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

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24 **Abstract**

25 The “ecology of fear” emphasizes the potential role of predation risk in shaping large herbivore
26 behaviour and the way they affect forest ecology. In this study we show how the presence or
27 absence of predation risk by hunters, together with or in the absence of carnivores, affect the
28 behaviour and ecological effects of Sitka black-tailed deer introduced to the islands of Haida
29 Gwaii, (British Columbia, Canada) or native to coastal BC. Deer in risk-free population showed
30 remarkable tolerance to human presence while deer exposed to severe culling in the recent past,
31 exhibited more costly anti-predator behaviors (long flight initiation distances and long travel
32 distances when fleeing; reluctance to consume foreign bait or to investigate baited traps; increased
33 night-time foraging) and were more likely to use exposed habitats. Contrasts in hunting histories
34 translated into dramatic variation in the nature, distribution and abundance of the understory
35 vegetation deer depended on.

36 The experimental translocation of unwary deer from an island without hunting to an island where
37 culls had partially restored the vegetation, showed that the lack of costly anti-predator behaviors
38 was not significantly affected by the presence of abundant and higher quality forage. We
39 interpreted these results as evidence that the experience of risk was key in explaining the observed
40 behavioral contrasts between deer populations with different risk histories. We strengthened this
41 conclusion by analysing the proportion of stable isotopes in deer bone collagen to show that deer
42 foraged less in the exposed intertidal zone when predation risk was higher.

43 Our results provide novel insights into how predation risk affects ecological networks, ecosystem
44 complexity and animal behaviour. By revealing the role of key species, they may enable better
45 strategies for future ecosystem restoration.

46

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

49

50

Introduction

51 From its outset, Ecology was defined as the science of interactions (Haeckel 1866, Elton 1927).
52 Interactions were first assessed by observing direct relationships among species. Over time, the
53 increasing sophistication of empirical and experimental approaches improved our understanding
54 of ecological systems and revealed the importance and intricacies of indirect interactions. This
55 brought key insights into the central role that herbivores and their predators play in the structure,
56 function and stability of ecological systems [(Paine 1966, 1969, Estes et al. 2011) and review in
57 (Martin et al. 2020)]. Consequently, while the loss of species or populations across the world's
58 ecosystems is dire, the loss of species interactions is perhaps even more insidious, because often
59 unnoticed (Janzen 1974, Soulé et al. 2003, Valiente-Banuet et al. 2015). The loss (or addition) of
60 key players in the ecological fabric will affect, directly or indirectly, day to day processes in an
61 ecosystem, and, over time, potentially select for traits and behaviors better adapted to the new state
62 of the ecological network (Bøhn and Amundsen 2004, Ellers et al. 2012, Estes et al. 2013).

63 The key role animal behavior plays in species interactions and in ecosystems has been dramatically
64 highlighted by the emergence of the conceptual framework proposed in what was named the
65 “ecology of fear” (Brown et al. 1999). This framework focused on the profound non-consumptive
66 effect predator presence can have on prey behavior and on how prey interact with their habitat,
67 giving rise to the idea of a “landscape of fear”. It fostered predictions about the consequences risk
68 variation in space and time could have, not only on predator-prey interactions, but also on the
69 functioning of ecosystems at large (Palmer et al. 2022).

70 Focusing on ungulates, and deer in particular, Altendorf et al. (2001), building on the pioneering
71 work of Brown et al. (1999), predicted that, in presence of risk, animals should spend less time
72 foraging overall, and spent less time foraging at any given location. Presence or absence of risk
73 should therefore influence the avoidance or use of certain portions of their habitat, perceived either
74 as more exposed to, or as refuges from, predation (Williams et al. 2008, Bonnot et al. 2017).

75 In large areas of North America and Europe dramatic increases in large herbivore populations
76 resulted in the partial recovery of their main predators, wolves. In this context, concepts related to
77 an “ecology of risk” have created a need to better understand how predator-prey interactions affect
78 ecological systems and their conservation (Chitwood et al. 2022).

79 Furthermore, the increasing understanding of the complex range of interactions ungulates and
80 wolves have with human activities, such as farming, livestock husbandry, or forestry, opened new
81 research avenues to better understand the role of predation risk in mitigating the undesirable
82 ecological and societal impacts of large herbivores (Kuijper et al. 2016, Martin et al. 2020). Such
83 studies emphasized the need to better integrate the study of animal and ecosystem ecology with
84 the study of animal temperament and its evolution (Réale et al. 2007, Sih et al. 2012) if we want
85 to embrace the full complexity of natural systems (Chitwood et al. 2022).

86 In this study we tested how the effects of high deer abundance on the ecology of forests are
87 modulated by the presence or absence of hunting or predation. We took advantage of the
88 introduction, at the end of the 19th century, of Sitka black-tailed deer (*Odocoileus hemionus*
89 *sitkensis*) to Haida Gwaii, a remote archipelago in British Columbia, western Canada (Fig. 1),
90 (Golumbia et al. 2008). The archipelago provided islands with and without deer, and, where deer
91 were present, islands with and without a history of hunting by people. This arrangement provided
92 a quasi-experimental context in which to study how predation risk shapes deer behaviour, their
93 resources and forest vegetation by comparing islands with deer that varied in hunting history.
94 Studies on Haida Gwaii were compared with a mainland coastal site where deer have always faced
95 natural predators in addition to hunters (Darimont et al. 2007).

96 Specifically, we asked: (1) Does deer habitat use, shyness, avoidance, and activity rhythms vary
97 with the presence or absence of hunting or predation risk? (2) Do risk-related contrasts in deer
98 behavior modify how deer affect the forest ecosystem?

99 We show that risk histories were key in explaining the observed behavioral contrasts between deer
100 populations and their effects on forest ecology. These results emphasize the importance of
101 predation risk, and its loss, in the dynamics of ecological networks.

102

103

Material and Methods

104 Haida Gwaii and the study sites

105 Haida Gwaii is characterized by a humid temperate-oceanic climate, with mean annual
106 temperature of 8.5°C (Banner et al. 2014). Most of the archipelago is covered by temperate
107 rainforests dominated by western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*),
108 and Sitka spruce (*Picea sitchensis*).

109 Native to coastal British Columbia, Sitka black-tailed deer were introduced to Haida Gwaii in the
110 late 19th century (Golumbia et al. 2008). They colonized all but a few small islands. The
111 occurrence of a few reference islands that never supported deer made it possible to demonstrate
112 that, on islands with long-term deer presence, independent of island size, deer herbivory was the
113 main factor structuring plant and animal communities (Martin and Baltzinger 2002, Gaston et al.
114 2006, Martin et al. 2010, Chollet et al. 2013), with important consequences on belowground
115 processes (Chollet et al. 2021a, Maillard et al. 2021). Recurrent experimental culls on two islands
116 allowed us to monitor the response of the aboveground vegetation and avifauna for 13 years
117 (Chollet et al. 2016).

118 The three islands in Laskeek Bay (52°53'12"N, 131°35'20"W) where we focused our study [Reef
119 249 ha, Kunga 395 ha, and East Limestone Island 48 ha] (Table 1) have all had deer present for
120 over 60 years at the time of study (Vila et al. 2004) and had no history of hunting (Fig. 1). Their
121 initial deer density was estimated at approximately 30 deer / km² (Daufresne and Martin 1997).

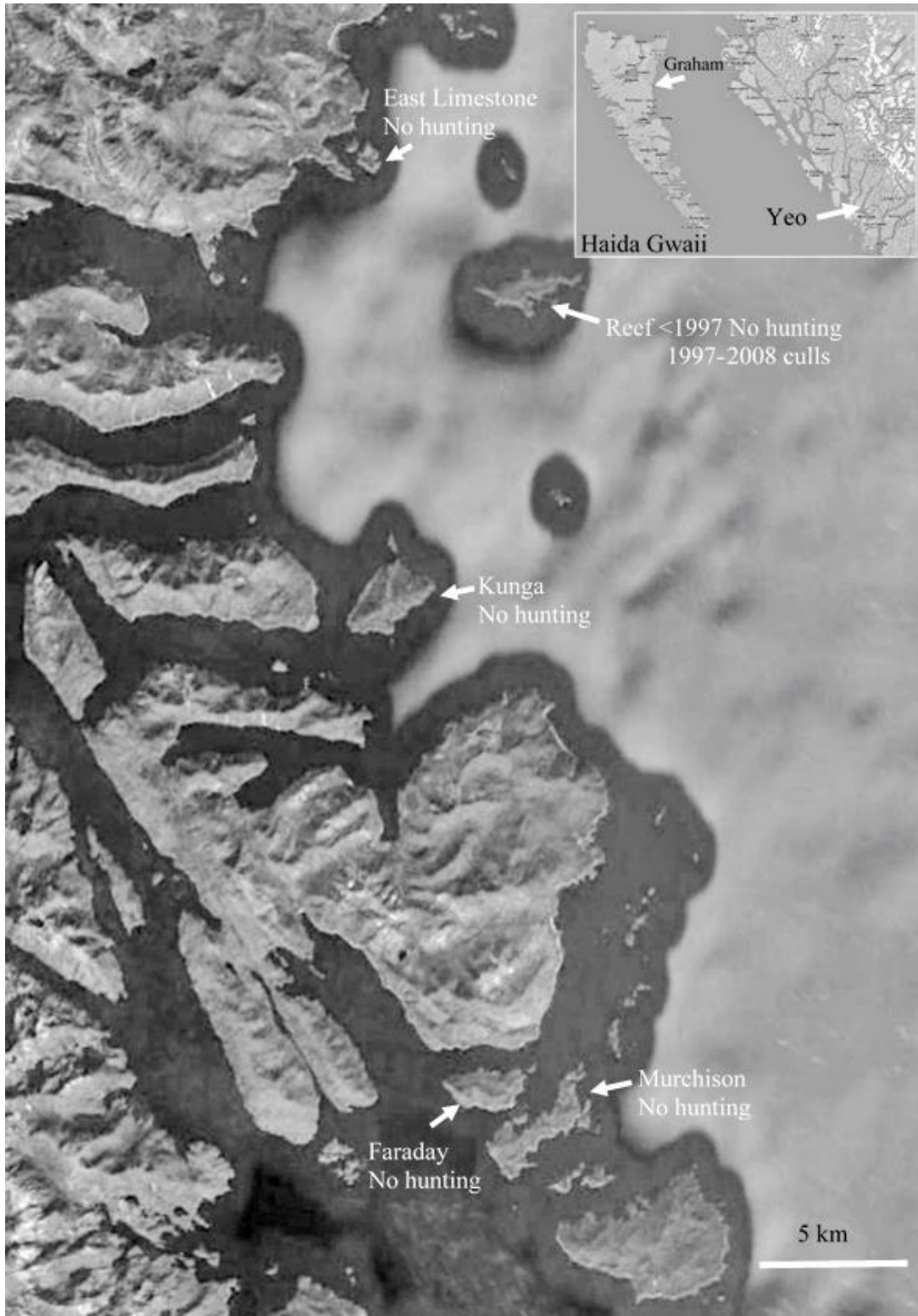
122 Covered by mature forests without human settlements or activities, they were all initially
 123 characterized by open and species poor understories (Martin et al. 1995, Stockton et al. 2005,
 124 Martin et al. 2010) representative of severe deer impacts that we documented at the scale of the
 125 archipelago (Martin et al. 2010, Chollet et al. 2015).

