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

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

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

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

[1] CEFE, Univ Montpellier, CNRS, EPHE, IRD - Montpellier, France

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

[3] University of Montpellier, UMR 5554 CNRS/IRD/EPHE, CC061 - Montpellier, France

[4] University of Rennes, CNRS, ECOBIO Ecosystèmes, biodiversité, évolution, UMR 6553 - Rennes, France

[5] PO Box 792, 408 2nd Ave - Daajing Giids,Canada

[6] 81 rue Marius Carrieu, 34080 Montpellier, France

[7] National Wildlife Research Center, Environment and Climate Change Canada - Ottawa, Canada

*Jean-Louis Martin

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

Abstract

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

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

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

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

Introduction

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

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

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

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

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

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

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

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

Material and Methods

Haida Gwaii and the study sites

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

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

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

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

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

Risk hist.	Island	Region	Area	Hunting	Predators	Vegetation	Isotope
No-risk	East Limestone	Haida Gwaii	48 ha	N	N	Y	Y
No-risk	Kunga	Haida Gwaii	395 ha	N	N	Y	Y
No-risk	Faraday*	Haida Gwaii	308 ha	N	N	N	Y
No-risk	Murchison*	Haida Gwaii	425 ha	N	N	N	Y
No-risk	Reef <1997	Haida Gwaii	249 ha	N	N	Y	Y
Risk	Reef >1997	Haida Gwaii	249 ha	Y (cull)	N	Y	Y
Risk	Graham	Haida Gwaii	6361 km²	Y	N	Y	Y
Risk	Yeo	Coastal BC	95 km²	Y	Y	Y	Y

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

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

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

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

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

Is vegetation cover and diversity shaped by predation risk?

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

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

Is deer behaviour shaped by predation risk?

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

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

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

Is risk affecting Flight Initiation Distance, and Distance travelled?

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

δX gives the deviation between the samples isotopic ratio and the ratio obtained from an international standard, “R in sample” is the isotopic ratio considered, in our case 13C/12C and 15N/14N. For Carbon, “R in reference” refers to the standard Pee Dee Belemnite (PDB) originally derived from a Cretaceous marine fossil, Belemnitella americana, from the Peedee Formation in South Carolina, for Nitrogen the accepted standard is atmospheric N2.

δ15N typically get enriched by about 3‰ when going from one trophic level to the next. At the consumer level the whole animal body δ13C closely reflects its concentration in the diet but its fractioning varies among tissues. Values of concentration gain vary from + 1.5‰ in muscle, to + 5‰ in consumer’s collagen tissue when compared to whole body values (DeNiro and Epstein 1978, 1981, Bocherens 1999, Kelly 2000, Bocherens and Drucker 2003, Camin et al. 2016).

