

1 **QUANTIFYING THE EFFECTS OF RECENT GLACIAL HISTORY AND**
2 **FUTURE CLIMATE CHANGE ON A UNIQUE POPULATION OF**
3 **MOUNTAIN GOATS**

4
5 Kiana B. Young ^{a, b, *}, Tania M. Lewis ^b, Kevin S. White ^c Aaron B.A. Shafer ^a

6
7 ^a *Department of Environmental and Life Sciences, Trent University, Peterborough, ON K9L 0G2,*
8 *Canada*

9 ^b *National Park Service, Glacier Bay National Park and Preserve, P.O. Box 140, Gustavus, AK*
10 *99826 USA*

11 ^c *Division of Wildlife Conservation, Alaska Department of Fish and Game, 802 3rd Street,*
12 *Douglas, AK, 99824 USA*
13

* Corresponding author at present address: 1714 414th St East Eatonville, WA 98328
Phone: 1-253-777-6803
Email: kianayoung@trentu.ca

14 **Abstract**

15 Human disturbance and climate change can impact populations by disrupting movement
16 corridors and reducing important habitat. Characterizing how animals respond to such
17 environmental changes is valuable for conservation as many species, especially habitat
18 specialists, can experience reduced genetic diversity when deleterious habitat change occurs,
19 leading to an increased likelihood of extirpation. Mountain goats (*Oreamnos americanus*)
20 exemplify this conservation challenge; their geographically isolated habitat can inhibit gene
21 flow, making them susceptible to population declines in the face of anthropogenic-induced
22 landscape change. To facilitate biologically informed population management of mountain goats
23 in Glacier Bay National Park, Alaska, we characterized the fine-scale genetic population
24 structure and examined how future climate change could impact the population density of these
25 mountain goats. We used DNA samples to estimate diversity and depict the genealogical history.
26 Climate response models allowed us to simulate changes to suitable habitat and predict how this
27 might influence future population structure. Our results indicated that three genetically distinct
28 subpopulations exist in Glacier Bay and that the population structure is reflective of the historic
29 landscape patterns. Climate modeling predicted that demographic productivity was likely to be
30 reduced for all subpopulations; additionally, we found that climate change likely degrades the
31 suitability of movement corridors that facilitate gene flow between subpopulations, ultimately
32 increasing the cost of travel. Understanding such fine-scale patterns are key to managing
33 subpopulations, particularly with impending changes to the landscape.

34

35 **Keywords:** biogeography, population genetic structure, landscape genetics, gene flow, mountain
36 goat, Alaska

37 1. INTRODUCTION

38 The colonization of landscapes is a central question in biogeography (Lomolino et al. 2017) that
39 can often be revealed by mapping the genetic diversity and differentiation of populations. For
40 example, plotting genetic diversity across the landscape can retrace the route individuals took
41 (i.e. stepping-stone model; Kimura and Weiss 1964, Baltazar-Soares et al. 2020), while more
42 complex models can estimate divergence times and infer population size changes (i.e. Csilléry et
43 al. 2010). When colonization follows a disturbance, quantifying the genetic response can aid in
44 predicting changes to the demography of that population as the landscape continues to change.
45 This information can help inform management decisions, for example, by minimizing
46 disturbance to those subpopulations with lower genetic diversity (Bouzat 2010, Stronen et al.
47 2019).

48 Landscape disturbances come in a variety of forms, and while each type of disturbance
49 has unique characteristics, there are similarities between regimes (Newman 2019). Glaciation
50 and subsequent deglaciation events provide opportunities to learn about animal movement across
51 broad scales (Hewitt 1999). The most recent large-scale ice age, during the Pleistocene Epoch,
52 ended around 11,700 years ago, and led to a range of species' responses, particularly in North
53 America (Lister 2004, Pearson 2013, Bibi and Kiessling 2015, Puzachenko and Markova 2019).
54 During the Last Glacier Maximum, two major refugia existed in western North America:
55 Beringia and the Pacific Northwest (Hultén 1937, Pielou 1991). While those areas are widely
56 accepted as refugia for species during this ice age, there is evidence of additional, smaller refugia
57 along coastal Alaska and British Columbia (Shafer et al. 2010). Beyond the major ice ages,
58 smaller-scale glaciation events have also occurred in North America. Notably, Glacier Bay
59 National Park and Preserve (GBNPP), located in Southeast Alaska, experienced a small
60 glaciation event, a product of the Little Ice Age, only ~300 years ago (Connor et al. 2009). The
61 native wildlife was forced to leave the area that is now Glacier Bay fjord to escape the advancing
62 glacier. Glaciers have since retreated, allowing flora and fauna to recolonize the landscape
63 (Milner et al. 2007, Boggs et al. 2010).

64 The origin of many recolonized species in GBNPP is unknown. Brown bears (*Ursus*
65 *arctos*) and black bears (*Ursus americanus*) recolonized GBNPP from both the northeast and
66 northwest after the Little Ice Age with Glacier Bay fjord and glacier-covered mountains acting as
67 barriers to dispersal (Lewis et al. 2015, 2020). While other mammals might have recolonized in a
68 similar way, the habitat associations of a species likely play a role in their movement across the
69 landscape. Bears, for example, might travel along coastlines or through forests, while alpine
70 ungulates such as mountain goats (*Oreamnos americanus*) likely select high elevation,
71 mountainous terrain leading to different movement patterns (Rice 2008). However, marine
72 waterways and steep glacier covered mountains or icefields likely inhibit movement of mountain
73 goats. Interestingly, while mountain goat habitat selection models suggest avoidance of glaciers
74 in coastal Alaska (Shafer et al. 2012), both expert opinion and landscape modeling suggested a
75 minimal effect of glaciers on movement in the Cascade Mountains (Shirk et al. 2010).

76 Reconstructing the historical colonization of a species can help predict future movements
77 in response to disturbance and is particularly relevant as land management agencies develop
78 plans to mitigate impacts to vulnerable and climate sensitive wildlife populations. Climate
79 change is expected to result in widespread changes in glaciers and landscape configurations and
80 learning about those processes in a place like GBNPP, where major deglaciation has occurred in

81 recent times, provides an important opportunity to gain insights about how predicted climate
82 change may impact ecological systems more broadly. Here, we used non-invasive genetic
83 samples to examine the population genetic structure of mountain goats in and surrounding
84 GBNPP. We use a Bayesian computational approach to reconstruct the demographic history and
85 climate projections to model how these subpopulations and movement corridors might be
86 impacted by climate change.

87

88 **2. METHODS**

89 *2.1 Study area and sample collection*

90 Glacier Bay National Park and Preserve is located in Southeast Alaska and is characterized by
91 glacial- and river-made valleys surrounded by mountain peaks and fjords (Boggs et al. 2010).
92 Within the boundary of GBNPP, four mountain goat study areas were identified based on
93 geographic patterns of distribution, abundance, and management interest. These study areas were
94 Mount Wright, Tidal Inlet, Marble Mountain, and Table Mountain (Figure 1). We included
95 samples from the adjacent Haines-Skagway and the Bering Glacier areas (Figure 1). These latter
96 two areas were studied because they were considered putative source populations for Glacier
97 Bay.

