

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

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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 risk is key in shaping, and potentially selecting for,  
50 lasting behavioural contrasts between deer populations, contrasts intimately connected to deer  
51 effects on plant cover and diversity, ecological networks, and ecosystem complexity.

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53

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

## Introduction

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

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

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

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

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

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

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

130 lack of cover in intertidal areas, the limitation of escape routes by the ocean, and wave sounds  
131 hindering auditory detection, might decrease shoreline use in presence of risk from predators or  
132 hunters. We tested this prediction indirectly by comparing the proportion of marine algae in deer  
133 diet under contrasting risk contexts.

134

## Material and Methods

### 135 Haida Gwaii and the study sites

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

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

152 The three islands in Laskeek Bay (52°53'12"N, 131°35'20"W) where we focused our study on deer  
153 behaviour (Reef 249 ha, Kunga 395 ha, and East Limestone Island 48 ha) (Table 1, Fig. 1) have  
154 all had deer present for over 60 years at the time of study (Vila et al. 2004b, 2004a) and had no  
155 history of hunting. Covered by mature forests without human settlements or activities, these  
156 islands were characterized by closed canopy forests with open species-poor understories (Martin  
157 et al. 1995, Stockton et al. 2005, Martin et al. 2010) representative of severe deer impacts that we  
158 documented at the scale of the archipelago (Martin et al. 2010; Chollet et al. 2015, 2021a). Rocky  
159 shorelines and areas exposed at low tide fringe the islands. On most islands, deer density was  
160 estimated around 30 deer / km<sup>2</sup> (Daufresne & Martin, 1997; Martin et al., 2010; Stockton et al.,  
161 2005) an estimate that has been repeatedly confirmed in the course of deer culls (Gaston et al.  
162 2008a; Irvine & Thorley 2024).

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

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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 <sup>2</sup>	Y	N	20	N	Y
Risk	Y	Yeo	Coastal BC	95 km <sup>2</sup>	Y	Y	7	N	Y <sup>+</sup>

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

180 Reef Island, devoid of hunting prior to 1997, was subjected to repeated and severe deer culls  
181 between 1997 and 2008 (Chollet et al. 2016). From September 1997 to February 1999, over 80%  
182 of the initial deer population was culled (Gaston et al. 2008b). Recent archipelago-wide genetic  
183 analyses confirmed that these culls caused a severe population bottleneck and that the current deer  
184 population of Reef Island consists of descendants from the handful of animals left after the culls  
185 (Burgess et al. 2022a, 2022b, 2023). As local deer survival is typically less than 10 years (JLM et  
186 al. unpubl.), most or all individuals involved in our study during 2011-2014 must have been born  
187 after the initial culls. In 2014, Reef Island had a deer population of about 15 deer / km<sup>2</sup>, thus an  
188 estimated 30 to 40 deer present, representing about half of the pre-cull population, and a partially,  
189 but dramatically, recovered understory vegetation (Chollet et al. 2016).

190 We also studied a portion of Graham Island (6,361 km<sup>2</sup>), the largest island of the Haida Gwaii  
191 archipelago, where deer have been widespread since the early 20th century (Golumbia et al. 2008)  
192 and have been exposed to human hunting ever since. Graham is also home to a population of black  
193 bear (*Ursus americanus*) that sometimes prey on deer fawns (Mathews & Porter 1988; Ballard et  
194 al. 2001). Deer densities on Graham have been estimated to exceed 13 deer / km<sup>2</sup> (Engelstoft 2001;  
195 Engelstoft et al. 2008). Its forests are characterized by low vegetation cover in the understory [this  
196 study and (Chollet et al. 2021a)].

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

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

## 210 **Does vegetation cover and diversity vary with predation risk?**

211 To assess the links between the vegetation and predation risk, we compared the understory  
212 vegetation among sites with different risk histories (Table 1). We used 3.6 m radius (50 m<sup>2</sup>)  
213 vegetation plots (Table 1) to estimate the % cover of plant species in the 0 to 1.5 m vegetation  
214 layer directly accessible to deer browsing for all islands, except Murchison and Faraday. Details  
215 for Graham Island sites can be found in Chollet et al. (2021a) and for the other islands from Haida  
216 Gwaii in Stockton et al. (2005). We grouped the plant species data into six groups: young conifers,



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

## 222 **Does deer fear vary with predation risk?**

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

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

246 Data on FID was obtained on islands without risk (Kunga and East Limestone), and on an island  
247 initially without risk but subjected to culling (Post-culls Reef). As the expression of fear can be  
248 affected by resource availability (Cooper 2008) we created a translocation experiment by moving  
249 six adult does from Kunga island, where they were not exposed to hunting and where the  
250 understory was heavily browsed, to Reef Island, where heavy culling in the 1990s had created a  
251 much denser understory. On Kunga, the translocated does had been box-trapped, marked and  
252 collared as adults in 2011 and had been recaptured multiple times (5 to 21 times each) (Le Saout  
253 et al. 2014a; Bonnot et al. 2016). Three of the six translocated animals had been subjected to five,

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

259 We analysed the two distance variables for these deer samples with a linear model (lm function in  
260 R) to fit the linear regression model with the distance variable (FID or Dtravel, both log<sub>10</sub>  
261 transformed to ensure normality) used as a response variable to compare treatments. We also  
262 analysed, when feasible within deer samples, the effect of deer status (marked/unmarked), sex  
263 (M/F) and age class (adult, young) as well as effect of year on FID and Dtravel. We used pairwise  
264 comparisons of the linear models with the emmeans package in R which provided t-tests to  
265 compare the effects of these variables on our distance variables within deer samples.

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

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

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

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

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

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

316 
$$\delta X = [(R \text{ in sample} / R \text{ in reference}) - 1] * 1000 \text{ (‰)}$$

317  $\delta X$  gives the deviation between the samples’ isotopic ratio and the ratio obtained from an  
318 international standard, “R in sample” is the isotopic ratio considered, in our case  $^{13}\text{C}/^{12}\text{C}$  and  
319  $^{15}\text{N}/^{14}\text{N}$ . For Carbon, “R in reference” refers to the standard Pee Dee Belemnite (PDB).