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

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

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

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

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

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

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

Results

Understory vegetation varied with risk history

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

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

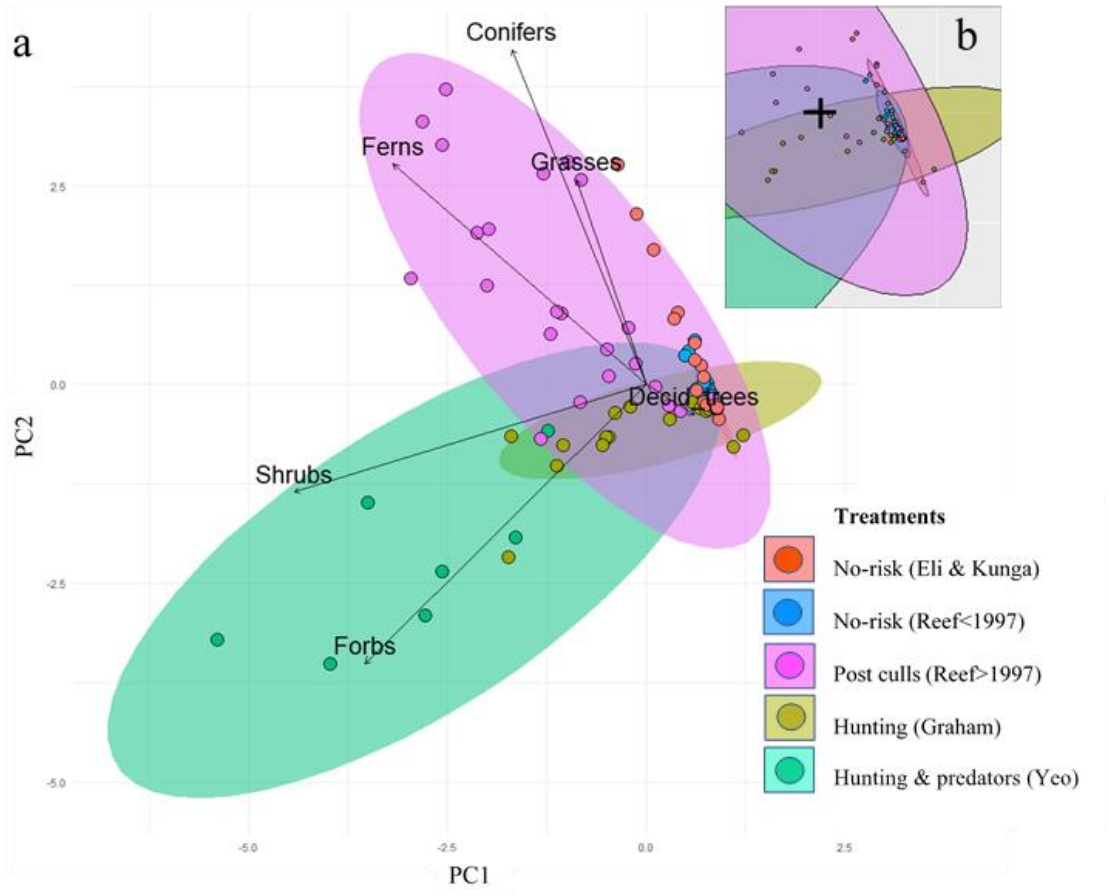


Figure 2. a: Scores of the vegetation plots on the two first components of the Principal Component Analysis on understory vegetation in relation to the main categories of understory vegetation. Treatments were color coded post analysis. Treatments are: No hunting represented by [No-risk (East Limestone (Eli) & Kunga)] = East Limestone and Kunga islands, in red, and [No-risk (Reef<1997)] = Reef island before the cull (1997), in blue; Presence of risk through hunting with [Past culls (Reef>1997)] = Reef Island after the1997 to 2008 culls, in pink, and [Hunting (Graham)] = long history of yearly hunting, in kaki; Presence of risk through regular hunting and presence of deer natural predators [Hunting + predators (Yeo)] = Yeo island, in green. **b:** zoom around plot center showing the ellipses corresponding to the [No-risk (Eli & Kunga)] (small red shade) and [No-risk (Reef<1997)] (tiny blue shade). Their small extent expresses the extreme similarity among vegetation plots in these samples. Note the five outliers from Kunga in the [No-risk (Eli & Kunga)]sample.

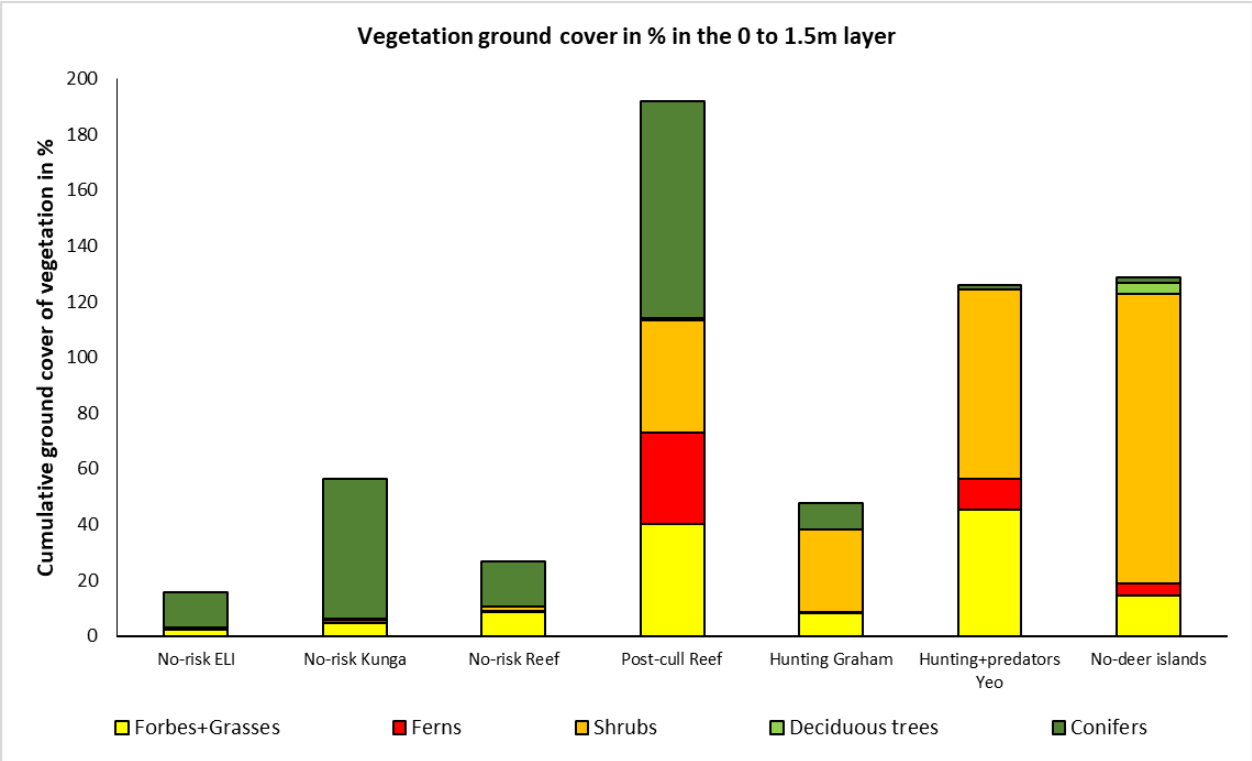


Figure 3. Cumulative percent cover recorded in the 0 to 1.5 m strata for the main understory plant categories in the different sampling units of our treatment categories: absence of predation risk (No-risk East Limestone and Kunga islands), and No-risk Reef island before the culls (1997); short recent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

