

Dietary shifts and behavioral adjustments of North American beaver (*Castor canadensis*) in a novel California riparian ecosystem

Alyssa L. Bartoo¹, Keatyn R. Bucknam² and Melanie L. Truan³

¹ Department of Animal Biology, University of California, Davis, California, USA.
albartoo@ucdavis.edu

² Department of Animal Biology, University of California, Davis, California USA.
krbucknam@ucdavis.edu

³ Museum of Wildlife and Fish Biology, Department of Wildlife, Fish & Conservation Biology, University of California, Davis, California, USA. mltruan@ucdavis.edu

DECLARATION OF AUTHORSHIP: ALB, KRB AND MLT conceived and designed the experiments. ALB and KRB performed the experiments, analyzed the data, and wrote the first draft. MLT commented on previous drafts and guided the development of the manuscript. All authors read and approved the final version.

1 Abstract

2 Rapid anthropogenic change can create novel ecosystems—human-modified environments
3 with no natural analogs—that confront species with new habitat conditions and new species
4 assemblages. Streams and rivers are particularly affected, especially those in arid and
5 Mediterranean climates. Little is known about California’s beaver (*Castor canadensis*) populations,
6 despite the fact that they are once-again becoming widespread and are assuming important roles in
7 riparian communities. We examined beaver foraging behavior and preferences in a novel riparian
8 ecosystem in California’s Central Valley, placing our results in the context of optimal foraging
9 theory. We found that, consistent with previous studies, beaver foraging patterns were heavily
10 influenced by plant species composition, structure, and distance from the creek. Plants closest to
11 the creek were foraged more frequently, but not more intensively, than those further away. Smaller
12 stems were consumed significantly more frequently and intensively at all distances. Contrary to
13 expectations, we found strong evidence of dietary shifts to a nonnative but widely available food
14 source, Himalayan blackberry (*Rubus armeniacus*), suggesting that beavers might modify their
15 foraging behavior to take advantage of new resources in altered plant communities. We also found
16 evidence that beavers may relax their adherence to central place foraging strategies as a result of
17 reduced predator pressure. We discuss the implications of these findings and provide
18 recommendations for restoration strategies and future research.

19 Key words: *Castor canadensis*, *Rubus armeniacus*, foraging theory, novel ecosystem, California

20 Introduction

21 Human induced rapid environmental change (Sih 2013) coupled with shifting human
22 values about nature and ecosystems continue to modify ecosystems at a rapid pace worldwide
23 (Pereira et al. 2010; Sanderson et al. 2002; Vitousek et al. 1997). These rapid changes tend to foster
24 the development of novel ecosystems—human-modified environments with no natural analogs—
25 that confront species with novel conditions that few have encountered previously (Hobbs et al.

26 2013; Perring et al. 2013; Wong and Candolin 2015). Novel ecosystems are particularly prevalent
27 in streams and rivers, especially those in arid and Mediterranean climates where damming and
28 diversion to provide water for human use result in irrevocable changes to ecosystems (Moyle 2014).
29 Here, riparian organisms must deal with a host of disturbances and altered conditions that affect
30 their diversity and survivorship (Levick et al. 2008).

31 As keystone species and ecosystem engineers, beavers are intimately tied to the riparian
32 environment and are responsible for the creation of wetlands that are used by many other species
33 (Naiman et al. 1986; Rossell et al. 2014). Beavers can wield positive effects in novel riparian
34 ecosystems by ameliorating some of the negative impacts of damming and diversion. But they can
35 also create conflicts with humans by causing flooding, blocking culverts and irrigation ditches,
36 burrowing into levees, and impacting vegetation growth, survival and recruitment (Lundquist and
37 Dolman 2016).

38 Beavers are herbivores, consuming a wide range of woody and herbaceous plant types and
39 exerting profound effects on the vegetative structure and species composition of a region. They are
40 especially fond of species in the *Populus* and *Salix* genera (Havens et al. 2013; Roberts and Arner
41 1984; Tappe 1942). It is unclear, however, how beaver foraging preferences might play out in novel
42 ecosystems with their altered ecosystem processes and unique combinations of native and exotic
43 plant species. Most studies have centered on the Eurasian beaver (*Castor fiber*) and/or populations
44 of the North American beaver (*C. canadensis*) residing in the eastern and mid-western continental
45 United States and Canada. Less is known about the ecology of *C. canadensis* in California and the
46 American West, where rivers and streams are highly altered and where differences in habitat,
47 behavior, and ecosystem processes make it difficult to extrapolate data across regions (Baker and
48 Hill 2003; Lanman et al. 2013).

49 Beavers are central-place-foragers, seeking to gain the most benefit (energy) for the lowest
50 cost during foraging (Havens et al. 2013; McGinley and Whitham 1985; Pyke et al. 1977). In
51 general, foraging costs and selectivity increase with distance from the central place while foraging

52 severity decreases (McGinley and Whitham 1985; Rockwood and Hubbell 1987). Considerable
53 debate exists, however, as to whether beavers always follow these patterns and under what
54 conditions they might deviate from them (McGinley and Whitham 1985). In addition, most beaver
55 herbivory studies have been performed in the fall when beavers cut woody plants to cache for
56 winter storage (Busher 1996). Much less is known about the foraging behavior of beavers during
57 the spring months when they allegedly switch to herbaceous material such as aquatic plants and
58 sedges, leaves, and grasses.

