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1 **From fear to food: predation risk shapes deer behaviour, their resources and forest**
2 **vegetation**

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5 Jean-Louis Martin^{*1}, Simon Chamaille-Jammes¹, Anne Salomon², Devana Veronica Gomez
6 Pourroy¹, Mathilde Schlaeflin¹, Soizic Le Saout¹, Annick Lucas¹, Ilham Bentaleb³, Simon
7 Chollet⁴, Jake Pattison⁵, Soline Martin-Blangy⁶, Anthony J. Gaston⁷

8
9 ¹ CEFE, CNRS, Univ Montpellier, EPHE, IRD - Montpellier, France

10 ² School of Resource & Environmental Management, Simon Fraser University - Burnaby, Canada

11 ³ University of Montpellier, UMR 5554 CNRS, IRD, EPHE, CC061 - Montpellier, France

12 ⁴ University of Rennes, CNRS, ECOBIO Ecosystèmes, biodiversité, évolution, UMR 6553 -
13 Rennes, France

14 ⁵ Laskeek Bay Conservation Society - Daajing Giids and Skidegate, Canada

15 ⁶ 81 rue Marius Carrieu, 34080 Montpellier, France

16 ⁷ National Wildlife Research Center, Environment and Climate Change Canada - Ottawa, Canada
17 K1A 0H3

18
19 *Jean-Louis Martin

20 Correspondence: jean-louis.martin@cefe.cnrs.fr

21

22 **Abstract**

23 The “ecology of fear” posits that predation risk shapes the behaviour of large herbivores, their
24 foraging patterns, their habitat selection and their consequent effect on forest ecology. To test
25 some of these predictions we used the extensive empirical and experimental data on vegetation
26 cover and composition, and on deer anti-predator behaviour, collected at study sites with different
27 histories of hunting and natural predation in the Haida Gwaii archipelago and in nearby areas of
28 coastal British Columbia (Canada). Because these deer also forage in the intertidal, an habitat
29 hypothetically more exposed to risk, we also analysed how risk affected intertidal foraging by
30 measuring the proportion of marine versus terrestrial stable isotopes in deer bone collagen.

31 In absence of risk, deer had a strong negative effect on understory vegetation cover and plant
32 composition. In these populations deer had a remarkable tolerance to human presence (short flight
33 initiation and travel distances when disturbed), a willingness to consume foreign bait or to
34 investigate baited traps, and a propensity to be active at daytime.

35 Where deer faced long term hunting and natural predators, understories were denser and more
36 diverse and resembled those of forests never exposed to deer. Severe deer culling in sites initially
37 without risk dramatically increased the cover of understory vegetation, although different in
38 composition from the one in forests with long-term presence of predators and hunting, or that
39 never had deer. Deer born after culling exhibited longer flight initiation distances and travel
40 distances when fleeing, a reluctance to consume foreign bait or to investigate baited traps, and
41 increased night-time foraging.

42 The translocation of unwary deer from a population without risk to the island where culls had
43 partially restored the vegetation, showed that their unwary behaviour was not significantly
44 modified in the presence of abundant and higher quality forage. This contrasted with the wary
45 behaviour observed in the local deer born after the culls.

46 Finally, deer in populations exposed to risk from hunters and/or predators were less likely to forage
47 in the intertidal, although this trend might be, to some extent, affected by resources in the
48 understory.

49 We interpreted our results as evidence that ~~experience or absence of risk~~ **were** key in shaping, and
50 potentially selecting for, lasting behavioural contrasts between deer populations, contrasts
51 intimately connected to deer effects on plant cover and diversity, ecological networks, and
52 ecosystem complexity.

53

54

55 **Keywords:** herbivore habitat effects, ecology of fear, behaviour and predation risk, anti-predator
56 behaviour, behavioural change, fear and habitat selection

58 From its outset, Ecology was defined as the science of interactions (Haeckel 1866; Elton 1927).
59 Initially centered on direct relationships among species, research increasingly emphasized the
60 importance of indirect interactions, highlighting the interplay between herbivores and their
61 predators and how it affected the structure, function and stability of ecosystems [(Paine 1966,
62 1969; Estes et al. 2011) and review in (Martin et al., 2020)]. Consequently, while the loss of
63 species or populations across the world's ecosystems is dire, the loss of species interactions is
64 perhaps even more insidious, because it often goes unnoticed (Janzen 1974; Soulé et al. 2003;
65 Valiente-Banuet et al. 2015).

66 **The ecology of fear, connecting behaviour, ecology and evolution** – Studies on large herbivores
67 and their predators suggest that, whether predators are present or absent, prey will alter their
68 behaviours in response to perceived risk. The non-consumptive effects of predator presence,
69 including human hunters, and its consequences on how prey interact with their habitat, is central
70 to the conceptual framework of "the ecology of fear" (Brown et al. 1999; Zhanette & Clinchy 2020;
71 Potratz et al. 2024), and to the idea of a "landscape of fear" (Laundré et al. 2001; Gaynor et al.
72 2019, 2021; Zhanette & Clinchy 2020; Palmer et al. 2022). Focusing on ungulates, and deer in
73 particular, Altendorf et al. (2001) predicted that, in presence of predators, deer should spend less
74 time foraging at any given location, limit or avoid using portions of their habitat perceived as more
75 exposed to predation (e.g. because of high visibility), or favour sites perceived as refuges from
76 risk (e.g. dense vegetation) (Williams et al. 2008; Kuijper et al. 2013; Padié et al. 2015; Bonnot et
77 al. 2017; Martin et al. 2018; Clare et al. 2023). Conversely, absence of risk should eliminate the
78 spatial effects of risk on foraging (Zhanette & Clinchy 2020; Wójcicki & Borowski 2023) and
79 intensify use of the vegetation. Beyond these direct or indirect **day to day** impacts on ecological
80 processes (e.g. Sih et al. 2012), prey behavioural adjustments to the level of risk, could also, over
81 time, select for prey traits and behaviours better adapted to the risk level of a given community
82 (Bøhn & Amundsen 2004; Sih et al. 2004; Réale et al. 2007; Eilers et al. 2012; Estes et al. 2013;
83 Zhanette & Clinchy 2020; Wójcicki & Borowski 2023).

84 **Questions to address** - Despite recent advances, we still need to better understand how animal
85 behaviour, ecology and evolution interact to shape ecological dynamics, behavioural traits, and
86 habitat selection (Réale et al. 2007; Sih et al. 2012; Potratz et al. 2024). Such an understanding
87 would also improve conservation strategies (Kuijper et al. 2016; Martin et al. 2020; Chitwood et
88 al. 2022; Potratz et al. 2024). Here, we use empirical and experimental studies carried out since
89 1989 on the interplay between deer, vegetation and predation risk, to assess (1) the links between
90 the presence of risk and the effects that deer have on forest ecosystems, (2) whether different
91 metrics of behavioural response varied in relation to the presence or absence of hunting and natural
92 predators, (3) **whether different risk contexts affected what individual behaviour became dominant**
93 **in different populations**, and (4) how risk affected deer habitat selection.

94 **A life-size laboratory** - We took advantage of the introduction, at the end of the 19th century, of
95 Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) to Haida Gwaii, a remote archipelago in
96 British Columbia, western Canada (Fig. 1) lacking the natural predators these deer are exposed to
97 on the adjacent mainland (Golumbia et al. 2008). The archipelago provided islands with and
98 without deer, and, where deer were present, islands with and without a history of hunting by
99 people. On two islands, severe culling was carried out on a deer population previously without
100 predation risk and where deer browsing had a dramatic impact on vegetation and fauna (Allombert
101 et al. 2005b, 2005a; Stockton et al. 2005; Martin et al. 2010). We complemented our long-term
102 data on Haida Gwaii with data from the Central Coast of British Columbia where deer always
103 faced natural predators in addition to hunters (Darimont & Paquet 2001, 2002; Darimont et al.
104 2007). There, black-tailed deer represent over 80% of wolf diet (Darimont & Paquet 2001).

105 **Fear and vegetation** - Based on prior studies, we expected that absence of risk would be
106 associated with severe impact on forest vegetation cover and diversity (Côté et al., 2004; Martin
107 et al., 2010; Stockton et al., 2005), with understory vegetation restricted to a small group of deer-
108 resistant species, even if only represented as severely browsed and stunted individuals (Martin et
109 al., 2010). We also expected that culling, in a deer population initially not exposed to risk, would
110 trigger a positive response in vegetation cover.

111 **Fear and behaviour** – We predicted that severe experimental culls and associated changes in
112 perception of risk would affect anti-predator behaviours, possibly years after the culls (Martin &
113 Baltzinger 2002; Gaynor et al. 2019; Clare et al. 2023; Wójcicki & Borowski 2023). In particular
114 we expected to see longer deer flight initiation distance (FID) after detection of a potential human
115 threat, longer distance travelled after detection, a reduction in deer use of foreign bait and a lower
116 likelihood of deer being trapped in the post-culls deer population. We also predicted changes in
117 deer diel activity towards being more nocturnal when compared to populations not exposed to risk
118 from day-hunting humans (Kilgo et al. 1998; Bonnot et al. 2020). Conversely, we predicted that
119 in populations not exposed to risk, lower levels of anti-predator behaviours would be key in
120 explaining the observed severity of deer impact on the vegetation.

121 **Fear and habitat selection** - Previous studies have shown that, in some systems, prey favoured
122 foraging in more open habitats because of better visibility of an approaching threat (Gigliotti et al.
123 2021; Kamaru et al. 2024). In other studies, in particular on deer, elevated risk resulted in prey
124 avoiding open habitats for foraging (Kilgo et al. 1998; Creel et al. 2005; Bonnot et al. 2013;
125 Dellinger et al. 2019). When wolves were introduced to Coronation Island in SE Alaska (Klein
126 1995) their extensive use of shorelines came with a dramatic shift by deer away from the coastal
127 portions of the island [for use of shorelines by foraging wolves see also Darimont & Reimchen
128 (2002) on deer seasonal use of salmon, and Roffler et al. (2023)]. Hunters access to deer on the
129 BC Central Coast, essentially roadless, and on Haida Gwaii, is often by boat [L. Vigneault pers.
130 com. and Irvine & Thorley (2024)]. This, and our observations of deer foraging frequently on
131 seaweeds beached or attached on intertidal shores (Bonnot et al., 2016) led us to predict that the

132 lack of cover in intertidal areas, the limitation of escape routes by the ocean, and wave sounds
133 hindering auditory detection, might negatively affect the ability of deer foraging in intertidal sites
134 **to detect hunters** approaching from the water and/or natural predators scouting the area for its
135 resources. We tested this prediction indirectly by comparing the proportion of marine algae in deer
136 diet under contrasting risk contexts.

137

138

Material and Methods

139 Haida Gwaii and the study sites

140 Haida Gwaii is characterized by a humid temperate-oceanic climate, with mean annual
141 temperature of 8.5°C (Banner et al. 2014). Most of the archipelago is covered by temperate
142 rainforests dominated by western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*),
143 and Sitka spruce (*Picea sitchensis*). Open terrestrial habitats are restricted to the alpine zones and
144 to extensive bogs on NE Graham Island.