Flight initiation distance varied with risk category

We collected FID data over several years at East Limestone, Kunga and Reef islands (post-cull): values among years did not differ significantly ($p = 0.60$). Nor did sex or age have any effect ($p = 0.30$, $p = 0.62$ respectively). Combining sexes, ages and years, FID varied significantly among samples ($p < 0.001$; $F = 49.28$ [on 3 predictors, DF = 233], residual standard error = 0.24, $R2 = 0.38$). All pairwise comparisons differed significantly (Fig. 4a, Table 2). FID was lowest for "No-risk" samples and highest for the Reef Island post-cull sample. Among the "No-risk" samples, FID was lowest for the East Limestone Island sample and highest for the Kunga deer translocated to Reef Island (Fig. 4a, Table 2).

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

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

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

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

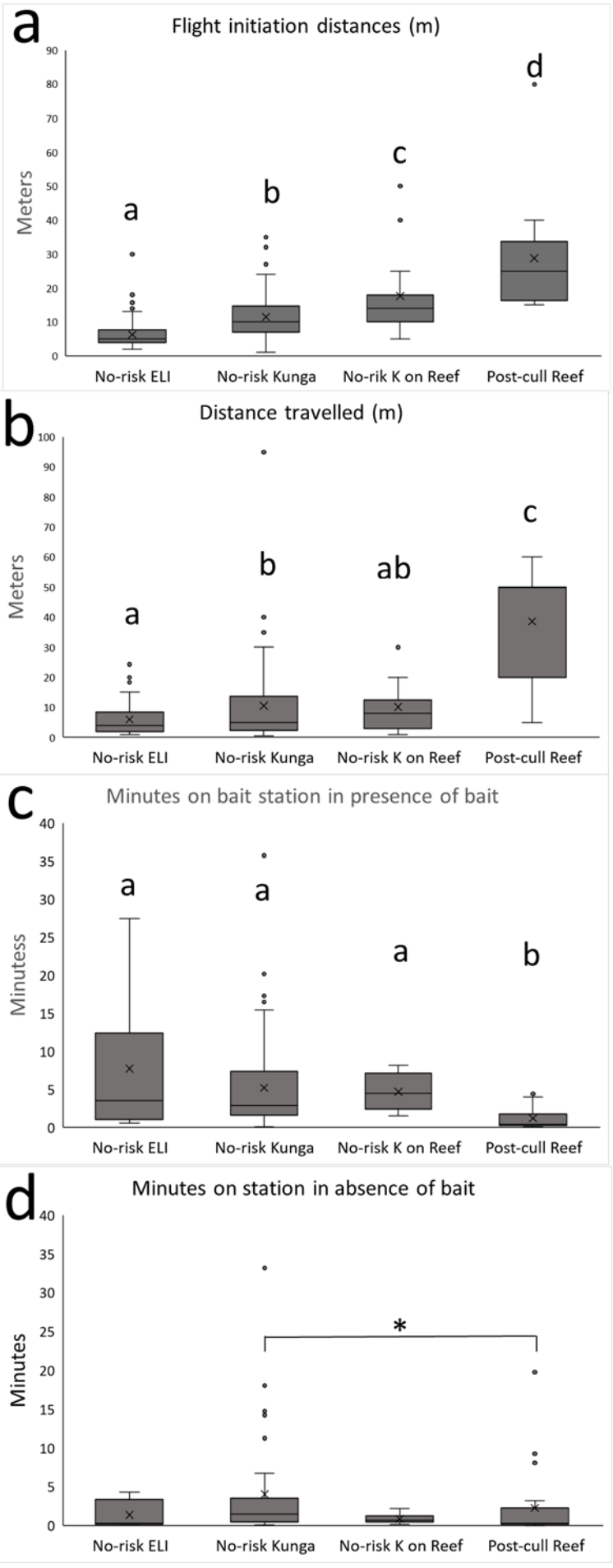


Figure 4. Boxplots on Flight and travel distance and on time spent at bait stations with bait present or absent. No-risk ELI = East Limestone deer, No-risk Kunga = Kunga deer on Kunga Island, No-risk K on Reef = Kunga deer after translocation to Reef Island, Post-cull Reef = Reef Island deer born into a population that survived the 1997 to 2008 culls. X in box = mean value, solid line in box = median value. Letters indicate results of post-hoc tests on the linear regression model on FID (log10 transformed) as a function of deer categories. **a.** Flight Initiation Distance (FID). All pairwise comparisons were significant: most had p-values < 0.001 except No-risk Kunga – No-risk K on Past culls Reef (p = 0.02) and No-risk K on Post-cull Reef – Post-cull Reef (p = 0.03). **b.** Distance travelled after flight initiation (Dtravel). For Post-cull Reef Median = 50 m. All pairwise comparisons were significant except for No-risk (ELI – No-risk K on Reef (p = 0.12) and No-risk Kunga – No-risk K on Post-cull Reef (p = 0.96). For the pairwise comparisons that were significant all p-values were <0.001 except No risk ELI – No-risk Kunga (p = 0.01). **c.** Time spent at bait stations with bait present. All comparisons among No risk categories were non-significant (p-values>0.80). For the pairwise comparisons that were significant, all p-values were <0.05. **d.** Time spent at bait stations by deer when bait was missing (consumed since station was re-provisioned). All comparisons among No risk categories were non-significant (p-values>0.50, except for No-risk Kunga – No-risk K on Post-cull Reef (p = 0.37). Only for the No-risk Kunga – Post-cull Reef comparison did Kunga deer spent significantly more time at stations with no bait left than did deer native to Post-cull Reef (p = 0.04).