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

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

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

346 We ground dry bone and plant samples to a granulometry of less than 0.7mm. We followed  
347 protocols defined by late F. Catzeflis based on DeNiro & Epstein (1981), Bocherens et al. (1988),  
348 and Bochérens, Hervé et al. (1991) to extract bone collagen from bone powder in the laboratory.  
349 We analysed the isotopic composition of the plant and collagen samples on CO<sup>2</sup> and N<sup>2</sup> obtained  
350 by sample combustion and analysed on a mass spectrometer. On the basis of isotopic similarities,  
351 plants, except conifers and the evergreen shrub Salal *Gaultheria shallon*, were combined in one  
352 group (DecHerbs). All seaweeds had a similar, restricted spread of isotopic signatures and we  
353 pooled them into a single group (Seaweed).

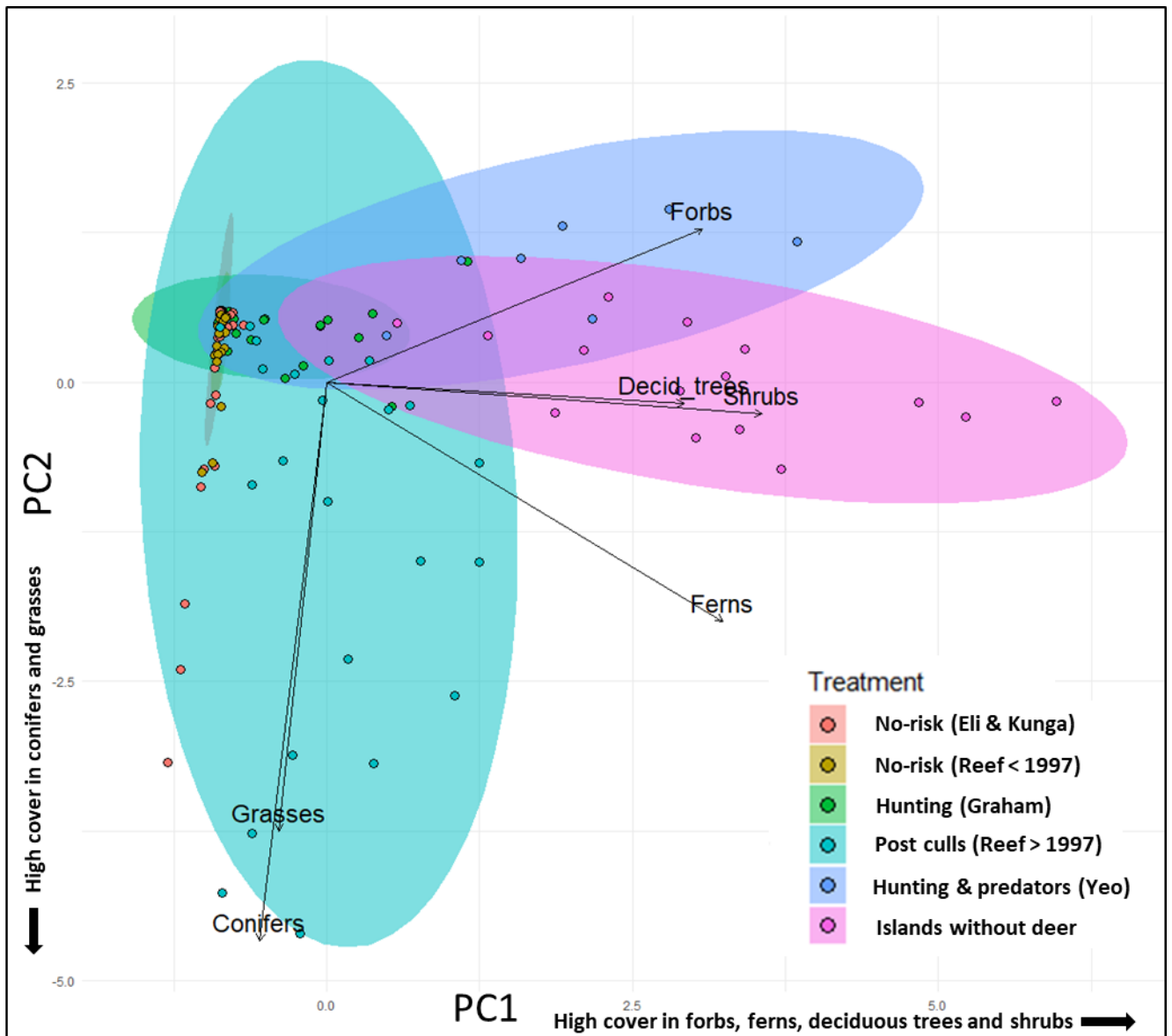
354 We analysed the isotopic ratios obtained for our samples using a Bayesian multiple source mixing  
355 model (MixSIAR package in R) (Stock et al. 2018a, 2018b) which estimates the proportions of  
356 source contributions (here terrestrial and marine plants) to a mixture (bones used as a proxy for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