98 During the summers of 2017 through 2020, we collected pellet samples from GBNPP.
99 Once a pellet group was determined to be fresh using protocols from Poole et al. (2011), we
100 swabbed the outside of multiple pellets from the same pellet group and stored the swabs in a vial
101 of Longmire's solution, a lysis buffer designed to preserve DNA and prevent contamination
102 (100mM Tris, 100mM EDTA, 10mM NaCl, 0.5% SDS, 0.2% sodium azide). Samples were
103 stored at -20 degrees C. Tissue samples adjacent to GBNPP were collected by Alaska
104 Department of Fish & Game (ADFG) through harvest and research sampling following field
105 sampling methods described in Shafer et al. (2011) and White et al. (2021a, 2021b).

106 *2.2 DNA extraction and lab methods*

107 DNA was extracted using a Qiagen DNeasy Blood and Tissue Kit (Qiagen Inc., Valencia,
108 California, USA), following the manufacturer's protocols. We amplified 17 polymorphic
109 microsatellites over 3 multiplex PCR pools using previously published non-invasive genotyping
110 protocol (White et al. 2021a). We used the software program Geneious (v 10.1.2, Kearse et al.
111 2012) to manually call alleles requiring a minimum strength of 250 RFUs. Pellet samples were
112 genotyped in triplicate and samples where fewer than two of the replicate genotypes matched
113 were dropped following the approach of White et al. (2021a). Samples with genotypes less than
114 80% complete were dropped from the analysis. Positive and negative controls were included in
115 all steps.

116 *2.3 Genetic variation*

117 We used the R package ALLELEMATCH (Galpern et al. 2012) to determine if individuals were
118 sampled multiple times (alleleMismatch = 2). To test for deviations from Hardy-Weinberg
119 Equilibrium (HWE) and linkage disequilibrium (LD), we used the R package genepop (Rousset
120 2008). We checked for allelic dropout using the program Micro-Checker (v2.2.3 Van Oosterhout
121 et al. 2004). For each study area we estimated the mean and private allelic richness using ADZE.

122 GENHET (Coulon 2010) and adegenet (Jombart 2008) were used to estimate individual- and
123 subpopulation-level heterozygosity, respectively. We estimated the effective population size (N_e)
124 using NeEstimator (v2.1, Do et al. 2014), and used the program SPAGeDi (Hardy and Vekemans
125 2002) to calculate the F_{ST} and Nei's D . We calculated spatial autocorrelation using the parameter
126 Moran's I at 5 km distance bins.

127 *2.4 Population structure and demographic history*

128 We visualized clusters of samples using a principal components analysis (PCA) and plotted
129 individual principal component scores against latitude and longitude as a proxy for isolation-by-
130 distance. The Bayesian clustering program STRUCTURE (Pritchard et al. 2000, Falush et al.
131 2003, 2007, Hubisz et al. 2009) was used to identify subpopulations using the admixture model
132 with independent runs from $K=1$ to $K=20$ and a burn-in period of 5×10^5 and 1×10^6 MCMC
133 iterations. We used a combination of Evanno et al. (2005) and Puechmaille (2016) methods
134 determine the optimal K . Admixed individuals were considered when $q < 0.8$.

135 The Bayesian approximate computation software DIYABC (v2.0, Cornuet et al. 2014)
136 was run to reconstruct the demographic history both within GBNPP and GBNPP and adjacent
137 populations (Bering Glacier and Haines-Skagway) where we assessed four different
138 recolonization scenarios (Figure S1, S2). We simulated 1×10^5 datasets for each scenario and
139 recorded the following summary statistics: mean number of alleles, genic diversity, mean Garza-
140 Williamson's M , and F_{ST} . Parameters were adjusted based on their posterior distribution and the
141 optimal model was selected by using measures of posterior probabilities of scenarios. Time
142 estimates in number of generations were converted to years by multiplying by a generation time
143 of 6 years following Martchenko et al. (2020).

144 *2.5 Climate change predictions*

145 We used a population model developed by White et al. (2018) to simulate demographic
146 responses of each genetically distinct subpopulation to predicted changes in climate. This
147 approach simulates climate effects by modeling how changes in mean July/August temperature
148 and total annual snowfall [derived from precipitation as snow (PAS)], influence sex- and age-
149 specific survival (White et al. 2011); a key predictor of population performance (Hamel et al.
150 2006). Temperature and PAS predictions were generated with the ClimateNA software package
151 (v5.10, Wang et al. 2016), and baseline values were calculated by taking the average temperature
152 and PAS over the past 20 years. Five GCM models were used to predict the changes in
153 temperature and PAS: CCSM4, GFDL-CM3, GISS-E2-H, IPSL-CM5B-LR, and MRI-CGCM3 (White et al. 2018). For each model we considered two emission scenarios (RCP 4.5 and RCP
155 8.5), and predicted out to year 2025, 2055, and 2085. Snowfall variability was modeled using
156 total annual snowfall measurements collected at the Gustavus Airport during 1965-2019.
157 Subpopulation size for each study area was derived based on aerial survey data collected during
158 2012 (Lewis and White 2015) and adjusted for sightability bias following analytical methods
159 described in White et al. (2016). The stable age distribution was used to determine the age and
160 sex structure for each initial population size following White et al. (2018). Age-specific density
161 dependent fecundity and kid survival was also parameterized as per White et al. (2018). We ran
162 each model 1000 times and calculated how many times the subpopulation size fell below $N = 2$
163 by the year 2085 to estimate the probability of quasi-extinction, a general metric of population
164 performance over time.

165 We used ecological niche modelling (ENM) and Least Cost Path (LCP) analysis to
166 predict how movement corridors might change in response to climate change. We used
167 coordinates of both the invasive and non-invasive research samples collected in the field
168 combined with a suite of climate raster data layers. The current and future cost landscape rasters
169 were created using the ENM software Maxent (v3.3.3, Phillips et al. 2006) and ArcGIS Pro (v
170 2.6.3) software. We evaluated the predictive capability of the model using cross-validation
171 methods with 75% of the samples as training samples to build the model; the remaining 25% of
172 the samples were omitted from the model building process and later used to test the model. We
173 ran the model using a variety of combinations of parameters and compared Area Under the
174 Curve (AUC) to measure model performance. We used 19 bioclimatic variables, downloaded
175 from WorldClim (<https://www.worldclim.org/>) for current climate data. Additionally, we used
176 landcover type and digital elevation model (DEM) rasters downloaded from the United States
177 Geologic Survey database (<https://apps.nationalmap.gov/downloader/#/>). The DEM raster was
178 used to calculate the heat load index which is a measure of the incident radiation in a location
179 based on the slope and aspect; this attribute has previously been found to affect mountain goat
180 space use (Shafer et al. 2012) and is subject to change with climate. All layers had a resolution of
181 30 arc-seconds. A jackknife test of variable contributions was used to determine which variables
182 contributed to the model; variables that did not contribute were removed and the model was re-
183 run. Future climate variables were downloaded from the GCM Downscaled Data Portal
184 (http://www.ccafs-climate.org/data_spatial_downscaling/). We used the Representative
185 Concentration Pathways models RCP 4.5 and RCP 8.5 from the GFDL_CM3 model projected
186 for the year 2080 (Donner et al. 2011), used in the IPCC Fifth Assessment Report (Shukla et al.
187 2019).