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

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

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

Distance travelled after flight varied with risk category

Dtravel varied among samples with a significant contrast between the "No-risk" and the "post-cull" samples: $p < 0.001$; F-statistic = 18.04 (on 3 predictors, DF = 229), Residual standard error = 0.42, R2 = 0.18. (see Fig. 4b). Dtravel observed on East Limestone Island (No-risk) was significantly shorter than on Kunga Island (No-risk) (p = 0.01), and was much shorter Reef Island post-cull (Fig. 4b) ($p < 0.001$). Dtravel for Kunga Island deer after translocation to Reef was similar to that observed on Kunga itself (p = 0.96), and to that on East Limestone Island (No-risk) (p = 0.12), but much shorter than that observed for deer native to Reef ("post-cull Reef") ($p < 0.001$) (Fig. 4b, Table 4).

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

Attraction versus aversion varied with risk category

Response to bait – Risk category had a significant effect on time spent at bait stations when bait was present (log10 transformed): p = 0.007, F-statistic = 4.29 (on 3 predictor, DF=79); Residual standard error = 0.63, R2 = 0.14 (Fig. 4c).

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

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

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

In absence of bait because of previous consumption, mean visit length by deer at a station were shorter (Fig. 4d versus Fig. 4c). Sample still had a significant effect on length of visit at a station (log10 transformed): $p = 0.05$, F-statistic = 2.72 (on 3 predictor, DF=84), Residual standard error = 0.64, $R2 = 0.09$ (Table 5, Fig. 4d), but this effect was unrelated to risk history. Visits were longer on average on Kunga essentially through the effect of outliers spending long periods at sites that had bait recently (Fig. 4d). Whatever the sample, time spent at a station never exceeded 4 minutes (Table 5). Median values equaled 36 s or less, with the exception of Kunga deer (median = 84 s). When time was spent at a station without bait, it was spent sniffing at the location where bait had been present.

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

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

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

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

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

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

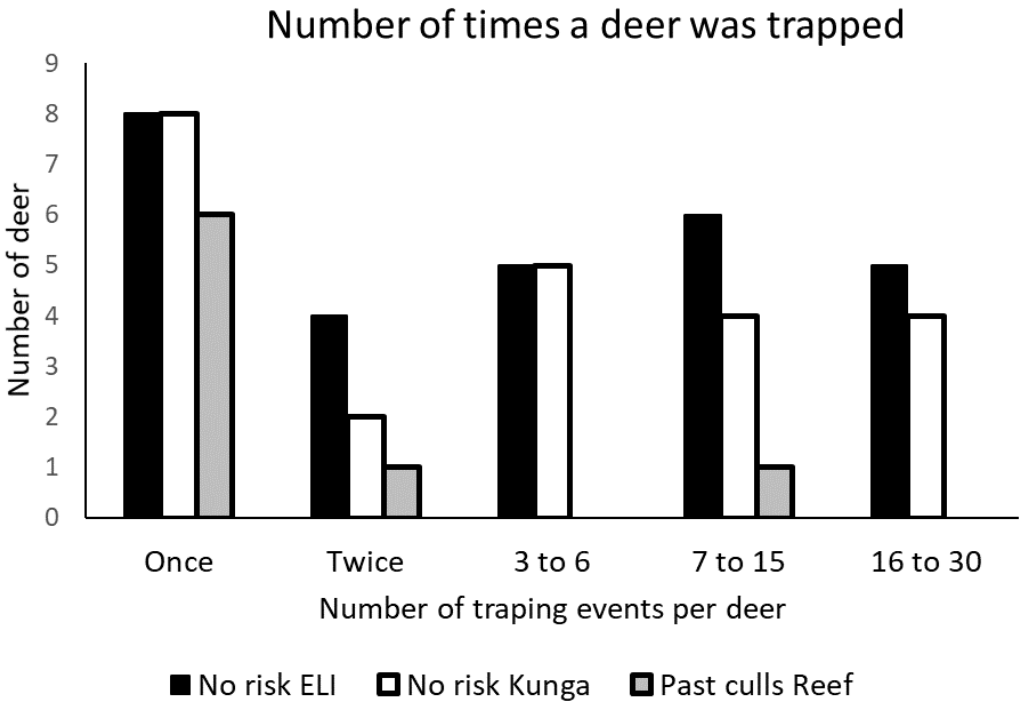


Figure 5. Summary of the capture and recapture histories for the deer native to the three sites and two categories of hunting histories. ELI = East Limestone Island.