358

## Results

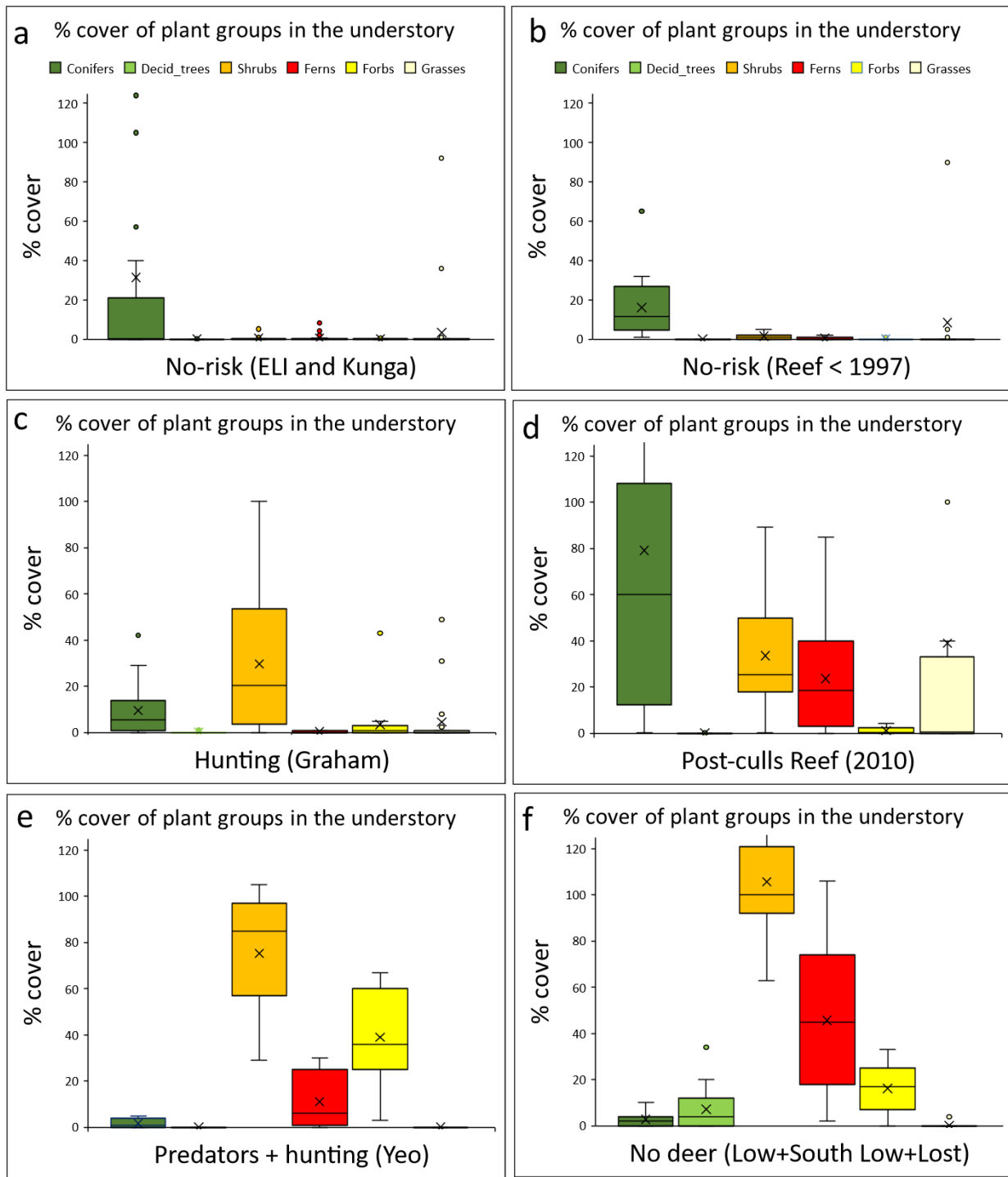
### 360 Understory vegetation varied with risk history

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



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



395 **Deer fear varied with predation risk**

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

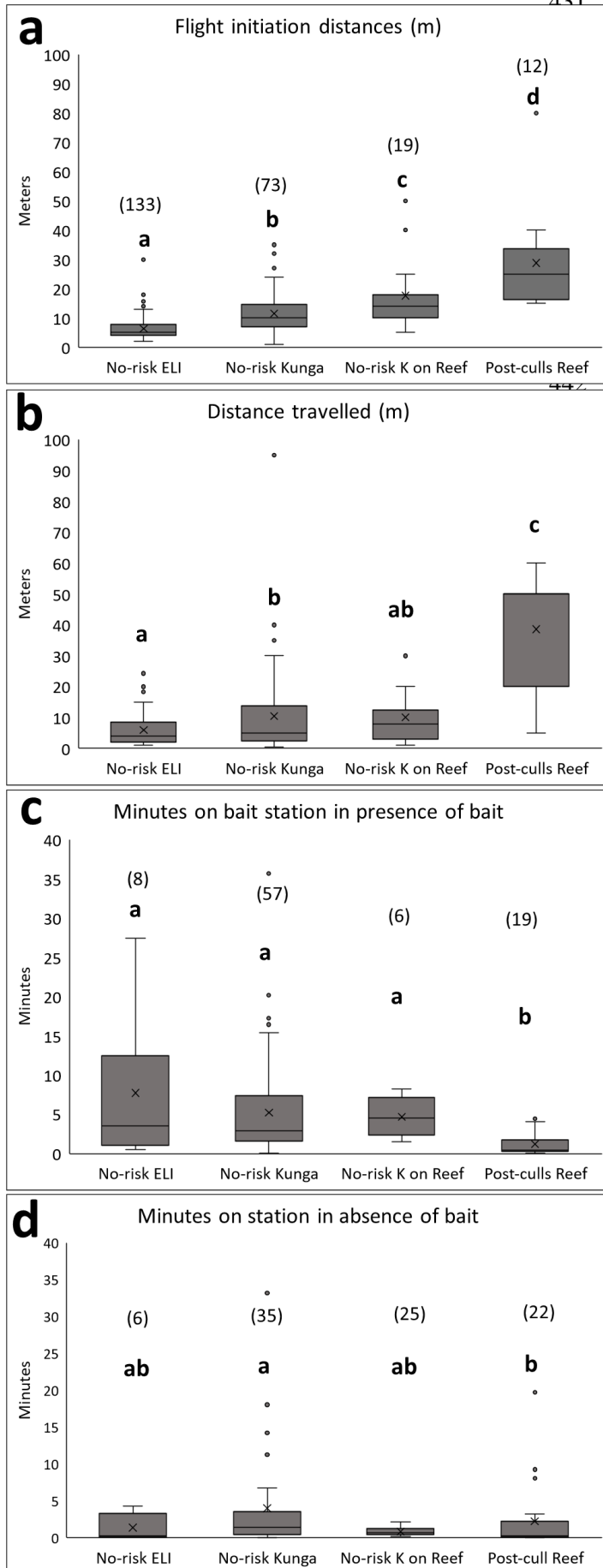
401 Values did not differ significantly among years within samples ( $p = 0.60$ ). Nor did sex or age have  
402 any effect ( $p = 0.30$ ,  $p = 0.62$  respectively). Thus we combined sexes, ages and years.

403 FID varied significantly among treatments [ $R^2 = 0.38$ ,  $F_{(3, 233)} = 49.28$ ,  $p < 0.001$ ] (Fig. 4a). FID  
404 was lowest for islands without hunting and highest for Post-culls Reef. Among the islands without  
405 hunting, FID was lowest on East Limestone and highest for Kunga deer translocated to Reef (Fig.  
406 4a).

407 Samples from No-risk East Limestone and from Post-culls Reef included marked and unmarked  
408 deer. Differences in FID between marked and unmarked deer were non-significant [for East  
409 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  
410 versus 23.6 m)].