145 Native to coastal British Columbia, but not to Haida Gwaii, Sitka black-tailed deer were
146 introduced to the archipelago in the late 19th century (Golumbia et al. 2008), colonizing all but a
147 few small islands. The absence of natural predators on the archipelago allowed the deer population
148 to thrive. The occurrence of a few reference islands that never supported deer made it possible to
149 demonstrate that, on islands with long-term deer presence, independent of island size, deer
150 herbivory was the main factor structuring plant and animal communities (Martin and Baltzinger
151 2002, Gaston et al. 2006, Martin et al. 2010, Chollet et al. 2013), with important consequences on
152 belowground processes (Chollet et al. 2021b; Maillard et al. 2021). Recurrent experimental culls
153 on two islands allowed us to monitor the response of the aboveground vegetation and avifauna for
154 13 years (Chollet et al. 2016). These results accumulated over the different phases of the long-
155 term RGIS project <https://rgis.cefe.cnrs.fr/>.

156 The three islands in Laskeek Bay (52°53'12"N, 131°35'20"W) where we focused our study on deer
157 behaviour (Reef 249 ha, Kunga 395 ha, and East Limestone Island 48 ha) (Table 1, Fig. 1) have
158 all had deer present for over 60 years at the time of study (Vila et al. 2004b, 2004a) and had no
159 history of hunting. Covered by mature forests without human settlements or activities, these
160 islands were characterized by closed canopy forests with open species-poor understories (Martin
161 et al. 1995, Stockton et al. 2005, Martin et al. 2010) representative of severe deer impacts that we
162 documented at the scale of the archipelago (Martin et al. 2010; Chollet et al. 2015, 2021a). Rocky
163 shorelines and areas exposed at low tide fringe the islands. On most islands, deer density was
164 estimated around 30 deer / km² (Daufresne & Martin, 1997; Martin et al., 2010; Stockton et al.,
165 2005) an estimate that has been repeatedly confirmed in the course of deer culls (Gaston et al.
166 2008a; Irvine & Thorley 2024).

167 **Table 1.** List of islands included in the study and their key characteristics. Risk hist. = Risk history; Deer:
 168 Y = present, N = absent; Island = island name; Hunting: Y = seasonal hunting, Y(cull) = repeated culls; N
 169 = no hunting; Predators: Y = present (wolves and possibly cougar and grizzly bear), N = absent; Veg. plots:
 170 figures = number of standardized plots on vegetation structure and composition, N = no standardized
 171 sampling; Behav.: Y = all behavioural data collected, N = none collected; Isotope = collection of bones for
 172 the stable isotope study (section 2.3.4.): Y = collected and analyzed, N = none collected; Reef <1997 =
 173 conditions on Reef prior to experimental culls; Reef >1997 = conditions after the culls that occurred
 174 between 1997 and 2008; * = Islands that provided data only for the study on stable isotopes (section 2.3.4).
 175 + = bones were sampled in the area of BC Central Coast between Yeo and Bella Bella.

176

Risk hist.	Deer	Island	Region	Area	Hunting	Hunting + Predators	Veg. plots	Behav.	Isotope
No-risk	N	Low	Haida Gwaii	9 ha	N	N	5	N	N
No-risk	N	South-Low	Haida Gwaii	13 ha	N	N	5	N	N
No-risk	N	Lost	Haida Gwaii	5 ha	N	N	5	N	N
No-risk	Y	East Limestone	Haida Gwaii	48 ha	N	N	10	Y	Y
No-risk	Y	Kunga	Haida Gwaii	395 ha	N	N	20	Y	Y
No-risk	Y	Faraday*	Haida Gwaii	308 ha	N	N	N	N	Y
No-risk	Y	Murchison*	Haida Gwaii	425 ha	N	N	N	N	Y
No-risk	Y	Reef <1997	Haida Gwaii	249 ha	N	N	22	N	Y
Risk	Y	Reef >1997	Haida Gwaii	249 ha	Y (cull)	N	22	Y	Y
Risk	Y	Graham	Haida Gwaii	6361 km ²	Y	N	20	N	Y
Risk	Y	Yeo	Coastal BC	95 km ²	Y	Y	7	N	Y ⁺



178

179 **Figure 1.** Map of the study area. Inset = localisation of Haida Gwaii and of Graham and Yeo islands in
 180 western British Columbia, Canada. Main map = location of the islands studied in the central east coast of
 181 Haida Gwaii, BC, Canada. Yeo = hunting and natural predators. © of map Gowgaia Institute.

182 Reef Island, devoid of hunting prior to 1997, was subjected to repeated and severe deer culls
183 between 1997 and 2008 (Chollet et al. 2016). From September 1997 to February 1999, over 80%
184 of the initial deer population was culled (Gaston et al. 2008b). Recent archipelago-wide genetic
185 analyses confirmed that these culls caused a severe population bottleneck and that the current deer
186 population of Reef Island consists of descendants from the handful of animals left after the culls
187 (Burgess et al. 2022a, 2022b, 2023). As local deer survival is typically less than 10 years (JLM et
188 al. unpubl.), most or all individuals involved in our study during 2011-2014 must have been born
189 after the initial culls. In 2014, Reef Island had a deer population of about 15 deer / km², thus an
190 estimated 30 to 40 deer present, representing about half of the pre-cull population, and a partially,
191 but dramatically, recovered understory vegetation (Chollet et al. 2016).

192 We also studied a portion of Graham Island (6,361 km²), the largest island of the Haida Gwaii
193 archipelago, where deer have been widespread since the early 20th century (Golumbia et al. 2008)
194 and have been exposed to human hunting ever since. Graham is also home to a population of black
195 bear (*Ursus americanus*) that sometimes prey on deer fawns (Mathews & Porter 1988; Ballard et
196 al. 2001). Deer densities on Graham have been estimated to exceed 13 deer / km² (Engelstoft 2001;
197 Engelstoft et al. 2008). Its forests are characterized by low vegetation cover in the understory [this
198 study and (Chollet et al. 2021a)].

199 Finally, we complemented the sites selected on Haida Gwaii with data on the vegetation from Yeo
200 Island (Table 1, Fig.1), situated about 15 km north of Bella Bella, close to the mainland of British
201 Columbia. Deer are native to Yeo and exposed there to predators such as wolves (*Canis lupus*)
202 (Darimont et al. 2007), black and brown (*Ursus arctos*) bears, and cougars (*Felis concolor*), and
203 to human hunting. Forestry operations occur in parts of Yeo and Graham islands but we restricted
204 our investigations to unlogged mature forests. We lack reliable estimates of current deer densities
205 for the coastal region. However, a modelling exercise analysing the relationships between habitat,
206 deer and wolves posited that, in the long term, a dense understory would be compatible with high
207 deer densities exposed to predation by wolves (Kirchhoff & Person 2008).

208 We thus had access to study sites varying in history of deer presence, in hunting history and in
209 deer exposure to large carnivores. On East Limestone, Kunga and Reef we also had access to 27,
210 23 and 8 marked deer respectively that we ear-tagged and GPS collared during a project that took
211 place from 2011 to 2013.

212 **Does vegetation cover and diversity vary with predation risk?**

213 To assess the links between the vegetation and predation risk, we compared the understory
214 vegetation among sites with different risk histories (Table 1). We used 3.6 m radius (50 m²)
215 vegetation plots (Table 1) to estimate the % cover of plant species in the 0 to 1.5 m vegetation
216 layer directly accessible to deer browsing for all islands, except Murchison and Faraday. Details
217 for Graham Island sites can be found in Chollet et al. (2021a) and for the other islands from Haida
218 Gwaii in Stockton et al. (2005). We grouped the plant species data into six groups: young conifers,

219 young deciduous trees, shrubs, ferns, forbs, and other herbaceous plants. We used a Principal
220 Component Analysis (PCA) on centered and standardized cover data in R (R-4.1.0) (Racine 2012)
221 [prcomp function in R (Team 2018)] to characterize variation in the cover of these plant groups in
222 the understory when deer are present or not and under different contexts of risk from hunters
223 and/or predators.

224 **Does deer fear vary with predation risk?**

225 To assess, quantify and compare deer behaviour in relation to risk history we studied deer Flight
226 Initiation Distance (FID), Distance travelled during flight (Dtravel), and deer response to bait and
227 traps in the different deer populations. We also compared deer diel activity patterns in relation to
228 risk by using activity data collected by automatic cameras.

229 **FID experiments** - FID (Flight Initiation Distance) is the distance at which an animal starts
230 moving away at the approach of what it perceives as a potential threat (Ydenberg & Dill 1986).
231 FID has been considered as a key method to disentangle the “economics” of anti-predatory
232 behaviour, as flight occurs where the decreasing value of remaining, and the increasing cost of not
233 fleeing, intercept (Cooper Jr 2008). According to Lima & Dill (1990) FID should, under equal
234 resource level, be shorter in safe areas, and longer in risky areas. We therefore used FID as a metric
235 of wariness, using the following protocol: once the observer detected an individual, it was
236 identified by means of its ear tag number or its morphological features. Then the observer walked
237 slowly and calmly (~2 km/hr) towards the deer, avoiding eye contact. The observer stopped
238 walking when the deer changed its initial behaviour and started moving away, but continued
239 observing the animal. We recorded and used as focal variables two distances: distance from the
240 observer at which the deer starts to move away (FID), and Distance travelled (Dtravel) by the deer
241 between its first location (when flight began) and its second location where it stopped moving
242 away and resumed (foraging) activity. We measured these distances by footstep lengths calibrated
243 in meters after each encounter. For deer native to Reef, FID data included deer moving out of sight
244 from the observer. In these four instances we recorded the distance to where it disappeared. This
245 led to a conservative estimate of Dtravel for such cases. To avoid the confounding effects of
246 pseudo-replication and deer habituation to the experiment, we discarded repeated measurements
247 on the same individual ~~during an encounter with an individual~~ and only considered the first FID
248 experiment done in a given sequence.

249 Data on FID was obtained on islands without risk (Kunga and East Limestone), and on an island
250 initially without risk but subjected to culling (Post-culls Reef). As the expression of fear can be
251 affected by resource availability (Cooper 2008) we created a translocation experiment by moving
252 six adult does from Kunga island, where they were not exposed to hunting and where the
253 understory was heavily browsed, to Reef Island, where heavy culling in the 1990s had created a
254 much denser understory. On Kunga, the translocated does had been box-trapped, marked and
255 collared as adults in 2011 and had been recaptured multiple times (5 to 21 times each) (Le Saout

256 et al. 2014a; Bonnot et al. 2016). Three of the six translocated animals had been subjected to five,
257 seven and 19 FID measures on Kunga in 2011 and 2012. We replaced their GPS collars before
258 their translocation to Reef in September 2013 where these animals settled among the local deer
259 born after the culls [(Burgess et al. 2022a, 2023) and M.A. Russello pers. com.]. In spring 2014,
260 five of the translocated animals were still present on Reef. We tested FID behaviours of
261 translocated and local deer in the same way as on Kunga.

262 We analysed the two distance variables for these deer samples with a linear model (lm function in
263 R) to fit the linear regression model with the distance variable (FID or Dtravel, both log₁₀
264 transformed to ensure normality) used as a response variable to compare treatments. We also
265 analysed, when feasible within deer samples, the effect of deer status (marked/unmarked), sex
266 (M/F) and age class (adult, young) as well as effect of year on FID and Dtravel. We used pairwise
267 comparisons of the linear models with the emmeans package in R which provided t-tests to
268 compare the effects of these variables on our distance variables within deer samples.