188 To calculate the LCP between the locations of each research sample collected in northern
189 Southeast Alaska, we used the R package ‘gdistance’ (van Etten 2017). Least cost path matrices
190 were produced and compared for current, future (year 2085) under the RCP 4.5 scenario, and
191 future (year 2085) under the RCP 8.5 scenario. We compared the cost distance to the genetic
192 distance parameter Moran’s I to determine how the genetic distance changed as the spatial LCP
193 distance increased and the cost distance to the Euclidean distance to compare the cost and
194 distance values. We used a multiple regression on distance matrices (MRM) method in the R
195 package ‘ecodist’ (Goslee and Urban 2007) that used Euclidean distance and current LCP
196 distance as predictor variables, with the genetic distance as the response variable.

197

198 **3. RESULTS**

199 *3.1 Population genetic diversity statistics*

200 A total of 68 unique samples from pellets in all four sampling areas in GBNPP were genotyped
201 at 17 polymorphic microsatellites (Table 1). An additional 69 (3 pellet, 66 tissue) samples were
202 added from areas surrounding the GBNPP focal areas to investigate connectivity of mountain
203 goats across the GBNPP boundary. Nei’s D between the sampling areas ranged from 0.01 to 0.18
204 with the lowest levels of genetic differentiation between Mt. Wright and Tidal Inlet and the
205 highest between Marble Mountain and Table Mountain (Table 2). The PCA showed clustering of
206 individuals according to sampling area, but Mt. Wright and Table Mountain samples overlapped
207 (Figure 2A). The first principal component versus latitude and longitude analysis did not show a
208 clear relationship ($p > 0.05$, Figure S3); however, an IBD and spatial autocorrelation pattern was

209 present, with genetic relatedness decreasing slightly as spatial distance increased (Figures S4,
210 S5). There was no correlation between H_O , F_{IS} , and N_e and longitude or latitude in GBNPP
211 (Figure S6).

212 *3.2 Population structure and demography*

213 STRUCTURE analysis supported three distinct subpopulations of mountain goats in GBNPP
214 (Figure 2B, S7). When surrounding individuals were included in the analysis 5 subpopulations
215 were detected, the same three within the GBNPP boundary and two intermixed subpopulations
216 northeast of GBNPP (Figure 2B, S8). The amount of admixture was lowest for the three GBNPP
217 subpopulations (proportion of individuals that were admixed: 0.16-0.33) and highest for the
218 subpopulations to the north (0.38-0.41, Table S1). Demographic modelling indicated that within
219 GBNPP, the Table Mountain subpopulation split off first ~7,920 years ago (95% CI: 3,102-
220 37,500). Following that split, the Tidal Inlet/Mt. Wright subpopulations split from Marble
221 Mountain ~1,050 years ago (95% CI: 524-7,080; Figure S1 Scenario 2). Results from the broad
222 scale demographic analysis indicated that GBNPP mountain goats split off most recently from
223 the Northeast in the Haines-Skagway area ~12,480 years ago (95% CI: 5,460-45,600; Figure S2
224 Scenario 1).

225 *3.4 Climate change population modeling*

226 Subpopulations showed numeric declines under all climate scenarios. For all four sampling
227 areas, the CCS and GFDL GCMs under the RCP 4.5 emissions scenarios showed subpopulations
228 reaching quasi-extinction by the year 2085 (Table 3). The CCS, GDFL, and ISPL GCMs showed
229 subpopulations reaching quasi-extinction for all runs in the RCP 8.5 scenario (Table 3). The
230 optimal Maxent model (AUC = 0.942) was based off 118 sample locations and included 13
231 environmental variables (Table S2) and indicated that the ecological niche for mountain goats in
232 Southeast Alaska, given their current location and these environmental layers, is reduced in
233 response to climate change (Figure 3A). The mean cost of travel between all individuals for the
234 current LCP analysis was 1.84×10^6 ; conversely, mean cost of travel between all individuals for
235 the future RCP 8.5 LCP analysis was 1.40×10^{16} (Figure 3B). Multiple regressions indicated that
236 geographic distance is negatively correlated with Moran's I ($R^2 = 0.22$, $p < 0.01$), while
237 including LCP did not improve the model fit (Table S3).

238

239 **4. DISCUSSION**

240 *4.1 Patterns of genetic differentiation*

241 Alaska has a dynamic geologic history with multiple glaciation events that have shaped the
242 current landscape and biodiversity (Svenning et al. 2015, Antonelli et al. 2018). Our results
243 suggest that the mountain goats in GBNPP originated from a local source population in
244 Southeast Alaska rather than dispersing from Southcentral Alaska, or more distant refugial
245 populations. Shafer et al. (2011) provided evidence for a hot spot of mountain goat genetic
246 diversity around Haines, Alaska with peripheral populations appearing to radiate to the
247 surrounding areas. We hypothesize that the common ancestors of GBNPP mountain goats likely
248 originated from this area before splitting off and colonizing GBNPP after the Last Glacial
249 Maximum. The grouping of outer coast Table Mountain subpopulation with two samples from
250 Yakutat indicate that mountain goats in that area could also have a route north of the park

251 boundary that followed the coast down to Table Mountain. The demographic analysis indicated
252 that GBNPP was likely colonized by mountain goats between the retreat of the Last Glacial
253 Maximum and the early stages of the Holocene. Consistent with this is data suggesting many
254 mammalian species colonized northern Southeast Alaska during this period, including rodents
255 (Runck and Cook 2005), mustelids (Cook et al. 2001), carnivores (Klein 1965), and ungulates
256 (Klein 1965, MacDonald and Cook 2009). During this time, glaciers still filled many of today's
257 fjords, allowing for the possibility of a more direct route of colonization across the landscape.

258 Mountain goats in GBNPP exhibit some subtle patterns of IBD and spatial
259 autocorrelation, which has been shown with other mountain goat populations, (Shafer et al. 2011,
260 Parks et al. 2015, White et al. 2021a). The IBD patterns and lack of a PC versus latitude and
261 longitude relationship indicates a relatively rapid wave of colonization across GBNPP, which is
262 not unexpected at a small scale. Mountain goats exhibit female philopatry which results in
263 patterns of closely related individuals staying together (Côté and Festa-Bianchet 2008). These
264 patterns along with low N_e values suggest that genetic drift is the main driver of genetic diversity
265 for these mountain goat subpopulations. Mountain goats are alpine specialists and have the
266 unique ability to traverse across steep, rocky 'escape terrain' that most predators cannot access
267 (Côté and Festa-Bianchet 2008, Shafer et al. 2012). Beyond the mountainous and forested
268 landscapes, GBNPP is also made up of numerous deep inlets and fjords which likely act as
269 barriers to contemporary mountain goat movement. Similar to what has been found for brown
270 and black bears (Lewis et al. 2015, 2020), the recently deglaciated Glacier Bay fjord isolates
271 subpopulations unless there is suitable habitat to facilitate movement around the fjord.

272 On the west side of Glacier Bay, mountain goats are consistently observed on Marble
273 Mountain, despite its isolated geographic position relative to other groups of mountain goats
274 (Lewis and White 2015). Marble Mountain had the lowest estimated genetic diversity and
275 smallest estimated population size ($n = 49$; Lewis and White 2015); with few neighboring
276 mountains inhabited by mountain goats, the amount of gene flow is likely decreased causing this
277 reduction in genetic diversity (e.g. Shirk et al. 2010). Additionally, gene flow is not only a
278 function of distance, but also population size, further causing small subpopulations, like that of
279 Marble Mountain, to experience low gene flow and genetic diversity (Frankham 1996).
280 Interestingly, clustering analysis showed that two of the study areas (Mt. Wright and Tidal Inlet)
281 are not genetically distinct from one another, indicating that gene flow between the study areas is
282 either currently ongoing, separation has occurred recently, or that colonization was recent. A 2
283 km wide fjord separates these two areas but was covered in ice in the late 1800s and movement
284 between them was likely more feasible during that time.

