to more labile policies.

187 Second, the infrequent and inconsistent inclusion of climate change in ESA species conservation
188 may be a consequence of chronic underfunding and imbalanced funding of species recovery. In
189 fiscal year 2012, 62% of species recovery funding was spent on the conservation of 10% of US listed
190 species, resulting in as little as \$60 for some species (e.g., Cumberland bean mussel [*Villosa trabalis*]
191 whose ESA documents did not mention climate change)^{14,29,30}. Another analysis of yearly
192 appropriations from 1980-2014 found that <25% of required recovery funding has been allocated
193 annually³¹. Increased funding to the agencies responsible for species recovery, paired with a more
194 informed allocation of resources, could help redress this problem^{15,31}.

195 Finally, climate change itself is a formidable conservation challenge that agencies generally lack
196 the logistical tools and capacity to address. The broad spatial and temporal scales and uncertainty of
197 specific threats mean that agencies should pair conceptual models with mechanistic approaches to
198 identify stressors that materialize as species threats^{2,32}. Agencies would benefit from embracing the
199 frameworks designed to enable systematic planning, implementing, and monitoring of complex
200 conservation challenge, and integrate climate change with other threats^{33,34}. Additionally, agencies
201 should proactively seek and embrace innovative tools that enable efficient management of the
202 2,300+ imperiled species listed on the ESA. The assessment used in this study is one such example,
203 offering a time-efficient method for preliminary evaluations of species sensitivity to climate change.

204 Our study reveals that US government agencies have yet to adequately evaluate climate change
205 threats to endangered animals listed under the ESA and plan commensurate action. The consistency
206 between our US results and recent findings from Australia^{10,11} suggest it is possible that many
207 countries are similarly failing to protect imperiled species from climate change impacts. Climate
208 change poses an ongoing and accelerating threat to many, if not most, imperiled species, and

209 recovery will be unattainable unless a feasible process is in place to account for and ameliorate its
210 impacts.

211

212 **Methods**

213 We compared the climate change sensitivity of species to agency evaluation and management
214 planning of climate change threats for ESA-listed endangered animals in the US. First, since
215 systematic data did not exist for the climate change impacts on endangered species, we developed
216 and conducted a trait-based, rapid assessment for evaluating climate change sensitivity. We focused
217 the assessment on one element of species vulnerability: a species' potential "sensitivity" to the effects
218 of climate change. Sensitivity "refers to innate characteristics of a species or system and considers
219 tolerance to changes in such things as temperature, precipitation, fire regimes, or other key
220 processes"³⁵. We created and answered eight yes-or-no questions based on whether the species'
221 habitat, ecology, physiology, or life cycle might be affected by changes in climate (Table 1). In doing
222 so, we employed a biological approach to assessing sensitivity that considered the ecological impact
223 to the species from the primary manifestations of climate change, including indirect impacts from
224 effects on interacting species²⁴. We derived the questions, or sensitivity factors, from factors listed in
225 existing vulnerability assessment protocols, particularly the NatureServe Climate Change
226 Vulnerability Index³⁶ and US Forest Service's System for Assessing Vulnerability of Species³⁷.
227 Though not exhaustive, our questions covered the main categories of species sensitivity (or
228 sometimes categorized under adaptive capacity) in these and other assessment frameworks³⁸. We
229 were thus able to assess many of the elements of vulnerability that can be addressed via management
230 planning, while also completing most species in 30-60 minutes. This assessment could be useful to
231 agencies for evaluating large numbers of species while still capturing the most critical elements of
232 potential species sensitivity.

233 We assessed the climate change sensitivity of all animal species listed as endangered under the
234 ESA (as of December 31, 2018) that are found in US states, territories, and surrounding waters
235 (n=459; see <http://www.fws.gov/endangered>), with the exception of those deemed likely to be
236 extinct by agencies or which have not been observed for 20+ years and are likely extinct in the wild.
237 We answered the assessment questions using freely-accessible species information from species
238 listing decisions and other publicly available information published by agencies and conservation
239 organizations about the species and its threats. We predominantly referenced the FWS'
240 Environmental Conservation Online System (ECOS; <https://ecos.fws.gov/ecp>), NMFS'
241 Endangered Species Conservation Directory ([https://www.fisheries.noaa.gov/species-
242 directory/threatened-endangered](https://www.fisheries.noaa.gov/species-
242 directory/threatened-endangered)), and the NatureServe Explorer (<http://explorer.natureserve.org>).
243 Using publicly available information enables the assessment to be used by the public or government,
244 the latter of which requires decision data to be publicly visible^{39,40}.