126

127 **Table 1.** List of islands included in the study and their key characteristics. Risk hist. = Risk history;
 128 Vegetation = standardized data on vegetation structure and composition; Isotope = collection of bones for
 129 the stable isotope study (section 2.3.4.); Reef <1997 = conditions on Reef prior to experimental culls; Reef
 130 >1997 = conditions after the culls that occurred between 1997 and 2008; Hunting Y = seasonal hunting,
 131 Y(cull) = repeated culls; N = no hunting; Predators Y = present (wolves and possibly cougar and grizzly
 132 bear), N = absent; Vegetation Y = standardized sampling done, N = no standardized sampling; Isotope Y
 133 = bone samples collected. * Islands that provided data only for the study on stable isotopes (section 2.3.4).

Risk hist.	Island	Region	Area	Hunting	Predators	Vegetation	Isotope
No-risk	East Limestone	Haida Gwaii	48 ha	N	N	Y	Y
No-risk	Kunga	Haida Gwaii	395 ha	N	N	Y	Y
No-risk	Faraday*	Haida Gwaii	308 ha	N	N	N	Y
No-risk	Murchison*	Haida Gwaii	425 ha	N	N	N	Y
No-risk	Reef <1997	Haida Gwaii	249 ha	N	N	Y	Y
Risk	Reef >1997	Haida Gwaii	249 ha	Y (cull)	N	Y	Y
Risk	Graham	Haida Gwaii	6361 km ²	Y	N	Y	Y
Risk	Yeo	Coastal BC	95 km ²	Y	Y	Y	Y

134



135

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

139

140 Reef Island, initially devoid of hunting, had been subjected to repeated and severe experimental
141 deer culls between 1997 and 2008 (Chollet et al. 2016). During September 1997 to February 1999,
142 over 80% of the initial deer population was culled. Recent archipelago-wide genetic analyses
143 confirmed that these culls caused a severe population bottleneck and that the current deer
144 population of Reef Island consists of descendants from the handful of animals left after the culls
145 (Burgess et al. 2022a, b, 2023). As local deer survival is typically less than 10 years (JLM et al.
146 unpubl.), all individuals involved in this study (2011-2014) were presumably born after the initial
147 culls. At that time, Reef Island had a deer population density estimated at about 15 deer/km², with
148 an estimated 30 to 40 deer present, and a partially, but dramatically, recovered understory
149 vegetation (Chollet et al. 2016).

150 We added to these three islands a portion of Graham Island (6,361 km²), the largest island of the
151 Haida Gwaii archipelago, where deer have been widespread since the early 20th century
152 (Golumbia et al. 2008) and have been exposed to human hunting ever since. Graham is also home
153 to a population of black bear (*Ursus americanus*) that sometime prey on deer fawns (Mathews and
154 Porter 1988, Ballard et al. 2001). Deer densities on Graham have been estimated to exceed 13
155 deer/km² (Engelstoft 2001, Engelstoft et al. 2008). Its forests are characterized by low vegetation
156 cover in the understory [this study and Chollet et al. (2021b)].

157 Finally, we complemented the sites selected on Haida Gwaii with a site on coastal British
158 Columbia, Yeo Island, situated about 15 km north of Bella Bella, where deer are native and
159 exposed to both human hunting, and predators such as wolves (*Canis lupus*) (Darimont et al.
160 2007), black and brown (*Ursus arctos*) bears, and cougars (*Felis concolor*). Forestry operations
161 occur in parts of Yeo and Graham islands.

162 We thus had access to study sites varying in history of deer presence, in hunting history and in
163 deer exposure to large carnivores. On East Limestone, Kunga and Reef we also had access to 27,
164 23 and 8 marked deer respectively that we ear-tagged and GPS collared during a project that took
165 place from 2011 to 2013.

166 **Is vegetation cover and diversity shaped by predation risk?**

167 To assess the links between the vegetation and predation risk, we compared the understory
168 vegetation among sites with different risk histories (Table 1). We estimated the % cover of plant
169 species in the 0 to 1.5 m vegetation layer directly accessible to deer browsing. We used 3.6 m
170 radius (50 m²) vegetation plots: 20 on Kunga and 10 on East Limestone Islands (long term
171 presence of deer, no-risk); 22 on Reef [long term presence of deer, sampled before the deer culls
172 (no-risk) and after the deer culls (past risk)]; 20 on Graham (long term presence of deer, limited
173 but yearly hunting pressure); and 7 on Yeo (predators present and deer hunting). Details of Graham
174 Island sites can be found in Chollet et al. (2021b). We grouped the plant species data into six
175 groups: young conifers, young deciduous trees, shrubs, ferns, forbs, and other herbaceous plants.
176 To characterize the understory cover of these plant groups in the different study sites we used a

177 Principal Component Analysis (PCA) on normalised data in R (R-4.1.0) (Racine 2012)[prcomp
178 function in R (Team 2018)].

179 **Is deer behaviour shaped by predation risk?**

180 To assess and, when appropriate, quantify and compare deer behaviour in relation to risk history
181 we experimentally studied deer Flight Initiation Distance (FID), Distance travelled during flight
182 (Dtravel), and deer response to bait and traps among deer populations. We also compared deer
183 diel activity pattern in relation to risk.

184 We obtained behaviour data on islands without risk (Kunga and East Limestone), with no-risk but
185 subject to previous culling (Reef), with hunting risk (Graham) and with risk from both hunting
186 and natural predators (Yeo). To tease apart the roles of risk history and understory food availability
187 in explaining deer behaviour, we carried out a translocation experiment. We moved deer
188 unexposed to hunting and living in a heavily browsed understory (No-risk Kunga Island), to a
189 post-cull island where a much denser understory had resulted from the past experimental reduction
190 in deer density (post-cull Reef Island). We therefore had behaviour data for seven distinct deer
191 samples that varied in the risk contexts to which they were or had been exposed.

192 Finally, we repeatedly observed deer feeding on beached and attached seaweeds in the intertidal
193 area of rocky shores and beaches, particularly at low tides. These observations led us to conclude
194 that beach feeding exposed deer to higher predation risk than feeding within the forest, because of
195 the open environment where escape routes towards cover were limited by the ocean, and where
196 wave sounds hindered the ability to detect danger by ear [for use of shorelines for by foraging
197 wolves see Klein (1995), Darimont and Reimchen (2002), Roffler et al. (2023)]. To test this
198 hypothesis, we used an indirect approach based on stable isotopes to assess if shores were used
199 less at sites with hunting or with hunting and natural predators than no risk sites. For this we
200 collected bones from deer belonging to all the study populations, to which we added samples from
201 Murchison and Faraday Islands, both without hunting (Fig.1 and Table 1).

202 **Is risk affecting Flight Initiation Distance, and Distance travelled?**

203 FID (Flight Initiation Distance) is the distance at which an animal will start moving away at the
204 approach of a potential predator (Ydenberg and Dill 1986). FID has been considered as a key
205 method to disentangle the “economics” of anti-predatory behaviour, as flight occurs where the
206 decreasing value of remaining, and the increasing cost of not fleeing, intercept (Cooper 2008).
207 According to Lima and Dill (Lima and Dill 1990) FID should, under equal resource level, be
208 shorter in safe areas, and longer in risky areas. We therefore used FID as a comparative metric of
209 wariness, using the following protocol: once the observer detected an individual, it was identified
210 by means of its ear tag number or its morphological features. Then the observer walked slowly
211 and calmly (1.8-2 km/hr) towards the deer, avoiding eye contact. The observer stopped walking
212 when the deer changed its initial behaviour and started moving away, but continued observing the

213 animal. We recorded and used as focal variables two distances: distance from the observer at which
214 the deer starts to move away (FID), and Distance travelled (Dtravel) by the deer between its first
215 location (when flight began) and its second location where it stopped moving away and resumed
216 (foraging) activity. We measured these distances by footstep lengths calibrated in meters after
217 each encounter. In the few instances when flight included deer moving out of sight from the
218 observer we estimated a conservative distance travelled by recording the distance to where it
219 disappeared.

220 We ran such FID experiments during four field seasons from spring 2011 to spring 2014, most
221 during 2011-2012. To avoid the confounding effects of pseudo-replication and deer habituation to
222 the experiment, we discarded repeated measurements on the same individual and only considered
223 the first FID experiment during each encounter of an individual. We retained 218 FID
224 experiments: 73 from Kunga, 133 from East Limestone, and 12 from Reef islands. We had no FID
225 data for Graham or Yeo islands. We included 19 FID observations for the Kunga deer eight months
226 after their translocation to Reef Island, making up four deer samples for this analysis: Kunga and
227 East Limestone (No-risk), Reef (post-cull), and Kunga-translocated.

228 We analysed the two distance variables for these deer samples with a linear model (lm function in
229 R) to fit the linear regression model with the distance variable (FID or Dtravel, both log 10
230 transformed) used as a response variable to assess the effects of risk category. We also analysed,
231 when feasible within deer samples, the effect of deer status (marked/unmarked), sex (M/F) and
232 age class (adult, young) as well as effect of year on FID and Dtravel. We used pairwise
233 comparisons on the linear models with the emmeans package in R which provided t-tests to
234 compare the effects of these variables on our distance variables within deer samples.

235 **Does risk history affect the use of bait and traps, and diel activity?**

236 Neophobia, an adverse reaction to novelty, is an important trait that allows animals to minimize
237 exposure to threats and how to respond to new resources (Greenberg and Mettke-Hofmann 2001,
238 Monestier et al. 2017). We looked at deer use of stations baited with apples and quantified interest
239 in this foreign food by using camera traps (RECONYX PC900) (Le Saout et al. 2015). We also
240 used traps baited with apples to assess the propensity to get trapped as a proxy for exploration
241 behaviour in presence of a foreign object. We baited each bait station daily with 1.5 to 2 apples
242 unless weather impeded fieldwork. For trapping we placed one chopped apple outside the trap
243 entrance, and another one at the furthest end inside the trap near the trigger. Depending on the
244 requirements of each stage of the study, the cameras at bait stations were programmed to acquire
245 from ten to 99 pictures every time the motion sensors were triggered, with a 1s intervals between
246 pictures. A built-in infrared flash with no red glow allowed us to capture images at night or under
247 low light conditions. We recorded: whether or not the deer had been trapped (hence, marked); bait
248 presence at the station (i.e. that it had not been consumed by previous visitors) (yes/no); bait
249 consumption if bait present (yes/no), the time at the beginning and end of a sequence; we also

250 recorded if the deer investigated the ground area where the bait had been before (if bait was absent,
251 yes/no). We set up bait stations monitored with automatic camera for 15 days on East Limestone
252 (no-risk, 4 locations), 12 days on Kunga (no-risk, 4 locations) and 28 days on Reef (post-cull, 8
253 locations). These data were collected between 2011 to 2014, with most visits to bait stations
254 collected in 2011 and 2014.

255 We calculated the rate of visits at bait stations as follows:

256 Rate of visits (visits per day) = (Total visits)/(Nb stations * Nb days stations were monitored)

257 We recorded the tag identity of the marked individuals and identified unmarked individuals using
258 physical features.