Diel activity pattern varied with risk category

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

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

562

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

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

567

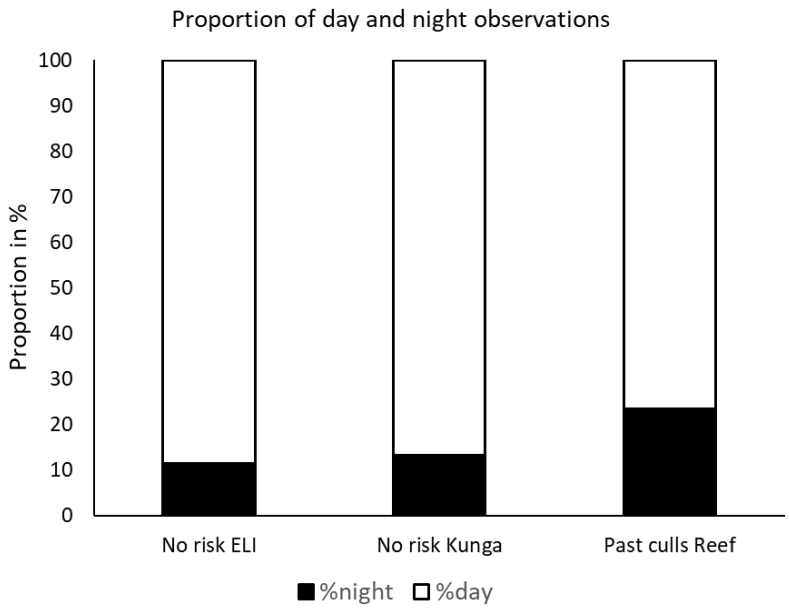


Figure 6. Temporal distribution between day and night of deer caught on automatic cameras near bait stations on islands in the absence of predation risk No-risk ELI (East Limestone) and No-risk Kunga (Kunga) and in presence of past risk (Post-cull Reef)

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

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

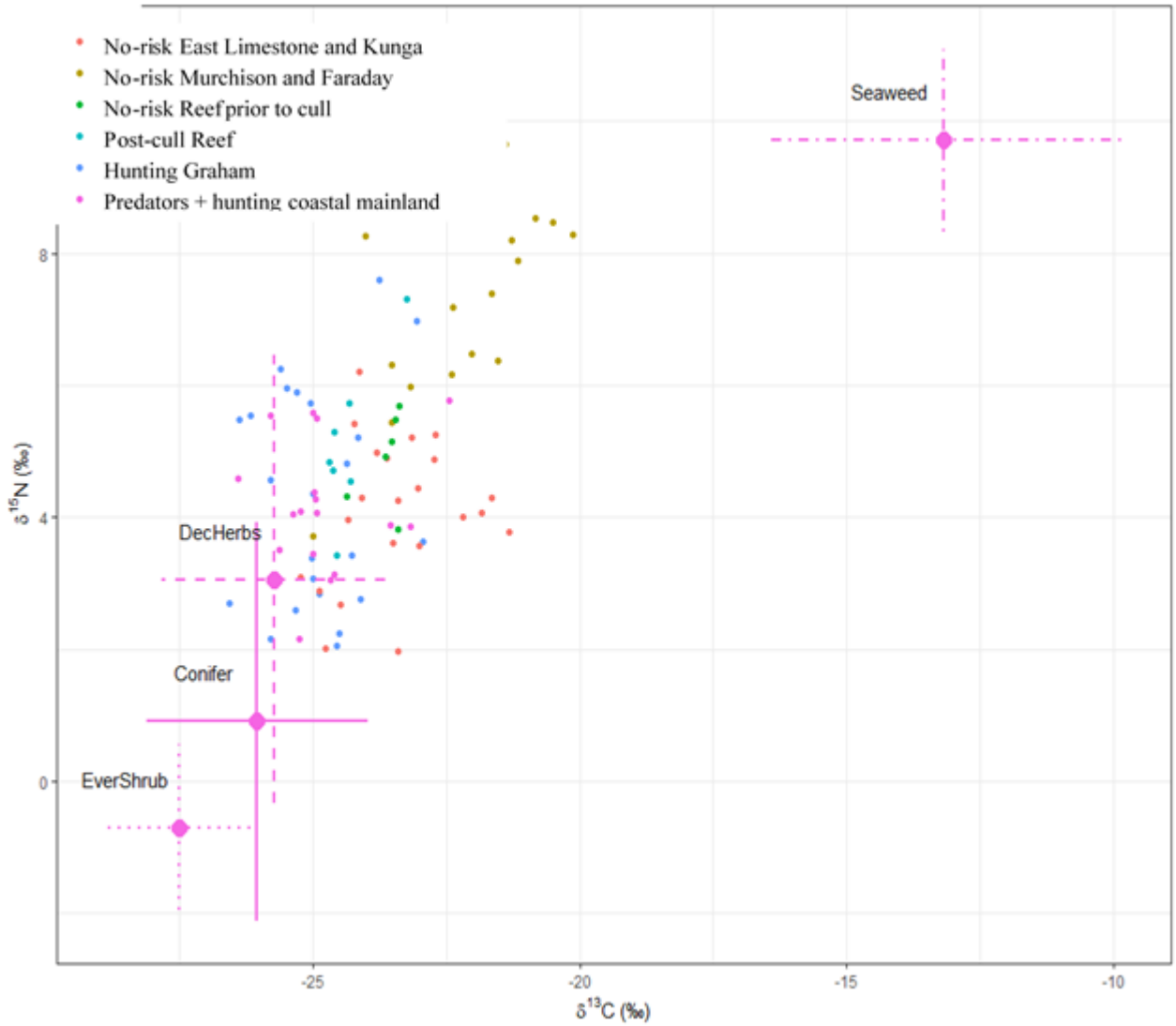
586 The isospace plot (Fig. 7) shows a spread of the isotopic signature in deer bone samples relative
587 to the proportion of seaweed and terrestrial plants in deer diet. The samples with the highest