59 In this study, we sought to better understand beaver behavioral responses to human-induced
60 rapid environmental change in California by assessing spring foraging preferences and placing
61 these findings in the context of optimal foraging theory. Specifically, we sought to quantify beaver
62 foraging preferences in light of plant species composition, plant size/age (diameter at knee height),
63 and distance from water. In addition to contributing to ecological theory and the generation of basic
64 life history and behavioral information, results from this study will be used to guide local and
65 regional restoration priorities and practices, formulate adaptive management strategies, and inform
66 public outreach efforts.

67 Materials and methods

68 The study was set within an active riparian restoration project on lower Putah Creek near the town
69 of Winters (Solano and Yolo County, California). Here, rapid and extensive changes over the last
70 few centuries have created a novel ecosystem with new environmental conditions and new species
71 combinations and interactions. Putah Creek flows out of the Vaca Mountains in the Coast Range,
72 flowing east into the Sacramento Valley of central California through one of the most productive
73 agricultural regions in the world (Fig. 1). Historically an intermittent stream for much of its length;
74 winter–spring floods created a vast swampy area through which the creek meandered in multiple
75 channels (Moyle 2014). In the 19th century, the creek was diked and forced into a single channel,
76 which became greatly incised. In 1957, the 93-m-high Monticello Dam was built for irrigation,
77 urban water supply, and flood control. At the same time, the Putah Creek Diversion Dam was

78 constructed 13 km downstream to send nearly all the water released from the reservoir to water
79 users in Solano County. The final 27-km reach between the diversion dam and the creek's mouth
80 in the Yolo Bypass was neglected, becoming dry in many years and subject to activities such as
81 gravel mining, widespread vegetation clearing, and trash dumping. Renewed interest in the creek
82 began in the 1980's, prompted by an extended drought, when local citizens and the University of
83 California sued to provide flows for fish below the Diversion Dam (Moyle et al. 1998). An accord
84 among the litigants was reached in 2000, which stipulated a flow regime designed to favor native
85 fishes and to maintain the creek as a living stream at all times. With the institution of permanent
86 flows, beaver, formerly extirpated by the fur trade but reintroduced in the early 20th Century, began
87 to flourish.

88 We established a 263-meter-long sampling area, centered on a known beaver den site, using
89 indirect and direct methods (scat and track identification, foraging marks, and visual detection)
90 (Scottish Beaver Trial 2011). The sampling area varied in width from 10m to 20m due to the
91 presence of a levee embankment intersecting the floodplain at an angle. To evaluate beaver foraging
92 preferences based on relative distance from the creek, we stratified the sampling area into two 263-
93 meter-long strip transects (strata) running relatively parallel to the creek (Fig. 2). Stratum 1 was 0.6
94 meters wide and ran along the water's edge. Stratum 2 was 1.5 meters wide. Stratum 2 was, by
95 necessity, wider than stratum 1 since its vegetative density was lower and more area was needed to
96 achieve a sufficient sample size. Because the floodplain varied in width due to the intersecting
97 embankment, stratum 2 was located approximately $\frac{3}{4}$ of the way between the creek and the toe of
98 the embankment to ensure that the entire width of the floodplain was represented.

99 We conducted preliminary observations and plant surveys beginning in January 2016 and
100 continuing every other week through March 2016. Six plant species dominated the survey area (in
101 order of decreasing cover): willow (*Salix exigua*), Arizona ash (*Fraxinus velutina*), coyote brush
102 (*Baccharis pilularis*), nonnative Himalayan blackberry (*Rubus armeniacus*), nonnative blue gum
103 (*Eucalyptus globulus*), and white alder (*Alnus rhombifolia*). These species were used in the final

104 surveys and analysis. During this time, we discovered that beavers strongly avoided dense thickets
105 of blackberry (*Rubus armeniacus*) and California rose (*Rosa californica*) brambles (see
106 Discussion). Thus, we modified our final sampling and assessment regime to avoid areas containing
107 dense thickets.

108 Final surveys were conducted on 21-May-2016 and 30-May-2016. For each stratum, all
109 plants were counted and tagged. Since individual blackberry bushes were variable in size and
110 consisted of multiple stems, we quantified plants in units of one square meter. For stratum 1, we
111 counted 126 coyote brush shrubs, 240 ash trees, 230 willow shrubs, 10 alder trees, 14 blue gum
112 trees, and 49 blackberry units. Thirty individuals or units were then chosen randomly for final
113 measurement and analysis. Due to their small sample sizes, all alder and blue gum were included.
114 This process was duplicated for the second stratum where we counted 46 willow shrubs, 50 coyote
115 brush shrubs, and 6 blue gum trees. Again, 30 individuals or units of each species were randomly
116 chosen for analysis and all blue gum trees were included due to small sample sizes.

117 For each species within each stratum, we recorded degree of foraging (DF) by beavers and
118 measured diameter at knee height (DKH) to the nearest cm. We considered both basal and lateral
119 stems as they are known to more accurately reflect plant structure in mixed growth form
120 communities (Rossell et al. 2014). For plants with multiple shoots, we took an average of up to ten
121 trunks or branches. DKH for saplings shorter than knee height was recorded as 0.25cm. We
122 established four DF classes: “0” meant the plant showed no signs of foraging, “1” indicated that
123 fewer than 20% of the plant’s branches had been removed, “2” indicated that between 20 and 75%
124 of the branches had been removed, and “3” indicated that more than 75% of the branches had been
125 removed or that the tree had been felled. Beaver foraging was determined by “double-grooved
126 marks” with sharp edges, which were clearly distinct from broken plant parts caused by flooding,
127 wind, or other animal activity (Scottish Beaver Trial 2011). We also used the presence of beaver
128 feeding trails originating from the creek and leading inland to upland foraging stations to further
129 distinguish beaver activity.