259 We used the recorded start time and end time of a feeding sequence to compute the time a deer
260 spent at a bait station when bait was present. We considered time spent at a bait station with bait
261 as a measure of bait friendliness as in Chamailé-Jammes et al. (2014). We used an analysis of
262 variance on log transformed minutes [aov and emmeans functions in R] to compare “time-spent”
263 among deer samples and between marked and unmarked deer within a deer sample. Time spent at
264 bait stations in the absence of bait was analysed similarly using the camera data collected at
265 stations where bait had been consumed during previous visits. We also analysed trapping rate and
266 the propension of individual deer to be trapped repeatedly.

267 To assess diel activity we used all deer observations obtained from automatic cameras during a
268 study on deer vigilance (Le Saout et al. 2015), and during our investigation on the use of bait
269 stations. We used the time recorded to assign observations to day or night, defining day as the
270 period between civil twilight start (morning) and end (evening) for that date, using Reef Island as
271 the reference locality for civil twilights (time difference with the two other localities is < 20s).
272 (<https://www.timeanddate.com/sun/@6118904?month=5&year=2011>). We compared the
273 proportion of day and night observations among sites with a Pearson’s Chi-squared test (R
274 function `chisq.test`).

275 **Translocation experiment: is deer behaviour shaped by food or fear?**

276 To tease apart the relative effects of resource abundance in the understory and of presence or
277 absence of hunting history, we translocated six adult does from heavily browsed Kunga Island
278 (no-risk). These deer had been trapped repeatedly and had been part of the animals subjected to
279 FID. We translocated them in September 2013 to better vegetated Reef Island (post-cull) where
280 they settled among the local deer born post culls [(Burgess et al. 2022a, 2023) and M.A. Russello
281 pers. com.]. We compared their behaviour on Reef Island with their behaviour on their native
282 island and with the behaviour of the post-cull deer native to Reef.

283 The translocated does had been box-trapped, marked and collared as adults in 2011 and had been
284 recaptured multiple times (5 to 22 times each) (Le Saout et al. 2014, Bonnot et al. 2016). We
285 replaced their GPS collars before translocation. In spring 2014 five translocated animals were still

286 present on Reef. No hunting took place on Reef Island during the eight months the translocated
287 animals spent there from September 2013 to May 2014. In May 2014 we tested them for FID,
288 distance travelled and bait avoidance in the same way they had been tested previously on Kunga.
289 We used six bait stations, set up in spring 2014 and distributed across five locations on Reef Island,
290 keeping them active for fourteen consecutive days.

291 **Stable isotope approach: is deer use of exposed shorelines shaped by food or fear?**

292 To determine the proportion of marine algae in deer diets (a measure of shoreline use) on different
293 islands, we examined stable isotope ratios of Nitrogen and Carbon in deer jaw bones collected
294 from all study sites (Table 1). Because marine plants are enriched in ^{13}C compared to terrestrial
295 plants (Balasse et al. 2005, Richards et al. 2006, Schulting et al. 2008), the isotopic signatures of
296 tissues from coastal herbivores can be used to estimate the relative contribution of terrestrial versus
297 marine plants in their diet (DeNiro and Epstein 1978). We collected bones either from hunting,
298 where hunting occurred, or from the forest floor where deer had died from natural causes. On the
299 larger islands [Kunga, Graham and Yeo] we restricted bone collecting to areas less than 1000 m
300 from the shoreline. We obtained jaw bones from East Limestone (10), Kunga (12), Murchison
301 (10) and Faraday islands (6), from pre-cull Reef Island (7), post-cull Reef Island (6), collected 10
302 years or more after the initial culls (2008 to 2014), Graham Island (23), and from the coastal
303 mainland (17).

304 Stable isotope ratios are expressed in the standard delta (δ) notation, defined as parts per mil (‰)
305 deviation from a standard:

$$306 \delta X = [(R \text{ in sample} / R \text{ in reference}) - 1] * 1000 (\text{‰})$$

307 δX gives the deviation between the samples isotopic ratio and the ratio obtained from an
308 international standard, “R in sample” is the isotopic ratio considered, in our case $^{13}\text{C}/^{12}\text{C}$ and
309 $^{15}\text{N}/^{14}\text{N}$. For Carbon, “R in reference” refers to the standard Pee Dee Belemnite (PDB) originally
310 derived from a Cretaceous marine fossil, *Belemnitella americana*, from the Peedee Formation in
311 South Carolina, for Nitrogen the accepted standard is atmospheric N_2 .

312 $\delta^{15}\text{N}$ typically get enriched by about 3‰ when going from one trophic level to the next. At the
313 consumer level the whole animal body $\delta^{13}\text{C}$ closely reflects its concentration in the diet but its
314 fractionation varies among tissues. Values of concentration gain vary from + 1.5‰ in muscle, to +
315 5‰ in consumer’s collagen tissue when compared to whole body values (DeNiro and Epstein
316 1978, 1981, Bocherens 1999, Kelly 2000, Bocherens and Drucker 2003, Camin et al. 2016).

317 To account for and assess spatial variability in isotopic composition of the food potentially
318 consumed by deer, we collected samples of 23 dominant plant species in Laskeek Bay (Reef and
319 East Limestone Islands) and on the coastal mainland, grouping them into: coniferous trees (4
320 species), deciduous trees (2 species), deciduous shrubs (9 species), evergreen shrubs (1 species),
321 ferns (5 species), grasses (5 species). We rinsed fresh samples in distilled water to avoid

322 contamination, pre-dried them in the field-camp cabin and fully dried them in the lab at 40°C for
323 24 hours.

324 We collected or had access to samples from one to thirty individuals of 41 seaweed species (19
325 species of brown, 5 green, and 19 red) collected on Reef Island, Louise Island, and Kunghit Island
326 on Haida Gwaii, and on the coastal mainland. We rinsed each sample collected in fresh water
327 immediately after collection and subsequently decarbonated them by a 5s treatment in acid
328 solution at 7.5%. Finally, we rinsed each sample twice in deionised water (Salomon et al. 2008).

329 Bone samples were cleaned and dried according to a protocol defined by late F. Catzefflis based
330 on (DeNiro and Epstein 1981, Bocherens et al. 1988, Bochérens, Hervé et al. 1991) and dry plant
331 and bone samples were ground into powder at a granulometry of less than 0.7mm. Collagen was
332 extracted from bone powder and treated through a standard protocol following the procedure
333 defined by DeNiro and Epstein (1981) slightly modified by Bocherens et al. (1988), and
334 Bocherens, Hervé et al. (1991).

335 We analysed the isotopic composition of the plant and collagen samples on CO₂ and N₂ obtained
336 by sample combustion and analysed on a mass spectrometer.

337 The isotopic signatures of deciduous trees, deciduous shrubs and forbs were extremely similar.
338 Hence, we grouped them into one cluster “DecHerbs”. Ferns and Grasses were also pooled with
339 the deciduous and forb cluster (DecHerbs) on the basis of palatability to deer (Taylor 1956, Pojar
340 1999). On the basis of their differences in isotopic signatures and their lower palatability to deer
341 we retained conifers as a distinct group (mainly represented by Sitka spruce and western hemlock
342 in the understory) (labelled Conifer), as well as salal (the evergreen shrub, labelled EverShrub).
343 Brown, green and red seaweeds had a restricted spread of isotopic signatures and we pooled them
344 into a single group labelled “Seaweed”.

345 We analysed the isotopic ratios obtained for these four groups of plants (Seaweed, DecHerbs,
346 Conifer and EverShrub) and for the bone samples using a Bayesian multiple source mixing model
347 (MixSIAR package in R) (Stock et al. 2018a, b) data to estimate the proportions of source
348 contributions (here terrestrial and marine plants) to a mixture (bones) (Bochérens and Drucker
349 2003).

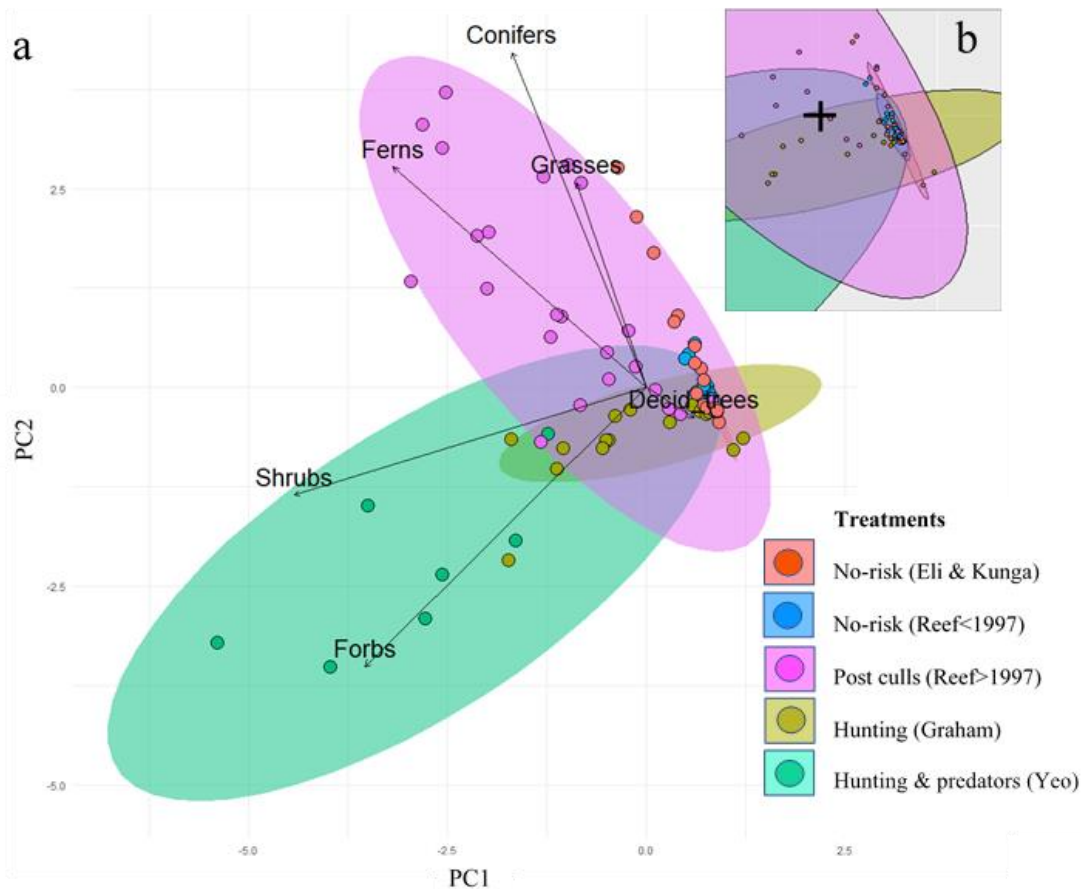
350 **Results**

351 **Understory vegetation varied with risk history**

352 Samples collected in forests with deer, but without a history of hunting (Reef Island prior to culls),
353 Kunga and East Limestone islands), had low vegetation cover in all understory plant groups (Figs.
354 2 and 3). Variability among plots was low (large overlap among samples and reduced spread of
355 plots, small ellipses), with only 4 outlying plots with high cover of conifer regeneration (spruce
356 and hemlock) (Figs. 2 and 3). All samples from sites with recent or current hunting, or hunting
357 plus predation (Reef Island post-cull, Graham, and Yeo islands), had a wider spread of plot

358 coordinates on the first and second principal component plane (Fig. 2). Variability among plots in
 359 understory vegetation was highest for the Yeo Island sample (hunting and predators), and the Reef
 360 Island post-cull sample. Yeo Island plots had a high shrub and forb cover (Figs. 2 and 3), while
 361 those on Reef Island post-cull showed high cover in conifers, ferns and grasses and an increase in
 362 forb and shrub cover (Figs. 2 and 3). Among plot variability was lower on Graham Island, exposed
 363 to a long history of yearly low intensity hunting (Fig. 2) and cover of shrubs, forbs and ferns was
 364 higher (Figs. 2 and 3).