285 *4.2 Response to climate change*

286 Mountain goat populations are projected to be negatively affected by climate change (White et
287 al. 2011, 2018) and our demographic simulation analyses suggest the same pattern is likely to
288 occur in GBNPP. These analyses are not intended to be literal space and time predictions, but
289 rather to heuristically examine whether predicted climate change is likely to be result in
290 favorable or unfavorable outcomes for mountain goats in a particular area. In GBNPP, the
291 projected decrease in winter snowfall and increase in summer temperature seen in climate
292 models suggested climate change is likely to negatively affect mountain goats in all four study
293 areas. These results are similar to that of White et al. (2018), who also found small populations
294 were more strongly influenced by climate-mediated perturbations. To avoid these negative

295 outcomes, mountain goats must either adapt to this changing environment by adjusting daily
296 activity budgets or move to more suitable habitat, which would likely mean moving higher in
297 elevation (Moritz et al. 2008). While behavioral adaptations are an important mechanism that can
298 enable mountain goats to adapt to a changing climate, we have limited understanding of their
299 ability to adapt or behaviorally mitigate these changes. The ability to move to more suitable
300 habitat becomes increasingly important as less habitat is available. Unfortunately, the cost of
301 travel across the landscape will likely increase because of climate change (Figure 3), further
302 highlighting the negative impact that climate change will have on mountain goats.

303 Surprisingly, genetic variation was correlated more with Euclidean distance than LCP
304 distance (Table S3). The LCP is reflective of the contemporary landscape and climatic patterns,
305 which often correlates better than geographic distance in mountain goats (Shirk et al. 2010,
306 Shafer et al. 2012). This correlation between genetic variation and Euclidean distance rather than
307 LCP distance variation supports our assertion that historical patterns of colonization are the
308 primary drivers of contemporary genetic patterns. During past glaciation events, ice filled the
309 fjords, allowing for a more direct route of colonization: this is reflected in the Euclidean
310 distances, all of which encompass the fjords when comparing the Mt. Wright to Marble
311 Mountain subpopulations, for example. Since the ice has retreated, the landscape and movement
312 corridors have changed and main fjord which allowed for the direct route is no longer
313 traversable, thus explaining the lack of correlation between contemporary LCP and genetic
314 variation. Any contemporary and future movement, however, will rely on the current landscape
315 and corridors (e.g. Shafer et al. 2012, Wolf et al. 2020); thus we would expect the future LCP
316 analysis to be more important for predicting future mountain goat connectivity. Additional
317 research on shifts in mountain goat movement across the landscape would be valuable for further
318 understanding how climate change will impact populations in Southeast Alaska. One limitation
319 to note is that locations were used from samples collected during late winter-summer which
320 potentially missed the full range of mountain goat habitat. For future studies on climate-induced
321 changes in mountain goat habitat, we suggest collecting representative year-round samples and
322 designing a complex model that incorporates finer-scale, climate-sensitive behavioral strategies
323 to thermal stress, explicitly considers seasonal differences in ecology and distribution, and
324 considers local climates and associated trajectories. Nevertheless, we feel that this model does
325 provide valuable insight into future climatic changes that will affect mountain goat survival and
326 movement across the landscape.

327 Movement corridors are crucial for maintaining connectivity and gene flow for isolated
328 subpopulations on patchy landscapes (Taylor et al. 1993, Kahilainen et al. 2014, Schlaepfer et al.
329 2018). Connectivity across a landscape can be obstructed by the addition of roads or
330 development which have been found to hinder mountain goat movement (Shirk et al. 2010). The
331 construction of new trails or increased tourism could also affect the landscape connectivity for
332 mountain goats and should be considered when making management decisions. Ecological niche
333 modeling suggested that the climate envelope mountain goats currently use in this area will be
334 greatly reduced and shifted, and may increase the cost of travel (i.e. connectivity) will increase.
335 With the incorporation of genetic information to the current knowledge of population dynamics
336 of mountain goats on a small scale, land managers can make more informed decisions to
337 minimize the disturbance on subpopulations of mountain goats that are more vulnerable to
338 disturbance.

339

340 **CRedit authorship contribution statement**

341 **Kiana B. Young:** Conceptualization, Methodology, Software, Validation, Formal analysis,
342 Investigation, Resources, Data Curation, Writing – Original Draft, Writing – Review & Editing,
343 Visualization, Project administration. **Tania M. Lewis:** Conceptualization, Writing – Review &
344 Editing, Supervision, Project administration, Funding acquisition. **Kevin S. White:**
345 Methodology, Writing – Review & Editing. **Aaron B. A. Shafer:** Conceptualization,
346 Methodology, Resources, Writing – Review & Editing, Supervision, Project administration,
347 Funding acquisition.

348 **Declaration of competing interest**

349 The authors declare they have no conflict of interest.

350 **Acknowledgements**

351 This work was funded by the CFI-JELF (36905; A.B.A.S.), Compute Canada Resources for
352 Research Groups (GME-665-01; A.B.A.S.), NSERC Discovery Grant (A.B.A.S.: RGPIN-2017-
353 03934) and Ontario Early Researcher Award (A.B.A.S.: ER18-14-209). This research was
354 conducted in collaboration with Trent University, the National Park Service, and Alaska
355 Department of Fish & Game. Thank you to the Glacier Bay National Park and Preserve boat
356 captains for providing us with safe transport to our study areas. We are also deeply grateful for
357 the citizen scientists for their assistance in collecting samples in areas that we were not able to
358 access.