130 Data was compiled in Excel and analyzed in JMP (Ver. 12, SAS Institute Inc., Cary, NC).
131 We analyzed correlations between foraging (both frequency and intensity) and plant species,
132 foraging and stratum, and foraging and DKH. We ran contingency tests and logistic regressions,
133 which have no assumptions for normality or homogeneity, for the categorical response variables
134 evidence of foraging and degree of foraging. A contingency test was run to analyze correlations
135 between strata as a categorical predictor variable and foraging status as the response variable.
136 Contingency tests were also run to determine relationships between plant species and foraging
137 status. Logistic regressions were run to determine the relationship between DKH as a continuous
138 variable and foraging status as a categorical response variable. Data were collected randomly which
139 satisfied assumptions for all tests.

140 Results

141 Foraging x Plant Species

142 Certain plant species, willow and blackberry, were selected by beaver significantly more
143 often than all other available species, $\chi^2(5, N = 218) = 86.58, p = <0.0001$ (Fig. 3). Due to the
144 large number of DF categories, combined with small sample sizes, the test for DF x species was
145 significant, but suspect since fewer than 20% of cells had an expected count of less than 5, $\chi^2(15,$
146 $N = 218) = 98.01, p = <0.0001$.

147 Foraging x Strata

148 Of the species found in both strata, significantly more plants were foraged in stratum 1 than
149 in stratum 2, $\chi^2(1, N = 149) = 3.93, p = .0473$ (Fig. 4). Due to small sample sizes, a Fisher's Exact
150 test was run, finding a strong correlation between variables ($p = .0347$). We found no significant
151 difference in the *intensity* of foraging between strata, however, $\chi^2(3, N = 149) = 4.88, p = .1805$.

152 Foraging x Size/Age

153 Plants with a smaller DKH were consumed significantly more frequently than those with
154 larger DKH, regardless of strata, $\chi^2(1, N = 218) = 6.87, p = .0088$ (Fig. 5). In addition, plants with

155 smaller DKH were foraged more intensively, as indicated by the number of foraging marks on a
156 single plant, $\chi^2(3, N = 218) = 15.27, p = .0016$.

157 Discussion

158 Foraging behavior

159 Foraging frequency varied with distance from the water's edge in accordance with central
160 place foraging theory. More plants were foraged in stratum 1 than in stratum 2. However, stratum
161 1 plants were not foraged more intensively than those in stratum 2, possibly reflecting constraints
162 on foraging pressure. Basey et al. (1988), for example, suggested that herbivory may elicit the
163 production of unpalatable secondary metabolites that compel beavers to travel further inland in
164 search of fresh browse and/or to switch to larger stems which lack these defensive compounds.
165 Alternatively, beavers may be deliberately managing their foraging resources to avoid depletion,
166 shifting their browsing patterns or relocating to other sites to allow the vegetation to regrow in their
167 absence (Hyvonen and Nummi 2008; Masslich et al. 1988). However, while moving to greener
168 pastures when local resources become diminished may be effective in large, uninterrupted expanses
169 of habitat, this strategy may be less viable in disturbed or fragmented ecosystems where habitats
170 are few and far-between. In these systems, beaver foraging pressure may become intensified in a
171 few areas, leading to further pressure on habitats and possibly increased human-beaver conflicts.

172 Size of branches consumed

173 Our beavers seemed to prefer smaller diameter branches, regardless of their distance from
174 the water's edge. While some studies indicate that to conserve energy beavers tend to forage less
175 and to forgo smaller branches at increasing distances from a central place, our data supports the
176 alternative theory that beavers tend to have a preference for either small or large branches regardless
177 of distance from the central place (McGinley and Whitham 1985). Note: while our data clearly
178 indicated that smaller stems were chosen more often than those with intermediate diameters (Fig.
179 5), results for plants with DKH of >2.0 may be suspect due to an accumulation of foraging marks
180 across multiple seasons.

181 Reduced predator pressure

182 That our beavers tended to forage widely across the floodplain might also be due to reduced
183 predator pressure at the site. Reduced predation risk is known to reduce the costs of foraging at
184 larger distances from safety as well as costs associated with high handling times (Salandre et al.
185 2017). We observed that that two of the three main beaver feeding stations were located in stratum
186 2 and that a large percentage of cut branches had been debarked on land in close proximity to the
187 cutting site. Beavers typically debark cut branches after hauling them to the safety of water,
188 presumably to avoid predation (McGinley and Whitham 1985) (Basey and Jenkins 1995) (Basey
189 and Jenkins 1995; Gallant et al. 2004). On Putah Creek, most of the beaver's major predators have
190 been extirpated as a result of habitat loss and human presence. Thus, beavers may be relaxing their
191 adherence to central place foraging strategies due to reduced predator pressure.