245 Consistency in measuring species sensitivity both within and between assessment tools is a
246 recognized and ongoing challenge^{41,42}. We took steps to ensure that sensitivity results were consistent
247 within and between species in our assessment. Each species was assessed by at least two and as
248 many as seven reviewers; species were initially reviewed by at least one of six reviewers (AC, KE,
249 RK, SM, KT and LV) and were finally crosschecking by an expert reviewer (AD). All reviewers went
250 through extensive training to ensure consistency in the application of the methodology (Table 1),
251 including assessing and comparing the same species to validate and align the approach.

252 We also evaluated the extent to which FWS' and NMFS' ESA documents discussed climate
253 change as a threat to species and included planned recovery actions to address climate change
254 impacts. First, for all endangered animals, we recorded whether climate change was considered as a
255 potential threat in each species' publicly available ESA documents (listing decisions, recovery plans
256 and outlines, critical habitat designations, and five-year reviews). We focused on the most recently

257 published agency documents, which should reflect cumulative knowledge about the species. Then,
258 for all endangered animals except those with only listing decisions, which are not management-
259 oriented and thus not appropriate for evaluating management planning (n=420; excluded species
260 n=39), we recorded what level of management action was discussed to address climate change in
261 species recovery. We recorded the level of discussion as: “Action,” indicating that the documents
262 articulated specific actions in response to climate change impacts; “Further study,” indicating that
263 the agency acknowledged they require additional information before an action plan could be
264 developed; “No threat, no action needed,” indicating that the documents discussed climate change
265 and decided that climate change is unlikely to impede species recovery; and “No discussion,”
266 indicating that climate change was not mentioned.

267 We examined patterns in sensitivity and climate change discussion by time, taxa, agency and
268 regional jurisdiction (see Supplemental Information for latter two). We tested the relationships
269 between the number of sensitivity factors and whether documents discussed climate change as a
270 potential threat (yes/no) or discussed management action (by reclassifying discussion categories to
271 create a binary variable of no action/action) using logistic regression run with the ‘stats’ package in R
272 v.3.5.0.

273

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280 **Author Contributions**

281 A.D. and A.C. designed the study; A.D., A.C., K.E., R.K., S.M., K.T., and L.V. collected data; A.D.
282 and J.R.B.M. analyzed data and wrote the manuscript; A.D., J.W.M., M.S., and J.R.B.M. interpreted
283 results; J.W.M. built the web app; all authors provided critical feedback on the manuscript.

284

285 **Data Availability**

286 Data is archived on Open Science Framework and available at <https://osf.io/r9uca>. A free,
287 interactive web application containing data and results from this study is available at [https://](https://defenders-cci.org/app/ESA_climate/)
288 defenders-cci.org/app/ESA_climate/.

289

290 **Competing Interests**

291 The authors declare no competing financial interests.

292

293 **Additional information**

294 Supplementary information is available in the online version of the paper.

295

296 **References**

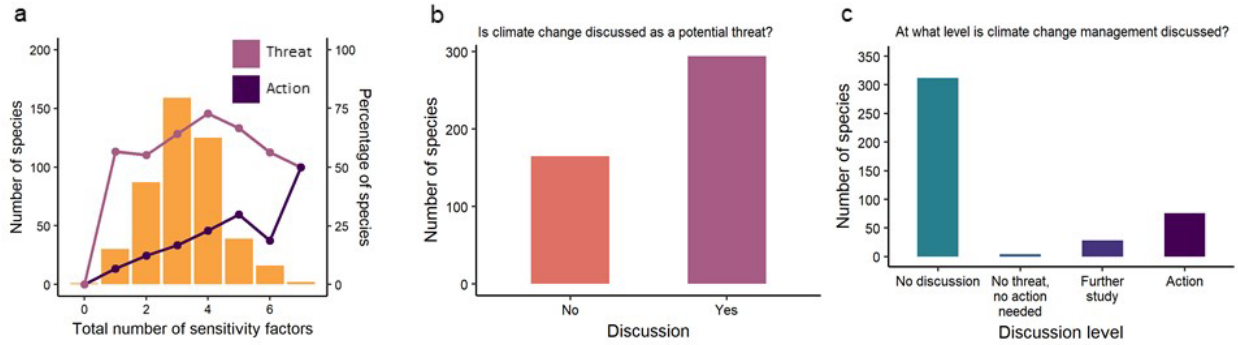
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383

