



**HAL**  
open science

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

Jean-Louis Martin, Simon Chamailé-Jammes, Anne Salomon, Devana  
Veronica Gomez Pourroy, Mathilde Schlaeflin, Soizic Le Saout, Annick Lucas,  
Ilham Bentaleb, Simon Chollet, Jake Pattison, et al.

### ► **To cite this version:**

Jean-Louis Martin, Simon Chamailé-Jammes, Anne Salomon, Devana Veronica Gomez Pourroy, Mathilde Schlaeflin, et al. From fear to food: predation risk shapes deer behaviour, their resources and forest vegetation. 2024. hal-04381108v4

**HAL Id: hal-04381108**

**<https://hal.science/hal-04381108v4>**

Preprint submitted on 10 Sep 2024

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

3  
4  
5 Jean-Louis Martin<sup>\*1</sup>, Simon Chamaille-Jammes<sup>1</sup>, Anne Salomon<sup>2</sup>, Devana Veronica Gomez  
6 Pourroy<sup>1</sup>, Mathilde Schlaeflin<sup>1</sup>, Soizic Le Saout<sup>1</sup>, Annick Lucas<sup>1</sup>, Ilham Bentaleb<sup>3</sup>, Simon  
7 Chollet<sup>4</sup>, Jake Pattison<sup>5</sup>, Soline Martin-Blangy<sup>6</sup>, Anthony J. Gaston<sup>7</sup>

8  
9 <sup>1</sup> CEFE, Univ Montpellier, CNRS, EPHE, IRD - Montpellier, France

10 <sup>2</sup> School of Resource & Environmental Management, Simon Fraser University - Burnaby, Canada

11 <sup>3</sup> University of Montpellier, UMR 5554 CNRS, IRD, EPHE, CC061 - Montpellier, France

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

14 <sup>5</sup> Laskeek Bay Conservation Society - Daajing Giids and Skidegate, Canada

15 <sup>6</sup> 81 rue Marius Carrieu, 34080 Montpellier, France

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

18  
19 \*Jean-Louis Martin

20 Correspondence: [jean-louis.martin@cefe.cnrs.fr](mailto:jean-louis.martin@cefe.cnrs.fr)

21

22 **Abstract**

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

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

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

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

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

51 We interpreted our results as evidence that experience of risk was key in shaping behavioural  
52 contrasts between deer populations and their effect on plant cover and diversity, ecological  
53 networks, and ecosystem complexity.

54

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

58 From its outset, Ecology was defined as the science of interactions (Haeckel 1866; Elton 1927).  
59 Interactions were first assessed by observing direct relationships among species. Over time, the  
60 increasing sophistication of empirical and experimental approaches improved our understanding  
61 of ecological systems and revealed the importance and intricacies of indirect interactions. This  
62 brought key insights into the central role of the interplay between herbivores and their predators  
63 in the structure, function and stability of ecological systems [(Paine 1966, 1969; Estes et al. 2011)  
64 and review in (Martin et al., 2020)]. Consequently, while the loss of species or populations across  
65 the world's ecosystems is dire, the loss of species interactions is perhaps even more insidious,  
66 because it often goes unnoticed (Janzen 1974; Soulé et al. 2003; Valiente-Banuet et al. 2015). The  
67 loss, or addition, of key players in the ecological fabric will affect, directly or indirectly, day to  
68 day processes in an ecosystem, and, over time, potentially select for traits and behaviors better  
69 adapted to the new state of the ecological network (Bøhn & Amundsen 2004; Ellers et al. 2012;  
70 Estes et al. 2013; Potratz et al. 2024).

71 The conceptual framework proposed by "the ecology of fear" (Brown et al., 1999; and reviewed  
72 in Zanette & Clinchy, 2020) emphasized the central role that animal behaviour plays in species  
73 interactions and their impact on ecosystems. It focused on the non-consumptive effects that  
74 predator presence, including human hunters, can have on prey behaviour and on the ways in which  
75 those prey interact with their habitat, giving rise to the idea of a "landscape of fear" (Laundré et  
76 al. 2001; Gaynor et al. 2019, 2021; Zanette & Clinchy 2020). This fostered predictions not only  
77 about how spatial and temporal variation in perceptions of risk directly affected predator-prey  
78 interactions, but also about how the presence of predators may shape the impact their prey have  
79 on ecosystems (Gaynor et al. 2019; Zanette & Clinchy 2020; Palmer et al. 2022). Focusing on  
80 ungulates, and deer in particular, Altendorf et al. (2001) predicted that, in presence of predators  
81 and in the absence of limitations in forage, deer should spend less time foraging at any given  
82 location, limit or avoid using portions of their habitat perceived as more exposed to (e.g. because  
83 of high visibility), or favour sites perceived as refuges from risk (e.g. through dense vegetation)  
84 (Williams et al. 2008; Padié et al. 2015; Bonnot et al. 2017; Martin et al. 2018; Clare et al. 2023).  
85 Conversely, absence of risk should eliminate spatial effects of risk on foraging (Zanette & Clinchy  
86 2020). However, studies on how risk affected habitat use by large herbivores remain limited. In  
87 some systems studies showed that prey favoured foraging in more open habitats because of better  
88 visibility of an approaching threat (Gigliotti et al. 2021; Kamaru et al. 2024). In other studies, in  
89 particular on deer, risk perception resulted in prey avoiding open habitats for foraging (Kilgo et  
90 al. 1998; Creel et al. 2005; Bonnot et al. 2013; Dellinger et al. 2019).

91 Although our understanding of the ecology of fear has made dramatic advances, we need to better  
92 integrate animal behaviour, ecology and evolution (Réale et al. 2007; Sih et al. 2012; Potratz et al.  
93 2024) to show how risk influences habitat selection and ecological dynamics. Our ambition is to

94 help address that need and to provide insights on how the ecology of fear can help better address  
95 conservation needs and strategies (Chitwood et al. 2022; Potratz et al. 2024) at a time when high  
96 deer populations in parts of Europe and North America, and their returning predators, wolves,  
97 interact in complex ways with human activities, such as farming, livestock husbandry, or forestry  
98 (Kuijper et al., 2016; Martin et al., 2020)

99 In this study we review and synthesize several studies carried out since 1997, supplemented by  
100 additional data, to evaluate how the presence or absence of predation risk affected the interplay  
101 between deer effects on forest ecology and deer behaviour. We took advantage of the introduction,  
102 at the end of the 19th century, of Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) to Haida  
103 Gwaii, a remote archipelago in British Columbia, western Canada (Fig. 1) lacking the natural  
104 predators these deer are exposed to on the adjacent mainland (Golumbia et al. 2008). The  
105 archipelago provided islands with and without deer, and, where deer were present, islands with  
106 and without a history of hunting by people. This arrangement of islands with varied hunting  
107 histories provided a quasi-experimental context in which to study how absence or presence of  
108 predation risk shaped deer impact on the forest vegetation and their behaviour. Our long-term  
109 study-sites on Haida Gwaii were complemented with data from the Central Coast of British  
110 Columbia where deer always faced natural predators in addition to hunters (Darimont & Paquet  
111 2001, 2002; Darimont et al. 2007). There, black-tailed deer represented over 80% of wolf diet  
112 (Darimont & Paquet 2001).

113 With this life-size laboratory, our objective was to explore the importance of predation risk in the  
114 ecological dynamics of these forests. We hypothesized that the absence of risk would reduce fear  
115 in deer, causing them to increase their impact on forest ecology through an even more dramatic  
116 reduction in forest vegetation cover and diversity (Côté et al., 2004; Martin et al., 2010; Stockton  
117 et al., 2005). We used data from our long-term studies on deer impact on their environment and  
118 more recent data on deer behaviour in presence or absence of risk. We predicted that understory  
119 vegetation would be restricted to a small group of plant species able to resist, even if only as  
120 severely browsed and stunted individuals (Martin et al., 2010). We also predicted that  
121 experimental culling, in a deer population initially not exposed to risk, would trigger a positive  
122 response in vegetation cover and affect anti-predator behaviours possibly years after the culls  
123 (Martin & Baltzinger 2002; Gaynor et al. 2019; Clare et al. 2023; Wójcicki & Borowski 2023). In  
124 particular we expected to see longer deer flight initiation distance (FID) after detection of a  
125 potential human threat, longer distance travelled after detection, a reduction in deer use of foreign  
126 bait and a lower likelihood of being trapped in the post-culls deer population. We also predicted  
127 these deer would differ in their diel activity towards being more nocturnal when compared to  
128 populations not exposed to risk from day-hunting humans (Kilgo et al. 1998; Bonnot et al. 2020).

129 Wolf introduction to Coronation Island in SE Alaska (Klein 1995) resulted in extensive use of  
130 shorelines by wolves and in a dramatic spatial shift in deer away from the coastal portions of the  
131 island [for use of shorelines by foraging wolves see also Darimont & Reimchen (2002); Roffler et

132 al. (2023)]. Access to hunting grounds by humans in the BC Central Coast, essentially roadless,  
133 and on Haida Gwaii is often by boat [L. Vigneault pers. com. and Irvine & Thorley (2024)]. This,  
134 and our own observations of deer foraging frequently on beached and attached seaweeds in the  
135 intertidal area of rocky shores and beaches (Bonnot et al., 2016) led us to predict that the lack of  
136 cover on beaches, the limitation of escape routes by the ocean, and wave sounds hindering the  
137 ability to detect danger by ear, might all negatively affect foraging in open intertidal sites with  
138 natural predators scouting the area and/or human hunters approaching from the water. We tested  
139 this prediction indirectly by comparing the proportion of marine algae in deer diet under  
140 contrasting risk contexts.

141

142

## Material and Methods

### 143 Haida Gwaii and the study sites

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

149 Native to coastal British Columbia, but not to Haida Gwaii, Sitka black-tailed deer were  
150 introduced to the archipelago in the late 19th century (Golumbia et al. 2008), colonizing all but a  
151 few small islands. The absence of natural predators on the archipelago allowed the deer population  
152 to thrive. The occurrence of a few reference islands that never supported deer made it possible to  
153 demonstrate that, on islands with long-term deer presence, independent of island size, deer  
154 herbivory was the main factor structuring plant and animal communities (Martin and Baltzinger  
155 2002, Gaston et al. 2006, Martin et al. 2010, Chollet et al. 2013), with important consequences on  
156 belowground processes (Chollet et al. 2021b; Maillard et al. 2021). Recurrent experimental culls  
157 on two islands allowed us to monitor the response of the aboveground vegetation and avifauna for  
158 13 years (Chollet et al. 2016). These results accumulated over the different phases of the long-  
159 term RGIS project <https://rgis.cefe.cnrs.fr/>.

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

168 estimated around 30 deer / km<sup>2</sup> (Daufresne & Martin, 1997; Martin et al., 2010; Stockton et al.,  
 169 2005) an estimate that has been repeatedly confirmed in the course of deer culls (Gaston et al.  
 170 2008a; Irvine & Thorley 2024).