192 Shifts to a novel food resource

193 While we expected beaver diet to be variable, we were surprised at the degree to which
194 nonnative Himalayan blackberry was selected. Beaver are known to be "fastidious generalists"
195 (Olson and Hubert 1994), consuming a wide variety of herbaceous and woody plant species
196 depending on current needs and what is available in the habitat (Baker and Hill 2003; Rosell et al.
197 2005). Yet, accounts of blackberry use by beaver are few and often contradictory. Tappe (1942)
198 reported California blackberry (*Rubus ursinus*) as being present in most of the habitats surveyed,
199 including Putah Creek, but made no mention of it as a food source. Jenkins (1981) reported that
200 beavers would consume raspberry (*Rubus idaeus*) to some degree while Roberts and Arner (1984)
201 reported that beavers would consume blackberry occasionally. Nixon and Ely (1969) reported that
202 beaver cut and utilized blackberry stems for dam construction, while Francis (2004) indicated that
203 beavers would eat blackberry cambium in winter months, but only when no other food was
204 available. Finally, Tirmenstein (1989) cited Van Dersal (1939), claiming that "porcupines and
205 beaver feed on the cambium, buds, and stems of many species of blackberries," while Van Dersal's

206 account claimed instead that *Rubus* spp. were of “considerable importance as food and cover for
207 rabbits; pica, red squirrel, black bear, beaver” (p242).

208 Behavioral innovations such as diet switching can enable organisms to exploit novel
209 resources that allow them to flourish in new environments (Wong and Candolin 2015). Putah
210 Creek’s riparian vegetation is composed of over 50% nonnative species that are confined to a
211 narrow riparian corridor (Truan 2010). Historical foraging habitat has been much reduced, willows
212 are not as extensive as they once were, and cottonwood trees (*Populus fremontii*), another preferred
213 species, suffer from poor survivorship and recruitment. Himalayan blackberry is abundant,
214 however, and beavers may be taking advantage of this resource to augment more traditional food
215 plants. Indeed, species of *Rubus* are known to be quite nutritious and to contain phytochemicals
216 and antioxidants—antioxidants whose concentrations are higher in the leaves than in the fruit
217 (Gonzalez-Hernandez and Silva-Pando 1999; Owen-Smith 2002; Van Saun 2017; Wang and Lin
218 2000). Consuming blackberry leaves and shoots may provide essential nutrients, especially in the
219 spring when nutritional needs are higher and the plants are actively translocating nutrients from the
220 crown to the growing tips (Strik and Bryla 2015). This may also explain our beavers’ observed
221 preferences for smaller, more-tender, and presumably more nutritious stems and branches.
222 Moreover, because Himalayan blackberry has been ubiquitous along Putah Creek for years, beaver
223 may already be predisposed to foraging on it.

224 Restoration implications: Creating native plant refugia

225 Beaver foraging can have deleterious effects on young plants, a fact that makes beavers
226 rather unpopular in habitat restoration circles. As mentioned previously, our beavers seemed averse
227 to entering thickets of blackberry, rose and coyote brush even though these thickets contained
228 willow, their most preferred food source. While these results were derived from a pilot study
229 involving only 60 willow trees set within two separate thickets, results were very convincing. Trees
230 along the thicket perimeters were foraged significantly more severely ($\chi^2(3, N = 60) = 50.42, p <$
231 $.0001$) and more frequently ($\chi^2(1, N = 60) = 48.65, p < .0001$) than trees within thickets. These

232 results suggest that a viable restoration strategy might be to plant sensitive species within thickets
233 of less-penetrable native species (eg. coyote brush and California rose) as a protection from beavers
234 and other browsers. The effectiveness of this strategy was documented in a study from California
235 in which Himalayan blackberry thickets promoted oak seedling recruitment to the sapling size class
236 by protecting them from browsing (Williams et al. 2006).

237 Research directions

238 For many species, behavioral adjustments represent the first response to altered
239 environmental conditions, determining in large part which species survive, thrive, or flounder
240 (Wong and Candolin 2015). An emerging conceptual framework predicting species responses in
241 novel ecosystems proposes that past selection pressures shape behavioral tendencies that determine
242 response to novel situations (Sih 2013; Sih et al. 2016). As a highly intelligent species evolved to
243 exploit ephemeral wetland resources, beavers have likely developed behavioral strategies that
244 enable them to take advantage of novel situations and resources. Additional inquiries are needed to
245 shed light on the nature of these strategies. For example, little is known about how beaver feed on
246 blackberry stems. Do they consume it at the cutting site or closer to the water's edge? Do they
247 cache it for later consumption or use it to build dams and other structures? And more pragmatically,
248 how do they deal with the thorns? Moreover, more studies are needed in novel ecosystems to
249 determine dietary preferences and behavioral patterns, including patterns of dispersal and nocturnal
250 versus diurnal activity. Research into how beavers utilize novel ecosystems and how they adjust
251 their life history strategies to deal with new habitat conditions and species assemblages may help
252 inform emerging conceptual models of species responses to novel ecosystems and further the
253 development of strategies for conservation and restoration of biodiversity in these rapidly changing
254 ecosystems.

255 Acknowledgements

256 We gratefully acknowledge Dr. Robert Kimsey for his guidance, Dr. Edwin Grosholz for
257 his expertise in statistical analysis, and Matthew Martin for helping to create tables and figures.