411 **Distance travelled** - Dtravel varied significantly among treatments [ $R^2 = 0.18$ ,  $F_{(3, 229)} = 18.04$ ,  $p$   
412  $< 0.001$ ]. Deer from populations without hunting travelled significantly shorter distances than deer  
413 on Reef after the culls (Fig. 4b). Dtravel on East Limestone Island was significantly shorter than  
414 on Kunga Island ( $p = 0.01$ ), and much shorter than on Post-culls Reef Island (Fig. 4b;  $p < 0.001$ ).  
415 Dtravel distances for Kunga deer translocated on Reef did not differ from those on Kunga ( $p =$   
416  $0.96$ ), or from Dtravel observed on East Limestone ( $p = 0.12$ ) and was only one third that of native  
417 Reef deer ( $p < 0.001$ ) (Fig. 4b). On East Limestone, marked deer moved significantly further than  
418 unmarked deer [ $t$ -ratio = 2.20,  $p = 0.03$ , (6.7 m versus 4.9)] but this did not apply to marked and  
419 unmarked deer on Reef [ $t$ -ratio = 0.17,  $p = 0.86$  (41m versus 36.7)].

420 **Response to bait** – Risk category had a significant effect on time spent at bait stations when bait  
421 was present ( $\log_{10}$  transformed): deer on islands without hunting and deer from Kunga translocated  
422 to Reef, spent significantly more time at bait stations with bait than native Reef deer ( $R^2 = 0.14$ ,  
423  $F_{(3, 79)} = 4.29$ ,  $p = 0.007$ ; Fig. 4c) and visited them five times more often (0.97 against 0.20; Fig.  
424 4c, Table 2). Bait consumption per visit was three times higher on Kunga and East Limestone than  
425 for native deer on Reef (75% against 20%) (Table 2). On East Limestone and Kunga marked deer  
426 consumed bait in 50-80% of their visits in contrast to native deer on Reef, where only three of the  
427 nine deer trapped and marked consumed bait at bait stations. None of the 14 unmarked deer  
428 observed on Reef touched bait which they investigated briefly or ignored altogether (mean visit  
429 length 24 s). Length of median values in time spent on a station, less affected by outliers, exceeded  
430 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 ( $p = 0.04$ ).

473 At Kunga, marked deer spent significantly more time at a station than unmarked deer (7.8 min on  
 474 average against 5.6 minutes) (t-ratio of contrast estimate = 4.64,  $p < 0.001$ ). Some unmarked  
 475 animals visited a bait station without eating bait (mean visit length 54 s). Among deer native to  
 476 Reef, marked individuals also spent longer at bait stations (t-ratio of contrast estimate = 3.00,  $p =$   
 477 0.004) and were the only deer consuming bait (mean visit length 3.0 minutes).

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

486

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

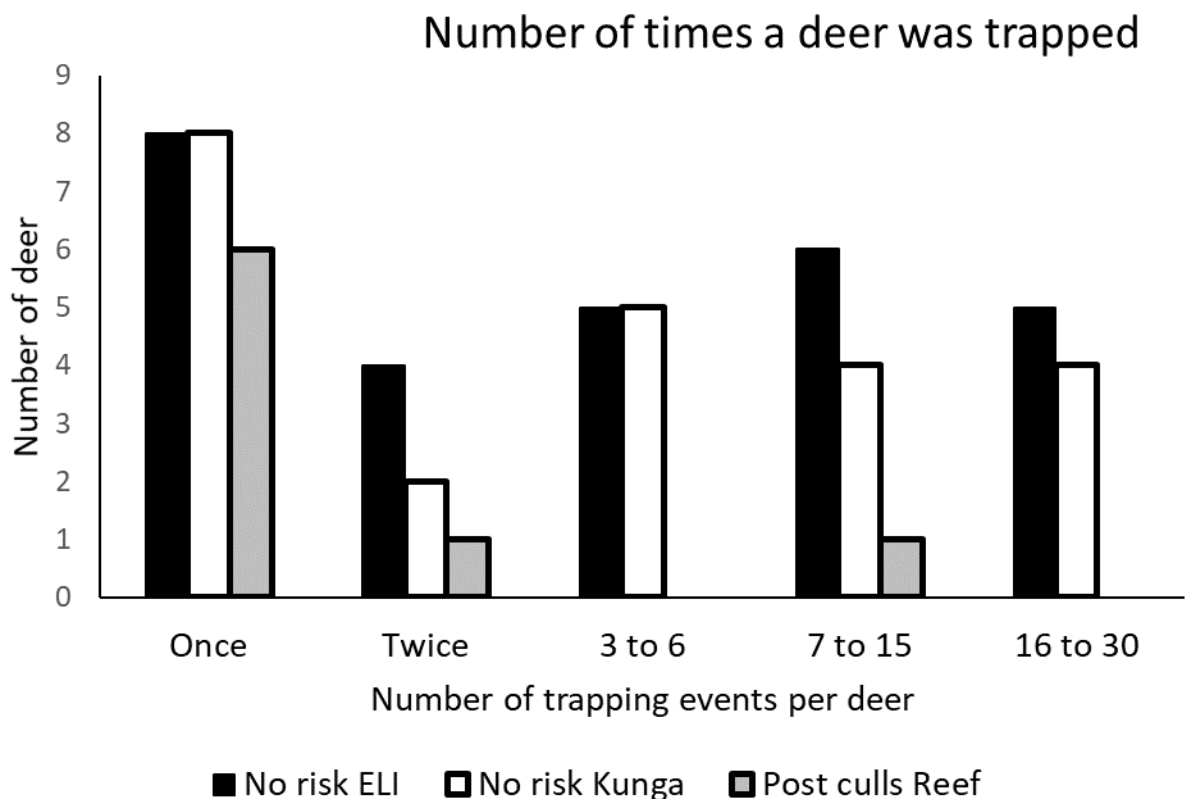
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497 **Response to traps** – On Reef Island (Post-culls) the capture rate was significantly lower than on  
 498 islands without hunting ( $p \leq 0.05$ ) (Table 3). On Reef only 2/8 deer were captured more than once,  
 499 compared to 35/51 for the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

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

508



509 **Figure 5.** Summary of the capture and recapture histories for the deer native to the three sites and two  
 510 categories of hunting histories. ELI = East Limestone Island.  
 511

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513

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

523

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

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531 Observer monitoring an unruffled wild deer foraging on remote Kunga Island (No-risk).