171

172 **Table 1.** List of islands included in the study and their key characteristics. Risk hist. = Risk history; Deer  
 173 = presence or absence of deer; Island = island name; Hunting: Y = seasonal hunting, Y(cull) = repeated  
 174 culls; N = no hunting; Predators: Y = present (wolves and possibly cougar and grizzly bear), N = absent;  
 175 Vegetation plots: figures = number of standardized plots on vegetation structure and composition, N = no  
 176 standardized sampling; Isotope = collection of bones for the stable isotope study (section 2.3.4.): Y = bone  
 177 samples collected and analyzed, N = no bone sampling done; Reef <1997 = conditions on Reef prior to  
 178 experimental culls; Reef >1997 = conditions after the culls that occurred between 1997 and 2008; \* =  
 179 Islands that provided data only for the study on stable isotopes (section 2.3.4). + = bones were sampled in  
 180 the area of BC Central Coast between Yeo and Bella Bella.

181

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

182  
 183  
 184  
 185



186

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



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

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

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

216 We thus had access to study sites varying in history of deer presence, in hunting history and in  
217 deer exposure to large carnivores. On East Limestone, Kunga and Reef we also had access to 27,  
218 23 and 8 marked deer respectively that we ear-tagged and GPS collared during a project that took  
219 place from 2011 to 2013.

## 220 **Does vegetation cover and diversity increase with predation risk?**

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

227 young deciduous trees, shrubs, ferns, forbs, and other herbaceous plants. We used a Principal  
228 Component Analysis (PCA) on centered and standardized cover data in R (R-4.1.0) (Racine  
229 2012)[prcomp function in R (Team 2018)] to characterize variation in the cover of these plant  
230 groups in the understory when deer are present or not and under different contexts of risk from  
231 hunters and/or predators.

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

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

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

257 Data on FID was obtained on islands without risk (Kunga and East Limestone), on an island  
258 initially without risk but subjected to culling (Post-culls Reef), and on an island with a hunting  
259 season (Graham). As the expression of fear can be affected by resource availability (Cooper 2008)  
260 we created a translocation experiment by moving six adult does from Kunga island, where they  
261 were not exposed to hunting and where the understory was heavily browsed, to Reef Island, where  
262 heavy culling in the 1990s had created a much denser understory. On Kunga, the translocated does  
263 had been box-trapped, marked and collared as adults in 2011 and had been recaptured multiple

264 times (5 to 21 times each) (Le Saout et al. 2014a; Bonnot et al. 2016). Three of the six translocated  
265 animals had been subjected to five, seven and 19 FID measures on Kunga in 2011 and 2012. We  
266 replaced their GPS collars before their translocation to Reef in September 2013 where these  
267 animals settled among the local deer born after the culls [(Burgess et al. 2022a, 2023) and M.A.  
268 Russello pers. com.]. In spring 2014, five of the translocated animals were still present on Reef.  
269 We tested FID behaviours of translocated and local deer in the same way as on Kunga.

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

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

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

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

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

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

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

$$326 \delta X = [(R \text{ in sample} / R \text{ in reference}) - 1] * 1000 \text{ (‰)}$$

327  $\delta X$  gives the deviation between the samples’ isotopic ratio and the ratio obtained from an  
328 international standard, “R in sample” is the isotopic ratio considered, in our case  $^{13}\text{C}/^{12}\text{C}$  and  
329  $^{15}\text{N}/^{14}\text{N}$ . For Carbon, “R in reference” refers to the standard Pee Dee Belemnite (PDB).

330  $\delta^{15}\text{N}$  typically gets enriched by about 3‰ when going from one trophic level to the next. At the  
331 consumer level the whole animal body  $\delta^{13}\text{C}$  closely reflects its concentration in the diet but its  
332 fractioning varies among tissues. Values of concentration gain vary from + 1.5‰ in muscle, to +  
333 5‰ in consumer’s collagen tissue when compared to whole body values (DeNiro & Epstein 1978,  
334 1981; Bocherens 1999; Kelly 2000; Bocherens & Drucker 2003; Camin et al. 2016).

335 To test our prediction that risk from hunters and/or predators could limit the use of the intertidal  
336 areas for foraging, we analysed the proportion of stable isotopes of terrestrial plant or seaweed

337 origin in deer diets on different islands, using deer jaw bones from all the study populations, to  
338 which we added bone samples available from Murchison and Faraday Islands, both hunting-free  
339 islands (Fig.1 and Table 1). We obtained these bones either from hunting, or from deer that had  
340 died from natural causes. On the larger islands (Kunga, Graham and the coastal area adjacent to  
341 Yeo) we restricted bone collecting to areas less than 1000 m from the shoreline. We obtained 10  
342 jaw bones from East Limestone, 12 from Kunga, 10 from Murchison, six from Faraday, seven  
343 from pre-cull Reef, all without hunting, six from Post-culls Reef, collected 10 years or more after  
344 the initial culls (2008 to 2014), 23 from Graham Island (hunting), and 17 from the central coast  
345 district between Bella Bella and Yeo Island (predators + hunting). We cleaned and dried bones in  
346 the field.

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

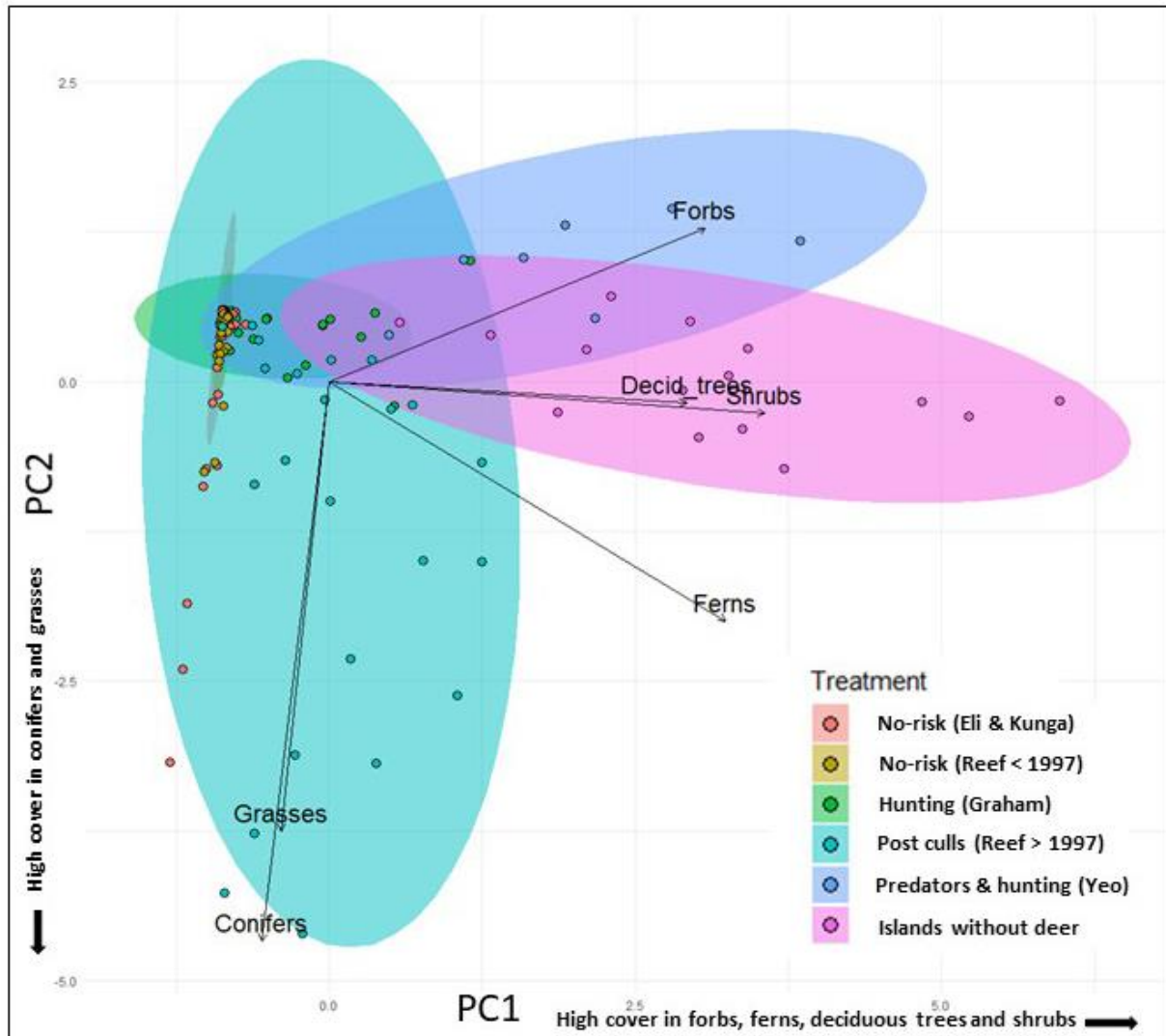
356 Dry bone and plant samples were ground to a granulometry of less than 0.7mm. Following  
357 protocols defined by late F. Catzeflis based on DeNiro & Epstein (1981), Bocherens et al. (1988),  
358 and Bochérens, Hervé et al. (1991). We extracted bone collagen from bone powder in the  
359 laboratory.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

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

368  
369  
370  
371  
372  
373

**375 Understory vegetation varied with risk history**

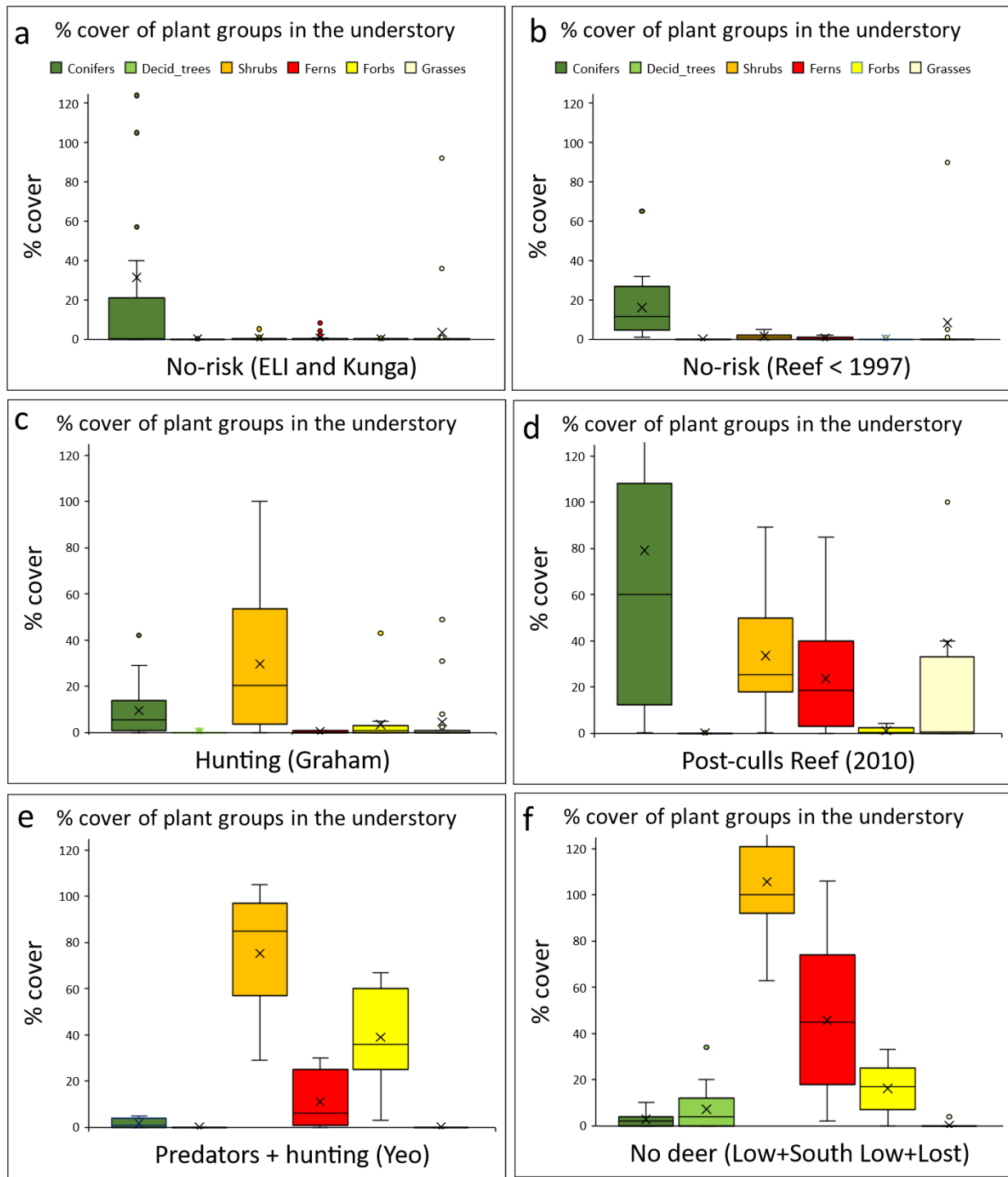
376 High vegetation cover and diversity was found on islands without deer and on those where deer  
377 were present but exposed to predators and hunting (Figs. 2 and 3). Their understories were  
378 dominated by forbs, shrubs, and ferns (Figs. 2 and 3). The samples from Reef Island (Post-culls)  
379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