258 Lit cited

259 Baker BW, Hill EP (2003) Beaver (*Castor canadensis*). In: Feldhamer GA, Thompson BC,
260 Chapman JA (eds) *Wild Mammals of North America: Biology, Management, and*
261 *Conservation*, 2nd ed.. The Johns Hopkins University Press, Baltimore, MD, pp 288-310

262 Basey JM, Jenkins SH (1995) Influences of predation risk and energy maximization on food
263 selection by beavers (*Castor canadensis*). *Can. J. Zool.* 73:2197-2208. doi: 10.1139/z95-
264 260

265 Basey JM, Jenkins SH, Busher PE (1988) Optimal central-place foraging by beavers: Tree-size
266 selection in relation to defensive chemicals of quaking aspen. *Oecologia* 76:278-282

267 Busher PE (1996) Food Caching Behavior of Beavers (*Castor canadensis*): Selection and Use of
268 Woody Species. *Am. Midl. Nat.* 135:343-348. doi: 10.2307/2426717

269 Francis JK (ed) (2004) *Wildland shrubs of the United States and its Territories: thamnnic*
270 *descriptions Vol. 1*. International Institute of Tropical Forestry, San Juan, PR and U.S.
271 Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ft.
272 Collins, CO

273 Gallant D, Bérubé CH, Tremblay E, Vasseur L (2004) An extensive study of the foraging ecology
274 of beavers (*Castor canadensis*) in relation to habitat quality. *Can. J. Zool.* 82:922-933.
275 doi: 10.1139/z04-067

276 Gonzalez-Hernandez MP, Silva-Pando FJ (1999) Nutritional attributes of understory plants
277 known as components of deer diets. *J. Range Manage.* 52:132-138

278 Havens RP, Crawford JC, Nelson TA (2013) Survival, Home Range, and Colony Reproduction of
279 Beavers in East-Central Illinois, an Agricultural Landscape. *Am. Midl. Nat.* 169:17-29.
280 doi: 10.1674/0003-0031-169.1.17

281 Hobbs RJ, Higgs ES, Hall CM (eds) (2013) *Novel Ecosystems: Intervening in the New*
282 *Ecological World Order*. Wiley-Blackwell, Oxford

283 Hyvonen T, Nummi P (2008) Habitat dynamics of beaver (*Castor canadensis*) at two spatial
284 scales. *Wildl. Biol.* 14:302-308

285 Jenkins SH (1981) Problems, progress, and prospects in studies of food selection by beaver. In:
286 Chapman JA, Pursley D (eds) *Proceedings of the worldwide furbearer conference*,
287 Frostburg, MD, pp 559-579

288 Lanman C et al. (2013) The historical range of beaver (*Castor canadensis*) in coastal California:
289 an updated review of the evidence. *Calif. Fish and Game* 99:193-221

290 Levick L et al. (2008) The ecological and hydrological significance of ephemeral and intermittent
291 streams in the arid and semi-arid American Southwest. *USDA/ARS Southwest*
292 *Watershed Res. Ctr, U.S. EPA*, 116pp.

293 Lundquist K, Dolman B (2016) *Beaver in California: Creating a Culture of Stewardship*. WATER
294 Institute, Occidental Arts and Ecology Center

295 Masslich WJ, Brotherson JD, Cates RG (1988) Relationships of aspen (*Populus tremuloides*) to
296 foraging patterns of beaver (*Castor canadensis*) in the Strawberry Valley of Central Utah.
297 *Gr. Basin Nat.* 48:250-262

298 McGinley MA, Whitham TG (1985) Central place foraging by beavers (*Castor canadensis*): a test
299 of foraging predictions and the impact of selective feeding on the growth form of
300 cottonwoods (*Populus fremontii*). *Oecologia* 66:558-562. doi: 10.1007/bf00379350

301 Moyle PB (2014) Novel aquatic ecosystems: the new reality for streams in California and other
302 Mediterranean climate regions. *River Res. & Appl.* 30:1335-1344. doi: 10.1002/rra.2709

303 Moyle PB, Marchetti MP, Baldrige J, Taylor TL (1998) *Fish Health and Diversity: Justifying*
304 *Flows for a California Stream*. *Fisheries* 23:6-15

305 Naiman RJ, Melillo JM, Hobbie JE (1986) Ecosystem Alteration of Boreal Forest Streams by
306 Beaver (*Castor canadensis*). *Ecology* 67:1254-1269. doi: 10.2307/1938681

307 Nixon CM, Ely J (1969) Foods Eaten by a Beaver Colony in Southeast Ohio. *Ohio J. Sci.* 69:313-
308 319

309 Olson R, Hubert W (1994) Beaver: Water resources and riparian habitat manager. University of
310 Wyoming, Laramie, Wyoming

311 Owen-Smith N (2002) Adaptive herbivore ecology: from resources to populations in variable
312 environments, Cambridge, UK

313 Pereira HM et al. (2010) Scenarios for Global Biodiversity in the 21st Century. *Science*
314 330:1496-1501. doi: 10.1126/science.1196624

315 Perring MP, Standish RJ, Hobbs RJ (2013) Incorporating novelty and novel ecosystems into
316 restoration planning and practice in the 21st century. *Ecol. Process.* 2:18. doi:
317 10.1186/2192-1709-2-18

318 Pyke GH, Pulliam HR, Charnov EL (1977) Optimal Foraging: A Selective Review of Theory and
319 Tests. *Q. Rev. Biol.* 52:137-154. doi: 10.1086/409852