269 **Response to bait and traps** - Neophobia, an adverse reaction to novelty, is an important trait that
270 allows animals to minimize exposure to threats (Greenberg & Mettke-Hofmann 2001; Monestier
271 et al. 2017). Between 2011-2014, we looked at deer use of stations baited with apples and
272 quantified interest in this foreign food by using camera traps (RECONYX PC900) (Le Saout et al.
273 2015). We also used traps baited with apples to assess the propensity to get trapped as a proxy for
274 exploration behaviour in the presence of a foreign object. We baited each bait station daily with
275 1.5 to 2 apples unless weather impeded fieldwork. For trapping we placed one chopped apple
276 outside the trap entrance, and another one at the furthest end inside the trap near the trigger.
277 Depending on the requirements of each stage of the study, the cameras at bait stations were
278 programmed to acquire from ten to 99 pictures every time the motion sensors were triggered, with
279 a 1s intervals between pictures. A built-in infrared flash with no red glow allowed us to capture
280 images at night or under low light conditions. The following data were recorded: whether or not
281 the deer had been trapped (unmarked/marked); bait presence at the station (in case consumed by
282 previous visitors) (yes/no); bait consumption if bait present (yes/no); the time at the beginning and
283 end of a sequence. We also recorded if the deer investigated the ground area where the bait had
284 been before (if bait was absent, yes/no). In 2011 bait stations were monitored with automatic
285 cameras for 15 days on East Limestone (no-risk, 4 locations), 12 days on Kunga (no-risk, 4
286 locations) and 28 days on Reef (post-culls, 8 locations).

287 In the context of the translocation experiment we applied similar protocols on Reef in the spring
288 of 2014, using six bait stations distributed across five locations, and keeping them active for
289 fourteen consecutive days. We compared responses to bait and traps on Reef Island with the past
290 behaviour of these deer on Kunga and with the behaviour of the deer resident on Reef. No hunting
291 took place on Reef Island during the eight months the translocated animals spent there from
292 September 2013 to May 2014.

293 We recorded the tag identity of the marked individuals and identified unmarked individuals using
294 physical features such as antler shape, fur marks, scars etc. We used the recorded start time and
295 end time of a feeding sequence to compute the time a deer spent at a bait station when bait was
296 present. We considered time spent at a bait station with bait as a measure of bait friendliness (the
297 willingness to check and consume bait) as in Chamaillé-Jammes et al. (2014). We used an analysis
298 of variance on \log_{10} transformed minutes (aov and emmeans functions in R) to compare “time-
299 spent” among treatments and between marked and unmarked deer within a treatment. We analysed
300 in the same way time spent at bait stations where bait had been consumed during previous visits.
301 We also compared trapping rates between categories using a Welch two sample t-test in R and
302 analysed the propensity of individual deer to be trapped repeatedly.

303 **Daily activity rythms** - To assess diel activity (e.g., if risk from daylight hunters led to more
304 nocturnal feeding) we used the time recorded by automatic cameras in all deer observations
305 collected during a study on deer vigilance (Le Saout et al. 2015), and during our investigation on
306 the use of bait stations. We used the time recorded at the outset of each observation to assign
307 observations to day or night. We defined day as the period between civil twilight start (morning)
308 and end (evening) for that date, using Reef Island as the reference locality for civil twilights (time
309 difference with the two other localities is < 20s).
310 (<https://www.timeanddate.com/sun/@6118904?month=5&year=2011>). We compared the
311 proportion of day and night observations among sites with a Pearson’s Chi-squared test (R
312 function `chisq.test`).

313 **Does shoreline use by deer vary with risk or amount of understory vegetation?**

314 Because marine plants are enriched in ^{13}C compared to terrestrial plants (Balasse et al. 2005;
315 Richards et al. 2006; Schulting et al. 2008), the isotopic signatures of tissues from coastal
316 herbivores can be used to estimate the relative contribution of terrestrial versus marine plants in
317 their diet (DeNiro & Epstein 1978). Stable isotope ratios are expressed in the standard delta (δ)
318 notation, defined as parts per mil (‰) deviation from a standard:

$$319 \delta X = [(R \text{ in sample} / R \text{ in reference}) - 1] * 1000 (\text{‰})$$

320 δX gives the deviation between the samples’ isotopic ratio and the ratio obtained from an
321 international standard, “R in sample” is the isotopic ratio considered, in our case $^{13}\text{C}/^{12}\text{C}$ and
322 $^{15}\text{N}/^{14}\text{N}$. For Carbon, “R in reference” refers to the standard Pee Dee Belemnite (PDB).

323 $\delta^{15}\text{N}$ typically gets enriched by about 3‰ when going from one trophic level to the next. At the
324 consumer level the whole animal body $\delta^{13}\text{C}$ closely reflects its concentration in the diet but its
325 fractioning varies among tissues. Values of concentration gain vary from + 1.5‰ in muscle, to +
326 5‰ in consumer’s collagen tissue when compared to whole body values (DeNiro & Epstein 1978,
327 1981; Bocherens 1999; Kelly 2000; Bocherens & Drucker 2003; Camin et al. 2016).

328 To test our prediction that risk from hunters and/or predators could limit the use of the intertidal
329 areas for foraging, we analysed the proportion of stable isotopes of terrestrial plant or seaweed
330 origin in deer diets on different islands, using deer jaw bones from all the study populations, to
331 which we added bone samples available from Murchison and Faraday Islands, both hunting-free
332 islands (Fig.1 and Table 1). We obtained these bones either from hunting, or from deer that had
333 died from natural causes. On the larger islands (Kunga, Graham and the coastal area adjacent to
334 Yeo) we restricted bone collecting whether through hunting or other means to less than 1000 m
335 from the shoreline. We obtained 10 jaw bones from East Limestone, 12 from Kunga, 10 from
336 Murchison, six from Faraday, seven from pre-cull Reef, all without hunting, six from Post-culls
337 Reef, collected 10 years or more after the initial culls (2008 to 2014), 23 from Graham Island
338 (hunting), and 17 from the central coast district between Bella Bella and Yeo Island (hunting +
339 predators). We cleaned and dried bones in the field.

340 For comparison of isotopic composition, we also collected seaweed and plant material across sites.
341 For seaweeds we collected or had access to samples from one to thirty individuals of 41 seaweed
342 species (19 species of brown, 5 green, and 19 red) collected on Reef Island, Louise Island, and
343 Kunghit Island on Haida Gwaii, and on the coastal mainland. We preserved them according to the
344 protocols of Salomon et al. (2008). We also collected samples of 23 dominant plant species in
345 Laskeek Bay (Reef and East Limestone islands) and on the coastal mainland, including 4 species
346 of coniferous trees, 2 deciduous trees, 9 deciduous shrubs, 1 evergreen shrub, 5 ferns and 5 grasses.
347 We rinsed fresh samples in distilled water to avoid contamination, pre-dried them in the field-
348 camp cabin and fully dried them in the lab at 40°C for 24 hours.

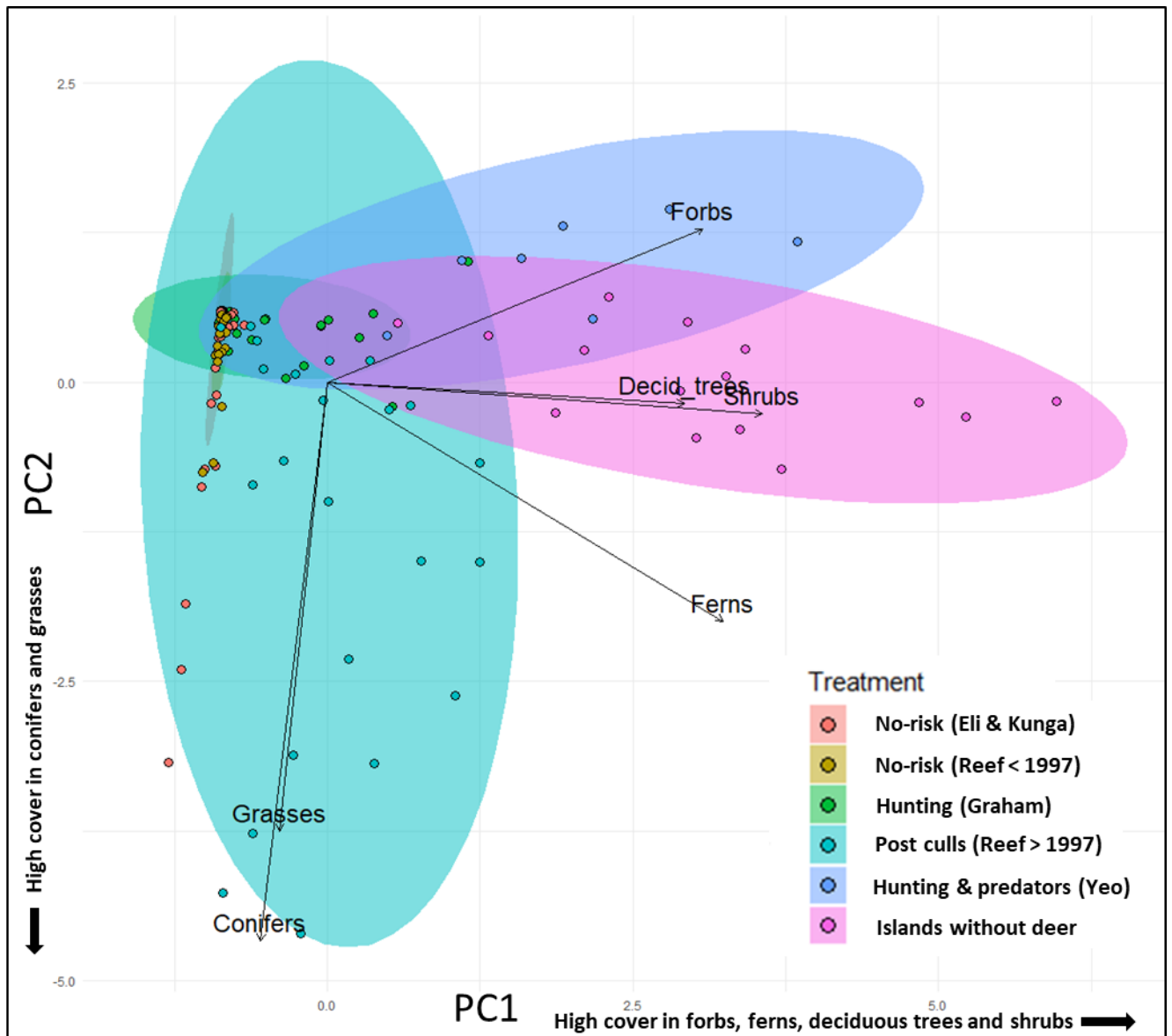
349 We ground dry bone and plant samples to a granulometry of less than 0.7mm. We followed
350 protocols defined by late F. Catzeflis based on DeNiro & Epstein (1981), Bocherens et al. (1988),
351 and Bochérens, Hervé et al. (1991) to extract bone collagen from bone powder in the laboratory.
352 We analysed the isotopic composition of the plant and collagen samples on CO² and N² obtained
353 by sample combustion and analysed on a mass spectrometer. On the basis of isotopic similarities,
354 plants, except conifers and the evergreen shrub Salal *Gaultheria shallon*, were combined in one
355 group (DecHerbs). All seaweeds had a similar, restricted spread of isotopic signatures and we
356 pooled them into a single group (Seaweed).