365

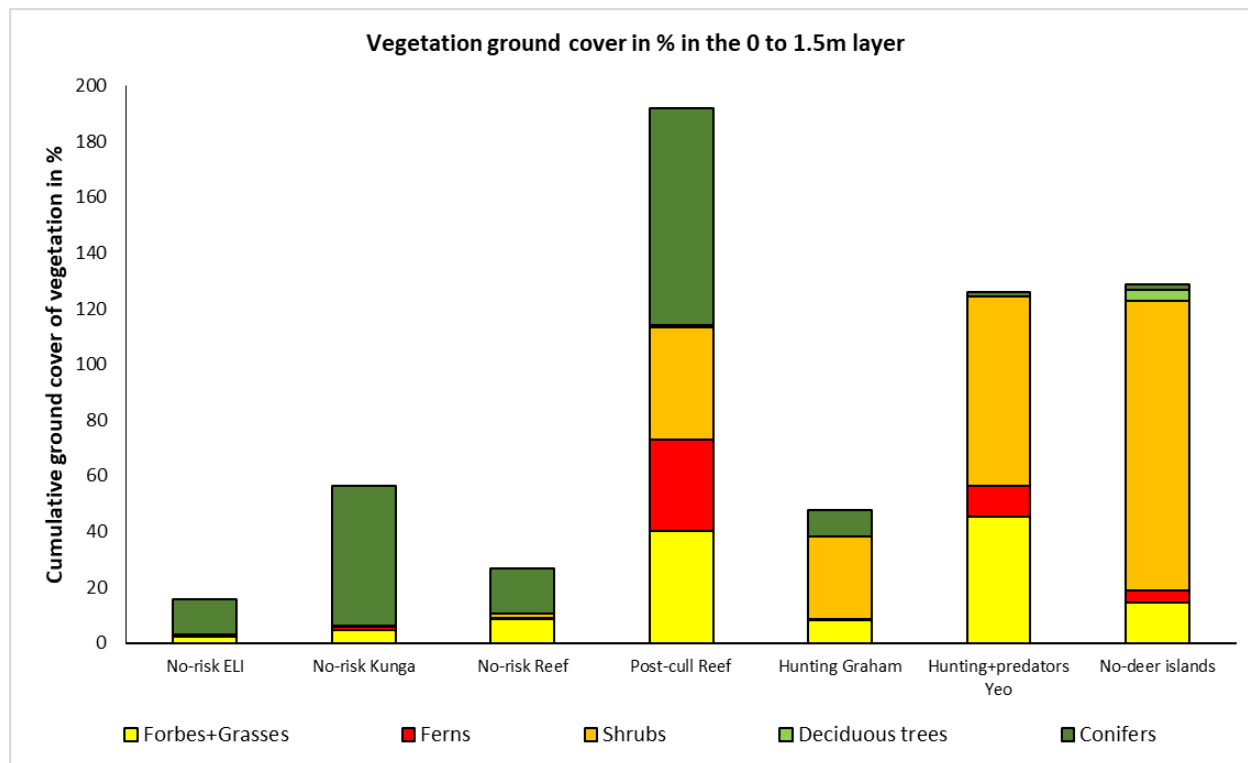


366

367 **Figure 2. a:** Scores of the vegetation plots on the two first components of the Principal Component
 368 Analysis on understory vegetation in relation to the main categories of understory vegetation. Treatments
 369 were color coded post analysis. Treatments are: No hunting represented by [No-risk (East Limestone (Eli)
 370 & Kunga)] = East Limestone and Kunga islands, in red, and [No-risk (Reef<1997)] = Reef island before
 371 the 1997, in blue; Presence of risk through hunting with [Past culls (Reef>1997)] = Reef Island after
 372 the 1997 to 2008 culls, in pink, and [Hunting (Graham)] = long history of yearly hunting, in kaki; Presence
 373 of risk through regular hunting and presence of deer natural predators [Hunting + predators (Yeo)] = Yeo
 374 island, in green. **b:** zoom around plot center showing the ellipses corresponding to the [No-risk (Eli &
 375 Kunga)] (small red shade) and [No-risk (Reef<1997)] (tiny blue shade). Their small extent expresses the
 376 extreme similarity among vegetation plots in these samples. Note the five outliers from Kunga in the [No-
 377 risk (Eli & Kunga)] sample.

378

379



380 **Figure 3.** Cumulative percent cover recorded in the 0 to 1.5 m strata for the main understory plant
381 categories in the different sampling units of our treatment categories: absence of predation risk (No-risk
382 East Limestone and Kunga islands), and No-risk Reef island before the culls (1997); short recent and severe
383 history of hunting (Post-cull Reef Island (2010); long history of only hunting (Hunting Graham); long
384 history of hunting and of natural predator presence (Hunting + predators Yeo); No-deer islands = data from
385 three islands on Haida Gwaii (Laskeek Bay) never colonized by deer (Martin et al., 2010). We lumped
386 herbaceous vegetation into one category.

387 **Flight initiation distance varied with risk category**

388 We collected FID data over several years at East Limestone, Kunga and Reef islands (post-cull):
389 values among years did not differ significantly ($p = 0.60$). Nor did sex or age have any effect ($p =$
390 0.30 , $p = 0.62$ respectively). Combining sexes, ages and years, FID varied significantly among
391 samples ($p < 0.001$; $F = 49.28$ [on 3 predictors, $DF = 233$], residual standard error = 0.24, $R^2 =$
392 0.38). All pairwise comparisons differed significantly (Fig. 4a, Table 2). FID was lowest for “No-
393 risk” samples and highest for the Reef Island post-cull sample. Among the “No-risk” samples,
394 FID was lowest for the East Limestone Island sample and highest for the Kunga deer translocated
395 to Reef Island (Fig. 4a, Table 2).

396

397 **Table 2.** Flight initiation distance (FID) in meter: FID_mean = mean values, FID_sd = standard deviation,
 398 and N = sample size for the different deer categories studied.

399

Deer category	Hunting	FID_mean (m)	FID_sd (m)	N
No-risk ELI (native)	none	6.3	3.7	133
No-risk Kunga (native)	none	11.5	6.8	73
No-risk K on Reef (from Kunga)	none	17.7	12.4	19
Post-cull Reef (native)	culls	28.7	18.0	12

400

401 **Table 3.** Flight initiation distances (FID) in meter and distance travelled after flight (Dtravel) in meter
 402 before resuming activity for the different treatment categories and for marked versus unmarked deer. Events
 403 = total number of visits recorded; Nb. Deer = total number of different deer individuals involved in a
 404 category; Total = total number of marked and unmarked individuals within a treatment. On No-risk Kunga
 405 only marked deer were involved in the FID experiments; the Kunga deer translocated to post-cull Reef
 406 (noted No-risk K on Reef) involved, by design, only marked individuals.

Deer Category	FID	Events	Nb. Deer	Total	Dtravel	Events	Nb. Deer	Total
No-risk East Limestone marked	6.9	78	13	31	6.7	78	13	31
No-risk East Limest. unmarked	5.5	55	18		4.9	56	18	
No-risk Kunga marked	11.5	73	10	10	10.5	72	10	10
No-risk K on Reef marked	17.7	19	5	5	10.1	17	5	5
Post-cull Reef marked	36	5	4	11	41	5	5	10
Post-cull Reef unmarked	23.6	7	7		36.7	6	6	

407

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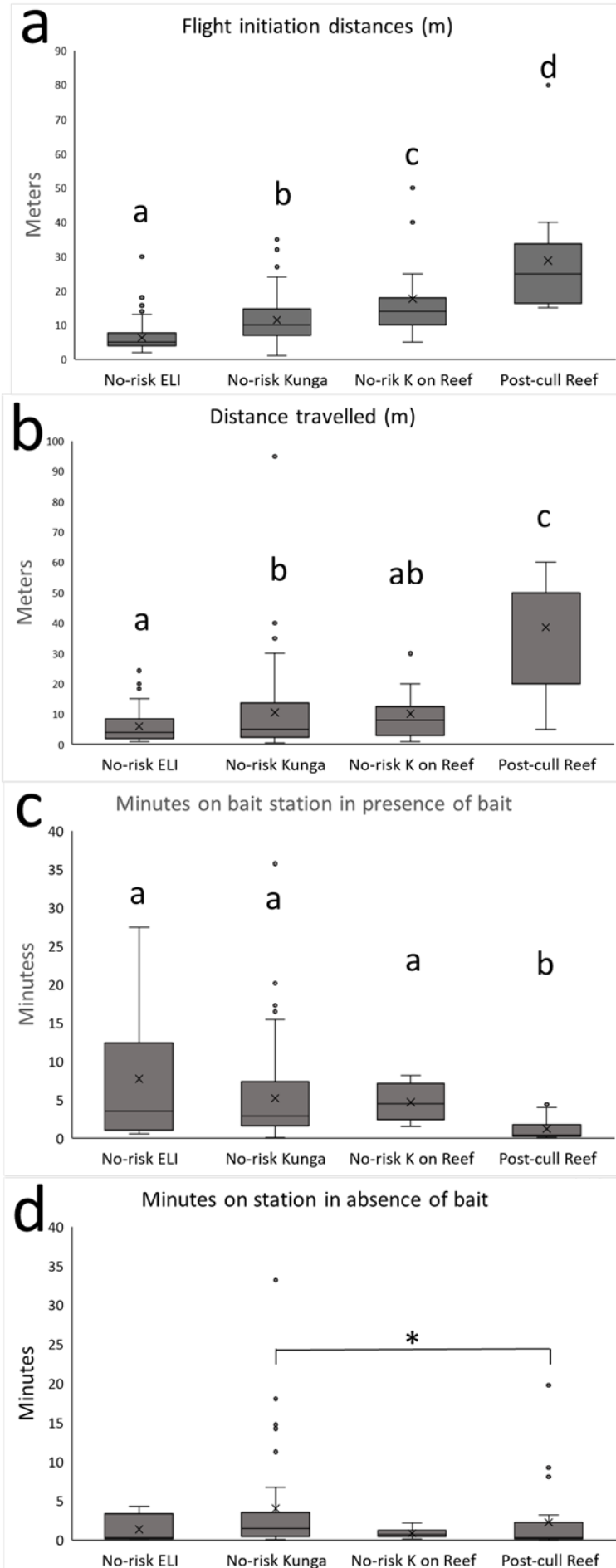


Figure 4. Boxplots on Flight and travel distance and on time spent at bait stations with bait present or absent. No-risk ELI = East Limestone deer, No-risk Kunga = Kunga deer on Kunga Island, No-risk K on Reef = Kunga deer after translocation to Reef Island, Post-cull Reef = Reef Island deer born into 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 (log₁₀ transformed) as a function of deer categories. **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-cull Reef – Post-cull Reef (p = 0.03). **b.** Distance travelled after flight initiation (Dtravel). For Post-cull 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-cull 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-cull Reef (p = 0.37). Only for the No-risk Kunga – Post-cull 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).