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

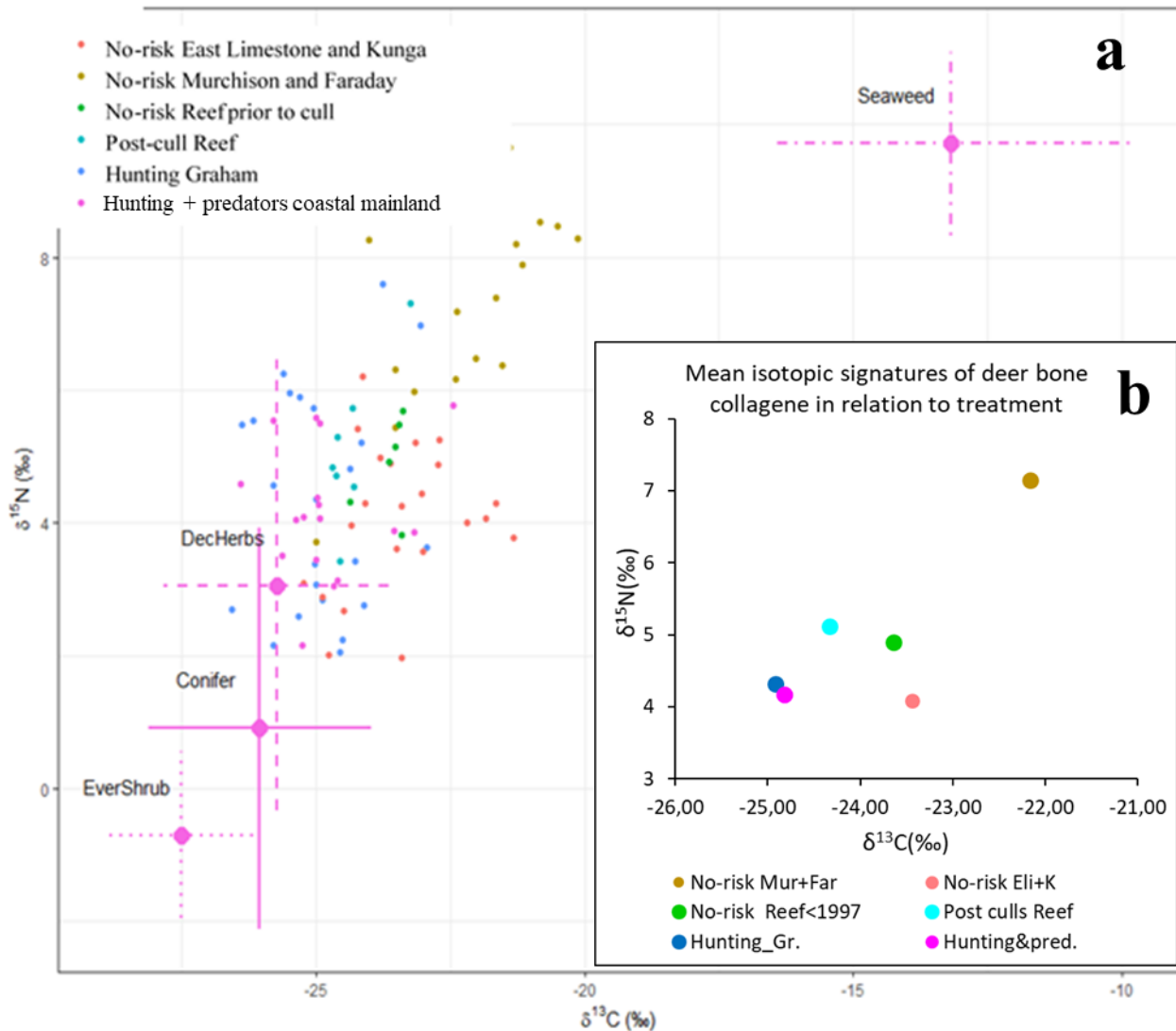
533 The following diagnostic and tests confirmed that our Markov Chain Monte Carlo (MCMC) chains  
534 converged in the MixSiar model. The Gelman-Rubin Diagnostic run after the MixSiar model  
535 indicated that only 2 of the 140 variables exceeded marginally the threshold value of 1.01. The  
536 Geweke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

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

546 The MixSIAR analysis quantifies the proportion of the four plant categories in deer diets in the  
547 samples (Figs. 6 and 7). Bayesian 95% credible intervals (Fig. 8) allow us to estimate the  
548 significance of differences in the proportion of seaweeds between the samples. Credible intervals  
549 from the samples without predation (Murchison, Faraday, East Limestone, Kunga and Reef before  
550 the culls) do not overlap with those of the two sites with hunting and/or predators (Graham and  
551 BC Central Coast). The credible interval of the Post-culls Reef sample was intermediate.

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

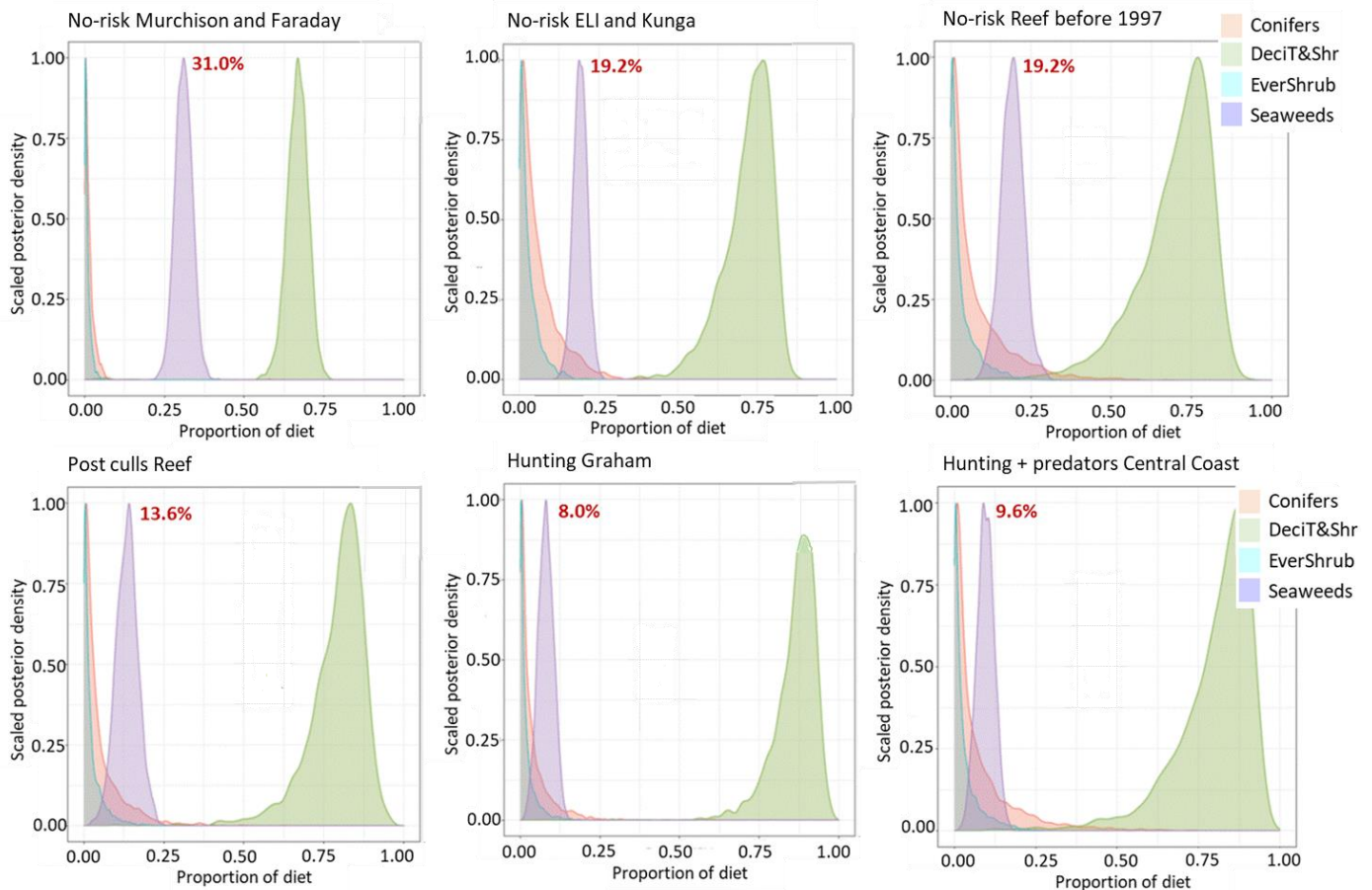
557 The proportion of the terrestrial plants in deer diets, which included deciduous trees and shrubs,  
558 ferns, forbs and grasses varied from 67% on Murchison and Faraday to 88% on Graham and on  
559 the coastal mainland. Conifers and evergreen shrubs stand out as a minor component of diet. It 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