359 **REFERENCES**

- 360 Antonelli, A., W. D. Kissling, S. G. A. Flantua, M. A. Bermúdez, A. Mulch, A. N. Muellner-
361 riehl, H. Kreft, H. P. Linder, C. Badgley, J. Fjeldså, S. A. Fritz, C. Rahbek, F. Herman, H.
362 Hooghiemstra, and C. Hoorn. 2018. Geological and climatic influences on mountain
363 biodiversity. *Nature Geoscience* 11:718–725.
- 364 Baltazar-Soares, M., J. D. Klein, S. M. Correia, T. Reischig, A. Taxonera, S. M. Roque, L. Dos
365 Passos, J. Durão, J. P. Lomba, H. Dinis, S. J. K. Cameron, V. A. Stiebens, and C.
366 Eizaguirre. 2020. Distribution of genetic diversity reveals colonization patterns and
367 philopatry of the loggerhead sea turtles across geographic scales. *Scientific Reports* 10.
- 368 Bibi, F., and W. Kiessling. 2015. Continuous evolutionary change in Plio-Pleistocene mammals
369 of eastern Africa. *Proceedings of the National Academy of Sciences of the United States of*
370 *America* 112:10623–10628.
- 371 Boggs, K., S. C. Klein, J. Grunblatt, T. Boucher, B. Koltun, M. Sturdy, and G. P. Streveler.
372 2010. Alpine and subalpine vegetation chronosequences following deglaciation in coastal
373 Alaska. *Arctic, Antarctic, and Alpine Research* 42:385–395.
- 374 Bouzat, J. L. 2010. Conservation genetics of population bottlenecks: The role of chance,
375 selection, and history. *Conservation Genetics* 11:463–478.
- 376 Connor, C., G. Streveler, A. Post, D. Monteith, and W. Howell. 2009. The Neoglacial landscape
377 and human history of Glacier Bay, Glacier Bay National Park and Preserve, southeast
378 Alaska, USA. *The Holocene* 19:381–393.
- 379 Cook, J. A., A. L. Bidlack, C. J. Conroy, J. R. Demboski, M. A. Fleming, A. M. Runck, K. D.
380 Stone, and S. O. MacDonald. 2001. A phylogeographic perspective on endemism in the
381 Alexander Archipelago of southeast Alaska. *Biological Conservation* 97:215–227.
- 382 Cornuet, J. M., P. Pudlo, J. Veyssier, A. Dehne-Garcia, M. Gautier, R. Leblois, J. M. Marin, and
383 A. Estoup. 2014. DIYABC v2.0: A software to make approximate Bayesian computation
384 inferences about population history using single nucleotide polymorphism, DNA sequence
385 and microsatellite data. *Bioinformatics* 30:1187–1189.
- 386 Côté, S. D., and M. Festa-Bianchet. 2008. *Mountain Goats: Ecology, Behavior, and*
387 *Conservation of an Alpine Ungulate*. Island Press, Washington D.C.
- 388 Coulon, A. 2010. Genhet: An easy-to-use R function to estimate individual heterozygosity.
389 *Molecular Ecology Resources* 10:167–169.
- 390 Csilléry, K., M. G. B. Blum, O. E. Gaggiotti, and O. François. 2010. Approximate Bayesian
391 Computation (ABC) in practice. *Trends in Ecology and Evolution* 25:410–418.
- 392 Do, C., R. S. Waples, D. Peel, G. M. Macbeth, B. J. Tillett, and J. R. Ovenden. 2014.
393 NeEstimator v2: Re-implementation of software for the estimation of contemporary
394 effective population size (Ne) from genetic data. *Molecular Ecology Resources* 14:209–214.
- 395 Donner, L. J., B. L. Wyman, R. S. Hemler, L. W. Horowitz, Y. Ming, M. Zhao, J. C. Golaz, P.
396 Ginoux, S. J. Lin, M. D. Schwarzkopf, J. Austin, G. Alaka, W. F. Cooke, T. L. Delworth, S.
397 M. Freidenreich, C. T. Gordon, S. M. Griffies, I. M. Held, W. J. Hurlin, S. A. Klein, T. R.

- 398 Knutson, A. R. Langenhorst, H. C. Lee, Y. Lin, B. I. Magi, S. L. Malyshev, P. C. D. Milly,
399 V. Naik, M. J. Nath, R. Pincus, J. J. Ploshay, V. Ramaswamy, C. J. Seman, E. Shevliakova,
400 J. J. Sirutis, W. F. Stern, R. J. Stouffer, R. J. Wilson, M. Winton, A. T. Wittenberg, and F.
401 Zeng. 2011. The dynamical core, physical parameterizations, and basic simulation
402 characteristics of the atmospheric component AM3 of the GFDL global coupled model
403 CM3. *Journal of Climate* 24:3484–3519.
- 404 van Etten, J. 2017. R package gdistance: Distances and routes on geographical grids. *Journal of*
405 *Statistical Software* 76:1–21.
- 406 Evanno, G., S. Regnaut, and J. Goudet. 2005. Detecting the number of clusters of individuals
407 using the software STRUCTURE: A simulation study. *Molecular Ecology* 14:2611–2620.
- 408 Falush, D., M. Stephens, and J. K. Pritchard. 2003. Inference of population structure using
409 multilocus genotype data: Linked loci and correlated allele frequencies. *Genetics* 164:1567–
410 1587.
- 411 Falush, D., M. Stephens, and J. K. Pritchard. 2007. Inference of population structure using
412 multilocus genotype data: Dominant markers and null alleles. *Molecular Ecology Notes*
413 7:574–578.
- 414 Frankham, R. 1996. Relationship of Genetic Variation to Population Size in Wildlife.
415 *Conservation Biology* 10:1500–1508.
- 416 Galpern, P., M. Manseau, P. Hettinga, K. Smith, and P. Wilson. 2012. Allelematch: An R
417 package for identifying unique multilocus genotypes where genotyping error and missing
418 data may be present. *Molecular Ecology Resources* 12:771–778.
- 419 Goslee, S. C., and D. L. Urban. 2007. The ecodist package for dissimilarity-based analysis of
420 ecological data. *Journal of Statistical Software* 22:1–19.
- 421 Hamel, S., S. D. Côté, K. G. Smith, and Fest. 2006. Population dynamics and harvest potential of
422 mountain goat herds in Alberta. *Journal of Wildlife Management* 70:1044–1053.
- 423 Hardy, O. J., and X. Vekemans. 2002. SPAGeDi: a versatile computer program to analyse spatial
424 genetic structure at the individual or population levels. *Molecular Ecology Notes* 2:618–
425 620.
- 426 Hewitt, G. M. 1999. Post-glacial re-colonization of European biota. *Biological Journal of the*
427 *Linnean Society* 68:87–112.
- 428 Hubisz, M. J., D. Falush, M. Stephens, and J. K. Pritchard. 2009. Inferring weak population
429 structure with the assistance of sample group information. *Molecular Ecology Resources*
430 9:1322–1332.
- 431 Hultén, E. 1937. Outline of the History of Arctic and Boreal Biota during the Quarternary
432 Period. Lehre J Cramer, New York.
- 433 Jombart, T. 2008. adegenet: a R package for the multivariate analysis of genetic markers.
434 *Bioinformatics* 24:1403–1405.
- 435 Kahilainen, A., M. Puurtinen, and J. S. Kotiaho. 2014. Conservation implications of species-