451 **Table 4.** Distance Travelled (Dtravel) after flight initiation: Dtravel_mean = mean values, Dtravel_sd =
 452 standard deviation and N = sample size for the different deer categories studied.

Deer category	Hunting	Dtravel_mean (m)	Dtravel_sd (m)	N
No-risk East Limestone (native)	none	6.0	5.8	133
No-risk Kunga (native)	none	10.5	13.7	72
No-risk K on Reef (from Kunga)	none	10.1	8.9	17
Post-cull Reef (native)	cull	38.6	18.4	11

453
 454 Only the samples from East Limestone and Reef Island (post-cull) included marked deer. There
 455 was a marginal trend for longer FID in “No-risk” East Limestone marked deer (t-ratio = 1.85, p =
 456 0.07) (6.9 versus 5.5 m). There was no statistically significant difference in FID between marked
 457 and unmarked deer in “post-cull Reef” (t-ratio = 0.95, p = 0.34) (36 versus 23.6 m) (Table 3).

458 **Distance travelled after flight varied with risk category**

459 Dtravel varied among samples with a significant contrast between the “No-risk” and the “post-
 460 cull” samples: $p < 0.001$; F-statistic = 18.04 (on 3 predictors, DF = 229), Residual standard error
 461 = 0.42, $R^2 = 0.18$. (see Fig. 4b). Dtravel observed on East Limestone Island (No-risk) was
 462 significantly shorter than on Kunga Island (No-risk) ($p = 0.01$), and was much shorter Reef Island
 463 post-cull (Fig. 4b) ($p < 0.001$). Dtravel for Kunga Island deer after translocation to Reef was
 464 similar to that observed on Kunga itself ($p = 0.96$), and to that on East Limestone Island (No-risk)
 465 ($p = 0.12$), but much shorter than that observed for deer native to Reef (“post-cull Reef”) ($p <$
 466 0.001) (Fig. 4b, Table 4).

467 Only the samples from “No-risk East Limestone” and “post-cull Reef” involved marked and
 468 unmarked deer. For “No-risk East Limestone”, Dtravel (log10 transformed) was significantly
 469 higher for marked deer (6.7 m versus 4.9, t-ratio = 2.20, $p = 0.03$). There was no significant
 470 difference in Dflight between marked and unmarked deer in “post-cull Reef” deer (41m versus
 471 36.7, t-ratio = 0.17, $p = 0.86$) (Table 3).

472 **Attraction versus aversion varied with risk category**

473 **Response to bait** – Risk category had a significant effect on time spent at bait stations when bait
 474 was present (log10 transformed): $p = 0.007$, F-statistic = 4.29 (on 3 predictor, DF=79); Residual
 475 standard error = 0.63, $R^2 = 0.14$ (Fig. 4c).

476 When bait was present, deer on islands with no risk, and deer from Kunga translocated to Reef,
 477 spent significantly more time at bait stations than the native Reef Island deer post-cull (Fig. 4c).
 478 The rate of visits at bait stations on islands with no risk history (East Limestone and Kunga)
 479 averaged 0.97 visits/day/station, against 0.20 (five folds lower) for the deer native to Reef post-

480 cull (Table 5.). Frequency of bait consumption per visit exceeded 75% on Kunga and East
481 Limestone (no-risk) (Table 5.) and was 20% for animals native to after the culls on Reef. In the
482 presence of bait, marked deer on East Limestone and Kunga consumed bait in over 80% of the
483 events whereas unmarked deer consumed bait in 61% and 50% respectively of the visits. This is
484 in striking contrast to native deer on Reef post-cull, where only three of the nine native deer
485 trapped and marked post-cull were seen consuming bait at bait stations. Bait remained untouched
486 by the 14 remaining (unmarked) Reef post-cull deer. Unmarked individuals, either briefly
487 investigated the bait (visually and/or olfactory) without consuming it, or ignored it altogether,
488 spending <30 s on site. When comparing median values, less affected by outliers, length of median
489 time spent on a station exceeded 3 min for deer with no hunting history and was less than 30 s for
490 post-cull deer on Reef.

491 As most deer on East Limestone (no-risk) were marked, all visits to a bait station with bait involved
492 marked deer. The deer translocated from Kunga to Reef islands were also all marked. On “No-
493 risk Kunga” and “post-cull Reef” our samples included both marked and unmarked deer. For “No-
494 risk Kunga” deer, seven marked and 21 unmarked deer consumed bait. Forty-two out of 56 visits
495 led to bait consumption. Time spent at a station was significantly higher in marked deer (7.8 min
496 on average) than in unmarked deer (5.6 minutes on average) (t-ratio of contrast estimate = 4.64, p
497 < 0.001). Only unmarked animals visited a bait station without eating the bait, and their mean visit
498 length was less than a minute on average (0.9 min). We observed a similar pattern of longer visits
499 by marked individuals among deer native to Reef post-cull (t ratio of contrast estimate = 3.00, p =
500 0.004). Bait was exclusively consumed by the 4 marked individuals (mean visit length 3.0
501 minutes). The 14 unmarked deer native to Reef Island post-cull visited bait stations on average for
502 0,4 minutes and never consumed any bait.

503 In absence of bait because of previous consumption, mean visit length by deer at a station were
504 shorter (Fig. 4d versus Fig. 4c). Sample still had a significant effect on length of visit at a station
505 (log10 transformed): p = 0.05, F-statistic = 2.72 (on 3 predictor, DF=84), Residual standard error
506 = 0.64, R^2 = 0.09 (Table 5, Fig. 4d), but this effect was unrelated to risk history. Visits were longer
507 on average on Kunga essentially through the effect of outliers spending long periods at sites that
508 had bait recently (Fig. 4d). Whatever the sample, time spent at a station never exceeded 4 minutes
509 (Table 5). Median values equaled 36 s or less, with the exception of Kunga deer (median = 84 s).
510 When time was spent at a station without bait, it was spent sniffing at the location where bait had
511 been present.

512 On Reef, post-cull marked native deer spent significantly longer at stations without bait than
513 unmarked native deer (means of 2.8min versus 0.13 respectively) (t-ratio of contrast estimate =
514 4.0, p < 0.001). On “No-risk Kunga”, there was no significant difference between marked and
515 unmarked deer in time spent at stations (84 versus 90 s) (t-ratio of contrast estimate = 1.42, p =
516 0.16).

517

518 **Table 5.** Deer visits and use of bait stations with bait present in relation to island/hunting history
 519 category. Stations (days) = number of stations set up and number of days each was active; Nb. Visits =
 520 total number of photographic sequences a deer was captured on camera at a bait station; With bait =
 521 number of visits when bait was present; Eat = number of visits in which bait was consumed when
 522 present; Mean length (median) min = mean value of a visit duration in minutes and the corresponding
 523 median value; Without bait = number of visits when bait was absent (= consumed during visits that
 524 followed the re-provisioning of the station; Nb. deer = total number of different individuals involved in
 525 the experiment; Marked = number of marked individuals among the total number of different individuals
 526 involved.

Island/hunting history	Stations (days)	Nb visits	With bait	Eat	Mean length (median) min	No bait	Mean length (median) min	Nb. deer	Marked
No-risk East Limestone	4 (15)	15	8	7	7,7 (3,5)	6	1,4 (0,3)	3	3
No-risk Kunga	4 (12)	90	56	42	5,2 (2,9)	35	4,0 (1,4)	28	7
No-risk K on Reef	5 (16)	31	6	6	4,7 (4,5)	25	0,9 (0,6)	5	5
Post-cull Reef (2011)	8 (35)	9	6	0	1,2 (0,4)	25	2,25 (0,3)	18	4
Post-cull Reef (2014)	5 (16)	35	13	4					

527

528 **Response to traps** – On Reef Island post-cull the capture rate was 90% lower than on East
 529 Limestone and 80% lower than on Kunga (Table 6). Only one third as many animals were captured
 530 on Reef Island post-cull as on the two “No-risk” islands, despite a larger number of capture days
 531 in the former than on the latter (five-fold versus six-fold respectively) (Table 6). The difference in
 532 recapture rates is even more dramatic: 45% and 33% of the deer captured on “No-risk” East
 533 Limestone and Kunga islands were recaptured three times or more (up to 30 times for some
 534 individuals on “No-risk East Limestone”) (Fig. 5). On East Limestone Island, 19 out of 27, and
 535 on Kunga, 15 out of 23 deer, were captured more than once. Even more, 13 of the deer captured
 536 on each island were recaptured three times or more. In contrast, among the deer native to post-cull
 537 Reef Island, only two of nine deer were captured more than once: one twice, and the other
 538 individual repeatedly (Fig. 5).

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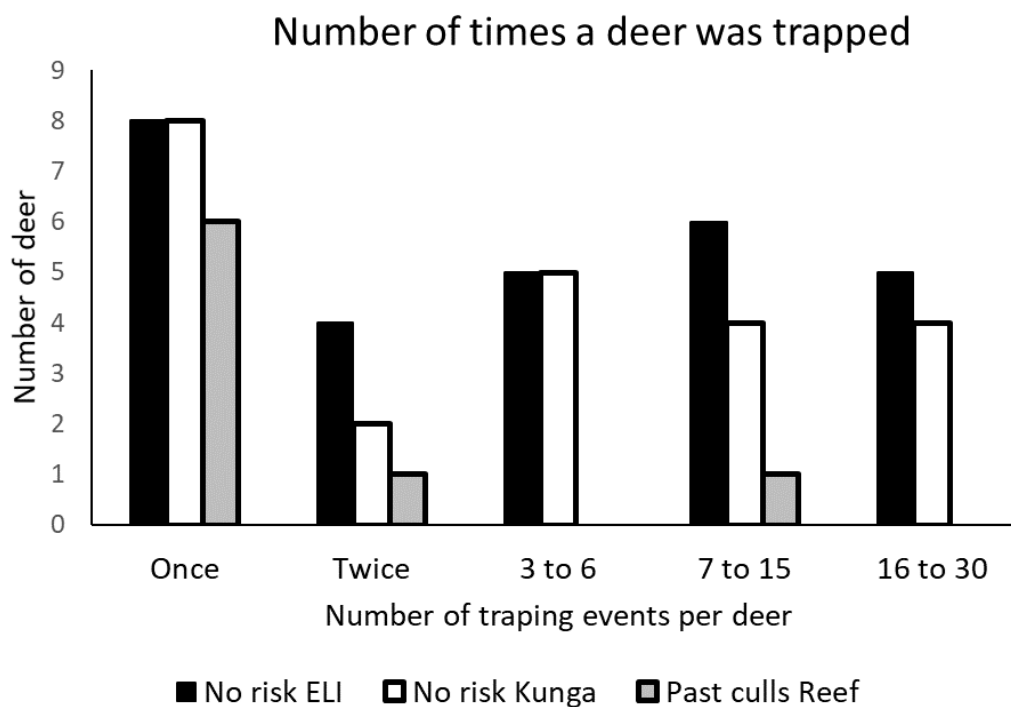
542

543

544 **Table 6.** Summary of box-trap capture data of animals on their native island for all sessions. Total
 545 captures include new deer (i.e. first time captured and marked) and recaptures of the marked individuals.
 546 ELI = East Limestone Island.