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

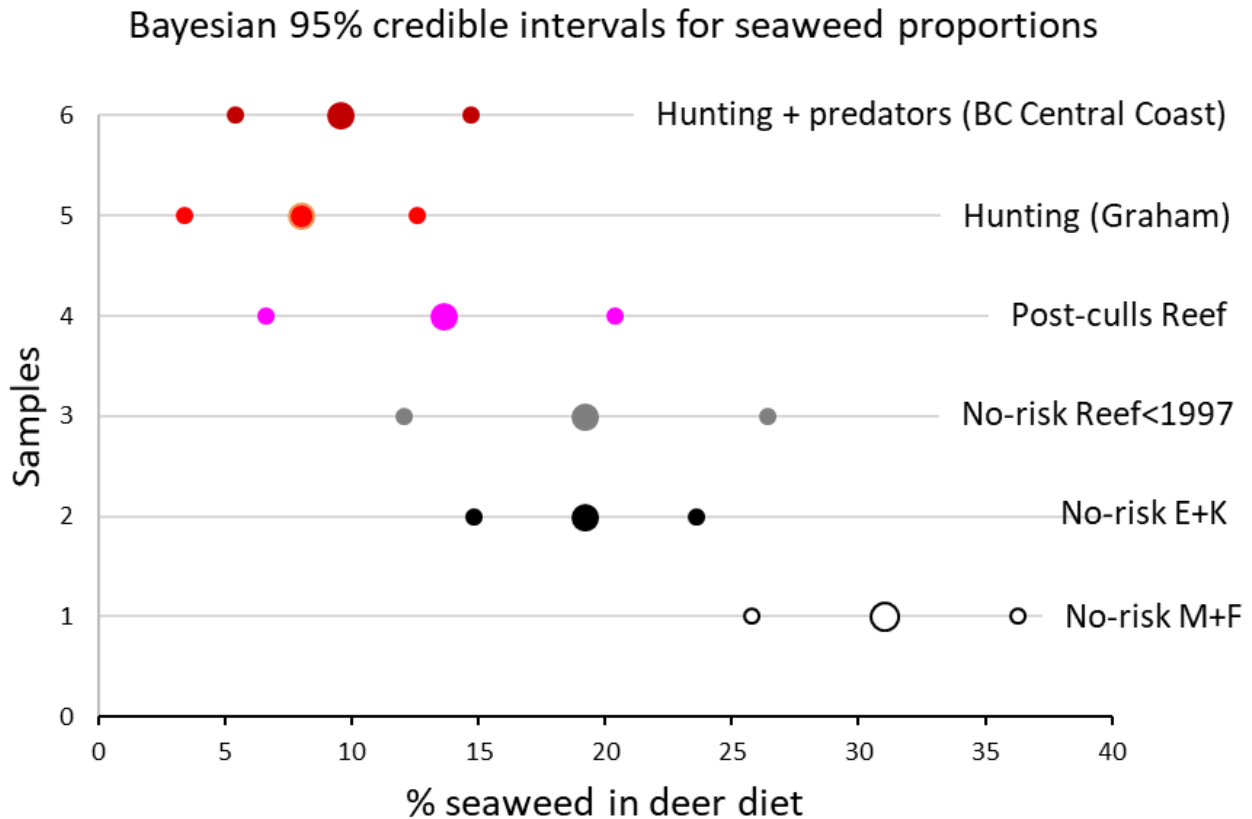
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**Figure 7.** MixSiar posterior plots of overall deer diet in relation to predation risk. N = number of bone samples per site. No-risk history, four sites: Murchison (N = 10), Faraday (N = 6), East Limestone (ELI) (N = 10), Kunga (N = 12) and Reef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



597

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

601

## Discussion

### 602 **How did understory vegetation cover and composition change with predation risk?**

603 Our results illustrated the well-established effect that large herbivores can have on forest  
 604 vegetation cover (Côté et al. 2004; Martin et al. 2010, 2011; Cardinal et al. 2012; Chollet et al.  
 605 2013, 2021a; Waller & Reo 2018). They also illustrated the relationship between the level of  
 606 impact on the vegetation and the risk history a deer population has been exposed to (Callan et al.  
 607 2013; Waller & Reo 2018). The severe culls on one of our sites (Reef Island) resulted, over a  
 608 decade, in an upsurge of understory vegetation and regenerating conifers in an initially heavily-  
 609 browsed open understory (Figs. 2 and 3), combined with an increase in diversity among plots  
 610 [(Fig. 2 and Chollet et al. (2016)]. However, there are intrinsic differences between this recovering  
 611 understory vegetation and the understory vegetation we sampled on Yeo Island where deer have  
 612 always been subject to their natural predators in addition to hunters. On Reef, the high proportion  
 613 of regenerating conifers in the understory following the culls resulted from the release of heavily

614 browsed dwarfed spruce and hemlock (Chollet et al. 2016), while the high cover of grasses resulted  
615 from a rapid colonisation of bare ground (Chollet et al. 2016). By contrast, the vegetation profile  
616 we observed in the presence of large carnivores and hunting on Yeo was remarkably similar to the  
617 understory vegetation profile we observed on three islands in Laskeek Bay never colonized by  
618 deer [see details in (Stockton et al. 2005, Martin et al. 2010)]. Their understories lack the  
619 significant cover of conifer regeneration we observed on Reef after the culls and are dominated  
620 by shrubs and forbs (Fig. 3).