384 **Figure 1. Despite sensitivity to one or more climate factors (a), US endangered animals are**

385 **not often assessed for whether climate change is a potential threat (b) and most do not**

386 **receive planning for management actions to address climate change impacts (c). (a) Species**

387 that are sensitive to more climate factors are more likely to receive management action planning

388 (dark purple line; $p < 0.05$) than species sensitive to fewer factors, and are marginally more likely to

389 receive evaluation of climate change as a threat (light pink line; $p = 0.07$). All endangered animals

390 except one (Hawaiian goose [*Branta sandvicensis*]) are sensitive to one or more of eight climate factors

391 (see Table 1 for description of factors). The two most sensitive species (seven factors) were a fish,

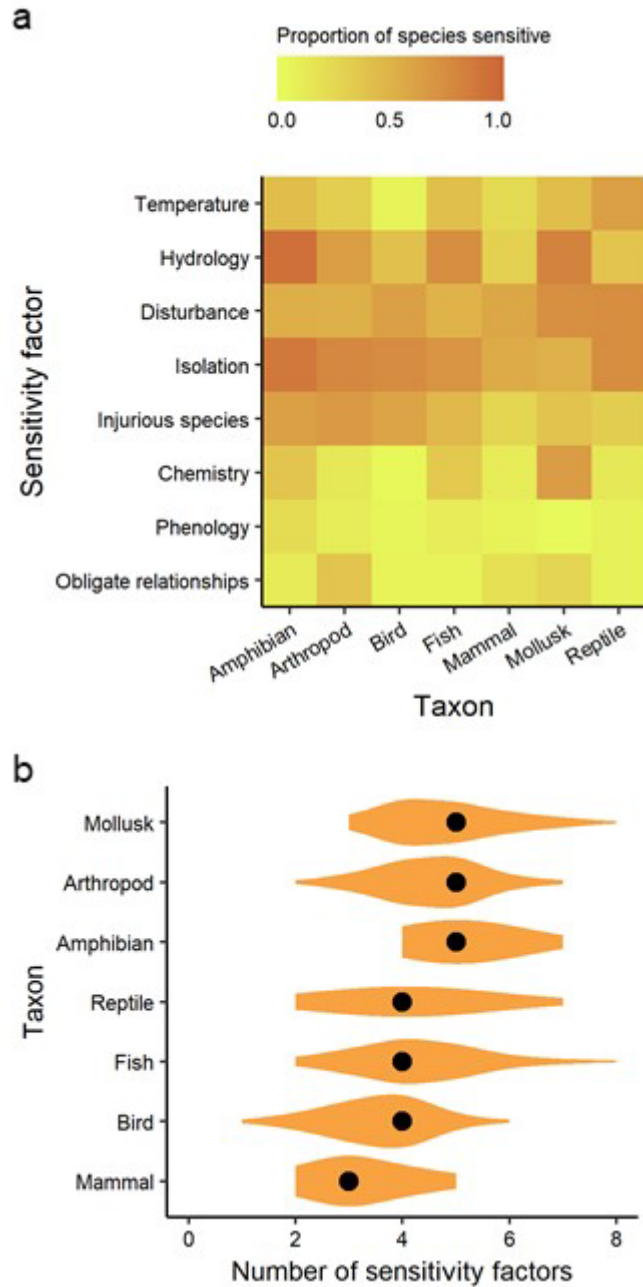
392 the Clear Creek gambusia (*Gambusia heterochir*), and a mollusk, the shinyrayed pocketbook (*Lampsilis*

393 *subangulata*). Bars represent the number of species; lines represent the proportion of species within

394 each number of sensitivity factors. Analysis in (a) and (b) contain all endangered animals on the

395 ESA ($n = 459$); analysis in (c) excludes species for which only listing decisions exist (excluded $n = 39$;

396 included $n = 420$; see text for details). Colors correspond to Fig. 2, 3, and 4.