395

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

404



405  
 406  
 407  
 408  
 409  
 410  
 411

**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.



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

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

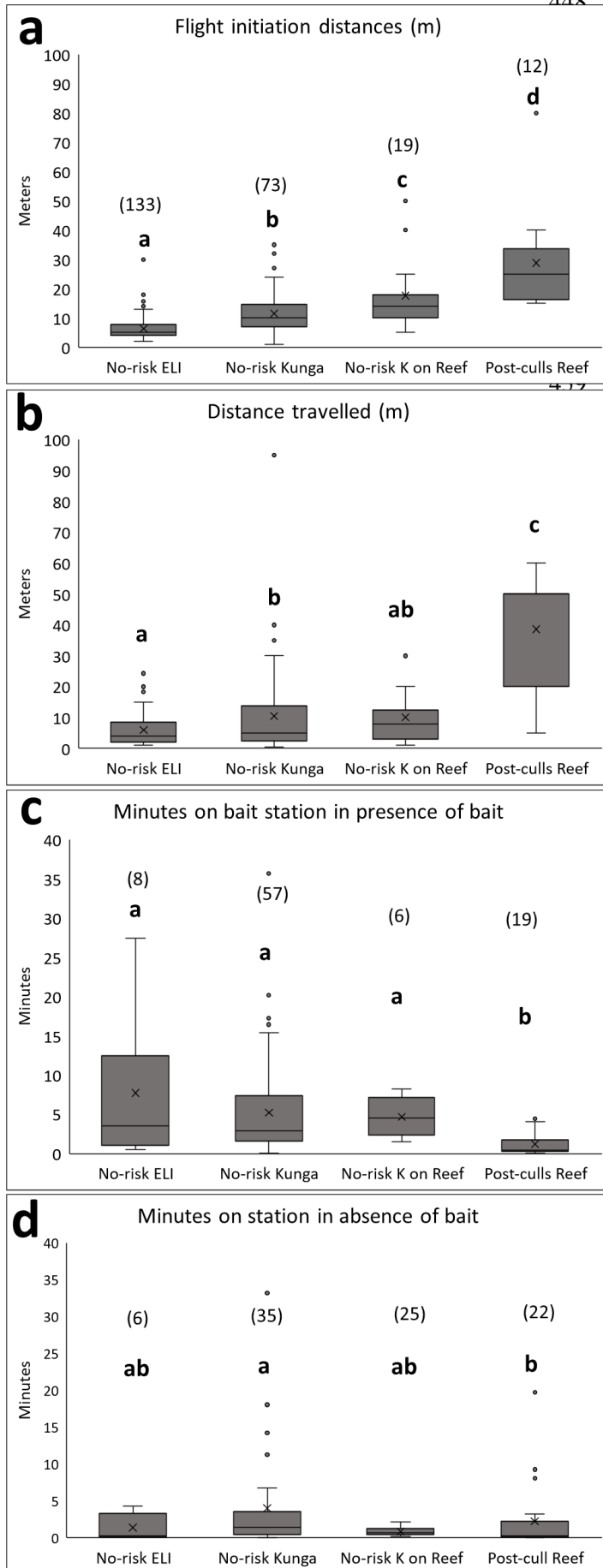
418 Values did not differ significantly among years within samples ( $p = 0.60$ ). Nor did sex or age have  
419 any effect ( $p = 0.30$ ,  $p = 0.62$  respectively). Thus we combined sexes, ages and years.

420 FID varied significantly among treatments [ $R^2 = 0.38$ ,  $F_{(3, 233)} = 49.28$ ,  $p < 0.001$ ] (Fig. 4a). FID  
421 was lowest for islands without hunting and highest for Post-culls Reef. Among the islands without  
422 hunting, FID was lowest on East Limestone and highest for Kunga deer translocated to Reef (Fig.  
423 4a).

424 Samples from No-risk East Limestone and from Post-culls Reef included marked and unmarked  
425 deer. Differences in FID between marked and unmarked deer were non-significant [for East  
426 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  
427 versus 23.6 m)].

428 **Distance travelled** - Dtravel varied significantly among treatments [ $R^2 = 0.18$ ,  $F_{(3, 229)} = 18.04$ ,  $p$   
429  $< 0.001$ ]. Deer from populations without hunting travelled significantly shorter distances than deer  
430 on Reef after the culls (Fig. 4b). Dtravel on East Limestone Island was significantly shorter than  
431 on Kunga Island ( $p = 0.01$ ), and much shorter than on Post-culls Reef Island (Fig. 4b;  $p < 0.001$ ).  
432 Dtravel distances for Kunga deer translocated on Reef did not differ from those on Kunga ( $p =$   
433  $0.96$ ), or from Dtravel observed on East Limestone ( $p = 0.12$ ) and was only one third that of native  
434 Reef deer ( $p < 0.001$ ) (Fig. 4b). On East Limestone, marked deer moved significantly further than  
435 unmarked deer [ $t$ -ratio = 2.20,  $p = 0.03$ , (6.7 m versus 4.9)] but this did not apply to marked and  
436 unmarked deer on Reef [ $t$ -ratio = 0.17,  $p = 0.86$  (41m versus 36.7)].

437 **Response to bait** – Risk category had a significant effect on time spent at bait stations when bait  
438 was present ( $\log_{10}$  transformed): deer on islands without hunting and deer from Kunga translocated  
439 to Reef, spent significantly more time at bait stations with bait than native Reef deer ( $R^2 = 0.14$ ,  
440  $F_{(3, 79)} = 4.29$ ,  $p = 0.007$ ; Fig. 4c) and visited them five times more often (0.97 against 0.20; Fig.  
441 4c, Table 2). Bait consumption per visit was three times higher on Kunga and East Limestone than  
442 for native deer on Reef (75% against 20%) (Table 2). On East Limestone and Kunga marked deer  
443 consumed bait in 50-80% of their visits in contrast to native deer on Reef, where only three of the  
444 nine deer trapped and marked consumed bait at bait stations. None of the 14 unmarked deer  
445 observed on Reef touched bait which they investigated briefly or ignored altogether (mean visit  
446 length 24 s). Length of median values in time spent on a station, less affected by outliers, exceeded  
447 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 ( $p = 0.04$ ).

490 At Kunga marked deer spent significantly more time at a station than unmarked deer (7.8 min on  
 491 average against 5.6 minutes) (t-ratio of contrast estimate = 4.64,  $p < 0.001$ ). Some unmarked  
 492 animals visited a bait station without eating bait (mean visit length 54 s). Among deer native to  
 493 Reef, marked individuals also spent longer at bait stations (t-ratio of contrast estimate = 3.00,  $p =$   
 494 0.004) and were the only deer consuming bait (mean visit length 3.0 minutes).

495 In absence of bait because of previous consumption visit length at a station were short (Fig. 4d  
 496 versus Fig. 4c). They were longest on Kunga through the effect of outliers spending long periods  
 497 at sites that had bait recently (Fig. 4d). Time spent at a station never exceeded 4 minutes and was  
 498 spent sniffing at where bait had been present. On Reef, marked native deer spent significantly  
 499 longer at stations without bait than unmarked native deer (means of 2.8min versus 0.13  
 500 respectively) (t-ratio of contrast estimate = 4.0,  $p < 0.001$ ). On No-risk Kunga, there was no  
 501 significant difference between marked and unmarked deer in time spent at stations without bait  
 502 (84 versus 90 s) (t-ratio of contrast estimate = 1.42,  $p = 0.16$ ).

503

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

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

512

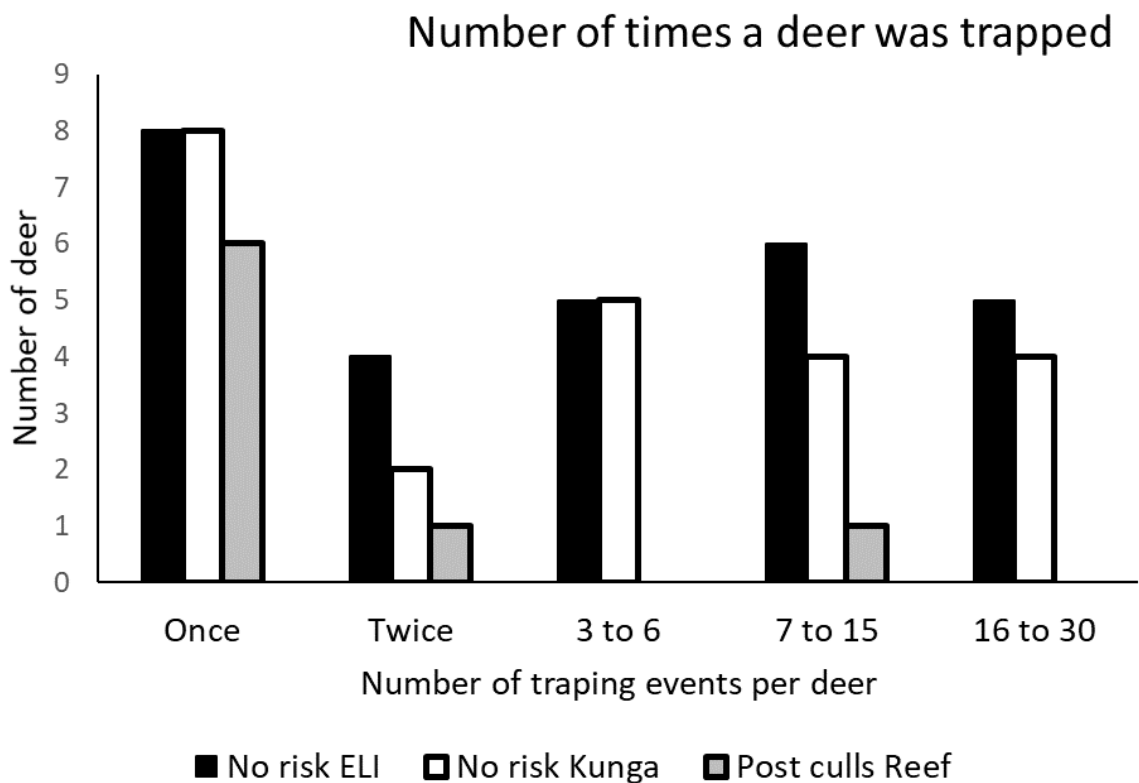
513

514 **Response to traps** – On Reef Island (Post-culls) the capture rate was 80-90% lower than on islands  
 515 without hunting (Table 3) and only 2/8 were captured more than once, compared to 35/51 for the  
 516 others including a majority of individuals captures more than 3 three times (Fig. 5).