320 Roberts TH, Arner DH (1984) Food Habits of Beaver in East-Central Mississippi. *J. Wildl.*
321 *Manag.* 48:1414-1419. doi: 10.2307/3801808

322 Rockwood LL, Hubbell SP (1987) Host-plant selection, diet diversity, and optimal foraging in a
323 tropical leafcutting ant. *Oecologia* 74:55-61. doi: 10.1007/bf00377345

324 Rosell F, Bozser O, Collen P, Parker H (2005) Ecological impact of beavers *Castor fiber* and
325 *Castor canadensis* and their ability to modify ecosystems. *Mamm. Rev.* 35:248-276. doi:
326 10.1111/j.1365-2907.2005.00067.x

327 Rossell CR, Arico S, Clarke HD, Horton JL, Ward JR, Patch SC (2014) Forage Selection of
328 Native and Nonnative Woody Plants by Beaver in a Rare-Shrub Community in the
329 Appalachian Mountains of North Carolina. *Southeast. Nat.* 13:649-662. doi:
330 10.1656/058.013.0415

331 Salandre JA, Beil R, Loehr JA, Sundell J (2017) Foraging decisions of North American beaver
332 (*Castor canadensis*) are shaped by energy constraints and predation risk. *Mamm. Res.*
333 62:229-239. doi: 10.1007/s13364-017-0312-6

334 Sanderson EW, Jaiteh M, Levy MA, Redford KH, Wannebo AV, Woolmer G (2002) The Human
335 Footprint and the Last of the Wild. *BioScience* 52:891-904. doi: 10.1641/0006-
336 3568(2002)052[0891:THFATL]2.0.CO;2

337 Scottish Beaver Trial (2011) Beaver media field signs: Trails and feeding stations. Online
338 multimedia. Royal Zool. Soc. Scotland, Scottish Wildlife Trust, Forestry Commission
339 Scotland

340 Sih A (2013) Understanding variation in behavioural responses to human-induced rapid
341 environmental change: a conceptual overview. *Anim. Behav.* 85:1077-1088. doi:
342 10.1016/j.anbehav.2013.02.017

343 Sih A, Trimmer PC, Ehlman SM (2016) A conceptual framework for understanding behavioral
344 responses to HIREC. *Curr. Opin. Behav. Sci.* 12:109-114. doi:
345 10.1016/j.cobeha.2016.09.014

346 Strik BC, Bryla DR (2015) Uptake and Partitioning of Nutrients in Blackberry and Raspberry and
347 Evaluating Plant Nutrient Status for Accurate Assessment of Fertilizer Requirements.
348 *HortTechnology* 25:452-459

349 Tappe DT (1942) The Status of Beavers in California. Dept. of Fish & Game, State of Calif.,
350 Dept. of Nat. Res.

351 Tirmenstein D (1989) *Rubus armeniacus* Fire Effects Information System [online]. Fire Sci. Lab.,
352 Rocky Mtn Res. Stn. USDA Forest Serv.

353 Truan ML (2010) Putah Creek Terrestrial Wildlife Monitoring Program Comprehensive Report,
354 1997-2009. Mus. of Wildl. & Fish Biol., Univ. of California, Davis

355 Van Dersal WR (1939) Native Woody Plants of the United States. Div. of Conserv. Operations,
356 Soil Conservation Service, U.S. Dept. of Agriculture, Washington D.C.

357 Van Saun RJ (2017) Effects of Forage Quality on a Camelid Feeding Program. Penn State
358 Extension, Penn. State Univ., Coll. of Agric. Sci.

359 Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human Domination of Earth's
360 Ecosystems. *Science* 277:494-499. doi: 10.1126/science.277.5325.494

361 Wang SY, Lin H-S (2000) Antioxidant Activity in Fruits and Leaves of Blackberry, Raspberry,
362 and Strawberry Varies with Cultivar and Developmental Stage. *J. Agric. and Food Chem.*
363 48:140-146. doi: 10.1021/jf9908345

364 Williams K, Westrick LJ, Williams BJ (2006) Effects of blackberry (*Rubus discolor*) invasion on
365 oak population dynamics in a California savanna. *For. Ecol. and Manag.* 228:187-196.
366 doi: 10.1016/j.foreco.2006.03.002

367 Wong BBM, Candolin U (2015) Behavioral responses to changing environments. *Behav. Ecol.*
368 26:665-673. doi: 10.1093/beheco/aru183

369

370 Figure 1. Site Map of lower Putah Creek, Yolo and Solano Counties, California, USA. Numbered
371 reaches in kilometers, beginning at the Putah Diversion Dam. Study site marked at km 6.

372

373 Figure 2. Schematic depiction of stratum measurements and distance extremes (10m and 20m)
374 between the toe of the embankment and the water for the 263m long sampling area, north bank of
375 Putah Creek, Winters, CA. Stratum 1 was 0.6m in width and was placed immediately adjacent to
376 the creek, while stratum 2 was 1.5m in width and was positioned at a point $\frac{3}{4}$ of the way between
377 the creek and the toe of the embankment. Stratum 2 was wider to accommodate a wider spacing
378 of plants.

379

380 Figure 3. Percent foraged for the six most abundant plant species. *Salix exigua* was foraged the
381 most frequently, followed by *Rubus armeniacus*, a nonnative species. *Alnus rhombifolia*,
382 *Fraxinus velutina*, *Eucalyptus globulus*, and *Baccharis pilularis* were only moderately or rarely
383 selected.