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

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

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

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



612

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

622

623

624

625

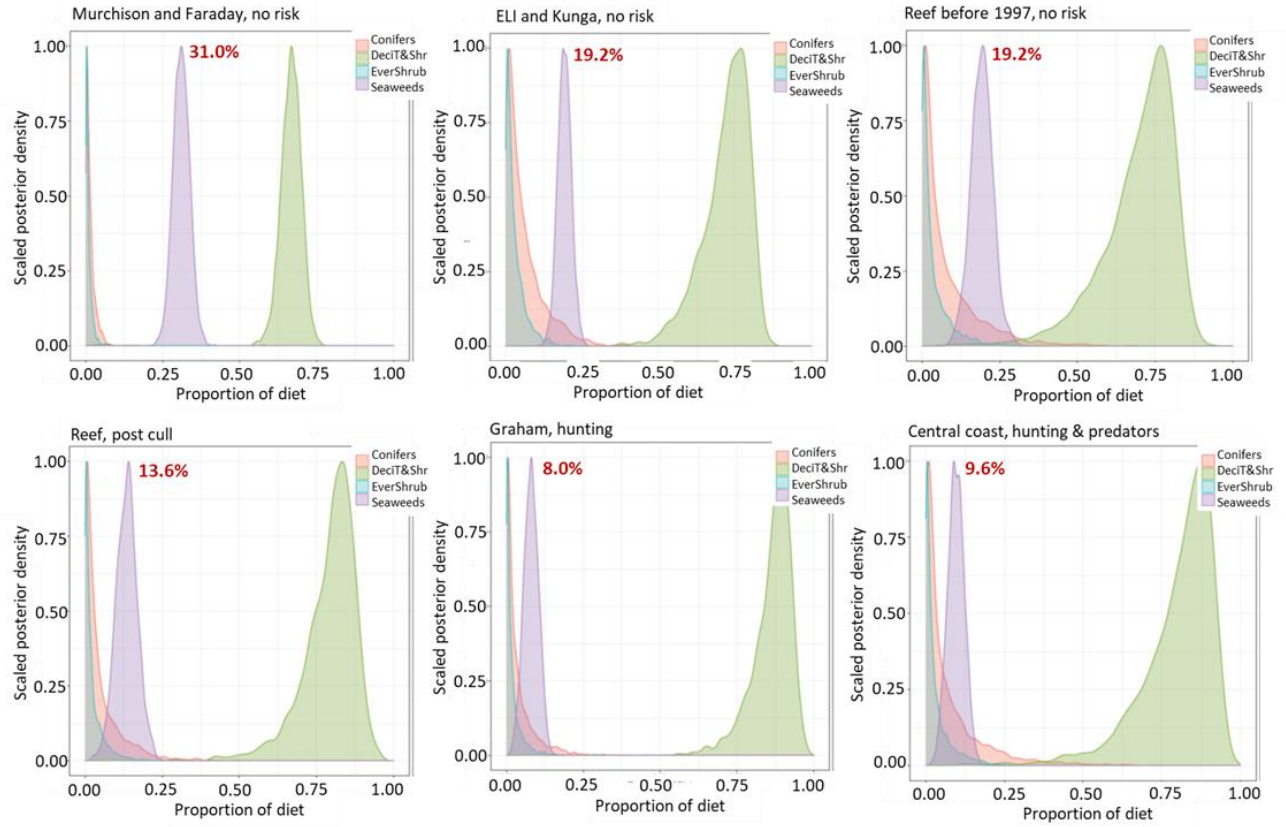


Figure 8. MixSiar posterior plots of overall deer diet in relation to predation risk. N = number of bone samples per site. No hunting history, four sites: Murchison (N=10), Faraday (N=6), East Limestone (ELI) (N= 10), Kunga (N=12) and Reef before the culls (N=7)) (see map in Fig. 1); Reef post-cull = 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); Coastal mainland, hunting and predators present (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).

Discussion

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

What lessons for ecology, population behavioural change and conservation?