- 436 genetic diversity correlations. *Global Ecology and Conservation* 2:315–323.
- 437 Kearse, M., R. Moir, A. Wilson, S. Stones-Havas, M. Cheung, S. Sturrock, S. Buxton, A.
438 Cooper, S. Markowitz, C. Duran, T. Thierer, B. Ashton, P. Meintjes, and A. Drummond.
439 2012. Geneious Basic: An integrated and extendable desktop software platform for the
440 organization and analysis of sequence data. *Bioinformatics* 28:1647–1649.
- 441 Kimura, M., and G. H. Weiss. 1964. The stepping stone model of population structure and the
442 decrease of genetic correlation with distance. *Genetics* 49:561–576.
- 443 Klein, D. R. 1965. Postglacial Distribution Patterns of Mammals in the Southern Coastal
444 Regions of Alaska. *Arctic* 18:7–20.
- 445 Lewis, T. M., S. Pyare, and K. J. Hundertmark. 2015. Contemporary genetic structure of brown
446 bears (*Ursus arctos*) in a recently deglaciated landscape. *Journal of Biogeography* 42:1701–
447 1713.
- 448 Lewis, T. M., and K. S. White. 2015. Distribution and abundance of mountain goats in Glacier
449 Bay National Park and Preserve. Fort Collins, Colorado.
- 450 Lewis, T., G. Roffler, A. Crupi, R. Maraj, and N. Barten. 2020. Unraveling the mystery of the
451 glacier bear: Genetic population structure of black bears (*Ursus americanus*) within the
452 range of a rare pelage type. *Ecology and Evolution* 10:7654–7668.
- 453 Lister, A. M. 2004. The impact of Quaternary Ice Ages on mammalian evolution. *Philosophical*
454 *Transactions of the Royal Society B: Biological Sciences* 359:221–241.
- 455 Lomolino, M. V., B. R. Riddle, and R. J. Whittaker. 2017. *Biogeography: Biological Diversity*
456 *Across Space and Time*. Sinauer Associates, Inc., Sunderland, MA.
- 457 MacDonald, S. O., and J. A. Cook. 2009. *Recent Mammals of Alaska*. University of Alaska
458 Press, Fairbanks, AK.
- 459 Martchenko, D., R. Chikhi, and A. B. A. Shafer. 2020. Genome assembly and analysis of the
460 north American mountain goat (*Oreamnos americanus*) reveals species-level responses to
461 extreme environments. *G3: Genes, Genomes, Genetics* 10:437–442.
- 462 Milner, A. M., C. L. Fastie, F. S. Chapin, D. R. Engstrom, and L. C. Sharman. 2007. Interactions
463 and linkages among ecosystems during landscape evolution. *BioScience* 57:237–247.
- 464 Moritz, C., J. L. Patton, C. J. Conroy, J. L. Parra, G. C. White, and S. R. Beissinger. 2008.
465 Impact of a century of climate change on small-mammal communities in Yosemite National
466 Park, USA. *Science* 322:261–264.
- 467 Newman, E. A. 2019. Disturbance ecology in the anthropocene. *Frontiers in Ecology and*
468 *Evolution* 7:1–6.
- 469 Van Oosterhout, C., W. F. Hutchinson, D. P. M. Wills, and P. Shipley. 2004. MICRO-
470 CHECKER: Software for identifying and correcting genotyping errors in microsatellite
471 data. *Molecular Ecology Notes* 4:535–538.
- 472 Parks, L. C., D. O. Wallin, S. A. Cushman, and B. H. McRae. 2015. Landscape-level analysis of
473 mountain goat population connectivity in Washington and southern British Columbia.

- 474 Conservation Genetics 16:1195–1207.
- 475 Pearson, O. M. 2013. Hominin evolution in the Middle-late Pleistocene: Fossils, adaptive
476 scenarios, and alternatives. *Current Anthropology* 54:221–233.
- 477 Phillips, S. B., V. P. Aneja, D. Kang, and S. P. Arya. 2006. Maximum entropy modeling of
478 species geographic distributions. *Ecological Modelling* 6:231–252.
- 479 Pielou, E. 1991. *After the Ice Age: the Return of Life to Glaciated North America*. University of
480 Chicago Press, Chicago.
- 481 Poole, K. G., D. M. Reynolds, G. Mowat, and D. Paetkau. 2011. Estimating mountain goat
482 abundance using DNA from fecal pellets. *Journal of Wildlife Management* 75:1527–1534.
- 483 Pritchard, J. K., M. Stephens, and P. Donnelly. 2000. Inference of population structure using
484 multilocus genotype data. *Genetics* 155:945–959.
- 485 Puechmaille, S. J. 2016. The program structure does not reliably recover the correct population
486 structure when sampling is uneven: Subsampling and new estimators alleviate the problem.
487 *Molecular Ecology Resources* 16:608–627.
- 488 Puzachenko, A. Y., and A. K. Markova. 2019. Evolution of mammal species composition and
489 species richness during the Late Pleistocene - Holocene transition in Europe: A general
490 view at the regional scale. *Quaternary International* 530–531:88–106.
- 491 Rice, C. G. 2008. Seasonal altitudinal movements of mountain goats. *Journal of Wildlife
492 Management* 72:1706–1716.
- 493 Rousset, F. 2008. GENEPOP'007: A complete re-implementation of the GENEPOP software for
494 Windows and Linux. *Molecular Ecology Resources* 8:103–106.
- 495 Runck, A. M., and J. A. Cook. 2005. Postglacial expansion of the southern red-backed vole
496 (*Clethrionomys gapperi*) in North America. *Molecular Ecology* 14:1445–1456.
- 497 Schlaepfer, D. R., B. Braschler, H. P. Rusterholz, and B. Baur. 2018. Genetic effects of
498 anthropogenic habitat fragmentation on remnant animal and plant populations: a meta-
499 analysis. *Ecosphere* 9:1–17.
- 500 Shafer, A. B. A., S. D. Côté, and D. W. Coltman. 2011. Hot spots of genetic diversity descended
501 from multiple Pleistocene refugia in an alpine ungulate. *Evolution* 65:125–138.
- 502 Shafer, A. B. A., C. I. Cullingham, S. D. Côté, and D. W. Coltman. 2010. Of glaciers and
503 refugia : a decade of study sheds new light on the phylogeography of northwestern North
504 America. *Molecular Ecology* 19:4589–4621.
- 505 Shafer, A. B. A., J. M. Northrup, K. S. White, M. S. Boyce, S. D. Côté, and D. W. Coltman.
506 2012. Habitat selection predicts genetic relatedness in an alpine ungulate. *Ecology* 93:1317–
507 1329.
- 508 Shirk, A. J., D. O. Wallin, S. A. Cushman, C. G. Rice, and K. I. Warheit. 2010. Inferring
509 landscape effects on gene flow: A new model selection framework. *Molecular Ecology*
510 19:3603–3619.

- 511 Shukla, P. R., J. Skea, E. C. Buendia, V. Masson-Delmotte, H.-O. Pörtner, D. C. Roberts, P.
512 Zhai, R. Slade, S. Connors, R. van Diemen, M. Ferrat, E. Haughey, S. Luz, S. Neogi, M.
513 Pathak, J. Petzold, J. P. Pereira, P. Vyas, E. Huntley, K. M. Kissick, and J. Malley. 2019.
514 IPCC, 2019: Climate Change and Land: an IPCC special report on climate change,
515 desertification, land degradation, sustainable land management, food security, and
516 greenhouse gas fluxes in terrestrial ecosystems.
- 517 Stronen, A. V., L. Iacolina, and A. Ruiz-Gonzalez. 2019. Rewilding and conservation genomics:
518 How developments in (re)colonization ecology and genomics can offer mutual benefits for
519 understanding contemporary evolution. *Global Ecology and Conservation* 17:e00502.
- 520 Svenning, J., W. L. Eiserhardt, S. Normand, A. Ordonez, and B. Sandel. 2015. The Influence of
521 Paleoclimate on Present-Day Patterns in Biodiversity and Ecosystems.
- 522 Taylor, P. D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity Is a Vital Element of
523 Landscape Structure. *Oikos* 68:571–573.
- 524 Wang, T., A. Hamann, D. Spittlehouse, and C. Carroll. 2016. Locally downscaled and spatially
525 customizable climate data for historical and future periods for North America. *PLoS ONE*
526 11:1–17.
- 527 White, K. S., D. P. Gregovich, and T. Levi. 2018. Projecting the future of an alpine ungulate
528 under climate change scenarios. *Global Change Biology* 24:1136–1149.
- 529 White, K. S., T. Levi, J. Breen, M. Britt, J. Merondun, D. Martchenko, Y. N. Shakeri, B. Porter,
530 and A. B. A. Shafer. 2021a. Integrating Genetic Data and Demographic Modeling to
531 Facilitate Conservation of Small, Isolated Mountain Goat Populations. *Journal of Wildlife*
532 *Management* 85:271–282.
- 533 White, K. S., G. W. Pendleton, D. Crowley, H. J. Griese, K. J. Hundertmark, T. McDonough, L.
534 Nichols, M. Robus, C. A. Smith, and J. W. Schoen. 2011. Mountain goat survival in coastal
535 Alaska: Effects of age, sex, and climate. *Journal of Wildlife Management* 75:1731–1744.
- 536 White, K. S., G. W. Pendleton, and J. N. Waite. 2016. Development of an aerial survey
537 population estimation technique for mountain goats in Alaska. Juneau.
- 538 White, K. S., D. E. Watts, and K. B. Beckmen. 2021b. Helicopter-Based Chemical
539 Immobilization of Mountain Goats in Coastal Alaska. *Wildlife Society Bulletin*:1–12.
- 540 Wolf, J. F., K. D. Kriss, K. M. MacAulay, and A. B. A. Shafer. 2020. Panmictic population
541 genetic structure of northern British Columbia mountain goats (*Oreamnos americanus*) has
542 implications for harvest management. *Conservation Genetics*.
- 543