517 **Table 3.** Summary of box-trap capture data of animals on their native island for all sessions. Total captures  
 518 include new deer (i.e. first time captured and marked) and recaptures of the marked individuals.

Island	Years	Effort boxes * days	Nb. deer captured	captures + recaptures	Trapping success deer/box*day/year
East Limestone	2011- 2013	494	27	207	0.42±0.21
Kunga	2011- 2013	591	23	150	0.22±0.16
Reef	2011- 2013	664	8	23	0.04±0.02

519



520

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

523

524

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

534

535 **Table 4.** Distribution of deer observations by automatic cameras across sites and their assignment to day  
 536 or night with day defined as the period between start of civil-twilight in the morning and end of civil-  
 537 twilight in the evening. Night was defined as the period between civil twilight end and civil twilight start  
 538 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%

539

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

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

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

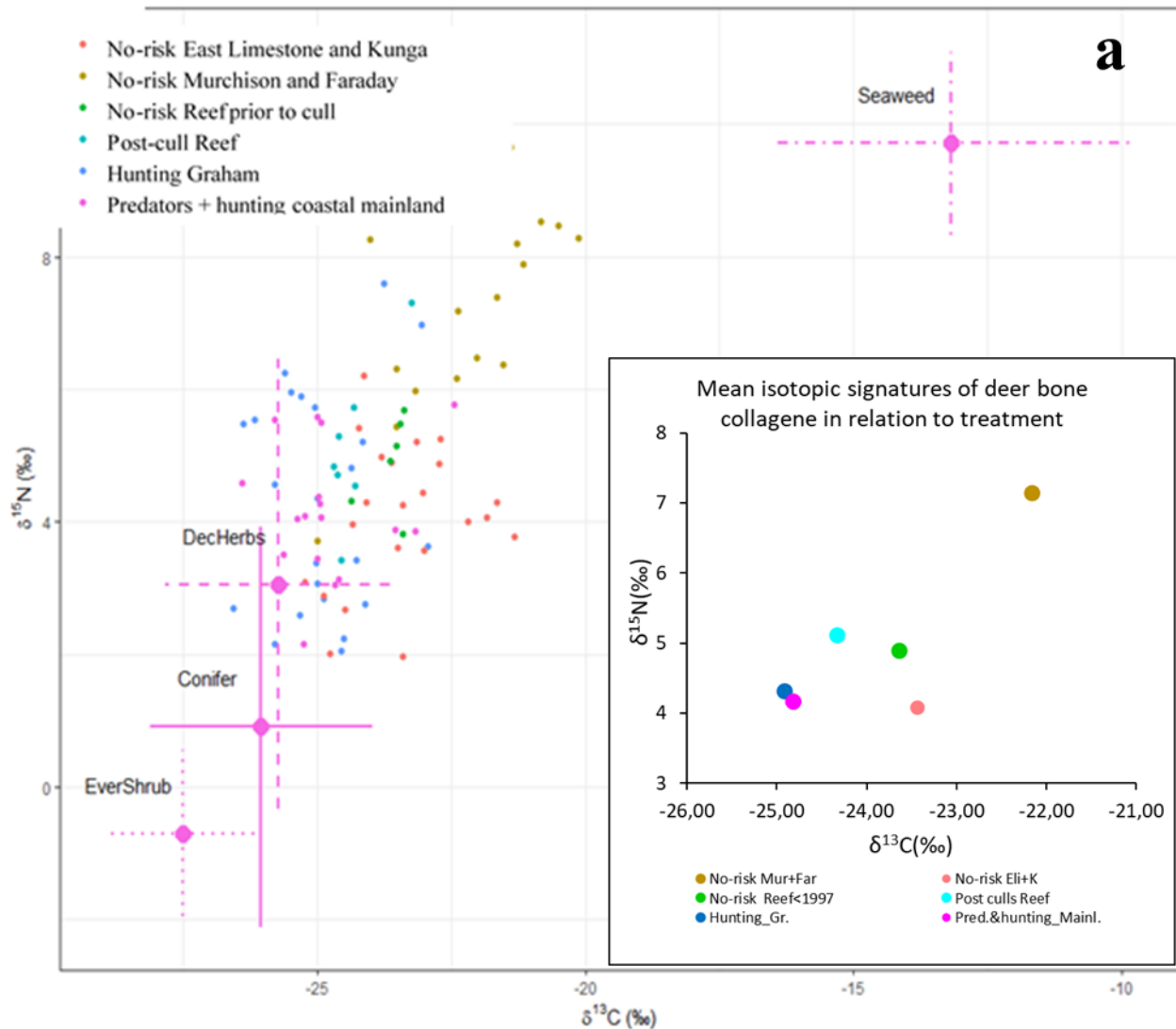
554 The MixSIAR analysis quantifies the proportion of the four plant categories in deer diets in the  
 555 samples (Figs. 6 and 7). Bayesian 95% credible intervals (Fig. 8) allow us to estimate the

556 significance of differences in the proportion of seaweeds between the samples. Credible intervals  
557 from the samples without predation (Murchison, Faraday, East Limestone, Kunga and Reef before  
558 the culls) do not overlap with those of the two sites with hunting and/or predators (Graham and  
559 BC Central Coast). The credible interval of the Post-culls Reef sample was intermediate.

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

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

571

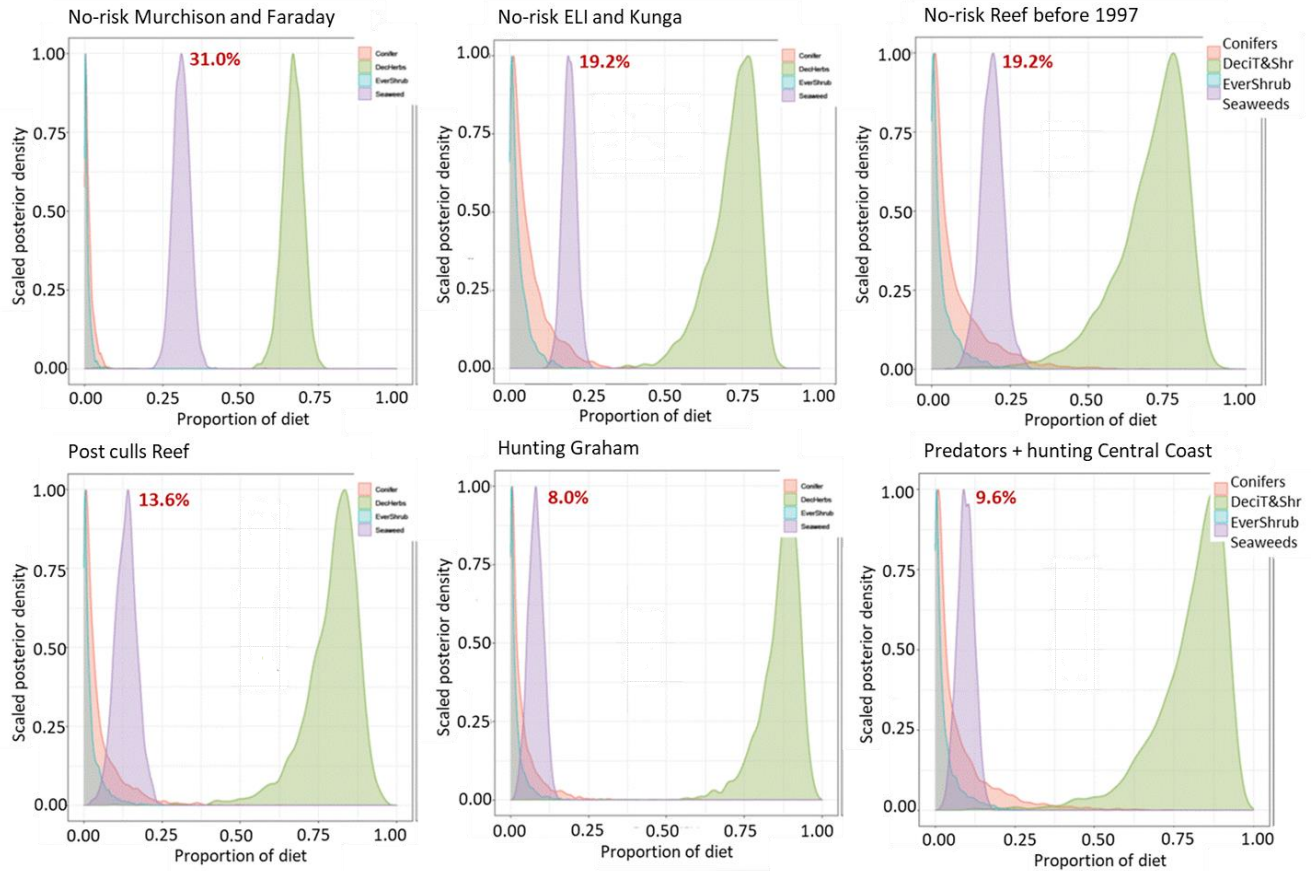


572

573 **Figure 6.** Isospace plots of deer bone collagen and plants Mixture data by risk category and islands. No-  
 574 risk Murchison and Faraday = No-risk samples from Murchison (N=10 bone samples) and Faraday (N =  
 575 6); No-risk samples from East Limestone (N = 10) and Kunga (N = 12); No-risk samples from Reef Island  
 576 prior to the culls (N = 7); Post-culls Reef = samples from Reef Island after the culls (N = 6); Hunting  
 577 Graham = samples from Graham Island (N = 23); Predators + hunting = samples from the BC Central  
 578 Copast (N = 17). Source data are by risk/island categories and have been adjusted by discrimination means  
 579 and SDs. Terrestrial plants: EverShrub = evergreen shrub (Salal), Conifer = conifers, DecHerbs =  
 580 deciduous trees and shrubs, forbs, ferns and grasses; Seaweed = Seaweeds (40 species). Error bars indicate  
 581 1 SD, the combined source+discrimination SD calculated under assumption of independence as:

582 
$$\sqrt{\sigma_{source}^2 + \sigma_{discr}^2}$$

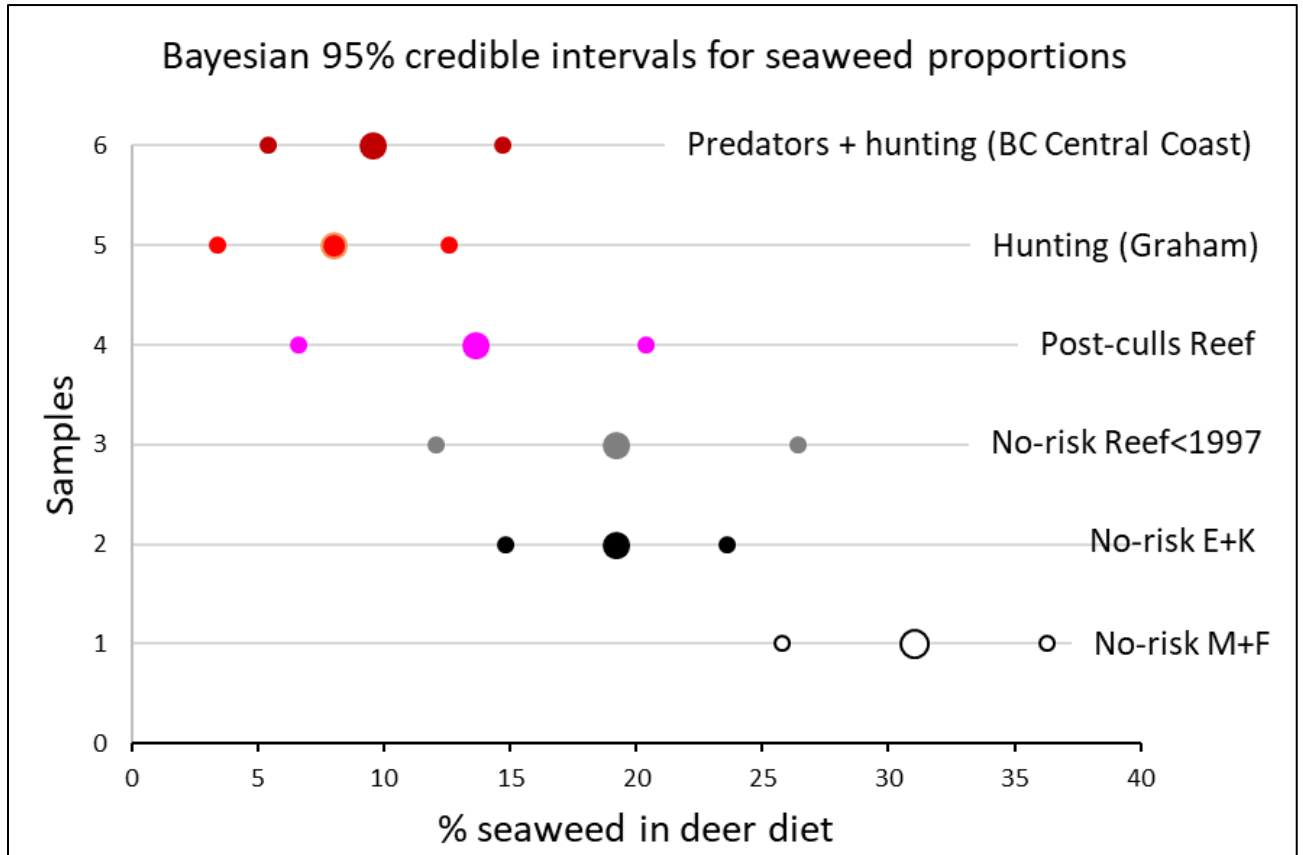
583



584  
 585  
 586  
 587  
 588  
 589  
 590  
 591  
 592  
 593  
 594  
 595  
 596  
 597  
 598  
 599

**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); Yearly relatively low intensity hunting without marked effect on high deer density (Engelstoft, 2001) Graham Island coastal area (N = 23); BC Centra Coast, predators and hunting (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 and western and yellow redcedar) (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).





600  
601

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

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

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

625 On Graham Island, where hunting is of low intensity and restricted to sites most accessible to  
626 the small local population of hunters (Martin and Baltzinger 2002), the diversity of cover  
627 among plots (spread of plots, Fig. 2) and the amount of shrub cover (Fig. 3) was higher than  
628 on No-risk islands but understory vegetation overall was still closer to the one observed on No-  
629 risk islands [for more details on the understory vegetation on Graham see (Engelstoft 2001;  
630 Engelstoft et al. 2008; Chollet et al. 2021a)]. This variation suggests an interplay among the  
631 presence of risk, its intensity, its nature (natural predators versus humans) and its duration in  
632 the interaction between deer and their habitat.

**633 Does absence of risk favor boldness over shyness and deer impact on the vegetation?**

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

641 though they showed slightly longer flight initiation distances in their novel environment. This  
642 was in stark contrast with the wary behaviour of the native deer on Reef after the culls, even  
643 more so as the flight and movement distances we recorded for the Reef deer were conservative:  
644 they often fled before being seen (heard running) and others were still running when they  
645 disappeared from view. As a result, actual values on Reef may have been closer to values  
646 reported for black-tailed deer populations on the mainland (FID ~ 60 to 70 m and Dtravel ~ 70  
647 to 120 m), where deer can be subject to hunting and carnivores (Stankowich & Coss 2006,  
648 2007; Stankowich 2008). Our field notes also indicated that native deer on Reef ran or trotted  
649 away, whereas deer from Kunga, even after translocation, and East Limestone (No-risk islands)  
650 usually performed a slow walk to a nearby location where they resumed their activities. On  
651 East Limestone, FID and distances travelled were significantly shorter than on Kunga, possibly  
652 reflecting some habituation to human presence (Rodriguez-Prieto et al. 2009; Schuttler et al.  
653 2017) on East Limestone Island, where people are present daily for two to three months each  
654 summer for ecological monitoring.

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

670 Food limitation and nutritional status have been proposed as mechanisms explaining individual  
671 attenuation in antipredator behaviours such as flight response (Stankowich 2008; Gaynor et al.  
672 2019). If so, we expect these behaviours to be reversed once food supply improves. Could a  
673 better food supply in the lush understory on Reef after the culls explain the higher values of  
674 FID and Dtravel for deer native to Reef, and would the apparent paucity of resources in the  
675 heavily browsed understories of East Limestone or Kunga explain the apparent lack of fear in  
676 their deer? This seems unlikely, given that we did not observe any significant change in the  
677 behaviour of the deer translocated from Kunga to Reef (Fig. 4). Our observations rather suggest  
678 a more indirect link between behaviour and resources, a link mediated by risk. Following the

679 reasoning of Kirchoff & Person (2008) we assumed that in the absence of risk intensive  
680 browsing would over time decrease the per capita availability of forage as well as the average  
681 quality of the diet. A reduction in anti-predator behaviour could be the necessary condition to  
682 allow increased foraging time in response to this progressive erosion of standing plant biomass  
683 and forage quality in an increasingly browsed understory. In these understories, resources,  
684 although sufficient to sustain a dense deer population (Stockton et al. 2005; Le Saout et al.  
685 2014a), are increasingly found in small increments of emerging vegetation or as subsidies  
686 fallen from the canopy (Le Saout et al. 2014a). Indeed, on No-risk islands less than 5% of the  
687 resources needed by these dense deer populations were provided by the rare standing biomass.  
688 The bulk was provided equally by the cryptic flux of growing vegetation and by canopy foliage  
689 fall, supplemented by seaweeds from the shorelines (Le Saout et al. 2014a). Our results from  
690 the stable isotope analysis are another illustration of the focus deer have to put on cryptic  
691 vegetation elements in the understory. On one hand conifers, the dominant element in the  
692 understory of No-risk sites (Fig. 3), make for only a tiny proportion of their diet (Fig. 7),  
693 whereas deciduous vegetation, a known preference in black-tailed deer diet (Taylor 1956; Pojar  
694 1999), make up the bulk of their diet (Fig. 7), its negligible presence as standing biomass (Fig.  
695 3) compensated by short lived emerging vegetation (Le Saout et al. 2014a). This need to feed  
696 on spatially dispersed food, occurring as small items, could be the ecological context forcing  
697 the emergence of populations expressing less anti-predator behaviours (Réale et al. 2010; Sih  
698 et al. 2012), or with less costly adjustments of spatial distribution in response to perceived  
699 distribution of risk (Williams et al. 2008; Gaynor et al. 2019). Such behavioural shifts could,  
700 in turn, help deer intensify their foraging pressure and, over time, aggravate the loss in  
701 understory standing vegetation, as was actually shown on these islands between 1989 and 2009  
702 (Chollet et al. 2015). This could further increase the shift towards bolder behaviours. The  
703 overall predominance of diurnal activity in East Limestone and Kunga deer compared to  
704 populations exposed to hunting (Bonnot et al. 2016) can also be interpreted as a change in  
705 favour of increased foraging time. This more diurnal behaviour has been shown to contrast  
706 with the more nocturnal behaviour commonly observed in hunted populations (Altendorf et al.  
707 2001; Bonnot et al. 2016, 2020; Palmer et al. 2022). However, anti-predator behaviours less  
708 costly in foraging time such as routine vigilance would be retained and not counter-selected as  
709 was actually observed for the populations of East Limestone and Kunga where routine  
710 vigilance persisted in an otherwise unwary population. (Chamailé-Jammes et al. 2014; Le  
711 Saout et al. 2015).

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

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

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

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

739 The lower proportion of seaweeds in diets at sites with predators and/or hunters seems to  
740 validate our prediction that deer would make less use of exposed shorelines where they face  
741 predation from wolves and/or humans. But, as the amount of standing vegetation in the  
742 understories tends to be much lower at sites without hunting (Fig. 3) it could be the greater  
743 availability of forage in the forest understorey that keeps deer from foraging on the shoreline  
744 at sites with hunting. Notably, Murchison and Faraday, where seaweed is especially prominent  
745 in the diet, have very open understoreys below their dense secondary closed canopy forests, with  
746 less than 4% of ligneous and herbaceous vegetation cover in the 0 to 1.5 m layer in addition to  
747 larger areas of intertidal than the other islands studied (Martin et al. 1995).

748 However, the two situations with the lowest and similar proportion of seaweed isotopes in  
749 jawbone collagen, Graham and the area of the BC Central Coast around Yeo Island, contrast  
750 in their cover of standing understory vegetation. On Yeo the permanent presence of predators  
751 and hunting is associated with a lush understory while on Graham the long history of moderate  
752 hunting, restricted to areas most accessible to a limited number of hunters (Martin and  
753 Baltzinger 2002), with limited impact on deer density (Engelstoft 2001; Engelstoft et al. 2008),

754 resulted in understory vegetation closer to those from No-risk sites than to those in sites where  
755 predators and hunting occur on the BC Central Coast (Figs. 2 and 8) (Pojar 1999; Chollet et al.  
756 2021a).

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

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

764 Our research contributes to the limited number of studies that connect animal behaviour with  
765 ecological dynamics, species interactions, population changes and ecosystems [see (Sih et al.  
766 2004, 2012; Réale et al. 2007; Chitwood et al. 2022)]. We show that the introduction of a new  
767 threat, such as hunting on Reef Island, led to a sudden change in behaviour. This change left  
768 the survivors exhibiting behaviours that were significantly different from those of animals on  
769 islands without hunting.

770 Our findings support the hypothesis that shifts in the “landscape of fear” (Gaynor et al. 2019;  
771 Palmer et al. 2022) can change the behavioural traits of a population. These changes may occur  
772 in response to intense selective pressures on particular behavioural traits caused by immediate  
773 risk (e.g. as in the case of severe culling), or, over longer periods of time, from the progressive  
774 reproductive advantage of behavioural profiles better adapted to a changing environment (e.g.  
775 a progressive increase in boldness driven by a progressive depletion of resources in absence of  
776 acute predation risk).