Island	Years	Effort boxes * days	Nb. deer captured	captures + recaptures	Trapping success deer/box*day/year
No-risk ELI	2011- 2013	494	27	207	0.42±0.21
No-risk Kunga	2011- 2013	591	23	150	0.22±0.16
Post-cull Reef	2011- 2013	664	8	23	0.04±0.02

547



548

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

551 **Diel activity pattern varied with risk category**

552 Between 2011 and 2014 we recorded 762 (Table 7) picture sequences of deer on automatic
 553 cameras. We used the time recorded on the first picture in a sequence to assign the sequence to
 554 day time or night time. These pictures were taken in spring and early summer, hence a period of
 555 the year of long days and short nights. After correcting for differences in duration of day and
 556 night, deer were more active by day than by night (Fig. 6). There was no significant difference in
 557 daily activity patterns between East Limestone and Kunga islands (no-risk) (Chi-squared = 0.29,
 558 df = 1, p = 0.59) but deer native to post-cull Reef were more nocturnal than either (Chi-squared =

559 10.38, $df = 1$, $p = 0.005$). There was no significant difference between marked and unmarked deer
 560 in diel activity either on Reef Island post-cull or on Kunga Island (Chi-squared = 0.05, $df = 1$, $p =$
 561 0.81).

562

563 **Table 7.** Distribution of deer observations by automatic cameras across sites and their assignment to day
 564 or night with day defined as the period between start of civil-twilight in the morning and end of civil-
 565 twilight in the evening. Night was defined as the period between civil twilight end and civil twilight start
 566 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-cull Reef	115	88	27	24%

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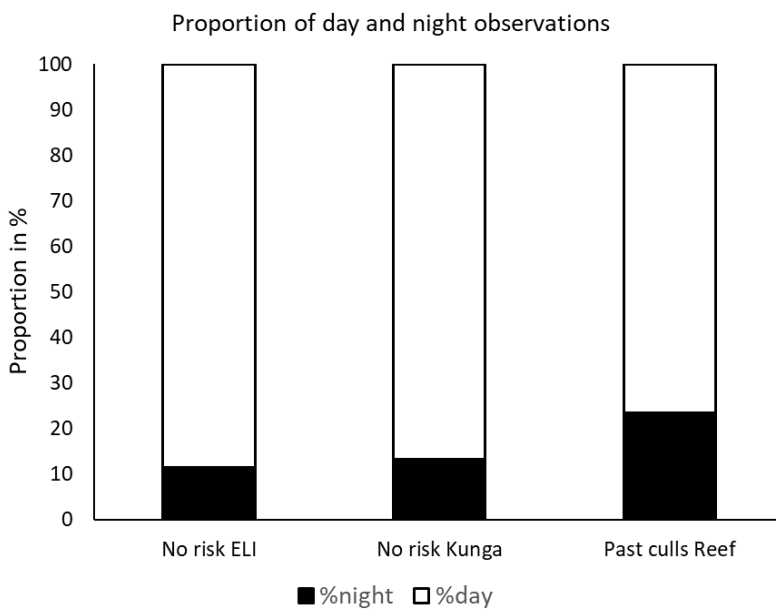


Figure 6. Temporal distribution between day and night of deer caught on automatic cameras near bait stations on islands in the absence of predation risk No-risk ELI (East Limestone) and No-risk Kunga (Kunga) and in presence of past risk (Post-cull Reef)

580 **Stable isotopes as indicator of the propensity to use exposed shorelines**

581 The Gelman-Rubin Diagnostic run after the MixSiar model indicated that only 2 of the 140
 582 variables exceed marginally the threshold value of 1.01. The Geweke diagnostic, a standard z-
 583 score to assess if less than 5% of the 140 variables were outside the +/-1.96 values in each chain
 584 indicated 3%, 5% and 1% for chains 1, 2 and 3 respectively. These diagnostic and tests confirmed
 585 that our Markov Chain Monte Carlo (MCM) chains converged.

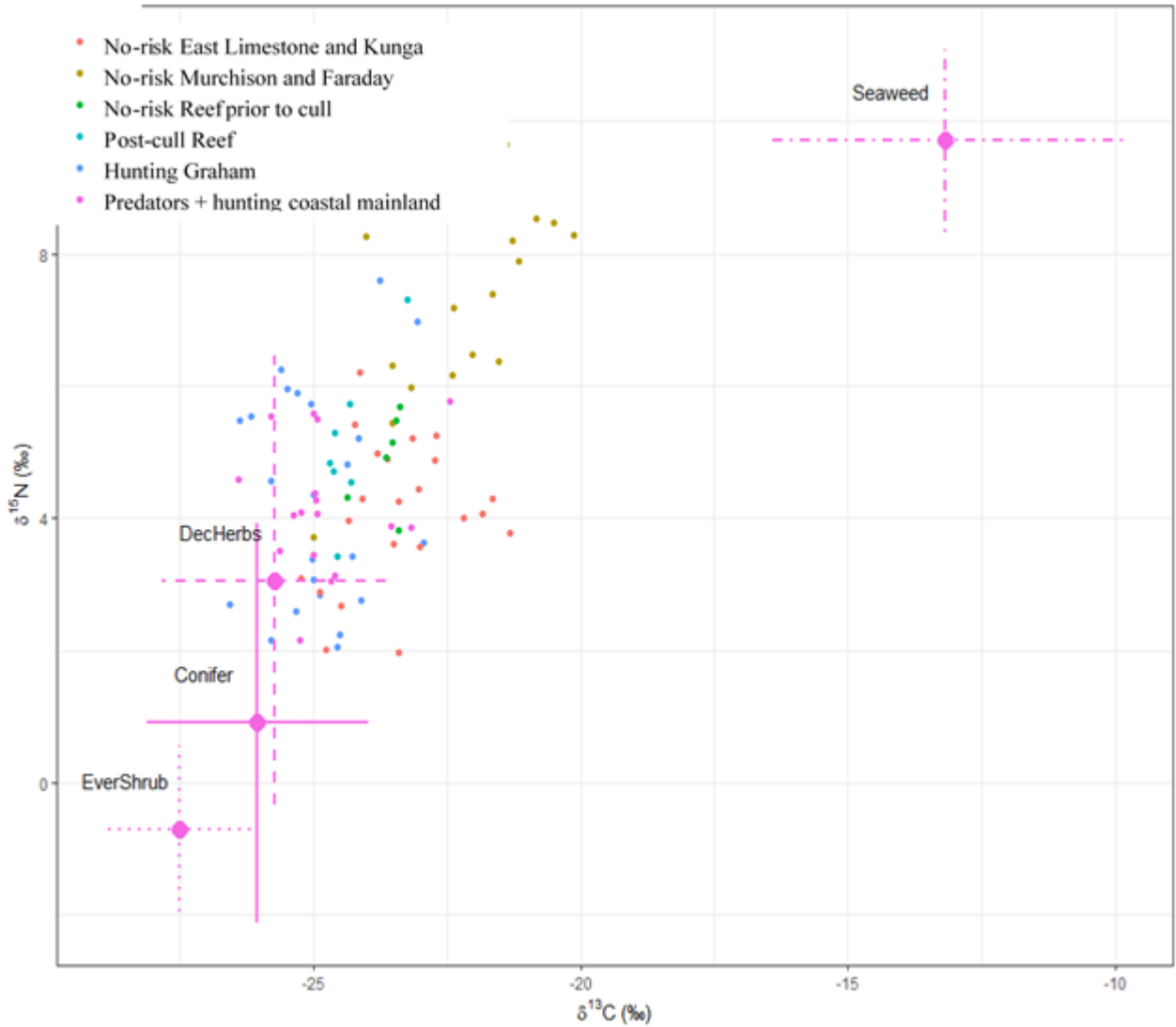
586 The isospace plot (Fig. 7) shows a spread of the isotopic signature in deer bone samples relative
 587 to the proportion of seaweed and terrestrial plants in deer diet. The samples with the highest

588 proportion of seaweed-isotopes in jawbone collagen were from the “No-risk” islands Murchison
589 and Faraday. Those with the least proportion of seaweed isotopes in jawbone collagen were from
590 the islands with risk, “Hunting Graham” and “Predators + hunting coastal mainland”. The plot
591 also indicates a ranking of the terrestrial sources in deer diet. The DecHerbs cluster (Deciduous
592 trees and shrubs, ferns, forbs and grasses) (Fig. 7) made up for the highest proportion. Conifers
593 came next and the evergreen shrub salal (*Gaultheria shallon*) last.

594 The MixSIAR posterior plots (Fig. 8) illustrate the proportion of the four plant categories retained
595 in deer diet in the different deer categories. The proportion of seaweed isotopes in bone collagen
596 reached 31% on “No-risk” Murchison and Faraday, and was 19.2% in “No-risk” sites in Laskeek
597 Bay (East Limestone, Kunga and Reef prior to the cull). It dropped to 8 and 9.6% respectively in
598 sites with hunting (“Hunting Graham”) or with predators and hunting (“Predators + hunting coastal
599 mainland”). It was intermediate (13.5%) in the post-cull Reef deer born after the cull.

600 Bayesian credible intervals at 95% of seaweed proportions (Fig. 8) confirm the contrast in the
601 proportion of seaweeds between the samples from no-risk situations (Murchison, Faraday, East
602 Limestone, Kunga and Reef before the cull), and the two sites with hunting and/or predators
603 (Graham and coastal mainland). They also illustrate the intermediate position of the post-cull Reef
604 sample.

605 In all situation the isotope data suggests that deer diets were dominated by the terrestrial plants
606 group that included deciduous trees and shrubs, ferns, forbs and grasses. Its proportion varied from
607 67% on “No-risk” Murchison and Faraday samples to 88% on “Hunting Graham” and in
608 “Predators + hunting coastal mainland” samples. Conifers and evergreen shrubs stand out as a
609 minor component of diet, despite their prevalence in the vegetation profiles of some of our study
610 sites (see Fig. 3). The proportion of seaweeds in the “No-risk” Murchison and Faraday samples
611 are remarkably high.