357 We analysed the isotopic ratios obtained for our samples using a Bayesian multiple source mixing
358 model (MixSIAR package in R) (Stock et al. 2018a, 2018b) which estimates the proportions of
359 source contributions (here terrestrial and marine plants) to a mixture (bones used as a proxy for
360 deer diet) (Bochérens and Drucker 2003).

361

363 Understory vegetation varied with risk history

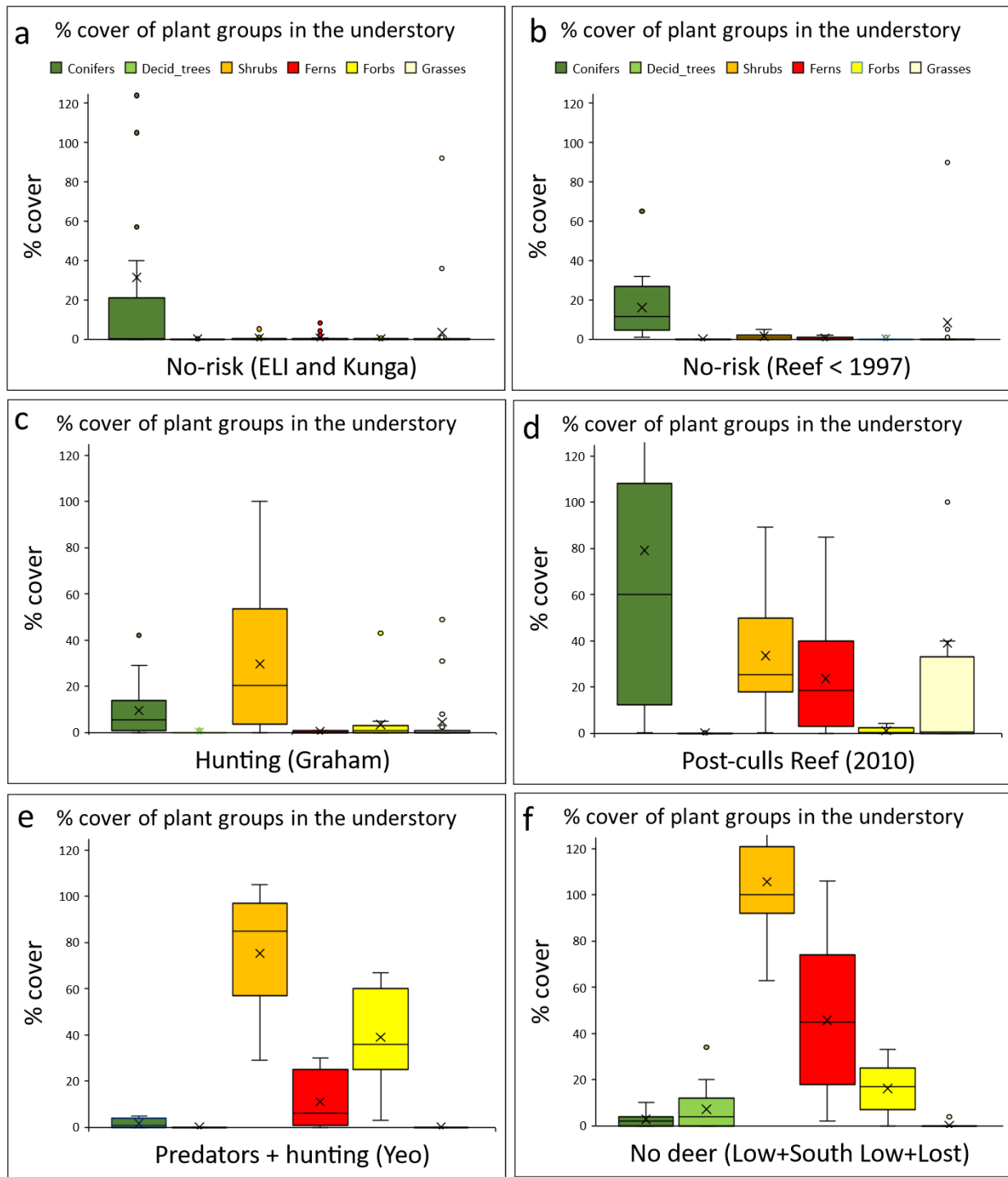
364 High vegetation cover and diversity was found on islands without deer and on those where deer
365 were present but exposed to predators and hunting (Figs. 2 and 3). Their understories were
366 dominated by forbs, shrubs, and ferns (Figs. 2 and 3). The samples from Reef Island (Post-culls)
367 showed an increase in cover and diversity after the culls, resulting in a large spread of plots. Most
368 had high vegetation cover in the understory (positive scores on PC1 and/or negative scores on
369 PC2), but their cover was dominated by conifer regeneration and grasses and some cover of ferns
370 and shrubs (negative scores on PC2 and low positive scores on PC1) (Figs. 2 and 3). Forests with
371 deer and no hunting (Reef Island prior to culls, Kunga and East Limestone), showed a stark
372 contrast with those from islands without deer or those where deer coexisted with hunters and
373 predators (small narrow ellipse along PC2, Fig. 2). Most plots had very low plant cover and
374 conifers were the only plant group with significant cover (Fig. 3): plots clustered around low cover
375 values for all understory plant groups (low negative scores on PC1 and low positive scores on
376 PC2, Fig. 2). Only three plots from pre-cull Reef and eight from the other islands without hunting
377 had high plant cover (negative scores along PC2, Fig. 2) consisting of conifer regeneration (spruce
378 and hemlock) (Fig. 3). The samples from Graham Island, where yearly moderate hunting has
379 occurred for over a century, were also dominated by plots with low plant cover in the understory
380 (Fig. 2) but had, in addition to conifer cover, more shrub cover and measurably more cover of ferns
381 and forbs in their understory than plots from the smaller islands without hunting (Fig. 3), hence
382 their higher spread along PC1 (Fig. 2).



383

384 **Figure 2.** Scores of the vegetation plots on the two first components of the Principal Component Analysis
 385 on understory vegetation cover below 1,5m. PC1 and PC2 summarize 37 and 19% respectively of the
 386 variance. Treatments were color coded post-analysis: orange = No-risk East Limestone and Kunga island
 387 samples, kahki = No-risk sample from Reef island before the cull (<1997), green = long history of yearly
 388 hunting (Graham island); blue = risk in the recent past through culls (Reef >1997), purple = hunting and
 389 deer predators (Yeo island), pink = reference islands without deer (Low, South Low and Lost islands). The
 390 dots refer to the actual coordinates of each plot. The ellipses are the most parsimonious graphical
 391 interpretation of the spread of plots in each sample.

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Figure 3. Percent cover recorded in the 0 to 1.5 m strata for the main understory plant categories in the different treatment categories. The vertical scale has been limited to 125% at the expense of a small number of outliers for conifers on graph 3d, and shrubs on graph 3f. Dark green = conifers, light green = deciduous trees, orange = shrubs, red = ferns, bright yellow = forbs, light yellow = grasses.

400 **Deer fear varied with predation risk**

401 **Flight initiation distance** - We ran FID assessments on the seven deer treatments during four
402 field seasons from spring 2011 to spring 2014. Most took place in 2011-2012. We retained 218
403 FID events: 73 from Kunga, 133 from East Limestone, both without risk, and 12 from Post-culls
404 Reef. We had no FID data for Graham and Yeo or for Reef prior to 1997. We recorded 19 FID
405 observations for the Kunga deer eight months after their translocation to Reef Island.

406 Values did not differ significantly among years within samples ($p = 0.60$). Nor did sex or age have
407 any effect ($p = 0.30$, $p = 0.62$ respectively). Thus we combined sexes, ages and years.

408 FID varied significantly among treatments [$R^2 = 0.38$, $F_{(3, 233)} = 49.28$, $p < 0.001$] (Fig. 4a). FID
409 was lowest for islands without hunting and highest for Post-culls Reef. Among the islands without
410 hunting, FID was lowest on East Limestone and highest for Kunga deer translocated to Reef (Fig.
411 4a).

412 Samples from No-risk East Limestone and from Post-culls Reef included marked and unmarked
413 deer. Differences in FID between marked and unmarked deer were non-significant [for East
414 Limestone t -ratio = 1.85, $p = 0.07$ (6.9 versus 5.5 m); for Reef island t -ratio = 0.95, $p = 0.34$ (36
415 versus 23.6 m)].

416 **Distance travelled** - Dtravel varied significantly among treatments [$R^2 = 0.18$, $F_{(3, 229)} = 18.04$, p
417 < 0.001]. Deer from populations without hunting travelled significantly shorter distances than deer
418 on Reef after the culls (Fig. 4b). Dtravel on East Limestone Island was significantly shorter than
419 on Kunga Island ($p = 0.01$), and much shorter than on Post-culls Reef Island (Fig. 4b; $p < 0.001$).
420 Dtravel distances for Kunga deer translocated on Reef did not differ from those on Kunga ($p =$
421 0.96), or from Dtravel observed on East Limestone ($p = 0.12$) and was only one third that of native
422 Reef deer ($p < 0.001$) (Fig. 4b). On East Limestone, marked deer moved significantly further than
423 unmarked deer [t -ratio = 2.20, $p = 0.03$, (6.7 m versus 4.9)] but this did not apply to marked and
424 unmarked deer on Reef [t -ratio = 0.17, $p = 0.86$ (41m versus 36.7)].

425 **Response to bait** – Risk category had a significant effect on time spent at bait stations when bait
426 was present (\log_{10} transformed): deer on islands without hunting and deer from Kunga translocated
427 to Reef, spent significantly more time at bait stations with bait than native Reef deer ($R^2 = 0.14$,
428 $F_{(3, 79)} = 4.29$, $p = 0.007$; Fig. 4c) and visited them five times more often (0.97 against 0.20; Fig.
429 4c, Table 2). Bait consumption per visit was three times higher on Kunga and East Limestone than
430 for native deer on Reef (75% against 20%) (Table 2). On East Limestone and Kunga marked deer
431 consumed bait in 50-80% of their visits in contrast to native deer on Reef, where only three of the
432 nine deer trapped and marked consumed bait at bait stations. None of the 14 unmarked deer
433 observed on Reef touched bait which they investigated briefly or ignored altogether (mean visit
434 length 24 s). Length of median values in time spent on a station, less affected by outliers, exceeded
435 3 min for deer on Kunga and East Limestone but was less than 30 s for native Reef deer.