544 **Tables and Figures**

545 Table 1. Diversity statistics for mountain goats in four sampling areas in Glacier Bay National
546 Park, Alaska (n = 68). Data were generated using Genalex v6.503 and NeEstimator v2.1.

547

<i>Sampling area</i>	<i>No. of samples</i>	<i>Assigned pop</i>	<i>Mean q-value</i>	<i>Observed heterozygosity</i>	<i>Expected heterozygosity</i>	F_{IS}	N_e (95% CI)
Marble Mountain	25	Marble Mtn	0.87	0.19 ± 0.049	0.24 ± 0.056	0.18 ± 0.078	6.6-50.7
Mt Wright	10	TidalInlet/ MtWright	0.76	0.34 ± 0.050	0.36 ± 0.054	0.02 ± 0.044	8.3-∞
Table Mountain	14	Table Mtn	0.92	0.32 ± 0.069	0.34 ± 0.047	0.07 ± 0.126	2.5-∞
Tidal Inlet	19	TidalInlet/ MtWright	0.82	0.30 ± 0.052	0.33 ± 0.045	0.17 ± 0.095	5.5-21.5

548 Table 2. Pairwise Nei's D (lower matrix) and F_{ST} (upper matrix) for mountain goats in eight
549 sampling areas in and around Glacier Bay National Park, Alaska and ($n = 137$). Data were
550 generated using SPAGeDi v1.5d.

	Yakutat	Chilkat	GLB	Marble Mtn	Mt Wright	Muir	Table Mtn	Tidal Inlet
Yakutat	-	0.2176	0.0966	0.209	0.1416	0.1097	0.1049	0.2159
Chilkat	0.1361	-	0.052	0.209	0.1243	0.1861	0.1511	0.1582
GLB	0.1094	0.047	-	0.1189	0.0657	0.0258	0.1081	0.1042
Marble Mtn	0.1283	0.124	0.0829	-	0.1439	0.2364	0.2589	0.1851
Mt Wright	0.1363	0.0679	0.0494	0.0857	-	0.0664	0.1355	0.1105
Muir	0.0948	0.1353	0.048	0.1562	0.0666	-	0.1461	0.1183
Table Mtn	0.0924	0.0939	0.0913	0.1766	0.0985	0.1104	-	0.169
Tidal Inlet	0.1019	0.0835	0.0807	0.1026	0.0285	0.0668	0.0988	-

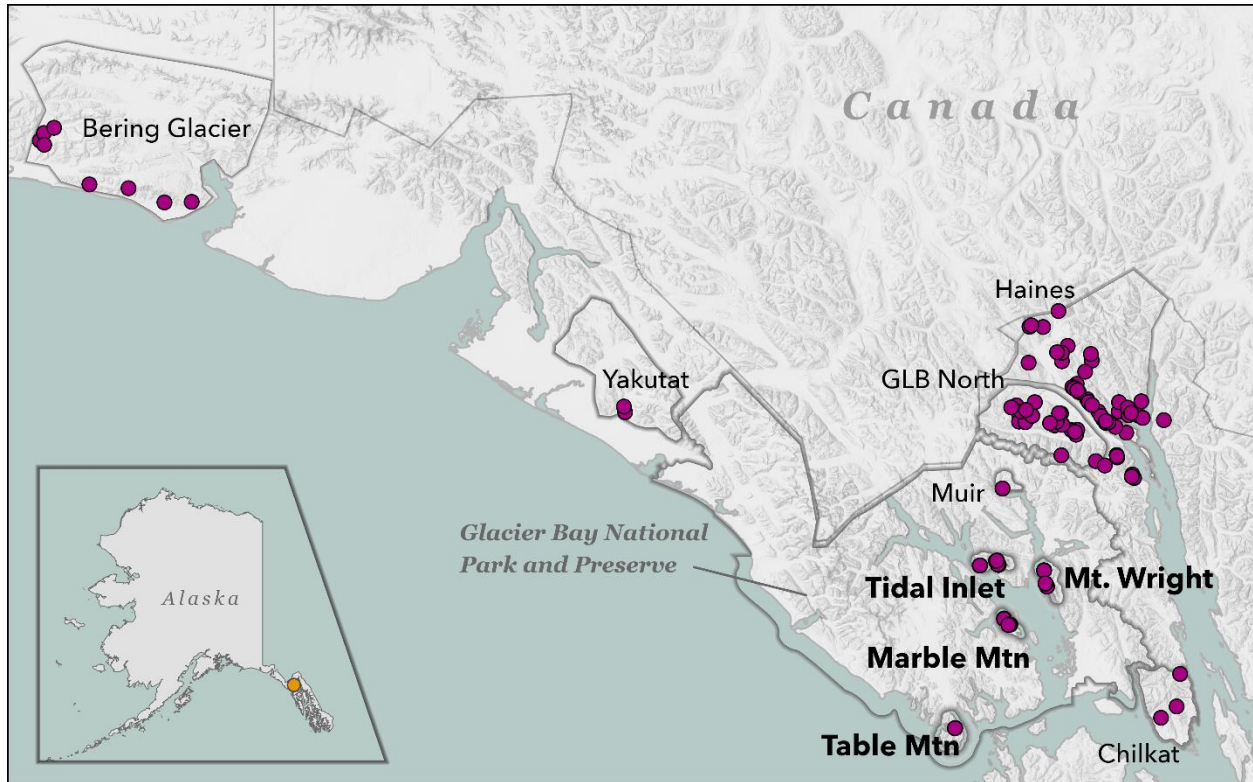
551

552 Table 3. Projected mountain goat population response to climate change over a 65-year period
 553 (2020–2085) for four subpopulations in Glacier Bay National Park, Alaska (total n = 68, Marble
 554 Mountain = 49, Mount Wright = 244, Table Mountain = 208, Tidal Inlet = 214). Subpopulations
 555 were simulated 1000 times under five global climate models (GCM) each with two emission
 556 scenarios (RCP 4.5 and 8.5). Initial population sizes were determined based on aerial surveys
 557 conducted in 2012 and corrected for sightability. Subpopulations were simulated 1,000 times
 558 each. *N* indicates the estimated population size of each study area.