777 While our interpretation of the non-wary behaviours we observed on islands without predation  
778 or hunting, or of the rapid shift towards shyness after the culls, remains speculative, it  
779 highlights the possibility for behaviour selection. The speed of behavioural change will be  
780 influenced by the intensity of the selective pressure (Blumstein 2002; Jolly et al. 2018; Moseby  
781 et al. 2023). It can be rapid if severe culling continues over generations but may be slower in  
782 the case of the relaxation of antipredator behaviours after the colonisation of a predator free  
783 environment (Blumstein 2002). The evolution of predator naivety in island organisms provides  
784 many classic examples of both gradual and rapid evolutionary changes in behaviour (Darwin  
785 1840; Lack 1968; Blumstein 2002), but see Blumstein and Daniel (2005).

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

790 management of overabundant populations through hunting. In such instances, a better grasp of  
791 behavioural responses to management actions can help design strategies that take into account  
792 the ability of species to adjust their spatial distribution and diel rhythms to the threat posed by  
793 management measures (Williams et al. 2008; Potratz et al. 2024). In general, by improving our  
794 understanding of mechanisms that lead to evolutionary shifts, our results help to better predict  
795 the full impact of neglecting the integrity of species assemblages. Hence, our evidence  
796 encourages the conservation and restoration of fully functioning ecosystems.

## 797 **Ethical note**

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

## 812 **Acknowledgements**

813 This is a publication of the Research Group on Introduced Species (RGIS,  
814 <https://rgis.cefe.cnrs.fr>). On top of funding (see below) we received critical logistic support  
815 from the Laskeek Bay Conservation Society, Environment and Climate Change Canada, the  
816 Gwaii Haanas National Park Reserve, National Marine Conservation Area Reserve and Haida  
817 Heritage Site, the Coast Sustainability Trust Matching Fund (CST-QCI-HG- 061– RGIS  
818 Infrastructure Upgrade), and the “Understanding Canada” program from the Canadian  
819 government. We are indebted to Todd Golumbia, Carita Bergman and Peter Dymont and  
820 colleagues from Gwaii Haanas for support in the field. Tibo Verchère, Ainsley Brown, Barbara  
821 and Keith Rowsell, Greg Martin, Jacques Morin, Erin Harris, Terry and Ron Husband, Mike  
822 Gillingham, Malcolm Hyatt, Georges Janeau, Jean-Luc Rames, Denis Picot, Nicolas Morellet,  
823 Bruno Cargnelutti, Nicolas Cebe, Helen Schwantje, Tom Smith and Keith Tipper provided  
824 critical help in the field and beyond. Chris Darimont, Eva Poilvé, H  l  ne Verheyden, and  
825 Maura Van Impe assisted with the treatment of samples in the stable isotope analysis. The  
826 Haida Watchmen program provided precious help through accommodation on Tanu Island.

827 Over the years, many people from all walks of life of the local communities provided  
828 invaluable support. We are deeply thankful to all. We also benefited from very insightful  
829 suggestions by two anonymous reviewers and by the recommender Gloriana Chaverri.

### 830 **Data, scripts, code, and supplementary information availability**

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

### 832 **Funding**

833 Funding for this research included grants from the French Ministry of Foreign Affairs, from  
834 the French National Agency for Research (#2010-BLAN-1718, BAMBI), the International  
835 Research Group (GDRI) Dynamics of Biodiversity and Life-History traits from CNRS, the  
836 South Moresby Forest Replacement Account (SMFRA) and Gwaii Forestry Charitable Trust  
837 (GF), and from National Geographic # 9266-13.

### 838 **Conflict of interest disclosure**

839 The authors declare that they comply with the PCI rule of having no financial conflicts of  
840 interest in relation to the content of the article. Jean-Louis Martin and Simon Chamailé-  
841 Jammes are listed as recommenders

842

843

### 844 **References**

- 845 Altendorf KB, Laundré JW, López González CA, Brown JS. 2001. Assessing effects of predation risk  
846 on foraging behavior of mule deer. *Journal of mammalogy* **82**:430–439. American Society of  
847 Mammalogists 810 East 10th Street, PO Box 1897, Lawrence ....
- 848 Balasse M, Tresset A, Dobney K, Ambrose SH. 2005. The use of isotope ratios to test for seaweed  
849 eating in sheep. *Journal of zoology* **266**:283–291. Wiley Online Library.
- 850 Ballard WB, Lutz D, Keegan TW, Carpenter LH, deVos Jr JC. 2001. Deer-predator relationships: a  
851 review of recent North American studies with emphasis on mule and black-tailed deer. *Wildlife*  
852 *Society Bulletin*:99–115. JSTOR.
- 853 Banner A, MacKenzie WH, Pojar J, MacKinnon A, Saunders SC, Klassen H. 2014. A field guide to  
854 ecosystem classification and identification for Haida Gwaii. *Land management handbook*.
- 855 Blumstein DT. 2002. Moving to suburbia: ontogenetic and evolutionary consequences of life on  
856 predator-free islands. *Journal of Biogeography* **29**:685–692. Wiley Online Library.
- 857 Blumstein DT, Daniel JC. 2005. The loss of anti-predator behaviour following isolation on islands.  
858 *Proceedings of the Royal Society B: Biological Sciences* **272**:1663–1668. The Royal Society  
859 London.
- 860 Bocherens H. 1999. Isotopes stables et reconstitution du régime alimentaire des hominidés fossiles: une  
861 revue. *Bulletins et Mémoires de la Société d'Anthropologie de Paris* **11**:261–287. Persée-  
862 Portail des revues scientifiques en SHS.
- 863 Bocherens H, Drucker D. 2003. Trophic level isotopic enrichment of carbon and nitrogen in bone  
864 collagen: case studies from recent and ancient terrestrial ecosystems. *International Journal of*  
865 *oste archaeology* **13**:46–53. Wiley Online Library.
- 866 Bocherens H, Fizet M, Cuif J-P, Jaeger J-J, Michard J-G. 1988. Premières mesures d'abondance  
867 isotopiques naturelles en <sup>13</sup>C et <sup>15</sup>N de la matière organique fossile de Dinosaur. Application  
868 à l'étude du régime alimentaire du genre *Anatosaurus* (*Ornithischia*, *Hadrosauridae*). *Comptes*



869 rendus de l'Académie des sciences. Série 2, Mécanique, Physique, Chimie, Sciences de  
870 l'univers, Sciences de la Terre **306**:1521–1525.

871 Bochérens, Hervé, Marc Fizet, Lange-Badre B, Vandermeersch B, Borel JP, Bellon G. 1991. Isotopic  
872 biogeochemistry (13C, 15N) of fossil vertebrate collagen: application to the study of a past  
873 food web including Neandertal man. *Journal of Human Evolution* **20**:481–492. Academic  
874 Press.

875 Bøhn T, Amundsen P-A. 2004. Ecological interactions and evolution: forgotten parts of biodiversity?  
876 *BioScience* **54**:804–805. American Institute of Biological Sciences.

877 Bonnot N, Morellet N, Verheyden H, Cargnelutti B, Lourtet B, Klein F, Hewison AM. 2013. Habitat  
878 use under predation risk: hunting, roads and human dwellings influence the spatial behaviour  
879 of roe deer. *European journal of wildlife research* **59**:185–193. Springer.

880 Bonnot NC, Couriot O, Berger A, Cagnacci F, Ciuti S, De Groeve JE, Gehr B, Heurich M, Kjellander  
881 P, Kröschel M. 2020. Fear of the dark? Contrasting impacts of humans versus lynx on diel  
882 activity of roe deer across Europe. *Journal of Animal Ecology* **89**:132–145. Wiley Online  
883 Library.

884 Bonnot NC, Hewison AM, Morellet N, Gaillard J-M, Debeffe L, Couriot O, Cargnelutti B, Chaval Y,  
885 Lourtet B, Kjellander P. 2017. Stick or twist: roe deer adjust their flight behaviour to the  
886 perceived trade-off between risk and reward. *Animal behaviour* **124**:35–46. Elsevier.

887 Bonnot NC, Morellet N, Hewison AM, Martin J-L, Benhamou S, Chamaillé-Jammes S. 2016. Sitka  
888 black-tailed deer (*Odocoileus hemionus sitkensis*) adjust habitat selection and activity rhythm  
889 to the absence of predators. *Canadian Journal of Zoology* **94**:385–394.

890 Brown JS, Laundré JW, Gurung M. 1999. The ecology of fear: optimal foraging, game theory, and  
891 trophic interactions. *Journal of Mammalogy* **80**:385–399.

892 Burgess BT, Irvine RL, Martin J-L, Russello MA. 2023. Past population control biases interpretations  
893 of contemporary genetic data: implications for future invasive Sitka black-tailed deer  
894 management in Haida Gwaii. *Biological Invasions* **25**:3871–3886. Springer.

895 Burgess BT, Irvine RL, Russello MA. 2022a. Population genomics of Sitka black-tailed deer supports  
896 invasive species management and ecological restoration on islands. *Communications Biology*  
897 **5**:223. Nature Publishing Group UK London.

898 Burgess BT, Irvine RL, Russello MA. 2022b. A genotyping-in-thousands by sequencing panel to inform  
899 invasive deer management using noninvasive fecal and hair samples. *Ecology and Evolution*  
900 **12**:e8993. Wiley Online Library.

901 Callan R, Nibbelink NP, Rooney TP, Wiedenhoef JE, Wydeven AP. 2013. Recolonizing wolves trigger  
902 a trophic cascade in Wisconsin (USA). *Journal of Ecology* **101**:837–845.

903 Camin F, Bontempo L, Perini M, Piasentier E. 2016. Stable isotope ratio analysis for assessing the  
904 authenticity of food of animal origin. *Comprehensive Reviews in Food Science and Food*  
905 *Safety* **15**:868–877. Wiley Online Library.

906 Cardinal E, Martin J-L, Tremblay J-P, Côté SD. 2012. An experimental study of how variation in deer  
907 density affects vegetation and songbird assemblages of recently harvested boreal forests.  
908 *Canadian Journal of Zoology* **90**:704–713.

909 Chamaillé-Jammes S, Malcuit H, Le Saout S, Martin J-L. 2014. Innate threat-sensitive foraging: black-  
910 tailed deer remain more fearful of wolf than of the less dangerous black bear even after 100  
911 years of wolf absence. *Oecologia* **174**:1151–1158.

912 Chitwood MC, Baruzzi C, Lashley MA. 2022. “Ecology of fear” in ungulates: Opportunities for  
913 improving conservation. *Ecology and Evolution* **12**:e8657. Wiley Online Library.

914 Chollet S. 2012. De la mise en évidence à la gestion de l'effet de cerf Leçons pratiques et théoriques  
915 fournies par l'introduction du cerf à queue-noire sur Haïda Gwaii. Université Montpellier II-  
916 Sciences et Techniques du Languedoc.

917 Chollet S, Baltzinger C, Maillard M, Martin J-L. 2021a. Deer exclusion unveils abiotic filtering in forest  
918 understorey plant assemblages. *Annals of Botany* **128**:371–381. Oxford University Press US.

919 Chollet S, Baltzinger C, Ostermann L, Saint-André F, Martin J-L. 2013a. Importance for forest plant  
920 communities of refuges protecting from deer browsing. *Forest Ecology and Management*  
921 **289**:470–477.