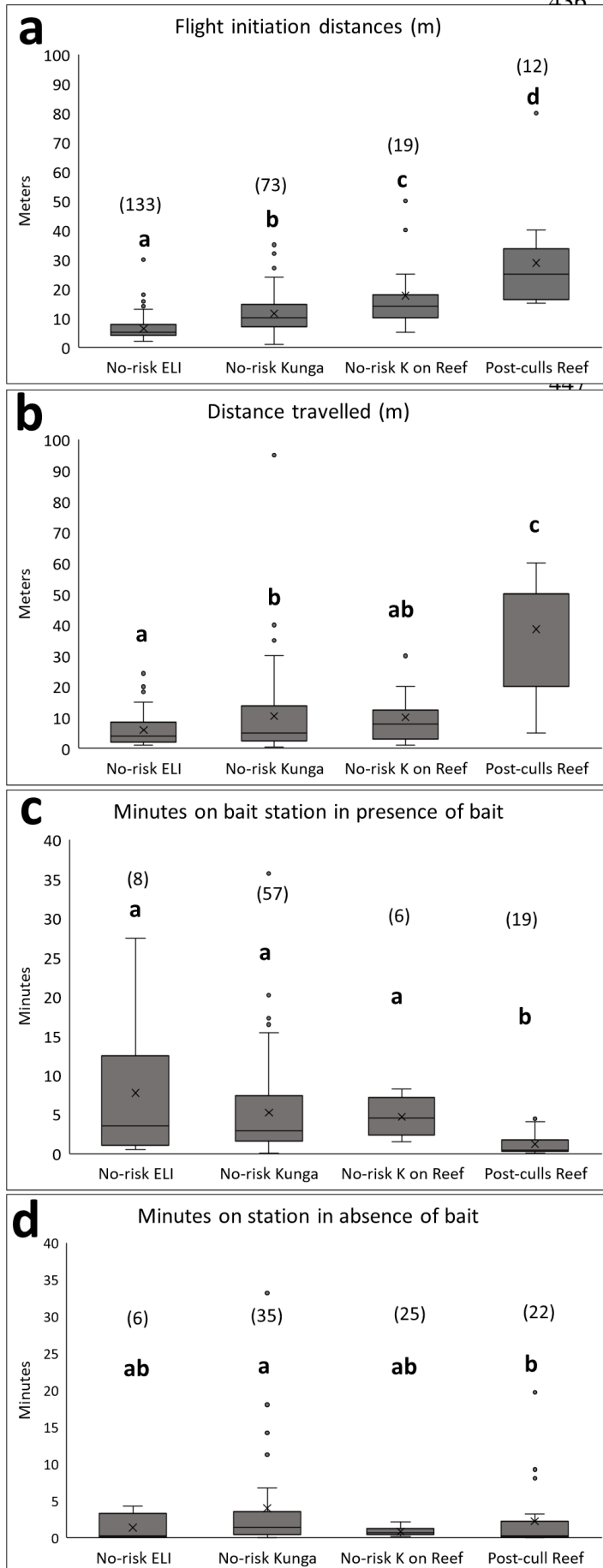


Figure 4. Boxplots on Flight and travel distance and on time spent at bait stations with bait present or absent. No-risk ELI = East Limestone deer, No-risk Kunga = Kunga deer on Kunga Island, No-risk K on Reef = Kunga deer after translocation to Reef Island, Post-culls Reef = Reef Island deer born into a population that survived the 1997 to 2008 culls. X in box = mean value, solid line in box = median value. Letters indicate results of post-hoc tests on the linear regression model on FID (\log_{10} transformed) as a function of deer categories. Numbers between parentheses = sample sizes.

a. Flight Initiation Distance (FID). All pairwise comparisons were significant: most had p -values < 0.001 except No-risk Kunga – No-risk K on Past culls Reef ($p = 0.02$) and No-risk K on Post-culls Reef – Post-culls Reef ($p = 0.03$).
b. Distance travelled after flight initiation (Dtravel). For Post-culls Reef median = 50 m. All pairwise comparisons were significant except for No-risk ELI – No-risk K on Reef ($p = 0.12$) and No-risk Kunga – No-risk K on Post-culls Reef ($p = 0.96$). For the pairwise comparisons that were significant all p -values were < 0.001 except No-risk ELI – No-risk Kunga ($p = 0.01$).

c. Time spent at bait stations with bait present. All comparisons among No-risk categories were non-significant (p -values > 0.80). For the pairwise comparisons that were significant, all p -values were < 0.05 .

d. Time spent at bait stations by deer when bait was missing (consumed since station was re-provisioned). All comparisons among No-risk categories were non-significant (p -values > 0.50 , except for No-risk Kunga – No-risk K on Post-culls Reef ($p = 0.37$)). Only for the No-risk Kunga – Post-culls Reef comparison did Kunga deer spent significantly more time at stations with no bait left than did deer native to Post-cull Reef ($p = 0.04$).

478 At Kunga marked deer spent significantly more time at a station than unmarked deer (7.8 min on
 479 average against 5.6 minutes) (t-ratio of contrast estimate = 4.64, $p < 0.001$). Some unmarked
 480 animals visited a bait station without eating bait (mean visit length 54 s). Among deer native to
 481 Reef, marked individuals also spent longer at bait stations (t-ratio of contrast estimate = 3.00, $p =$
 482 0.004) and were the only deer consuming bait (mean visit length 3.0 minutes).

483 In absence of bait because of previous consumption visit length at a station were short (Fig. 4d
 484 versus Fig. 4c). They were longest on Kunga through the effect of outliers spending long periods
 485 at sites that had bait recently (Fig. 4d). Time spent at a station never exceeded 4 minutes and was
 486 spent sniffing at where bait had been present. On Reef, marked native deer spent significantly
 487 longer at stations without bait than unmarked native deer (means of 2.8min versus 0.13
 488 respectively) (t-ratio of contrast estimate = 4.0, $p < 0.001$). On No-risk Kunga, there was no
 489 significant difference between marked and unmarked deer in time spent at stations without bait
 490 (84 versus 90 s) (t-ratio of contrast estimate = 1.42, $p = 0.16$).

491

492 **Table 2.** Deer visits and use of bait stations with bait present in relation to island/hunting history category.
 493 Stations (days) = number of stations set up and number of days each was active; Visits = total number of
 494 photographic sequences a deer was captured on camera at a bait station; With bait = number of visits when
 495 bait was present; Eat = number of visits in which bait was consumed when present; Mean length (median)
 496 = mean value of a visit duration in minutes and the corresponding median value; Without bait = number of
 497 visits when bait was absent (= consumed during visits that followed the re-provisioning of the station);
 498 Deer = total number of different individuals involved in the experiment; Marked = number of marked
 499 individuals among the total number of different individuals involved.

Island/hunting history	Stations (days)	Visits	With bait	Eat	Mean duration (median)	No bait	Mean duration (median)	Deer	Marked
East Limestone (2011) No-risk	4 (15)	14	8	7	7.7 (3.5)	6	1.4 (0.3)	3	3
Kunga (2011) No-risk	4 (12)	91	56	42	5.2 (2.9)	35	4.0 (1.4)	28	7
Kunga on Reef (2014)	5 (16)	31	6	6	4.7 (4.5)	25	0.9 (0.6)	5	5
Native Reef (2011) Post-culls	8 (35)	9	6	0	1.2 (0.4)	25	2.25 (0.3)	18	4
Native Reef (2014) Post-culls	5 (16)	35	13	4					

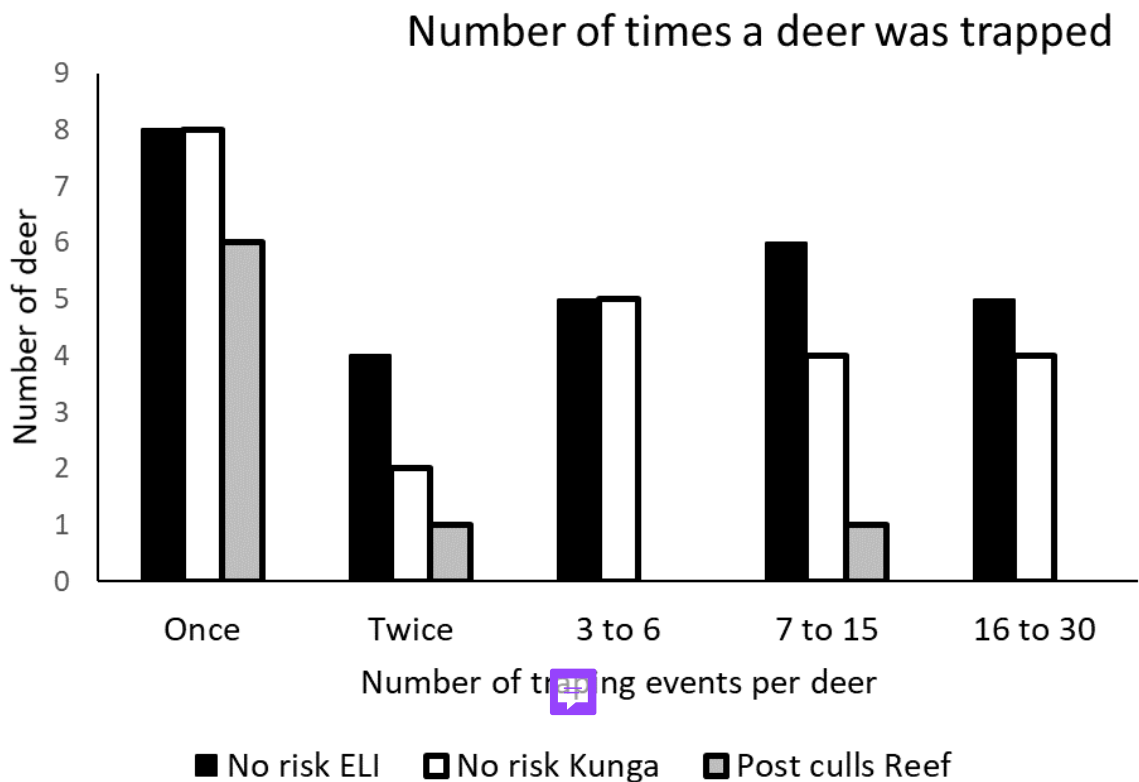
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501 **Response to traps** – On Reef Island (Post-culls) the capture rate was significantly lower than on
 502 islands without hunting ($p \leq 0.05$) (Table 3). On Reef only 2/8 deer were captured more than once,
 503 compared to 35/51 for the No-risk islands, with a majority of individuals captured more than three
 504 times (Fig. 5).

505 **Table 3.** Summary of box-trap capture data of animals on their native island for all sessions. Captures +
 506 recaptures = total number of captures including multiple recaptures of individuals within a session.
 507 Adjusted for outliers = for deer recaptured over 5 times within a capture session (ranged from 6 to 23 times)
 508 we capped their recapture scores in the session at 5 to limit variance inequality. This adjustment was
 509 conservative as it reduced the contrast between the no-risk and risk categories. Significance in differences
 510 in **adjusted** rates: East Limestone versus Reef: $t = 3.31$, $df = 3.19$, $p = 0.04$; Kunga versus Reef: $t = 2.84$, df
 511 $= 3.71$, $p = 0.05$; East Limestone versus Kunga: $t = 1.06$, $df = 3.50$, $p = 0.17$.

Island	Years	Effort boxes*days	Nb. Deer captured	Captures+recaptures		Adjusted captures
				All	Adjusted for outliers	Trapping rates deer/box*day/year
East Limestone	2011- 2013	494	27	207	140	0.30±0.13
Kunga	2011- 2013	591	23	150	102	0.16±0.07
Reef post culls	2011- 2013	664	8	23	18	0.04±0.02

512



513

514 **Figure 5.** Summary of the capture and recapture histories for the deer native to the three sites and two
 515 categories of hunting histories. ELI = East Limestone Island.

516

517

518 **Diel activity pattern** - Between 2011 and 2014 we recorded 762 (Table 4) picture sequences of
 519 deer on automatic cameras. We used the time recorded on the first picture in a sequence to assign
 520 the sequence to day time or night time. These pictures were taken in spring and early summer,
 521 hence a period of the year of long days and short nights. Deer were more active by day than by
 522 night (Table 4). There was no significant difference in daily activity patterns between East
 523 Limestone and Kunga islands (Chi-squared = 0.29, df = 1, p = 0.59) but deer native to Reef post-
 524 culls were more nocturnal than either (Chi-squared = 10.38, df = 1, p = 0.005). There was no
 525 significant difference in diel activity between marked and unmarked deer either on Reef or Kunga
 526 (Chi-squared = 0.05, df = 1, p = 0.81).