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

#### 629 **Does absence of risk favor boldness and deer impact on the vegetation?**

630 Our comparison between populations that had not been exposed to any risk (East Limestone and  
631 Kunga), with a population on Reef subjected, over a decade prior to the study, to a severe  
632 population reduction through culling, revealed clear behavioural contrasts. In absence of risk deer  
633 were easy to trap and unwary of people. They also willingly consumed foreign food at bait  
634 stations, and foreign food when associated with an unfamiliar object (trap). The significantly  
635 shorter flight initiation distances, and much shorter distances travelled, observed in non-hunted  
636 populations were retained by the Kunga deer translocated to Reef, even though they showed  
637 slightly longer flight initiation distances in their novel environment. This was in stark contrast  
638 with the wary behaviour of the native deer on Reef after the culls, even more so as the flight and  
639 movement distances we recorded for the Reef deer were conservative: they often fled before being  
640 seen (heard running) and others were still running when they disappeared from view. As a result,  
641 actual values on Reef may have been closer to values reported for black-tailed deer populations  
642 on the mainland (FID ~ 60 to 70 m and Dtravel ~ 70 to 120 m), where deer can be subject to  
643 hunting and carnivores (Stankowich & Coss 2006, 2007; Stankowich 2008). Our field notes also  
644 indicated that native deer on Reef ran or trotted away, whereas deer from Kunga, even after  
645 translocation, and East Limestone (No-risk islands) usually performed a slow walk to a nearby  
646 location where they resumed their activities. On East Limestone, FID and distances travelled were  
647 significantly shorter than on Kunga, possibly reflecting some habituation to human presence  
648 (Rodriguez-Prieto et al. 2009; Schuttler et al. 2017) on East Limestone Island, where people are  
649 present daily for two to three months each summer for ecological monitoring.

650 Despite minor differences in flight distances or time spent at bait, marked and unmarked deer of  
651 the same population had comparable flight initiation behaviours. Marked and unmarked, deer from  
652 Reef born after the culls were predominantly shy, as their poor trapping rate illustrated, even when  
653 we take into account that deer densities on Reef at the time of study were still at only 50% of their  
654 pre-cull density (originally ~30 deer/km<sup>2</sup>, i.e. >80 deer present; Chollet 2012). Only two (25%) of  
655 the eight deer captured on Reef were ever re-captured, and only one was recaptured repeatedly,  
656 mostly as a yearling and a juvenile, before becoming trap shy in the following years while still  
657 captured on cameras. This contrasts with deer unexposed to risk on East Limestone and Kunga. A  
658 significant proportion of the local deer were trapped, and over half of them re-trapped three times  
659 or more over the years (Fig. 5). The presence on Kunga and Reef of a fraction of animals never  
660 trapped, but captured on automatic cameras, indicated that within each population there was  
661 variation in trap-shyness among individuals (Sih et al. 2012). Overall, observed differences in  
662 behaviour between deer native to East Limestone and Kunga and those native to Reef after the  
663 culls, suggest that culling shifted the dominant behaviour profiles of Reef Island deer towards the  
664 shy-end of a boldness-shyness continuum.

665 Food limitation and nutritional status have been proposed as mechanisms explaining individual  
666 attenuation in antipredator behaviours such as flight response (Stankowich 2008; Gaynor et al.  
667 2019). If so, we expect these behaviours to be reversed once food supply improves. Could a better  
668 food supply in the lush understory on Reef after the culls explain the higher values of FID and  
669 Dtravel for deer native to Reef, and would the apparent paucity of resources in the heavily browsed  
670 understories of East Limestone or Kunga explain the apparent lack of fear in their deer? This seems  
671 unlikely, given that we did not observe any significant change in the behaviour of the deer  
672 translocated from Kunga to Reef (Fig. 4). Our observations rather suggest a more indirect link  
673 between behaviour and resources, a link mediated by risk. Following the reasoning of Kirchhoff  
674 & Person (2008) we assumed that in absence of risk, intensive browsing would, over time,  
675 decrease the per capita availability of forage as well as the average quality of the diet. A reduction  
676 in anti-predator behaviour could be the necessary condition to allow increased foraging time in  
677 response to this progressive erosion of standing plant biomass and forage quality in an increasingly  
678 browsed understory. In these understories, resources, although sufficient to sustain a dense deer  
679 population (Stockton et al. 2005; Le Saout et al. 2014a), are increasingly found in small increments  
680 of emerging vegetation or as subsidies fallen from the canopy (Le Saout et al. 2014a). Indeed, on  
681 No-risk islands less than 5% of the resources needed by these dense deer populations were  
682 provided by the rare standing biomass. The bulk was provided equally by the cryptic flux of  
683 growing vegetation and by canopy foliage fall, supplemented by seaweeds from the shorelines (Le  
684 Saout et al. 2014a).

685 Our results from the stable isotope analysis are another illustration of the focus deer have to put  
686 on cryptic vegetation elements in the understory. On one hand conifers, the dominant element in  
687 the understory of No-risk sites (Fig. 3), make for only a tiny proportion of their diet (Fig. 7),

688 whereas deciduous vegetation, a known preference in black-tailed deer diet (Taylor 1956; Pojar  
689 1999), make up the bulk of their diet (Fig. 7), its negligible presence as standing biomass (Fig. 3)  
690 compensated by short lived emerging vegetation (Le Saout et al. 2014a). This need to feed on  
691 spatially dispersed food, occurring as small items, could be the ecological context forcing the  
692 emergence of populations expressing less anti-predator behaviours (Réale et al. 2010; Sih et al.  
693 2012), or with less costly adjustments of spatial distribution in response to perceived distribution  
694 of risk (Williams et al. 2008; Gaynor et al. 2019). Such behavioural shifts could, in turn, help deer  
695 intensify their foraging pressure and, over time, aggravate the loss in understory standing  
696 vegetation, as was actually shown on these islands between 1989 and 2009 (Chollet et al. 2015).  
697 This could further increase the shift towards bolder behaviours. The overall predominance of  
698 diurnal activity in East Limestone and Kunga deer compared to populations exposed to hunting  
699 (Bonnot et al. 2016) can also be interpreted as a change in favour of increased foraging time. This  
700 more diurnal behaviour has been shown to contrast with the more nocturnal behaviour commonly  
701 observed in hunted populations (Altendorf et al. 2001; Bonnot et al. 2016, 2020; Palmer et al.  
702 2022). However, anti-predator behaviours less costly in foraging time such as routine vigilance  
703 would be retained and not counter-selected as was actually observed for the populations of East  
704 Limestone and Kunga where routine vigilance persisted in an otherwise unwary population.  
705 (Chamaillé-Jammes et al. 2014; Le Saout et al. 2015).