- 922 Chollet S, Baltzinger C, Saout SL, Martin J-L. 2013b. A better world for bryophytes? A rare and  
923 overlooked case of positive community-wide effects of browsing by overabundant deer.  
924 *Ecoscience* **20**:352–360.
- 925 Chollet S, Bergman C, Gaston AJ, Martin J-L. 2015. Long-term consequences of invasive deer on  
926 songbird communities: Going from bad to worse? *Biological Invasions* **17**:777–790. Springer.
- 927 Chollet S, Maillard M, Schörghuber J, Grayston SJ, Martin J-L. 2021b. Deer slow down litter  
928 decomposition by reducing litter quality in a temperate forest. *Ecology* **102**:e03235. Wiley  
929 Online Library.
- 930 Chollet S, Padié S, Stockton S, Allombert S, Gaston AJ, Martin J-L. 2016. Positive plant and bird  
931 diversity response to experimental deer population reduction after decades of uncontrolled  
932 browsing. *Diversity and Distributions* **22**:274–287.
- 933 Clare JD, Zuckerberg B, Liu N, Stenglein JL, Van Deelen TR, Pauli JN, Townsend PA. 2023. A  
934 phenology of fear: Investigating scale and seasonality in predator–prey games between wolves  
935 and white-tailed deer. *Ecology* **104**:e4019. Wiley Online Library.
- 936 Cooper Jr WE. 2008. Visual monitoring of predators: occurrence, cost and benefit for escape. *Animal*  
937 *Behaviour* **76**:1365–1372. Elsevier.
- 938 Côté SD, Rooney TP, Tremblay J-P, Dussault C, Waller DM. 2004. Ecological Impacts of Deer  
939 Overabundance. *Annual Review of Ecology, Evolution, and Systematics* **35**:113–147.
- 940 Creel S, Winnie Jr J, Maxwell B, Hamlin K, Creel M. 2005. Elk alter habitat selection as an antipredator  
941 response to wolves. *Ecology* **86**:3387–3397. Wiley Online Library.
- 942 Darimont CT, Paquet PC. 2001. The gray wolves (*Canis lupus*) of British Columbia’s coastal  
943 rainforests.
- 944 Darimont CT, Paquet PC. 2002. Gray wolves, *Canis lupus*, of British Columbia’s Central and North  
945 Coast: distribution and conservation assessment. *Canadian Field Naturalist* **116**:416–422.  
946 Ottawa, Ottawa Field-Naturalists’ Club.
- 947 Darimont CT, Paquet PC, Reimchen TE. 2007. Stable isotopic niche predicts fitness of prey in a wolf–  
948 deer system. *Biological Journal of the Linnean Society* **90**:125–137. Oxford University Press.
- 949 Darimont CT, Reimchen TE. 2002. Intra-hair stable isotope analysis implies seasonal shift to salmon  
950 in gray wolf diet. *Canadian Journal of zoology* **80**:1638–1642. NRC Research Press Ottawa,  
951 Canada.
- 952 Darwin C. 1840. *Journal of Researches into the Geology and Natural History of the Varoious Countries*  
953 *Visited by HMS Beagle, under the Command of Captain Fitzroy from 1832 to 1836 by Charles*  
954 *Darwin.* Colburn.
- 955 Daufresne T, Martin JL. 1997. Changes in vegetation structure and diversity as a result of browsing by  
956 a large herbivore: the impact of introduced Black-tailed deer in the primary forest of Haida  
957 Gwaii, British Columbia. *Laskeek Bay Research* **7**:2–26.
- 958 Dellinger JA, Shores CR, Craig A, Heithaus MR, Ripple WJ, Wirsing AJ. 2019. Habitat use of  
959 sympatric prey suggests divergent anti-predator responses to recolonizing gray wolves.  
960 *Oecologia* **189**:487–500. Springer.
- 961 DeNiro MJ, Epstein S. 1978. Influence of diet on the distribution of carbon isotopes in animals.  
962 *Geochimica et cosmochimica acta* **42**:495–506. Elsevier.
- 963 DeNiro MJ, Epstein S. 1981. Influence of diet on the distribution of nitrogen isotopes in animals.  
964 *Geochimica et cosmochimica acta* **45**:341–351. Elsevier.
- 965 Ellers J, Toby Kiers E, Currie CR, McDonald BR, Visser B. 2012. Ecological interactions drive  
966 evolutionary loss of traits. *Ecology letters* **15**:1071–1082. Wiley Online Library.
- 967 Elton C. 1927. *Animal ecology.* 207 pp. Sidgwick & Jackson, LTD. London.
- 968 Engelstoft C. 2001. Effects of Sitka Black-tailed Deer (*Odocoileus Hemionus Sitkensis*) on Understory  
969 in Old Growth Forest on Haida Gwaii (Queen Charlotte Islands), British Columbia. University  
970 of Victoria.
- 971 Engelstoft C, Kirchhoff MD, Eastman D. 2008. Herbivory and the missing understory on Haida Gwaii.  
972 Pages 78–86 *Lessons from the Islands: Introduced Species and What They Tell Us About How*  
973 *Ecosystems Work.* Canadian Wildlife Service, Environment Canada, Ottawa, Queen Charlotte  
974 City, Queen Charlotte Islands, British Columbia.
- 975 Estes JA et al. 2011. Trophic Downgrading of Planet Earth. *Science* **333**:301–306.

- 976 Estes JA, Brashares JS, Power ME. 2013. Predicting and detecting reciprocity between indirect  
977 ecological interactions and evolution. *The American Naturalist* **181**:S76–S99. University of  
978 Chicago Press Chicago, IL.
- 979 Gaston A, Golumbia T, Martin J, Sharpe S. 2008a. Lessons from the Islands: introduced species and  
980 what they tell us about how ecosystems work. Page Proceedings from the Research Group on  
981 Introduced Species 2002 Symposium Canadian Wildlife Service, Environment Canada, Ottawa.  
982 Canadian Wildlife Service, Queen Charlotte City, Queen Charlotte Islands, British Columbia.
- 983 Gaston AJ, Sharpe S, Stockton SA, Golumbia T, Martin J-L. 2008b. Reduction in deer numbers on Reef  
984 Island and SGang Gwaay: progress, results, and vegetation changes. Lessons from the  
985 Islands:103. Canadian Wildlife Service Ottawa, Canada.
- 986 Gaston AJ, Stockton SA, Smith JL. 2006. Species-area relationships and the impact of deer-browse in  
987 the complex phytogeography of the Haida Gwaii archipelago (Queen Charlotte Islands), British  
988 Columbia. *Écoscience* **13**:511–522.
- 989 Gaynor KM, Brown JS, Middleton AD, Power ME, Brashares JS. 2019. Landscapes of fear: spatial  
990 patterns of risk perception and response. *Trends in ecology & evolution* **34**:355–368. Elsevier.
- 991 Gaynor KM, Cherry MJ, Gilbert SL, Kohl MT, Larson CL, Newsome TM, Prugh LR, Suraci JP, Young  
992 JK, Smith JA. 2021. An applied ecology of fear framework: linking theory to conservation  
993 practice. *Animal Conservation* **24**:308–321. Wiley Online Library.
- 994 Gigliotti LC, Slotow R, Sholto-Douglas C, de Vos C, Jachowski DS. 2021. Short-term predation risk  
995 and habitat complexity influence cheetah antipredator behaviours. *Animal Behaviour* **178**:175–  
996 184. Elsevier.
- 997 Golumbia T, Bland L, Moore K, Bartier P. 2008. History and current status of introduced vertebrates  
998 on Haida Gwaii. Pages 8–31 Lessons from the islands: introduced species and what they tell us  
999 about how ecosystems work. Canadian Wildlife Service, Environment Canada, Ottawa, Queen  
1000 Charlotte City, Queen Charlotte Islands, British Columbia.
- 1001 Greenberg R, Mettke-Hofmann C. 2001. Ecological aspects of neophobia and neophilia in birds.  
1002 *Current ornithology*:119–178. Springer.
- 1003 Haeckel E. 1866. *Generelle Morphologie der Organismen. Allgemeine Grundzüge der organischen*  
1004 *Formen-Wissenschaft, mechanisch begründet durch die von C. Darwin reformirte Descendenz-*  
1005 *Theorie. Allgemeine Entwicklungsgeschichte.* De Gruyter., Berlin.
- 1006 Irvine RL, Thorley JL. 2024. Relative efficiency of hunting methods during an incomplete Sitka black-  
1007 tailed deer eradication on Haida Gwaii, Canada. *Ecological Solutions and Evidence* **5**:e12312.  
1008 Wiley Online Library.
- 1009 Janzen DH. 1974. The deflowering of central america. *Natural History Magazine* **83**:48–51.
- 1010 Jolly CJ, Webb JK, Phillips BL. 2018. The perils of paradise: an endangered species conserved on an  
1011 island loses antipredator behaviours within 13 generations. *Biology Letters* **14**:20180222. The  
1012 Royal Society.
- 1013 Kamaru DN, Palmer TM, Riginos C, Ford AT, Belnap J, Chira RM, Githaiga JM, Gituku BC, Hays  
1014 BR, Kavwele CM. 2024. Disruption of an ant-plant mutualism shapes interactions between  
1015 lions and their primary prey. *Science* **383**:433–438. American Association for the Advancement  
1016 of Science.
- 1017 Kelly JF. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic  
1018 ecology. *Canadian journal of zoology* **78**:1–27. NRC Research Press Ottawa, Canada.
- 1019 Kilgo JC, Labisky RF, Fritzen DE. 1998. Influences of hunting on the behavior of white-tailed deer:  
1020 implications for conservation of the Florida panther. *Conservation Biology* **12**:1359–1364.  
1021 Wiley Online Library.
- 1022 Kirchhoff MD, Person DK. 2008. The Alaska perspective—deer populations in the presence of wolves.  
1023 *Lessons from the Islands*:171.
- 1024 Klein DR. 1995. The introduction, increase, and demise of wolves on Coronation Island, Alaska.  
1025 *Ecology and conservation of wolves in a changing world* **275**:280. Canadian Circumpolar  
1026 Institute, University of Alberta Edmonton, Alberta, Canada.
- 1027 Kuijper DPJ, Sahlén E, Elmhagen B, Chamaillé-Jammes S, Sand H, Lone K, Cromsigt J. 2016. Paws  
1028 without claws? Ecological effects of large carnivores in anthropogenic landscapes. *Proc. R.*  
1029 *Soc. B* **283**. Available from <http://dx.doi.org/10.1098/rspb.2016.162>.
- 1030 Lack DL. 1968. *Ecological adaptations for breeding in birds.* Methuen, York.