527
 528 **Table 4.** Distribution of deer observations by automatic cameras across sites and their assignment to day
 529 or night with day defined as the period between start of civil-twilight in the morning and end of civil-
 530 twilight in the evening. Night was defined as the period between civil twilight end and civil twilight start
 531 the following day.

Island/hunting history	N	day	night	% at night
No-risk East Limestone	289	256	33	11%
No-risk Kunga	358	311	47	13%
Post-culls Reef	115	88	27	24%

532

533 **Shoreline use by deer varied with risk and forest understory vegetation**

534 The following diagnostic and tests confirmed that our Markov Chain Monte Carlo (MCMC) chains
 535 converged in the MixSiar model. The Gelman-Rubin Diagnostic run after the MixSiar model
 536 indicated that only 2 of the 140 variables exceeded marginally the threshold value of 1.01. The
 537 Geweke diagnostic, a standard z-score to assess if less than 5% of the 140 variables were outside
 538 the +/-1.96 values in each chain indicated 3%, 5% and 1% for chains 1, 2 and 3 respectively.

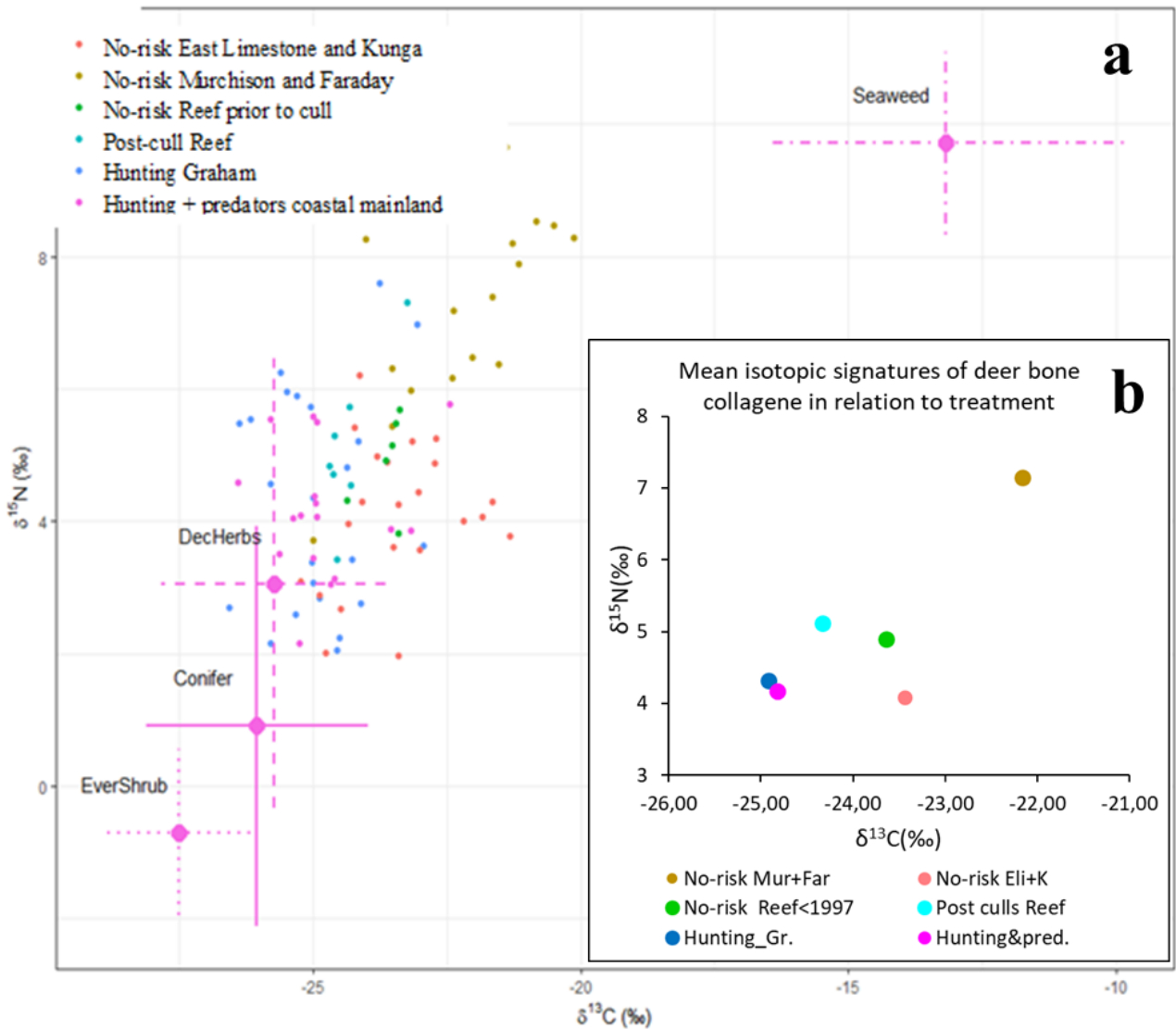
539 On the isospace plot (Fig. 6) the isotopic signature in deer bone samples were distributed in
 540 relation to the proportion of seaweeds in deer diet relative to terrestrial plants. Samples from the
 541 no-risk islands had a higher proportion of seaweeds in deer diet than samples from sites with a
 542 risk history (Fig. 6b). The samples from Murchison and Faraday showed the highest mean
 543 proportion of seaweeds, those from Graham and from the BC Central Coast, where hunting and/or
 544 predators occurred, the lowest (Fig. 6b). Among the terrestrial plant groups the cluster which
 545 included deciduous trees and shrubs, ferns, forbs and grasses, made up the highest proportion in
 546 deer diets. Conifers came next and salal last.

547 The MixSIAR analysis quantifies the proportion of the four plant categories in deer diets in the
 548 samples (Figs. 6 and 7). Bayesian 95% credible intervals (Fig. 8) allow us to estimate the
 549 significance of differences in the proportion of seaweeds between the samples. Credible intervals

550 from the samples without predation (Murchison, Faraday, East Limestone, Kunga and Reef before
551 the culls) do not overlap with those of the two sites with hunting and/or predators (Graham and
552 BC Central Coast). The credible interval of the Post-culls Reef sample was intermediate.

553 The proportion of seaweed in deer diets reached 31% on Murchison and Faraday, and 19.2% on
554 sites in Laskeek Bay (East Limestone, Kunga and Reef prior to the culls). It dropped to 8 and 9.6%
555 respectively in sites with hunting (Graham) or with predators and hunting (BC Central Coast). On
556 Reef after the culls the proportion of seaweed in diet (13.5%) was intermediate between the no-
557 risk and the values for the hunting or predators+hunting samples (Figs. 7 and 8).

558 The proportion of the terrestrial plants in deer diets, which included deciduous trees and shrubs,
559 ferns, forbs and grasses varied from 67% on Murchison and Faraday to 88% on Graham and on
560 the coastal mainland. Conifers and evergreen shrubs stand out as a minor component of diet. It
561 was always lower than 8% for conifers, despite their prevalence in the vegetation profiles of some
562 of our study sites (Fig. 3). The proportion of salal (evergreen shrub) never exceeded 4% in the
563 diets.



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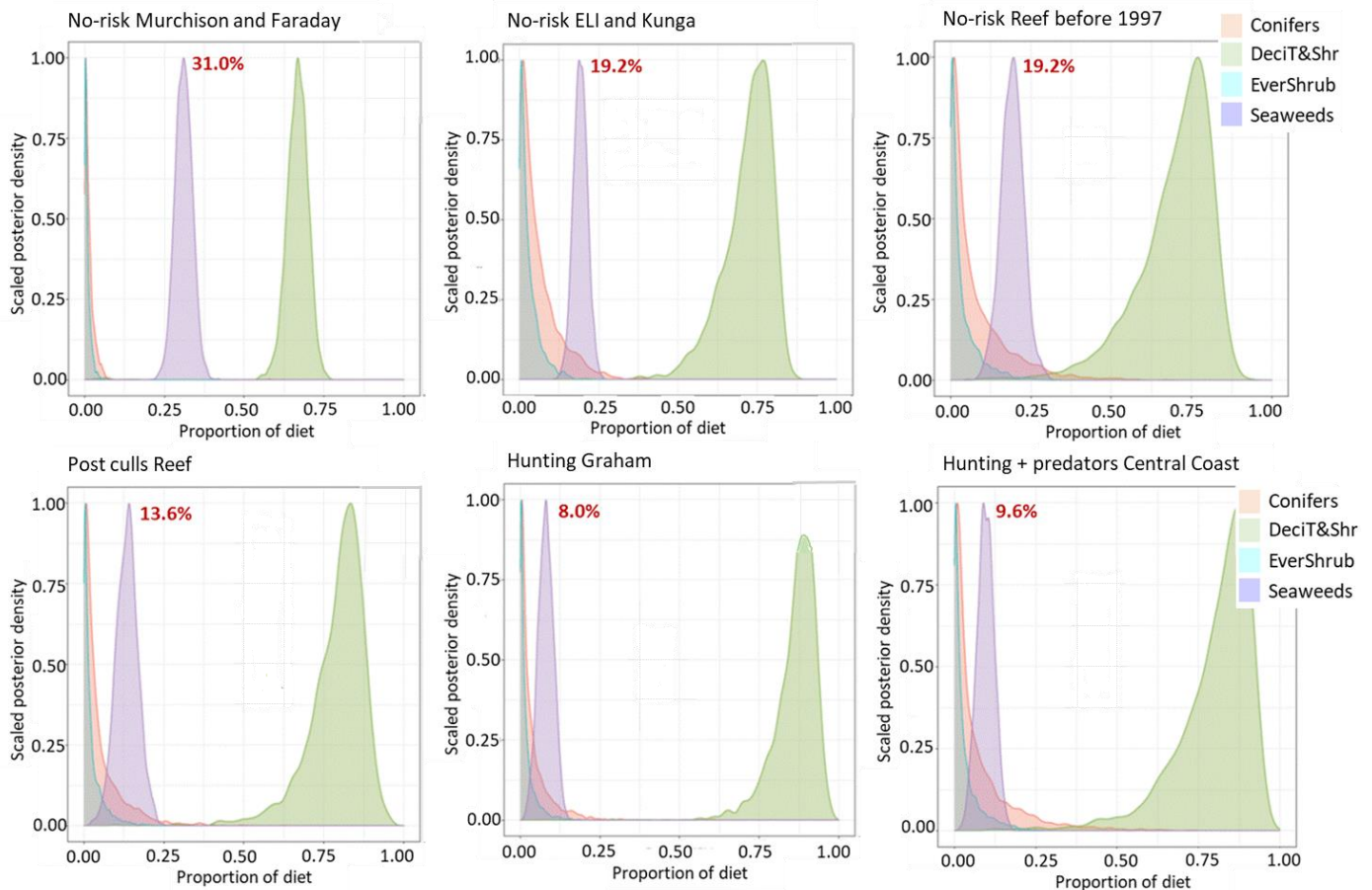
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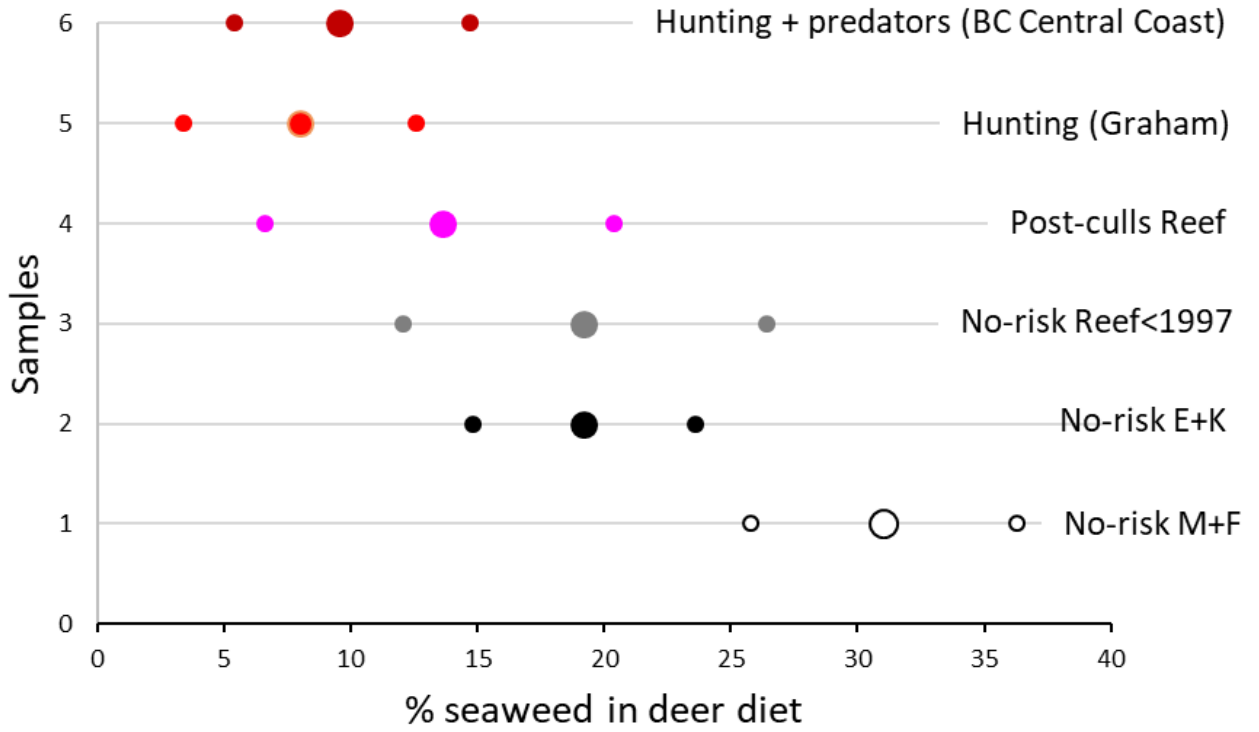
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Figure 6. Isospace plots of deer bone collagen and plants. Mixture data by risk category and islands. No-risk Murchison and Faraday = No-risk samples from Murchison (N=10 bone samples) and Faraday (N = 6); No-risk samples from East Limestone (N = 10) and Kunga (N = 12); No-risk samples from Reef Island prior to the culls (N = 7); Post-culls Reef = samples from Reef Island after the culls (N = 6); Hunting Graham = samples from Graham Island (N = 23); Predators + hunting = samples from the BC Central Coast (N = 17). Source data are by risk/island categories and have been adjusted by discrimination means and SDs. Terrestrial plants: EverShrub = evergreen shrub (Salal), Conifer = conifers, DecHerbs = deciduous trees and shrubs, forbs, ferns and grasses; Seaweed = Seaweeds (40 species). Error bars indicate 1 SD, the combined source+discrimination SD calculated under assumption of independence as: $\sqrt{\sigma_{source}^2 + \sigma_{discr}^2}$