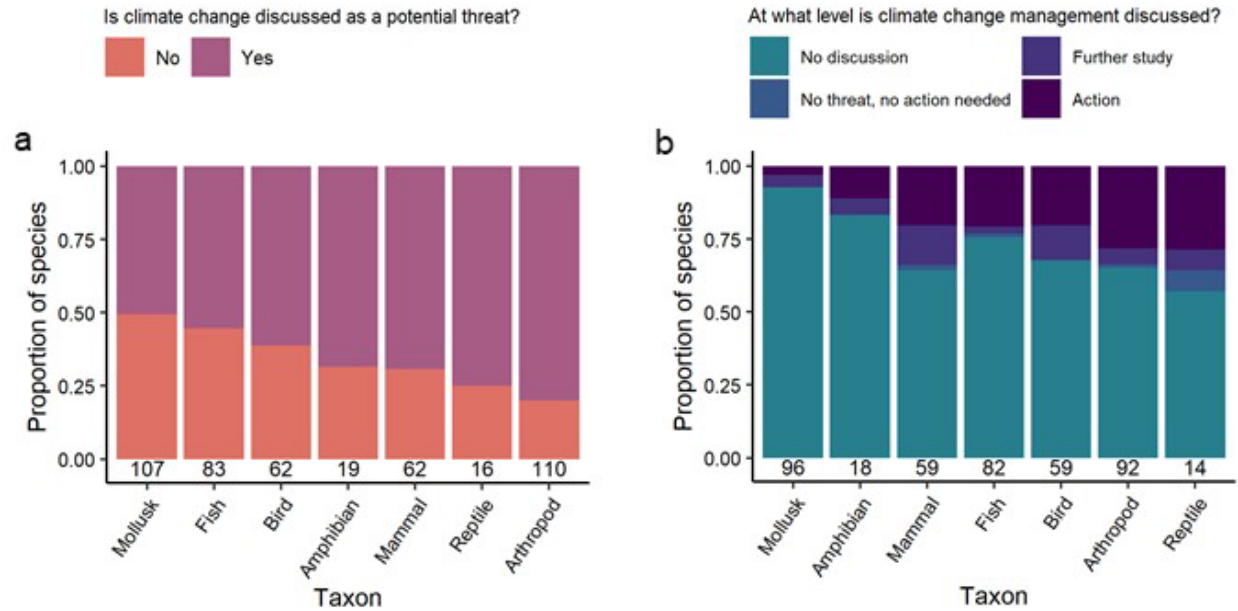
397

398 **Figure 2. Taxa differ in sensitivity to the (a) type and (b) total number of climate factors.**

399 Analysis includes all 459 endangered species listed on the Endangered Species Act. See Table 1 for

400 descriptions of factors, Supplementary Table 1 for the number of species in each taxa, and

401 Supplementary Figure S1 for taxa sensitivity by factor across management agency and region.



402

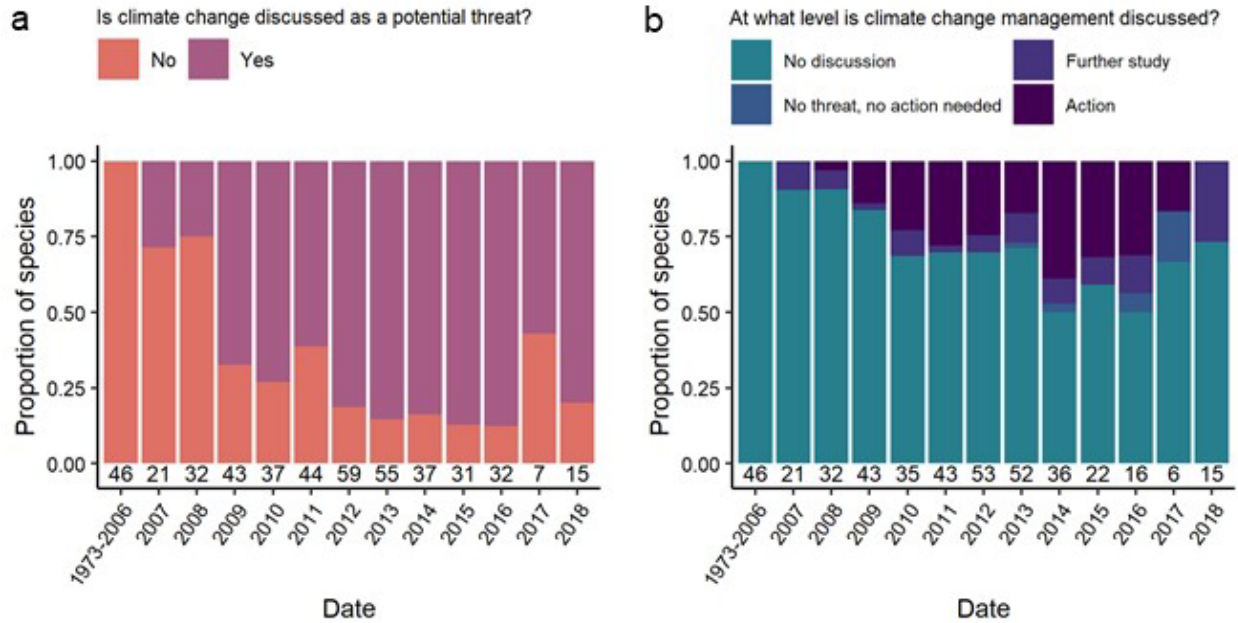
403 **Figure 3. Taxonomic differences occur in whether (a) and how (b) climate change is**