GCM	% quasi-extinction (N<2) by 2085				Years to extinction			
	<i>Marble Mtn</i>	<i>Mt. Wright</i>	<i>Table Mtn</i>	<i>Tidal Inlet</i>	<i>Marble Mtn</i>	<i>Mt. Wright</i>	<i>Table Mtn</i>	<i>Tidal Inlet</i>
RCP 4.5								
CCS	98.6	62.2	37.6	42.7	>65	>65	>65	>65
GFDL	100	88.4	83.0	62.5	55.51±0.15	>65	>65	>65
GISS	0.0	0.0	0.0	0.0	>65	>65	>65	>65
ISPL	0.0	0.0	0.0	0.0	>65	>65	>65	>65
MRI	0.0	0.0	0.0	0.0	>65	>65	>65	>65
RCP 8.5								
CCS	100	100	100	100	45.02±0.09	47.97±0.09	49.93±0.10	50.59±0.09
GFDL	100	100	100	100	48.10±0.10	52.12±0.10	54.17±0.10	52.00±0.10
GISS	0.0	0.0	0.0	0.0	>65	>65	>65	>65
ISPL	100	100	100	100	52.14±0.09	56.44±0.08	57.65±0.09	57.60±0.09
MRI	0.0	0.0	0.0	0.0	>65	>65	>65	>65
N	49	244	208	214				

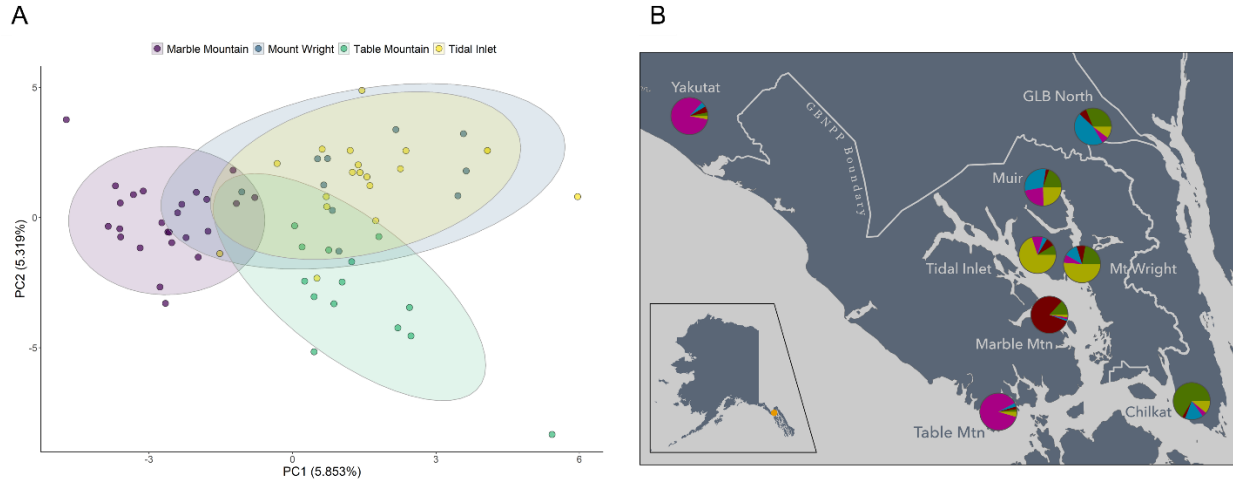
559

560



561

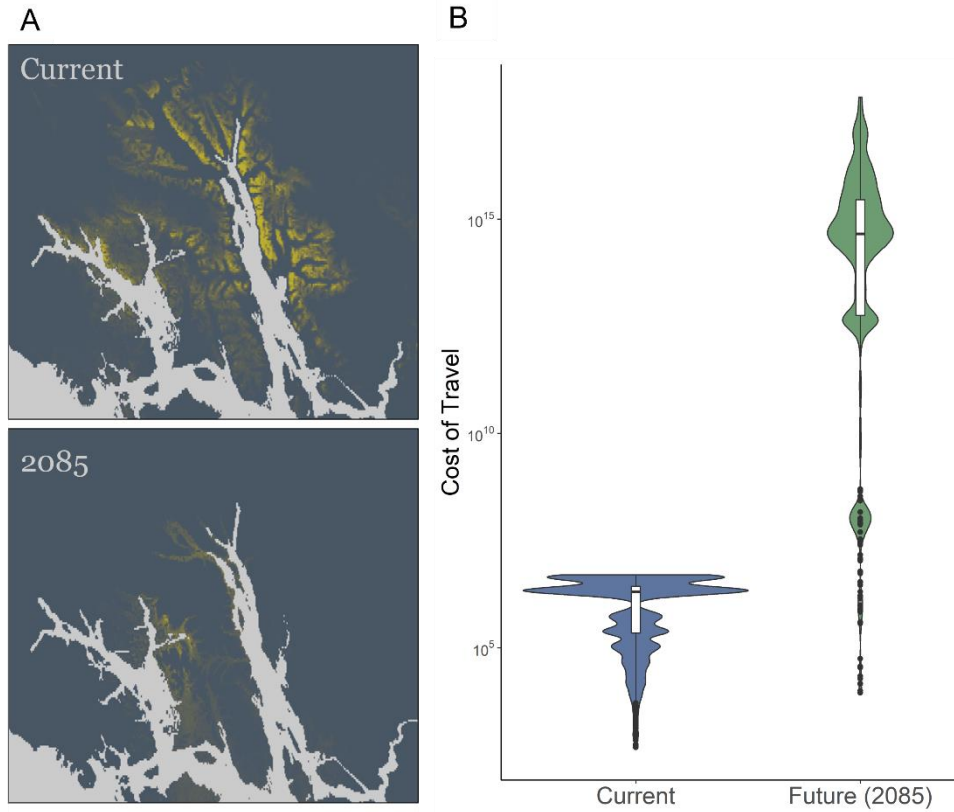
562 Figure 1. Map of mountain goat (*Oreamnos americanus*) samples for Glacier Bay National Park,
563 Alaska analysis. The four focal study areas are indicated in bold. All other study areas (not in
564 bold) were used for demographic and admixture analysis.



565

566 Figure 2. The population structure of mountain goats in and around Glacier Bay National Park
567 and Preserve. A) Principal Components Analysis (PCA) of mountain goats from four sampling
568 areas in Glacier Bay National Park, Alaska (n = 68). The proportion of variance explained by
569 each axis is shown in parentheses. Subpopulations are delineated by color and ellipses. B)
570 Average STRUCTURE subpopulation assignments for mountain goats in each of the four study
571 areas in Glacier Bay National Park, Alaska and areas surrounding Glacier Bay. Pie charts
572 indicate the q-value assignments for each K=5. The four GBNPP sampling areas are indicated in
573 bold.

574



575

576 Figure 3. The effects of climate change on mountain goats in northern Southeast Alaska. (A)
577 Maps of current (top) and year 2085 (bottom) habitat suitability for mountain goats in northern
578 Southeast Alaska based off Maxent analysis. Yellow indicates more suitable habitat and blue
579 indicates less suitable habitat. The global climate model GFDL-CM3 was used for this model. B)
580 Violin plot of the average current and future cost of travel for mountain goats between each
581 sample location in northern Southeast Alaska. Costs were calculated using Maxent suitability
582 layers and Least Cost Path analysis.