612

613 **Figure 7.** Isospace plots of deer and plants Mixture data (deer) by risk category and islands. No-risk
 614 Murchison and Faraday = No-risk samples from Murchison (N=10 bone samples) and Faraday (N=6); No-
 615 risk samples from East Limestone (N=10) and Kunga (N=12); No-risk samples from Reef Island prior to
 616 the culls (N=7); Post-cull Reef = samples from Reef Island after the culls (N=6); Hunting Graham =
 617 samples from Graham Island (N=23); Predators + hunting = samples from the coastal mainland (N=17).
 618 Source data are by risk/island categories and have been adjusted by discrimination means and SDs.
 619 Terrestrial plants, EverShrub = evergreen shrub, Conifer, DecHerbs = deciduous trees and shrubs, forbs,
 620 ferns and grasses; Seaweed (40 species). Error bars indicate 1 SD, the combined source+discrimination SD
 621 calculated under assumption of independence as:

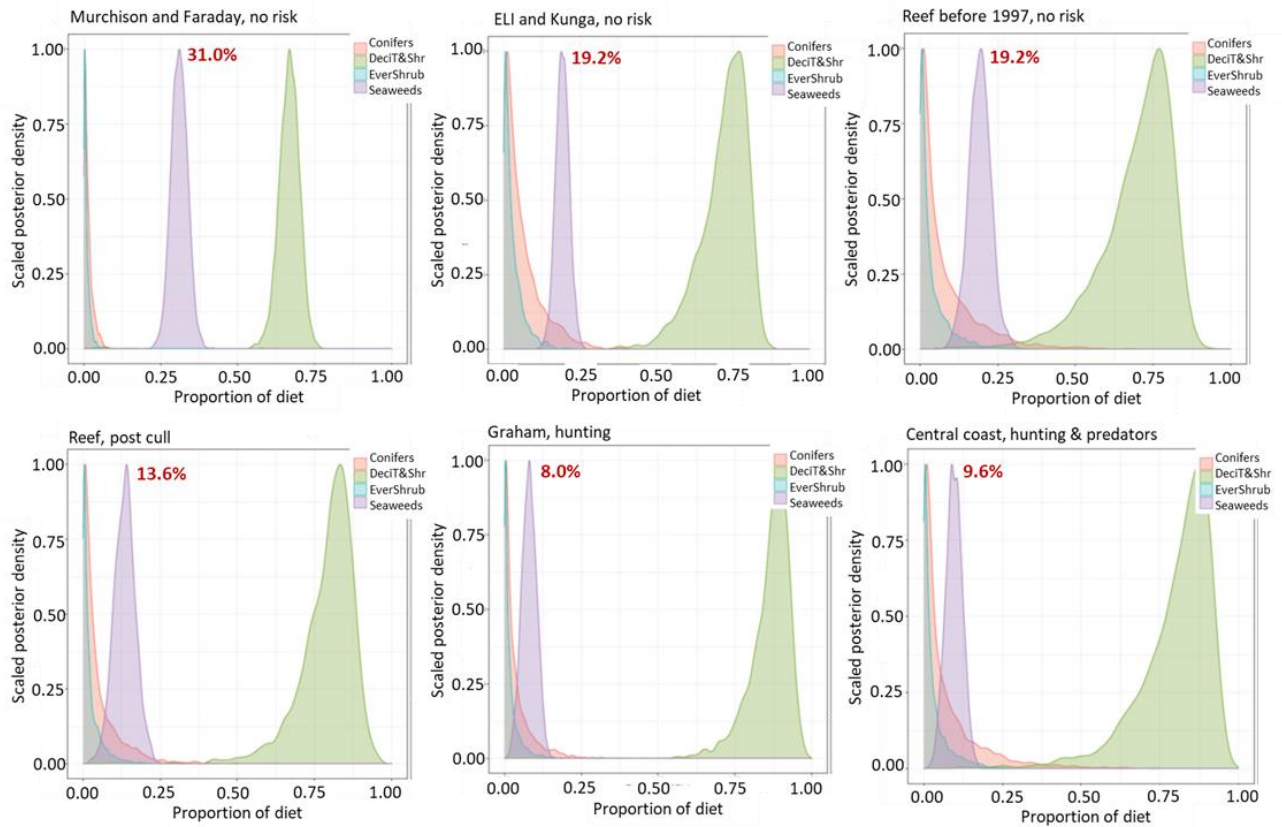
$$\sqrt{\sigma_{source}^2 + \sigma_{discr}^2}$$

622

623

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625



626 **Figure 8.** MixSiar posterior plots of overall deer diet in relation to predation risk. N = number of bone
 627 samples per site. No hunting history, four sites: Murchison (N=10), Faraday (N=6), East Limestone (ELI)
 628 (N= 10), Kunga (N=12) and Reef before the culls (N=7)) (see map in Fig. 1); Reef post-cull = samples
 629 from Reef Islands collected after the culls (2008-2014) (N=6); Yearly relatively low intensity hunting
 630 without marked effect on high deer density (Engelstoft, 2001) Graham Island coastal area (N=23); Coastal
 631 mainland, hunting and predators present (N=17). All profiles are at the same scale. Murchison and Faraday
 632 are two islands with vegetation poor understories (see text and Martin, Gaston & Hitier (1995)). The peaks
 633 of the shaded areas represent the median estimate of the proportion of the different sources in deer diet.
 634 Conifers (Sitka spruce, western hemlock and western and yellow redcedar) (pink shading) (4 species, 13
 635 samples), evergreen shrubs (light blue shading) (1 species (salal), 4 samples), green shading = deciduous
 636 trees and shrubs, forbs, ferns and grasses) (27 species, 86 samples). Seaweeds (purple shading) (40 species,
 637 237 samples). Red figures indicate median percent value).

638

639

640

642 How did understory vegetation cover and dynamics change with predation risk?

643 Our results illustrate the well-established effect that large herbivores have on vegetation in the
644 absence of predation risk (Côté et al. 2004, Martin et al. 2010a, 2011, Cardinal et al. 2012a, b,
645 Chollet et al. 2021b). They also illustrate the relationship between the impact of herbivory on
646 the vegetation and the risk history a deer population is exposed to (Callan et al. 2013, Waller
647 and Reo 2018). The severe culls on one of our sites (Reef Island) resulted, over a decade, in an
648 upsurge of understory vegetation and of regenerating conifers in an initially heavily-browsed
649 open understory (Figs. 2 and 3). The increase in beta diversity (spread of plots, Fig. 2) in the
650 post-cull Reef Island sample illustrates the response of vegetation cover and composition
651 (Chollet et al. 2016). However, there are intrinsic differences between this recovering
652 understory vegetation and the understory vegetation we sampled on Yeo Island where deer
653 have always been subject to their natural predators and hunters. On post-cull Reef Island, we
654 interpret the high proportion of regenerating conifers in the understory as the legacy of heavily
655 browsed pre-cull patches of dwarfed spruce and hemlock and their dramatic release after the
656 culls (Chollet et al. 2016). By contrast, the vegetation profile we observed in the presence of
657 large carnivores and hunting on Yeo, close to the coastal mainland, is remarkably similar to
658 the understory vegetation profile we observed on three islands in Laskeek Bay where we found
659 no evidence of deer [see details in (Stockton et al. 2005, Martin et al. 2010)]. Their understories
660 lack the significant conifer cover observed on post-cull Reef and are dominated by shrubs,
661 forbs and grasses (Fig. 3).

662 On Graham Island, where hunting is of low intensity and restricted to sites most accessible to
663 the small local population of hunters (Martin and Baltzinger 2002), hunting had a smaller effect
664 in mitigating deer over-browsing, resulting in a beta diversity (spread of plots, Fig. 2) and
665 proportions of different vegetation components (Fig. 3) intermediate between Yeo Island and
666 islands without predation (Engelstoft 2001, Engelstoft et al. 2008, Chollet et al. 2021b)]. This
667 suggests an interplay among the presence of risk, its intensity (hunting versus culling), its
668 nature (humans versus natural predators) and its duration in the interaction between deer and
669 their habitat.

670 Does lack of risk favor bold deer, and does presence of risk favor shy deer?

671 Our comparison of anti-predator behaviours between populations that had not been exposed to
672 hunting (East Limestone and Kunga Islands), with a population on Reef Island that had been
673 subject, over a decade prior to the study, to a severe population reduction through experimental
674 culling, revealed clear behavioural contrasts among these populations. Deer exposed to
675 different risk history responded differently to cues mimicking predation risk. They also differed
676 in their response to foreign food at bait stations, and to foreign food associated with an

677 unfamiliar object. The significantly shorter flight initiation distances, and much shorter
678 distances travelled, observed in non-hunted populations were retained by the Kunga deer
679 translocated to Reef, even though they showed slightly longer flight initiation distances in their
680 novel environment. This was in stark contrast with the wary behaviour of the deer native to
681 post-cull Reef, even more so as the flight and travel distances we recorded for the post-cull
682 Reef deer were likely conservative: they often fled before being seen (flight diagnosed by ear)
683 and often were still running when they disappeared from view. This suggests that we
684 underestimated distances travelled and that actual values on Reef may have been closer to
685 values reported in black-tailed deer populations on the mainland (FID ~ 60 to 70 m and Dtravel
686 ~ 70 to 120 m), where deer can be subject to hunting, poaching and carnivores (Stankowich
687 and Coss 2006, 2007, Stankowich 2008). Our field notes also indicated that animals native to
688 post-cull Reef ran or trotted away, whereas deer from Kunga and East Limestone (no-risk
689 islands) usually performed a slow walk to a nearby location where they resumed their activities.

690 Among the “No-risk” deer categories, FID and distances travelled were significantly shorter
691 on East Limestone than on Kunga. This may reflect some habituation to human presence
692 (Rodriguez-Prieto et al. 2009, Schuttler et al. 2017) on East Limestone Island where people are
693 present daily for two to three months each summer for ecological monitoring.

694 Despite minor differences in flight distances or time spent at bait, marked and unmarked deer
695 of the same island had comparable behavioural profiles. In particular, marked and unmarked,
696 deer from post-cull Reef Island were predominantly shy, as is illustrated by their poor trapping
697 rate, even when we take into account that deer densities on post-cull Reef were still at only
698 50% of their pre-cull density (~30 deer/km², i.e. >80 deer present) (Chollet 2012). Only two
699 (25%) of the eight deer captured on post-cull Reef were ever re-captured, and only one was
700 recaptured repeatedly, mostly as a yearling and a juvenile, before becoming trap shy the
701 following years while still captured on cameras. This contrasts with deer unexposed to risk on
702 East Limestone and Kunga, where over half of the deer trapped were re-trapped at least 3 times,
703 often much more often over the years (Fig. 8).

704 The presence on Kunga and Reef (post-cull) of a fraction of animals never trapped, but captured
705 on automatic cameras, indicated within population variation in trap-shyness of individuals (Sih
706 et al. 2012). Observed differences in behaviour between deer native to East Limestone and
707 Kunga Islands (no-risk) and those native to Reef Island post-cull, suggest that culling shifted
708 the dominant behaviour profiles of Reef Island deer towards the shy-end of a boldness-shyness
709 continuum.

710 Food limitation and nutritional status have also been proposed as mechanisms explaining
711 individual attenuation in antipredator behaviours such as flight response to an approaching
712 threat (Stankowich 2008, Gaynor et al. 2019). Such individual behavioural-adjustments,
713 motivated by food shortage, should be lifted once food supply improves. This could explain

714 the higher values of FID and Dtravel observed for Reef Island deer post-cull, as well as the less
715 wary behaviour of deer living in heavily browsed understories. However, we did not observe
716 any effect of food availability in the deer we translocated from Kunga to Reef. These animals
717 did not change their behaviour despite a large increase in their available food supply. Our
718 observations better fit the hypothesis that less wary behaviour was enabled by the absence of
719 risk. Less wary behaviour could progressively favour individuals investing more in foraging
720 and less in costly anti-predator behaviours. Less costly anti-predator behaviours such as routine
721 vigilance would be retained and not counter-selected as observed for the populations of East
722 Limestone and Kunga where routine vigilance persisted in an otherwise tame population.
723 (Chamaillé-Jammes et al. 2014, Le Saout et al. 2015).