384

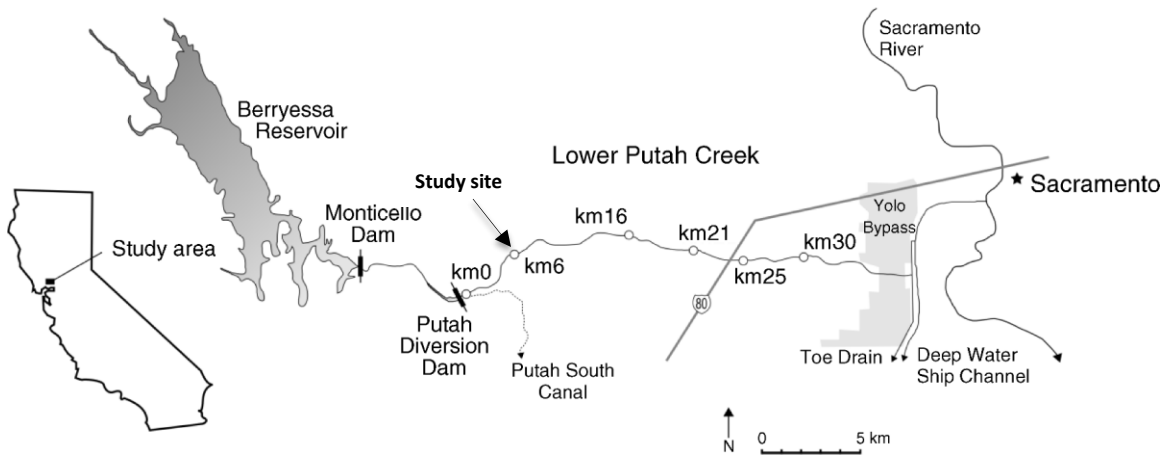
385 Figure 4. Percent foraged by stratum. Stratum 1 contained *Baccharis pilularis*, *Fraxinus velutina*,
386 *Rubus armeniacus*, *Salix exigua*, *Alnus rhombifolia*, and *Eucalyptus globulus*. Stratum 2
387 contained only *Salix exigua*, *Baccharis pilularis*, and *Eucalyptus globulus*. Of the species found in
388 both strata, significantly more plants were foraged in stratum 1 than in stratum 2.

389

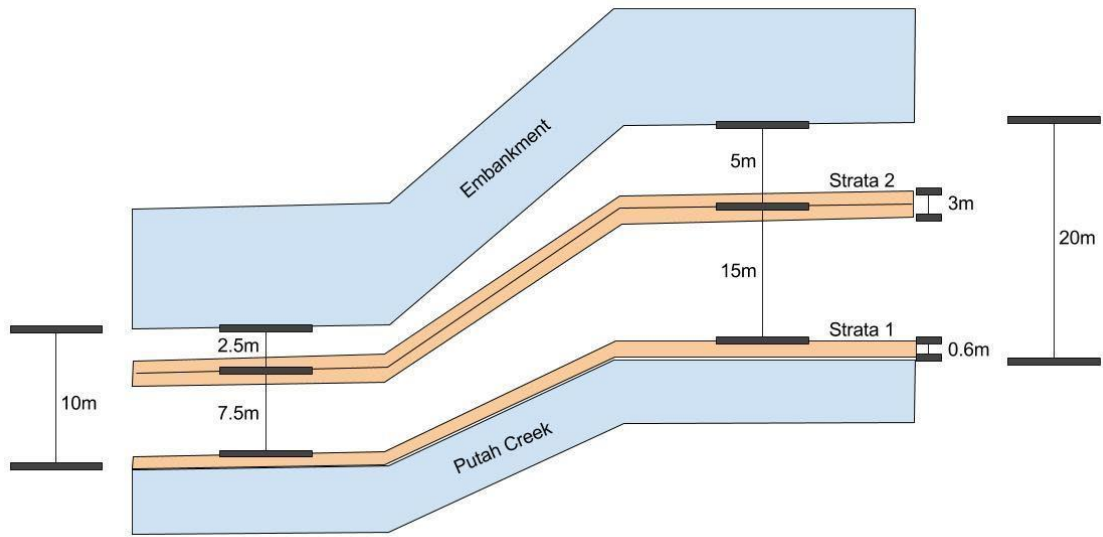
390 Figure 5. Severity of foraging, based on a predetermined scale, for the six most abundant plant
391 species as a function of diameter at knee height (DKH). Plants with smaller DKH were foraged
392 significantly more frequently, as well as more severely, than plants with larger DKH. Results for
393 plants with DKH of >2.0 may be suspect due to accumulation of foraging marks across multiple
394 seasons. Nevertheless, the relationship between foraging and DKH for the remaining size classes
395 was significant. DKH was graphed categorically for ease of interpretation.