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

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

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

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

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

Ethical note

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

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

Acknowledgements

This is a publication of the Research Group on Introduced Species (RGIS, https://rgis.cefe.cnrs.fr). On top of funding (see below) we received critical logistic support from the Laskeek Bay Conservation Society, Environment and Climate Change Canada, the Gwaii Haanas National Park Reserve, National Marine Conservation Area Reserve and Haida Heritage Site, the Coast Sustainability Trust Matching Fund (CST-QCI-HG- 061– RGIS Infrastructure Upgrade), and the "Understanding Canada" program from the Canadian government. We are indebted to Todd Golumbia, Carita Bergman and Peter Dyment and colleagues from Gwaii Haanas for support in the field. Tibo Verchère, Ainsley Brown, Barbara and Keith Rowsell, Greg Martin, Jacques Morin, Erin Harris, Terry and Ron Husband, Bruno Cargnelutti, Nicolas Cebe, Mike Gillingham, Malcolm Hyatt, Georges Janeau, Jean-Luc Rames, Denis Picot, Helen Schwantje, Tom Smith and Keith Tipper provided critical help in the field and beyond. Chris Darimont, Eva Poilvé and Maurah Van Impe assisted with the treatment of samples in the stable isotope analysis. The Haida Watchmen program provided precious help through accommodation on Tanu Island. Over the years, many members of the local communities provided invaluable support. We are deeply thankful to all.

Data, scripts, code, and supplementary information availability

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

Funding

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

Conflict of interest disclosure

The authors declare that they comply with the PCI rule of having no financial conflicts of interest in relation to the content of the article. JL Martin and Simon Chamaillé-Jammes are listed as recommenders

References

Altendorf, K. B., Laundré, J. W., López González, C. A., & Brown, J. S. (2001). Assessing effects of predation risk on foraging behavior of mule deer. Journal of Mammalogy, 82(2), 430–439.

Balasse, M., Tresset, A., Dobney, K., & Ambrose, S. H. (2005). The use of isotope ratios to test for seaweed eating in sheep. Journal of Zoology, 266(3), 283–291.

Ballard, W. B., Lutz, D., Keegan, T. W., Carpenter, L. H., & deVos Jr, J. C. (2001). Deer-predator relationships: A review of recent North American studies with emphasis on mule and black-tailed deer. Wildlife Society Bulletin, 99–115.

Banner, A., MacKenzie, W. H., Pojar, J., MacKinnon, A., Saunders, S. C., & Klassen, H. (2014). A field guide to ecosystem classification and identification for Haida Gwaii. Land Management Handbook.

Blumstein, D. T. (2002). Moving to suburbia: Ontogenetic and evolutionary consequences of life on predator-free islands. Journal of Biogeography, 29(5-6), 685–692.

Blumstein, D. T., & Daniel, J. C. (2005). The loss of anti-predator behaviour following isolation on islands. Proceedings of the Royal Society B: Biological Sciences, 272(1573), 1663–1668.

Bocherens, H. (1999). Isotopes stables et reconstitution du régime alimentaire des hominidés fossiles: Une revue. Bulletins et Mémoires de La Société d'Anthropologie de Paris, 11(3), 261–287.

Bocherens, H., & Drucker, D. (2003). Trophic level isotopic enrichment of carbon and nitrogen in bone collagen: Case studies from recent and ancient terrestrial ecosystems. International Journal of Osteoarchaeology, 13(1-2), 46–53.

Bocherens, H., Fizet, M., Cuif, J.-P., Jaeger, J.-J., & Michard, J.-G. (1988). Premières mesures d'abondance isotopiques naturelles en 13C et 15N de la matière organique fossile de Dinosaure. Application à l'étude du régime alimentaire du genre Anatosaurus (Ornitischia, Hadrosauridae). Comptes Rendus de l'Académie Des Sciences. Série 2, Mécanique, Physique, Chimie, Sciences de l'univers, Sciences de La Terre, 306(20), 1521–1525.

Bochérens, Hervé, Marc Fizet, Lange-Badre, B., Vandermeersch, B., Borel, J. P., & Bellon, G. (1991). Isotopic biogeochemistry (13C, 15N) of fossil vertebrate collagen: Application to the study of a past food web including Neandertal man. Journal of Human Evolution, 20(6), 481–492.

Bøhn, T., & Amundsen, P.-A. (2004). Ecological interactions and evolution: Forgotten parts of biodiversity? BioScience, 54(9), 804–805.

Bonnot, N. C., Couriot, O., Berger, A., Cagnacci, F., Ciuti, S., De Groeve, J. E., Gehr, B., Heurich, M., Kjellander, P., & Kröschel, M. (2020). Fear of the dark? Contrasting impacts of humans versus lynx on diel activity of roe deer across Europe. Journal of Animal Ecology, 89(1), 132–145.

Bonnot, N. C., Hewison, A. M., Morellet, N., Gaillard, J.-M., Debeffe, L., Couriot, O., Cargnelutti, B., Chaval, Y., Lourtet, B., & Kjellander, P. (2017). Stick or twist: Roe deer adjust their flight behaviour to the perceived trade-off between risk and reward. Animal Behaviour, 124, 35–46.

Bonnot, N. C., Morellet, N., Hewison, A. M., Martin, J.-L., Benhamou, S., & Chamaillé-Jammes, S. (2016). Sitka black-tailed deer (Odocoileus hemionus sitkensis) adjust habitat selection and activity rhythm to the absence of predators. Canadian Journal of Zoology, 94(6), 385–394.

Brown, J. S., Laundré, J. W., & Gurung, M. (1999). The ecology of fear: Optimal foraging, game theory, and trophic interactions. Journal of Mammalogy, 80(2), 385–399.

Burgess, B. T., Irvine, R. L., Martin, J.-L., & Russello, M. A. (2023). Past population control biases interpretations of contemporary genetic data: Implications for future invasive Sitka black-tailed deer management in Haida Gwaii. Biological Invasions, 25(12), 3871–3886.