724 In non-hunted populations we suggest that the need to adjust to an increasingly depleted
725 understory explains a progressive shift towards bolder behaviour in the population. On Reef,
726 we suppose that severe culling may have resulted in a strong selection of the wariest individuals
727 best equipped to elude hunters (Terry Husband pers.com). From an initial population not
728 hunted and living in a heavily browsed habitat (Martin et al. 1995, Chollet et al. 2016), those
729 animals that survived were shyer and with a tendency to be more active at night than the mean
730 for the pre-cull population. The higher proportion of night time activity in post-cull Reef deer
731 is consistent with the predicted shift towards more nocturnality in response to increased hunting
732 (Altendorf et al. 2001, Bonnot et al. 2020, Palmer et al. 2022). The overall predominance of
733 diurnal activity in the “No-risk” East Limestone and Kunga deer populations has been shown
734 to contrast with the behavioural patterns commonly observed elsewhere in hunted populations
735 (Bonnot et al. 2016). But a higher proportion daytime activity in non-hunted deer populations
736 on Haida Gwaii may also be interpreted as responding to the need for increased foraging time
737 in intensively browsed understories.

738 **Does attenuation of anti-predator behaviour favour deer density?**

739 Stockton et al. (2005) showed that, even on islands with the most severe deer impact on the
740 understory within our study area, deer densities remained high, exceeding 20 deer per km².
741 However, Le Saout et al. (2014) showed that less than 5% of the resources needed by these
742 dense deer populations were provided by the rare standing biomass. In summer the bulk of deer
743 forage was provided equally by a cryptic flux of growing vegetation and by canopy fall in the
744 form of foliage shed by wind. In winter canopy fall was the dominant source of forage
745 supplemented by seaweed available on the shorelines (Le Saout et al. 2014). But these
746 resources, while sufficient, occurred in small spatially-dispersed cryptic items in contrast with
747 the volume and distribution of palatable foliage and plant material in lush understories on
748 islands without deer (Martin et al. 2010) or with limited deer impact as on Yeo (Fig. 3).
749 Spatially dispersed food occurring as small items, could favour behaviour that increases
750 foraging time at the expense of time devoted to costly anti-predator behaviours (Réale et al.

751 2010, Sih et al. 2012) such as flight or dynamic adjustments of spatial distribution in response
752 to perceived distribution of risk (Williams et al. 2008, Gaynor et al. 2019). This could favour
753 a progressive decrease in understory vegetation, as was actually shown on these islands by
754 (Chollet et al. 2015) between 1989 and 2009.

755 **Did (the absence of) risk affect the use of exposed habitats?**

756 Cursorial predator hunting by sight should increase the reluctance in their prey to use open
757 habitats (Bonnot et al. 2017). In addition, the lush understory on Yeo Island, similar in cover
758 and diversity to the understory of islands never colonized by deer, or the lush understory on
759 post-cull Reef Island, may reduce the incentive to use the shoreline in these deer. The data on
760 understory vegetation (Fig. 3), also suggest a potential for a negative relationship between the
761 amount of vegetation in the understory and the proportion of seaweed signature in deer bone
762 collagen. The very high seaweed isotopic signature on “No-risk” Murchison and Faraday,
763 could, for instance, be interpreted as the consequences of a lack of understory forage on these
764 two islands. The vegetation data collected in 20 plots on “No-risk” Murchison Island in 1993
765 (Martin et al. 1995) indeed recorded less than 4% of ligneous and herbaceous vegetation cover
766 in the 0 to 1.5 m layer, making it one of the least vegetated understories in the archipelago [see
767 Fig. 2 in Martin et al. (1995), an observation confirmed by more recent visits to Murchison,
768 also see Chollet et al. (2015)]. In contrast to the other islands, Murchison and Faraday islands
769 had been subjected to extensive logging in the first half of the 20th century, resulting in a dense
770 canopy, further reducing forage for deer. Such a high proportion of seaweed in ruminant diet
771 is not unheard of, in particular in conditions where other resources were scarce or unavailable.
772 Seaweeds accounted for up to 50, and even 100%, of the diet of some sheep in primitive North
773 Ronaldsay (Orkey islands) sheep (Balasse et al. 2005) that were confined to the shoreline.

774 However, the two situations with the lowest and similar proportion of seaweed isotopes in
775 jawbone collagen, “Hunting Graham” on Haida Gwaii, and “Predators + hunting” on the
776 coastal mainland, show a dramatic contrast in their cover of understory vegetation. On Yeo
777 Island the permanent presence of predators and hunting is associated with the presence of a
778 lush understory. On Graham the long history of moderate hunting, restricted to areas most
779 accessible to a limited number of hunters (Martin and Baltzinger 2002), had a limited impact
780 on deer density (Engelstoft 2001, Engelstoft et al. 2008) and Graham understories were closer
781 to those on islands with deer but no hunting, than to Yeo understories where predators and
782 hunting occur (Figs. 2 and 8) (Pojar 1999, Chollet et al. 2021b).

783 Post-cull Reef Island represented an intermediate situation. The severe episode of hunting
784 during the experimental culls resulted in a severe, (temporary) reduction in deer abundance
785 triggering a rebound of understory vegetation; an upsurge of resources that could arguably
786 explain the decrease observed in the proportion of seaweeds in their diet after the culls.

787 However, given the lack of a perfect correlation between the proportion of seaweeds in deer
788 diet and the abundance of forage in the understory, our results are still consistent with a
789 prediction of an increased reluctance to use more exposed habitats or localities when risk is
790 higher (Williams et al. 2008, Bonnot et al. 2017). The regular decrease in seaweed signature in
791 bone collagen when going from islands without hunting history to islands where current
792 hunting and predators occur, and the reduced seaweed signature in the bones of deer from
793 Graham (hunting) and coastal mainland (predators and hunting), despite their contrast in the
794 abundance of understory vegetation, are suggestive that the risk history on a site negatively
795 affects deer propensity to feed on shorelines a habitat repeatedly shown of high value and use
796 for foraging wolves (Klein 1995, Darimont and Reimchen 2002, Roffler et al. 2023).

797 Our results from the stable isotope analysis also documented (Fig. 6) a preference for deciduous
798 vegetation in deer diet (Taylor 1956, Pojar 1999) that exceeded its relative abundance in the
799 understory (Fig. 3).

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

801 Our research adds to the small number of studies that attempted to integrate animal behaviour
802 with the study of the mechanisms that govern ecological dynamics, species interactions,
803 population change and ecosystems [see (Sih et al. 2004, 2012, Réale et al. 2007, Chitwood et
804 al. 2022)]. We demonstrate that the introduction of a novel threat (i.e., hunting on Reef Island)
805 caused an abrupt change in behaviour which afterwards left the norm for the survivors far
806 outside the range of observed behaviour on islands without hunting – the sort of behaviour seen
807 for Reef Island deer post-cull was never witnessed for deer never exposed to risk on Kunga or
808 East Limestone islands. The survivors on Reef probably included animals that modified their
809 behaviour more rapidly than those that were culled and, if some or all of that variation in
810 behaviour was under genetic control (Réale et al. 2007), subsequent generations will have been
811 shyer than the one that was culled. The consequent increases in FID, Dtravel, novelty aversion
812 and nocturnal foraging have persisted and been inherited or adopted by young reared
813 subsequently, so that the behaviour of the current population resembles that of populations
814 subject to natural predation and human hunting. However, there is little sign that the deer
815 translocated from Kunga Island and hence never exposed to predation threat, adopted any of
816 the modified behaviour of the local post-cull deer. This interpretation of a rapid change in
817 dominant behaviours in a population echoes the recent documentation of rapid differential
818 selection of inheritable antipredator behaviours and physical traits in a mammal in response to
819 novel predation (Moseby et al. 2023)

820 Our results are consistent with the hypothesis that changes in the landscape of fear (Gaynor et
821 al. 2019, Palmer et al. 2022) can alter the behaviour characteristic of a population. Such
822 changes can result from severe differential selection of certain behavioural syndromes driven
823 by acute risk (e.g. as in the case of severe culling), or, over longer periods of time, from the

824 progressive reproductive advantage of behavioural profiles better adapted to a changing
825 environment (e.g. driven by a progressive depletion of resources in absence of acute predation
826 risk). Although this remains speculative in the case of the non-wary behaviours we observed
827 on islands without predation or hunting, it illustrates a potential for long term selection. The
828 rapidity of adaptive behavioural change will depend on the magnitude of the selective pressure
829 (Blumstein 2002, Jolly et al. 2018, Moseby et al. 2023). It can be rapid if severe culling is
830 maintained over generations continuously but will presumably be slower in the case of the
831 relaxation of antipredator behaviours after the colonisation of a predator free environment
832 (Blumstein 2002). The evolution of predator naivety in island organisms provides numerous
833 text-book examples of long-term progressive (or fast) evolutionary shifts in behavioural traits
834 (Darwin 1840, Lack 1968, Blumstein 2002), but see Blumstein and Daniel (2005).

835 Our results on shifts in behaviour within a population when the risk context changes have
836 implications for conservation. They can help mitigate the problems posed by the adjustment of
837 focal species towards a novel threat, or facilitate success in species restoration programs where
838 the release of naïve captive bred individuals have to adjust to predators (Moseby et al. 2015,
839 2016, 2023). They can also bring insights to management of overabundant populations through
840 hunting. In such instances, a better grasp of behavioural responses to management actions can
841 help design strategies that prevent species adjusting their spatial distribution and diel rhythms
842 to the threat posed by novel management measures (Williams et al. 2008).

843 Improving our understanding of mechanisms that could, over time, lead to evolutionary shifts,
844 in addition to the multifaceted consequences of loosing species from ecological networks,
845 could help better foreseeing the full impact of neglecting the integrity of species assemblages.
846 It would fuel the arguments necessary to prevent such losses, and encourage the conservation
847 and restoration of fully functioning ecosystems. The role left to modern humans in these
848 systems, in place of the significant influence they certainly had on their dynamics for millennia
849 as gatherers and hunters, remains to be defined.

850

851 **Ethical note**

852 All research was conducted under the appropriate animal care permits from the Wildlife Act
853 of the Ministry of Natural Resources Operation of British Columbia (No. NA11-68421,
854 approved by Parks Canada Animal Care Task Force research permit No. 9059), and under the
855 Archipelago Management Board of Gwaii Haanas National Park Reserve and Haida Heritage
856 Site research permit No. GWA-2011-8373. All except 3 deer captures were done using box
857 traps specially designed for this project (the exceptions were one individual captured by a
858 clover trap and two by a netgun). We made over 400 deer captures or recaptures in the course
859 of the project. Traps were radio-monitored remotely and we dealt with captured animal
860 immediately after capture notification. The animals captured at night were treated the following

861 morning. We recorded no injury to deer, nor mortality associated to capture. The project
862 permits included the experimental culls on one island and the translocation of a small number
863 of deer from one island to another. Culls were conducted by local hunters under clear ethical
864 and practical rules. Carcasses were processed and the meat distributed to the local
865 communities.

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882

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

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

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891

892 **Conflict of interest disclosure**

893 The authors declare that they comply with the PCI rule of having no financial conflicts of
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896

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