577
 578 **Figure 7.** MixSiar posterior plots of overall deer diet in relation to predation risk. N = number of bone
 579 samples per site. No-risk history, four sites: Murchison (N = 10), Faraday (N = 6), East Limestone (ELI)
 580 (N = 10), Kunga (N = 12) and Reef before the culls (N = 7)) (see map in Fig. 1); Post-culls Reef = samples
 581 from Reef Islands collected after the culls (2008-2014) (N = 6); Graham Island coastal area = yearly
 582 relatively low intensity hunting without marked effect on high deer density (Engelstoft, 2001) (N = 23);
 583 BC Central Coast, hunting and predators (N = 17). All profiles are at the same scale. Murchison and Faraday
 584 are two islands with vegetation poor understories [see text and Martin, Gaston & Hitier (1995)]. The peaks
 585 of the shaded areas represent the median estimate of the proportion of the different sources in deer diet.
 586 Conifers (Sitka spruce, western hemlock, western redcedar, and yeellow cypress *Chamaecyparis*
 587 *nootkatensis*) (pink shading) (4 species, 13 samples), evergreen shrubs (light blue shading) [1 species
 588 (salal), 4 samples], green shading = deciduous trees and shrubs, forbs, ferns and grasses) (27 species, 86
 589 samples). Seaweeds (purple shading) (40 species, 237 samples). Red figures indicate median percent value
 590 for seaweeds).

Bayesian 95% credible intervals for seaweed proportions



591
592

593 **Figure 8.** 95% Bayesian credible intervals of the 50% quantile (large central dots = median proportion of
594 seaweeds in diet) as provided by the 2.5% and 97.5% quantiles (small dots). M+F= Muchison + Faraday
595 islands; E+K = East Limestone + Kunga islands.

597 How did understory vegetation cover and composition change with predation risk?

598 Our results illustrated the well-established effect that large herbivores can have on forest
599 vegetation cover (Côté et al. 2004; Martin et al. 2010, 2011; Cardinal et al. 2012; Chollet et al.
600 2013, 2021a; Waller & Reo 2018). They also illustrated the relationship between the level of
601 impact on the vegetation and the risk history a deer population has been exposed to (Callan et
602 al. 2013; Waller & Reo 2018). The severe culls on one of our sites (Reef Island) resulted, over
603 a decade, in an upsurge of understory vegetation and regenerating conifers in an initially
604 heavily-browsed open understory (Figs. 2 and 3), combined with an increase in diversity
605 among plots [(Fig. 2 and Chollet et al. (2016)]. However, there are intrinsic differences between
606 this recovering understory vegetation and the understory vegetation we sampled on Yeo Island
607 where deer have always been subject to their natural predators in addition to hunters. On Reef,
608 the high proportion of regenerating conifers in the understory following the culls resulted from
609 the release of heavily browsed dwarfed spruce and hemlock (Chollet et al. 2016), while the
610 high cover of grasses resulted from a rapid colonisation of bare ground (Chollet et al. 2016).
611 By contrast, the vegetation profile we observed in the presence of large carnivores and hunting
612 on Yeo was remarkably similar to the understory vegetation profile we observed on three
613 islands in Laskeek Bay never colonized by deer [see details in (Stockton et al. 2005, Martin et
614 al. 2010)]. Their understories lack the significant cover of conifer regeneration we observed on
615 Reef after the culls and are dominated by shrubs and forbs (Fig. 3).

616 On Graham Island, where hunting is of low intensity and restricted to sites most accessible to
617 the small local population of hunters (Martin and Baltzinger 2002), the diversity of cover
618 among plots (spread of plots, Fig. 2) and the amount of shrub cover (Fig. 3) was higher than
619 on No-risk islands but understory vegetation overall was still closer to the one observed on No-
620 risk islands [for more details on the understory vegetation on Graham see (Engelstoft 2001;
621 Engelstoft et al. 2008; Chollet et al. 2021a)]. This variation suggests an interplay among the
622 presence of risk, its intensity, its nature (natural predators present or not) and its duration in the
623 interaction between deer and their habitat.

624 Does absence of risk favor boldness and deer impact on the vegetation?

625 Our comparison between populations that had not been exposed to any risk (East Limestone
626 and Kunga), with a population on Reef subjected, over a decade prior to the study, to a severe
627 population reduction through culling, revealed clear behavioural contrasts. In absence of risk
628 deer were easy to trap and unwary of people. They also willingly consumed foreign food at
629 bait stations, and foreign food when associated with an unfamiliar object (trap). The
630 significantly shorter flight initiation distances, and much shorter distances travelled, observed
631 in non-hunted populations were retained by the Kunga deer translocated to Reef, even though

632 they showed slightly longer flight initiation distances in their novel environment. This was in
633 stark contrast with the wary behaviour of the native deer on Reef after the culls, even more so
634 as the flight and movement distances we recorded for the Reef deer were conservative: they
635 often fled before being seen (heard running) and others were still running when they
636 disappeared from view. As a result, actual values on Reef may have been closer to values
637 reported for black-tailed deer populations on the mainland (FID ~ 60 to 70 m and Dtravel ~ 70
638 to 120 m), where deer can be subject to hunting and carnivores (Stankowich & Coss 2006,
639 2007; Stankowich 2008). Our field notes also indicated that native deer on Reef ran or trotted
640 away, whereas deer from Kunga, even after translocation, and East Limestone (No-risk islands)
641 usually performed a slow walk to a nearby location where they resumed their activities. On
642 East Limestone, FID and distances travelled were significantly shorter than on Kunga, possibly
643 reflecting some habituation to human presence (Rodriguez-Prieto et al. 2009; Schuttler et al.
644 2017) on East Limestone Island, where people are present daily for two to three months each
645 summer for ecological monitoring.

646 Despite minor differences in flight distances or time spent at bait, marked and unmarked deer
647 of the same population had comparable flight initiation behaviours. Marked and unmarked,
648 deer from Reef born after the culls were predominantly shy, as their poor trapping rate
649 illustrated, even when we take into account that deer densities on Reef at the time of study were
650 still at only 50% of their pre-cull density (originally ~30 deer/km², i.e. >80 deer present; Chollet
651 2012). Only two (25%) of the eight deer captured on Reef were ever re-captured, and only one
652 was recaptured repeatedly, mostly as a yearling and a juvenile, before becoming trap shy in the
653 following years while still captured on cameras. This contrasts with deer unexposed to risk on
654 East Limestone and Kunga. A significant proportion of the local deer were trapped, and over
655 half of them re-trapped three times or more over the years (Fig. 5). The presence on Kunga and
656 Reef of a fraction of animals never trapped, but captured on automatic cameras, indicated that
657 within each population there was variation in trap-shyness among individuals (Sih et al. 2012).
658 Overall, observed differences in behaviour between deer native to East Limestone and Kunga
659 and those native to Reef after the culls, suggest that culling shifted the dominant behaviour
660 profiles of Reef Island deer towards the shy-end of a boldness-shyness continuum.