396 **Figure 1**

397

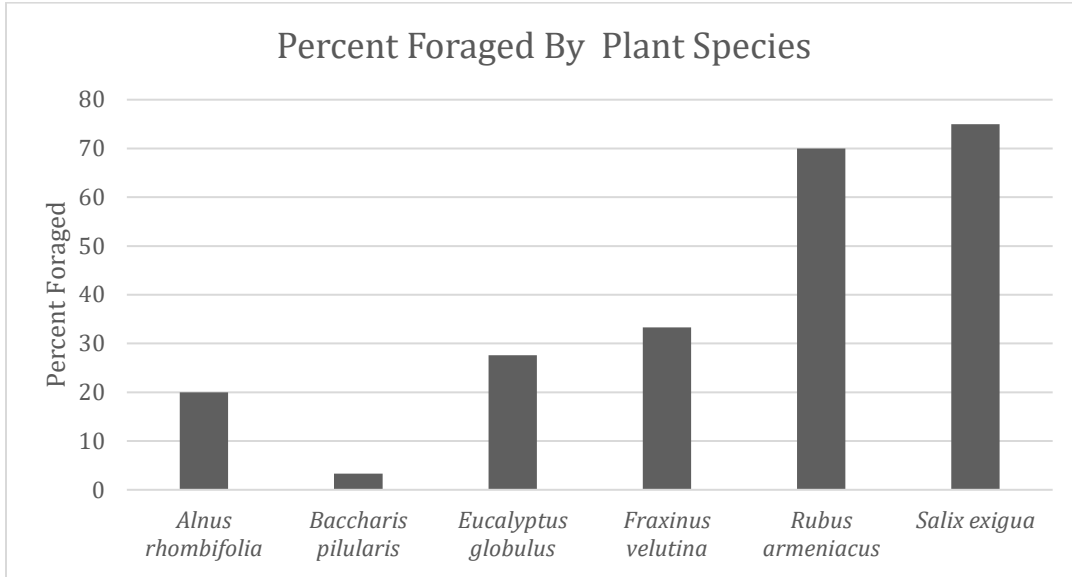


398 **Figure 2:**



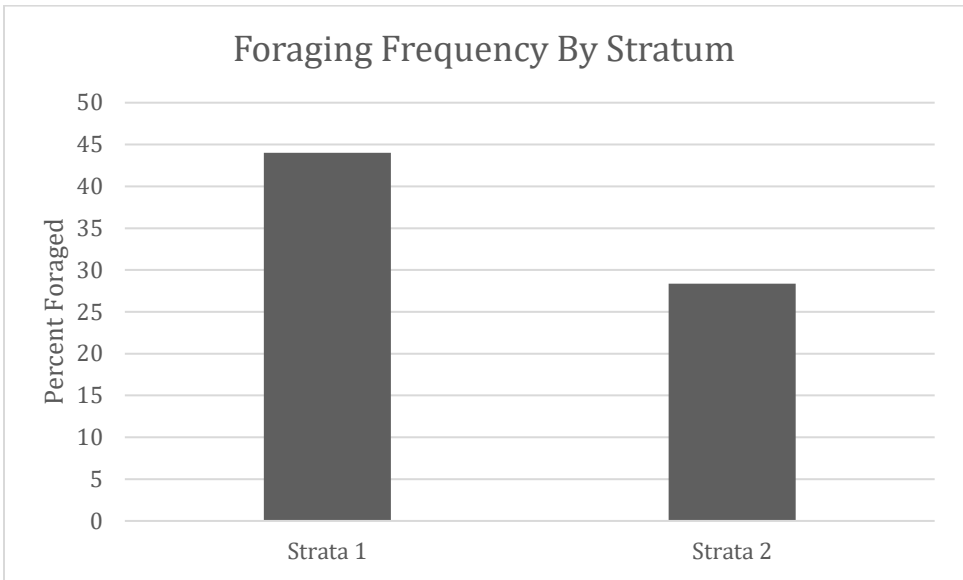
399

400 **Figure 3:**



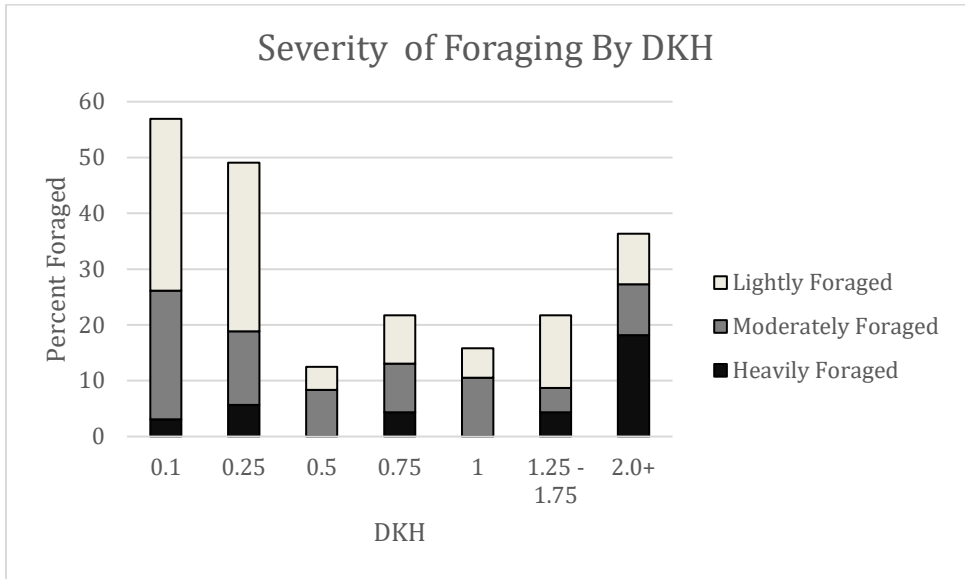
401

402 **Figure 4:**



403

404 **Figure 5:**



405