404 **discussed in official management documents for endangered animals.** Analysis in **a** contains

405 all 459 endangered animals listed on the Endangered Species Act; analysis in **b** excludes species for

406 which only listing decisions exist (excluded n=39; included n=420; see text for details). The number

407 of species in each group is shown above the x-axis.



408

409 **Figure 4. Over time US agencies have included discussions about climate change in official**

410 **documents for more endangered animals, but (a) baseline assessments of climate change as**

411 **a threat have increased at a substantially faster rate than (b) planning of management**

412 **action.** Analysis in **a** contains all 459 endangered animals listed on the Endangered Species Act;

413 analysis in **b** excludes species for which only listing decisions exist (excluded n=39; included n=420;

414 see text for details). The number of species in each group is shown above the x-axis.

415 **Table 1.** Questions in the rapid sensitivity assessment related to eight climate change sensitivity
416 factors.
417

| Factor | Question and description |
|---------------|---|
| Temperature | Does the species have specialized thermal tolerance or depend on habitat with an important temperature threshold? Species were considered temperature sensitive if available information indicated the species has or depends on habitats with obligate or preferential temperature thresholds (e.g., sea ice). |
| Hydrology | Is the species dependent on habitat with a specialized hydrology? Species were considered sensitive if available information indicated they require narrow ranges of water depths, flow rates, timing, or seasonality (e.g., vernal pools or intermittent streams). |
| Disturbance | Is the species or its habitat sensitive to or dependent on a specific disturbance regime? This includes species in fire-adapted systems, species that rely on certain flood regimes, and species impaired by disturbance, such as old-growth forest obligates and species sensitive to excessive flooding. |
| Isolation | Is the species or its habitat geographically restricted or does it face intrinsic or extrinsic barriers to shifting its range to maintain its climate space? While many endangered species are found in small, isolated populations, we scored species in this category if available information indicated they are confined to mountains, islands, or headwaters; are narrowly endemic to spatially discrete habitats, like caves, springs or rare soil types; or if species movement to other suitable habitat is limited by habitat loss, development, dams, or other anthropogenic pressures. |

| | |
|------------------------|--|
| Injurious species | Is the species or its habitat threatened by an invasive species, pest and/or disease organism that might benefit from climate change? We did not consider the species in question sensitive where the injurious species is ubiquitous or human-oriented (e.g., cats, rats, livestock). |
| Chemistry | Is the species sensitive to changes in chemical concentration, such as atmospheric CO ₂ , water pH, or dissolved oxygen? |
| Phenology | Does the species rely on specific triggers for life cycle events, such as breeding, migration, or color change, that are likely to become out of sync with seasonal changes in resource availability or environmental conditions (i.e., phenologic mismatch)? |
| Obligate relationships | Is the species dependent on one or a few species such as a host, dominant food source, with limited alternatives if the required species declines due to climate change? We did not consider the species sensitive if it requires a host but can succeed in association with four or more species. |

418