706 On Reef, after the first few days of culling, every animal remaining was much shyer than the  
707 animals observed pre-cull (AJG and T. Husband pers.com), showing that at least some animals in  
708 the pre-cull population, previously never hunted and living in a heavily browsed habitat for more  
709 than 50 years (Martin et al. 1995; Vila et al. 2004a; Chollet et al. 2016), had retained the ability to  
710 respond to a new threat [see also Chamaillé-Jammes et al. (2014)]. A study on the effects of low  
711 intensity and simulated hunting (Le Saout et al. 2014b) on the behaviour of deer on Kunga also  
712 documented the presence within the local deer population of individual personalities differing in  
713 their ability to respond to a threat. Some animals were easily seen and trapped, and showed little  
714 or no response to simulated hunting or to being trapped, whereas some animals were only observed  
715 through automatic cameras, were never trapped and shifted their habitat use away from the area  
716 exposed to simulated hunting.

717 On Reef, at the time of this study, the animals born several years later, offspring of those that  
718 survived the culls, were much shyer than those seen on Reef prior to the cull (AJG pers. obs.).  
719 These animals also had a tendency to be more active at night than deer on Kunga and East  
720 Limestone never exposed to hunting or to culls. The survivors on Reef may have included animals  
721 that modified their behaviour more rapidly and more radically than those that were killed. If some  
722 or all of that variation in behaviour was under genetic control (Réale et al. 2007), subsequent  
723 generations will have been shyer than the pre-cull population as a result of differential survival of  
724 shyer personalities during the culls. The consequent persistence of increases in FID, Dtravel,  
725 novelty aversion and nocturnal foraging would have been inherited or adopted by young reared

726 subsequently, so that the behaviour of the current population resembles that of populations subject  
727 to natural predation and human hunting. Rapid differential selection of heritable antipredator  
728 behaviours in response to novel predation were documented recently (Moseby et al. 2023).  
729 Conversely, there is little sign that the deer trapped and translocated from Kunga Island and hence  
730 never exposed to predation threat, adopted any of the modified behaviour of the local post-cull  
731 deer despite the better foraging resources.

### 732 **Did risk affect the use of habitats?**

733 The lower proportion of seaweeds in diets at sites with predators and/or hunters seems to validate  
734 our prediction that deer would make less use of exposed shorelines where they face predation from  
735 hunters and/or wolves. But, as the amount of standing vegetation in the understories tends to be  
736 much lower at sites without hunting (Fig. 3) it could be the lack of forage in the understories of  
737 No-risk islands that encouraged deer to forage in the intertidal. On Murchison and Faraday, where  
738 seaweed is especially prominent in the diet, the very open understories below dense secondary  
739 canopy, supported very little ligneous and herbaceous vegetation cover in the 0 to 1.5 m layer  
740 (<4%, Martin et al. 1995).

741 However, the two situations with the lowest and similar proportion of seaweed isotopes in jawbone  
742 collagen, Graham and Yeo Islands, differed in their cover of standing understory vegetation. On  
743 Yeo, the permanent presence of predators and hunting was associated with a lush understory. On  
744 Graham, the long history of moderate hunting, restricted to areas most accessible to a small  
745 number of hunters (Martin and Baltzinger 2002), had limited impact on deer density (Engelstoft  
746 2001; Engelstoft et al. 2008), resulting in understory cover closer to that at No-risk sites than to  
747 that at sites on the BC Central Coast (Figs. 2 and 8) (Pojar 1999; Chollet et al. 2021a). This partial  
748 decoupling of understory vegetation cover and proportion of seaweeds in deer diet remains  
749 suggestive that risk history on a site can negatively affect deer propensity to feed on shorelines.  
750 This would be consistent with the documented high use of shorelines by foraging wolves and its  
751 negative consequence on their use by deer (Klein 1995). It would also be consistent with the  
752 documented increased reluctance in deer to use more exposed habitats or localities when risk is  
753 higher (Williams et al. 2008; Bonnot et al. 2017).

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

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

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

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

781 Our results have implications for conservation. They can improve understanding of the problems  
782 posed by the adjustment of focal species towards a novel threat, thus improving the success of  
783 species restoration programs where naïve captive-bred individuals have to adjust to predators on  
784 release (Moseby et al. 2015, 2016, 2023). They also provide insights into the management of  
785 overabundant populations through hunting. In such instances, a better grasp of behavioural  
786 responses to management actions can help design strategies that take into account the ability of  
787 species to adjust their spatial distribution and diel rhythms to the threat posed by management  
788 measures (Williams et al. 2008; Potratz et al. 2024). A better understanding of the ramifications  
789 of consequences triggered in prey by the return of their predators will also help better address the  
790 challenges posed by high deer populations in parts of Europe and North America to human  
791 activities, such as farming, livestock husbandry, forestry (Kuijper et al. 2013, 2016; Raynor 2017;  
792 Martin et al. 2020) or road safety (Gilbert et al. 2017; Raynor et al. 2021; Bell et al. 2024). Finally,  
793 by improving our understanding of mechanisms that lead to evolutionary shifts, our results help  
794 to better predict the full impact of neglecting the integrity of species assemblages. Hence, our  
795 evidence encourages the conservation and restoration of fully functioning ecosystems.

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797



798 **Ethical note**

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

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830 **Data and scripts availability**

831 <https://zenodo.org/me/uploads?q=&f=allversions%3Atrue&l=list&p=1&s=10&sort=newest>

832

833

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840 **Conflict of interest disclosure**

841 The authors declare that they comply with the PCI rule of having no financial conflicts of interest  
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844

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