661 Food limitation and nutritional status have been proposed as mechanisms explaining individual
662 attenuation in antipredator behaviours such as flight response (Stankowich 2008; Gaynor et al.
663 2019). If so, we expect these behaviours to be reversed once food supply improves. Could a
664 better food supply in the lush understorey on Reef after the culls explain the higher values of
665 FID and Dtravel for deer native to Reef, and would the apparent paucity of resources in the
666 heavily browsed understories of East Limestone or Kunga explain the apparent lack of fear in
667 their deer? This seems unlikely, given that we did not observe any significant change in the
668 behaviour of the deer translocated from Kunga to Reef (Fig. 4). Our observations rather suggest
669 a more indirect link between behaviour and resources, a link mediated by risk. Following the

670 reasoning of Kirchhoff & Person (2008) we assumed that ~~in~~ the absence of risk-intensive
671 browsing would over time decrease the per capita availability of forage as well as the average
672 quality of the diet. A reduction in anti-predator behaviour could be the necessary condition to
673 allow increased foraging time in response to this progressive erosion of standing plant biomass
674 and forage quality in an increasingly browsed understory. In these understories, resources,
675 although sufficient to sustain a dense deer population (Stockton et al. 2005; Le Saout et al.
676 2014a), are increasingly found in small increments of emerging vegetation or as subsidies
677 fallen from the canopy (Le Saout et al. 2014a). Indeed, on No-risk islands less than 5% of the
678 resources needed by these dense deer populations were provided by the rare standing biomass.
679 The bulk was provided equally by the cryptic flux of growing vegetation and by canopy foliage
680 fall, supplemented by seaweeds from the shorelines (Le Saout et al. 2014a).

681 Our results from the stable isotope analysis are another illustration of the focus deer have to
682 put on cryptic vegetation elements in the understory. On one hand conifers, the dominant
683 element in the understory of No-risk sites (Fig. 3), make for only a tiny proportion of their diet
684 (Fig. 7), whereas deciduous vegetation, a known preference in black-tailed deer diet (Taylor
685 1956; Pojar 1999), make up the bulk of their diet (Fig. 7), its negligible presence as standing
686 biomass (Fig. 3) compensated by short lived emerging vegetation (Le Saout et al. 2014a). This
687 need to feed on spatially dispersed food, occurring as small items, could be the ecological
688 context forcing the emergence of populations expressing less anti-predator behaviours (Réale
689 et al. 2010; Sih et al. 2012), or with less costly adjustments of spatial distribution in response
690 to perceived distribution of risk (Williams et al. 2008; Gaynor et al. 2019). Such behavioural
691 shifts could, in turn, help deer intensify their foraging pressure and, over time, aggravate the
692 loss in understory standing vegetation, as was actually shown on these islands between 1989
693 and 2009 (Chollet et al. 2015). This could further increase the shift towards bolder behaviours.
694 The overall predominance of diurnal activity in East Limestone and Kunga deer compared to
695 populations exposed to hunting (Bonnot et al. 2016) can also be interpreted as a change in
696 favour of increased foraging time. This more diurnal behaviour has been shown to contrast
697 with the more nocturnal behaviour commonly observed in hunted populations (Altendorf et al.
698 2001; Bonnot et al. 2016, 2020; Palmer et al. 2022). However, anti-predator behaviours less
699 costly in foraging time such as routine vigilance would be retained and not counter-selected as
700 was actually observed for the populations of East Limestone and Kunga where routine
701 vigilance persisted in an otherwise unwary population. (Chamaillé-Jammes et al. 2014; Le
702 Saout et al. 2015).

703 On Reef, after the first few days of culling, every animal remaining was much shyer than the
704 animals observed pre-cull (AJG and T. Husband pers.com), showing that at least some animals
705 in the pre-cull population, previously never hunted and living in a heavily browsed habitat for
706 more than 50 years (Martin et al. 1995; Vila et al. 2004a; Chollet et al. 2016), had retained the
707 ability to respond to a new threat [see also Chamaillé-Jammes et al. (2014)]. A study on the

708 effects of low intensity and simulated hunting (Le Saout et al. 2014b) on the behaviour of deer
709 on Kunga also documented the presence within the local deer population of individual
710 personalities differing in their ability to respond to a threat. Some animals were easily seen and
711 trapped, and showed little or no response to simulated hunting or to being trapped, whereas
712 some animals were only observed through automatic cameras, were never trapped and shifted
713 their habitat use away from the area exposed to simulated hunting.

714 On Reef, at the time of this study, the animals born several years later, offspring of those that
715 survived the culls, were much shyer than those seen on Reef prior to the cull (AJG pers. obs.).
716 These animals also had a tendency to be more active at night than deer on Kunga and East
717 Limestone never exposed to hunting or to culls. The survivors on Reef may have included
718 animals that modified their behaviour more rapidly and more radically than those that were
719 killed. If some or all of that variation in behaviour was under genetic control (Réale et al. 2007),
720 subsequent generations will have been shyer than the pre-cull population as a result of
721 differential survival of shyer personalities during the culls. The consequent persistence of
722 increases in FID, Dtravel, novelty aversion and nocturnal foraging would have been inherited
723 or adopted by young reared subsequently, so that the behaviour of the current population
724 resembles that of populations subject to natural predation and human hunting. Rapid
725 differential selection of heritable antipredator behaviours in response to novel predation were
726 documented recently (Moseby et al. 2023). Conversely, there is little sign that the deer trapped
727 and translocated from Kunga Island and hence never exposed to predation threat, adopted any
728 of the modified behaviour of the local post-cull deer despite the better foraging resources.

729 **Did risk affect the use of habitats?**

730 The lower proportion of seaweeds in diets at sites with predators and/or hunters seems to
731 validate our prediction that deer would make less use of exposed shorelines where they face
732 predation from hunters and/or wolves. But, as the amount of standing vegetation in the
733 understories tends to be much lower at sites without hunting (Fig. 3) it could be the lack of
734 forage in the understories of No-risk islands that encouraged deer to forage in the intertidal.
735 On Murchison and Faraday, where seaweed is especially prominent in the diet, the very open
736 understories below dense secondary canopy, supported very little ligneous and herbaceous
737 vegetation cover in the 0 to 1.5 m layer (<4%, Martin et al. 1995).

738 However, the two situations with the lowest and similar proportion of seaweed isotopes in
739 jawbone collagen, Graham and Yeo Islands, differed in their cover of standing understory
740 vegetation. On Yeo, the permanent presence of predators and hunting was associated with a
741 lush understory. On Graham, the long history of moderate hunting, restricted to areas most
742 accessible to a small number of hunters (Martin and Baltzinger 2002) had limited impact on
743 deer density (Engelstoft 2001; Engelstoft et al. 2008), resulting in understory cover closer to
744 that at No-risk sites than to that at sites on the BC Central Coast (Figs. 2 and 8) (Pojar 1999;

745 Chollet et al. 2021a). This partial decoupling of understory vegetation cover and proportion of
746 seaweeds in deer diet remains suggestive that risk history on a site can negatively affect deer
747 propensity to feed on shorelines. This would be consistent with the documented high use of
748 shorelines by foraging wolves and its negative consequence on their use by deer (Klein 1995).
749 It would also be consistent with the documented increased reluctance in deer to use more
750 exposed habitats or localities when risk is higher (Williams et al. 2008; Bonnot et al. 2017).

751 **What lessons for ecology, population behavioural change and conservation?**

752 Our research contributes to the limited number of studies that connect animal behaviour with
753 ecological dynamics, species interactions, population changes and ecosystems [see (Sih et al.
754 2004, 2012; Réale et al. 2007; Chitwood et al. 2022)]. We show that the introduction of a new
755 threat, such as hunting on Reef Island, led to a sudden change in behaviour. This change left
756 the survivors exhibiting behaviours that were significantly different from those of animals on
757 islands without hunting.

758 Our findings support the hypothesis that shifts in the “ landscape of fear” (Gaynor et al. 2019;
759 Palmer et al. 2022) can change the behavioural traits of a population. These changes may occur
760 in response to intense selective pressures on particular behavioural traits caused by immediate
761 risk (e.g. as in the case of severe culling), or, over longer periods of time, from the progressive
762 reproductive advantage of behavioural profiles better adapted to a changing environment (e.g.
763 a progressive increase in boldness driven by a progressive depletion of resources in absence of
764 acute predation risk). Vourc’h et al. (2001, 2002) documented similar shifts in population
765 profiles in redcedars exposed or not to browsing by deer on Haida Gwaii. Trees with low levels
766 of chemical defenses dominated in populations not exposed to browsing, while individuals with
767 high levels of defenses dominated populations exposed to deer. These defence levels were
768 under genetic control (Vourc’h et al. 2002; Vourc’h et al. 2002).

769 While our interpretation of the non-wary behaviours we observed on islands without predation
770 or hunting, or of the rapid shift towards shyness after the culls, remains speculative, it
771 highlights the possibility for behaviour selection. The speed of behavioural change will be
772 influenced by the intensity of the selective pressure (Blumstein 2002; Jolly et al. 2018; Moseby
773 et al. 2023). It can be rapid if severe culling continues over generations but may be slower in
774 the case of the relaxation of antipredator behaviours after the colonisation of a predator free
775 environment (Blumstein 2002). The evolution of predator naivety in island organisms provides
776 many classic examples of both gradual and rapid evolutionary changes in behaviour (Darwin
777 1840; Lack 1968; Blumstein 2002), but see Blumstein and Daniel (2005)..

778 Our results have implications for conservation. They can improve understanding of the
779 problems posed by the adjustment of focal species towards a novel threat, thus improving the
780 success of species restoration programs where naïve captive-bred individuals have to adjust to
781 predators on release (Moseby et al. 2015, 2016, 2023). They also provide insights into the

782 management of overabundant populations through hunting. In such instances, a better grasp of
783 behavioural responses to management actions can help design strategies that take into account
784 the ability of species to adjust their spatial distribution and diel rhythms to the threat posed by
785 management measures (Williams et al. 2008; Potratz et al. 2024). A better understanding of
786 the ramifications of consequences triggered in prey by the return of their predators will also
787 help better address the challenges posed by high deer populations in parts of Europe and North
788 America to human activities, such as farming, livestock husbandry, forestry (Kuijper et al.
789 2013, 2016; Raynor 2017; Martin et al. 2020) or road safety (Gilbert et al. 2017; Raynor et al.
790 2021; Bell et al. 2024). Finally, by improving our understanding of mechanisms that lead to
791 evolutionary shifts, our results help to better predict the full impact of neglecting the integrity
792 of species assemblages. Hence, our evidence encourages the conservation and restoration of
793 fully functioning ecosystems.

794 **Ethical note**

795 All research was conducted under the appropriate animal care permits from the Wildlife Act
796 of the Ministry of Natural Resources Operation of British Columbia (No. NA11-68421,
797 approved by Parks Canada Animal Care Task Force research permit No. 9059), and under the
798 Archipelago Management Board of Gwaii Haanas National Park Reserve and Haida Heritage
799 Site research permit No. GWA-2011-8373. All except 3 deer captures were done using box
800 traps specially designed for this project (the exceptions were one individual captured by a
801 clover trap and two by a netgun). We made over 400 deer captures or recaptures in the course
802 of the project. Traps were radio-monitored remotely and we dealt with captured animal
803 immediately after capture notification. The animals captured at night were treated the following
804 morning. We recorded no injury to deer, nor mortality associated to capture. The project
805 permits included the experimental culls on one island and the translocation of a small number
806 of deer from one island to another. Culls were conducted by local hunters under clear ethical
807 and practical rules. Carcasses were processed and the meat distributed to the local
808 communities.

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828 **Data, scripts, code, and supplementary information availability**

829 <https://zenodo.org/me/uploads?q=&l=list&p=1&s=10&sort=newest>

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836 **Conflict of interest disclosure**

837 The authors declare that they comply with the PCI rule of having no financial conflicts of
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840

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