- 1031 Laundré JW, Hernández L, Altendorf KB. 2001. Wolves, elk, and bison: reestablishing the “landscape  
1032 of fear” in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology* **79**:1401–1409.
- 1033 Le Saout S et al. 2014a. Understanding the paradox of deer persisting at high abundance in heavily  
1034 browsed habitats. *Wildlife Biology* **20**:122–135.
- 1035 Le Saout S, Martin J-L, Blanchard P, Cebe N, Mark Hewison AJ, Rames J-L, Chamaillé-Jammes S.  
1036 2015. Seeing a ghost? Vigilance and its drivers in a predator-free world. *Ethology* **121**:651–  
1037 660. Wiley Online Library.
- 1038 Le Saout S, Padié S, Chamaillé-Jammes S, Chollet S, Côté S, Morellet N, Pattison J, Harris E, Martin  
1039 J-L. 2014b. Short-term effects of hunting on naïve black-tailed deer (*Odocoileus hemionus*  
1040 *sitkensis*): behavioural response and consequences on vegetation growth. *Canadian Journal of*  
1041 *Zoology* **92**:915–925. NRC Research Press.
- 1042 Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and  
1043 prospectus. *Canadian journal of zoology* **68**:619–640. NRC Research Press Ottawa, Canada.
- 1044 Maillard M, Martin J-L, Chollet S, Catomeris C, Simon L, Grayston SJ. 2021. Belowground effects of  
1045 deer in a temperate forest are time-dependent. *Forest Ecology and Management* **493**:119228.  
1046 Elsevier.
- 1047 Martin J, Vourc’h G, Bonnot N, Cargnelutti B, Chaval Y, Lourtet B, Goulard M, Hoch T, Plantard O,  
1048 Hewison AM. 2018. Temporal shifts in landscape connectivity for an ecosystem engineer, the  
1049 roe deer, across a multiple-use landscape. *Landscape ecology* **33**:937–954. Springer.
- 1050 Martin J-L, Baltzinger C. 2002. Interaction among deer browsing, hunting, and tree regeneration.  
1051 *Canadian Journal of Forest Research* **32**:1254–1264.
- 1052 Martin J-L, Chamaillé-Jammes S, Waller DM. 2020. Deer, wolves, and people: costs, benefits and  
1053 challenges of living together. *Biological Reviews* **93**:782–801.
- 1054 Martin J-L, Gaston AJ, Hitier S. 1995. The effect of island size and isolation on old growth forest habitat  
1055 and bird diversity in Gwaii Haanas (Queen Charlotte Islands, Canada). *Oikos*:115–131. JSTOR.
- 1056 Martin J-L, Stockton SA, Allombert S, Gaston AJ. 2010. Top-down and bottom-up consequences of  
1057 unchecked ungulate browsing on plant and animal diversity in temperate forests: lessons from  
1058 a deer introduction. *Biological Invasions* **12**:353–371.
- 1059 Martin TG, Arcese P, Scheerder N. 2011. Browsing down our natural heritage: deer impacts on  
1060 vegetation structure and songbird populations across an island archipelago. *Biological*  
1061 *Conservation* **144**:459–469.
- 1062 Mathews NE, Porter WF. 1988. Black bear predation of white-tailed deer neonates in the central  
1063 Adirondacks. *Canadian Journal of Zoology* **66**:1241–1242. NRC Research Press Ottawa,  
1064 Canada.
- 1065 Monestier C, Morellet N, Verheyden H, Gaillard J-M, Bideau E, Denailhac A, Lourtet B, Cebe N, Picot  
1066 D, Rames J-L. 2017. Neophobia is linked to behavioural and haematological indicators of stress  
1067 in captive roe deer. *Animal Behaviour* **126**:135–143. Elsevier.
- 1068 Moseby K, Van der Weyde L, Letnic M, Blumstein DT, West R, Bannister H. 2023. Addressing prey  
1069 naivety in native mammals by accelerating selection for antipredator traits. *Ecological*  
1070 *Applications* **33**:e2780. Wiley Online Library.
- 1071 Moseby KE, Blumstein DT, Letnic M. 2016. Harnessing natural selection to tackle the problem of prey  
1072 naïveté. *Evolutionary applications* **9**:334–343. Wiley Online Library.
- 1073 Moseby KE, Carthey A, Schroeder T. 2015. The influence of predators and prey naivety on  
1074 reintroduction success: current and future directions. *Advances in reintroduction biology of*  
1075 *Australian and New Zealand fauna*:29–42. CSIRO publishing Clayton South, Vic, Australia.
- 1076 Padié S, Morellet N, Hewison AM, Martin J-L, Bonnot N, Cargnelutti B, Chamaillé-Jammes S. 2015.  
1077 Roe deer at risk: teasing apart habitat selection and landscape constraints in risk exposure at  
1078 multiple scales. *Oikos* **124**:1536–1546. Wiley Online Library.
- 1079 Paine RT. 1966. Food web complexity and species diversity. *The American Naturalist* **100**:65–75.
- 1080 Paine RT. 1969. A Note on Trophic Complexity and Community Stability. *The American Naturalist*  
1081 **103**:91–93.
- 1082 Palmer MS, Gaynor KM, Becker JA, Abraham JO, Mumma MA, Pringle RM. 2022. Dynamic  
1083 landscapes of fear: understanding spatiotemporal risk. *Trends in Ecology & Evolution* **37**:911–  
1084 925. Elsevier.

- 1085 Pojar J. 1999. The effects of deer browsing on the plant life of Haida Gwaii. Pages 90–97 Proceedings  
1086 of the cedar symposium: growing western redcedar and yellowcypress on the Queen Charlotte  
1087 Islands/Haida Gwaii. BC Ministry of Forests/Canada–British Columbia South Moresby Forest  
1088 Replacement Account, Victoria, BC. Citeseer.
- 1089 Potratz EJ, Holt RD, Brown JS. 2024. Ecology of Fear: Acclimation and Adaptations to Hunting by  
1090 Humans. *Sustainability* **16**:1216. MDPI.
- 1091 Racine JS. 2012. RStudio: a platform-independent IDE for R and Sweave. JSTOR.
- 1092 Réale D, Garant D, Humphries MM, Bergeron P, Careau V, Montiglio P-O. 2010. Personality and the  
1093 emergence of the pace-of-life syndrome concept at the population level. *Philosophical  
1094 Transactions of the Royal Society B: Biological Sciences* **365**:4051–4063. The Royal Society.
- 1095 Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ. 2007. Integrating animal temperament  
1096 within ecology and evolution. *Biological reviews* **82**:291–318. Wiley Online Library.
- 1097 Richards MP, Fuller BT, Molleson TI. 2006. Stable isotope palaeodietary study of humans and fauna  
1098 from the multi-period (Iron Age, Viking and Late Medieval) site of Newark Bay, Orkney.  
1099 *Journal of Archaeological Science* **33**:122–131. Elsevier.
- 1100 Rodriguez-Prieto I, Fernández-Juricic E, Martín J, Regis Y. 2009. Antipredator behavior in blackbirds:  
1101 habituation complements risk allocation. *Behavioral Ecology* **20**:371–377. Oxford University  
1102 Press.
- 1103 Roffler GH, Eriksson CE, Allen JM, Levi T. 2023. Recovery of a marine keystone predator transforms  
1104 terrestrial predator–prey dynamics. *Proceedings of the National Academy of Sciences*  
1105 **120**:e2209037120. National Acad Sciences.
- 1106 Salomon AK, Shears NT, Langlois TJ, Babcock RC. 2008. Cascading effects of fishing can alter carbon  
1107 flow through a temperate coastal ecosystem. *Ecological Applications* **18**:1874–1887. Wiley  
1108 Online Library.
- 1109 Schulting RJ, Blockley SM, Bocherens H, Drucker D, Richards M. 2008. Stable carbon and nitrogen  
1110 isotope analysis on human remains from the Early Mesolithic site of La Vergne (Charente-  
1111 Maritime, France). *Journal of Archaeological Science* **35**:763–772. Elsevier.
- 1112 Schuttler SG, Parsons AW, Forrester TD, Baker MC, McShea WJ, Costello R, Kays R. 2017. Deer on  
1113 the lookout: how hunting, hiking and coyotes affect white-tailed deer vigilance. *Journal of  
1114 Zoology* **301**:320–327. Wiley Online Library.
- 1115 Sih A, Bell A, Johnson JC. 2004. Behavioral syndromes: an ecological and evolutionary overview.  
1116 *Trends in ecology & evolution* **19**:372–378. Elsevier.
- 1117 Sih A, Cote J, Evans M, Fogarty S, Pruitt J. 2012. Ecological implications of behavioural syndromes.  
1118 *Ecology letters* **15**:278–289. Wiley Online Library.
- 1119 Soulé ME, Estes JA, Berger J, Del Rio CM. 2003. Ecological effectiveness: conservation goals for  
1120 interactive species. *Conservation Biology* **17**:1238–1250.
- 1121 Stankowich T. 2008. Ungulate flight responses to human disturbance: a review and meta-analysis.  
1122 *Biological conservation* **141**:2159–2173. Elsevier.
- 1123 Stankowich T, Coss RG. 2006. Effects of predator behavior and proximity on risk assessment by  
1124 Columbian black-tailed deer. *Behavioral Ecology* **17**:246–254. Oxford University Press.
- 1125 Stankowich T, Coss RG. 2007. Effects of risk assessment, predator behavior, and habitat on escape  
1126 behavior in Columbian black-tailed deer. *Behavioral Ecology* **18**:358–367. Oxford University  
1127 Press.
- 1128 Stock B, Semmens B, Ward E, Parnell A, Jackson A, Phillips D. 2018a. Package ‘MixSIAR.’ Bayesian  
1129 Mixing Models in R, Version 3.
- 1130 Stock BC, Jackson AL, Ward EJ, Parnell AC, Phillips DL, Semmens BX. 2018b. Analyzing mixing  
1131 systems using a new generation of Bayesian tracer mixing models. *PeerJ* **6**:e5096. PeerJ Inc.
- 1132 Stockton SA, Allombert S, Gaston AJ, Martin J-L. 2005. A natural experiment on the effects of high  
1133 deer densities on the native flora of coastal temperate rain forests. *Biological Conservation*  
1134 **126**:118–128.
- 1135 Taylor WP. 1956. *The Deer of North America*. Stackpole Company and Wildlife Management Institute,  
1136 Washington.
- 1137 Team RC. 2018. *R: A language and environment for statistical computing*; 2018.

- 1138 Valiente-Banuet A, Aizen MA, Alcántara JM, Arroyo J, Cocucci A, Galetti M, García MB, García D,  
1139 Gómez JM, Jordano P. 2015. Beyond species loss: the extinction of ecological interactions in  
1140 a changing world. *Functional Ecology* **29**:299–307. Wiley Online Library.
- 1141 Vila B, Guibal F, Torre F, Martin J-L. 2004a. Assessing spatial variation in browsing history by means  
1142 of fraying scars. *Journal of Biogeography* **31**:987–995. Wiley Online Library.
- 1143 Vila B, Torre F, Guibal F, Martin J-L. 2004b. Can we reconstruct browsing history and how far back?  
1144 Lessons from *Vaccinium parvifolium* Smith in Rees. *Forest Ecology and Management*  
1145 **201**:171–185.
- 1146 Waller DM, Reo NJ. 2018. First stewards: ecological outcomes of forest and wildlife stewardship by  
1147 indigenous peoples of Wisconsin, USA. *Ecology and Society* **23**:45.
- 1148 Williams SC, DeNicola AJ, Ortega IM. 2008. Behavioral responses of white-tailed deer subjected to  
1149 lethal management. *Canadian Journal of Zoology* **86**:1358–1366.
- 1150 Wójcicki A, Borowski Z. 2023. The presence of wolves leads to spatial differentiation in deer browsing  
1151 pressure on forest regeneration. *Scientific Reports* **13**:17245.
- 1152 Ydenberg RC, Dill LM. 1986. The economics of fleeing from predators. *Advances in the Study of*  
1153 *Behavior* **16**:229–249. Elsevier.
- 1154 Zanette LY, Clinchy M. 2020. Ecology and neurobiology of fear in free-living wildlife. *Annual Review*  
1155 *of Ecology, Evolution, and Systematics* **51**:297–318. Annual Reviews.
- 1156