Burgess, B. T., Irvine, R. L., & Russello, M. A. (2022a). A genotyping-in-thousands by sequencing panel to inform invasive deer management using noninvasive fecal and hair samples. Ecology and Evolution, 12(6), e8993.

Burgess, B. T., Irvine, R. L., & Russello, M. A. (2022b). Population genomics of Sitka black-tailed deer supports invasive species management and ecological restoration on islands. Communications Biology, 5(1), 223.

Callan, R., Nibbelink, N. P., Rooney, T. P., Wiedenhoeft, J. E., & Wydeven, A. P. (2013). Recolonizing wolves trigger a trophic cascade in Wisconsin (USA). Journal of Ecology, 101(4), 837–845. https://doi.org/10.1111/1365-2745.12095

Camin, F., Bontempo, L., Perini, M., & Piasentier, E. (2016). Stable isotope ratio analysis for assessing the authenticity of food of animal origin. Comprehensive Reviews in Food Science and Food Safety, 15(5), 868–877.

960 Cardinal, E., Martin, J.-L., & Côté, S. D. (2012). Large herbivore effects on songbirds in boreal
961 forests: Lessons from deer introduction on Anticosti Island. Ecoscience, 19(1), 38–47.

962 Cardinal, E., Martin, J.-L., Tremblay, J.-P., & Côté, S. D. (2012). An experimental study of
963 how variation in deer density affects vegetation and songbird assemblages of recently harvested
964 boreal forests. Canadian Journal of Zoology, 90(6), 704–713.

965 Chamaillé-Jammes, S., Malcuit, H., Le Saout, S., & Martin, J.-L. (2014). Innate threat-sensitive
966 foraging: Black-tailed deer remain more fearful of wolf than of the less dangerous black bear
967 even after 100 years of wolf absence. Oecologia, 174(4), 1151–1158.

968 Chitwood, M. C., Baruzzi, C., & Lashley, M. A. (2022). "Ecology of fear" in ungulates:
969 Opportunities for improving conservation. Ecology and Evolution, 12(3), e8657.

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

973 Chollet, S., Baltzinger, C., Maillard, M., & Martin, J.-L. (2021b). Deer exclusion unveils
974 abiotic filtering in forest understorey plant assemblages. Annals of Botany, 128(3), 371–381.

975 Chollet, S., Baltzinger, C., Ostermann, L., Saint-André, F., & Martin, J.-L. (2013). Importance
976 for forest plant communities of refuges protecting from deer browsing. Forest Ecology and
977 Management, 289, 470–477. https://doi.org/10.1016/j.foreco.2012.10.043

978 Chollet, S., Bergman, C., Gaston, A. J., & Martin, J.-L. (2015). Long-term consequences of
979 invasive deer on songbird communities: Going from bad to worse? Biological Invasions, 17(2),
980 777–790.

981 Chollet, S., Maillard, M., Schörghuber, J., Grayston, S. J., & Martin, J.-L. (2021a). Deer slow
982 down litter decomposition by reducing litter quality in a temperate forest. Ecology, 102(2),
983 e03235.

984 Chollet, S., Padié, S., Stockton, S., Allombert, S., Gaston, A. J., & Martin, J.-L. (2016). Positive
985 plant and bird diversity response to experimental deer population reduction after decades of
986 uncontrolled browsing. Diversity and Distributions, 22(3), 274–287.
987 https://doi.org/10.1111/ddi.12393

988 Cooper Jr, W. E. (2008). Visual monitoring of predators: Occurrence, cost and benefit for
989 escape. Animal Behaviour, 76(4), 1365–1372.

990 Côté, S. D., Rooney, T. P., Tremblay, J.-P., Dussault, C., & Waller, D. M. (2004). Ecological
991 Impacts of Deer Overabundance. Annual Review of Ecology, Evolution, and Systematics, 35,
992 113–147.

993 Darimont, C. T., Paquet, P. C., & Reimchen, T. E. (2007). Stable isotopic niche predicts fitness
994 of prey in a wolf–deer system. Biological Journal of the Linnean Society, 90(1), 125–137.

995 Darimont, C. T., & Reimchen, T. E. (2002). Intra-hair stable isotope analysis implies seasonal
996 shift to salmon in gray wolf diet. Canadian Journal of Zoology, 80(9), 1638–1642.

997 Darwin, C. (1840). Journal of Researches into the Geology and Natural History of the Varoius
998 Countries Visited by HMS Beagle, under the Command of Captain Fitzroy from 1832 to 1836
999 by Charles Darwin. Colburn.

1000 Daufresne, T., & Martin, J. L. (1997). Changes in vegetation structure and diversity as a result
1001 of browsing by a large herbivore: The impact of introduced Black-tailed deer in the primary
1002 forest of Haida Gwaii, British Columbia. Laskeek Bay Research, 7, 2–26.

1003 DeNiro, M. J., & Epstein, S. (1978). Influence of diet on the distribution of carbon isotopes in
1004 animals. Geochimica et Cosmochimica Acta, 42(5), 495–506.

1005 DeNiro, M. J., & Epstein, S. (1981). Influence of diet on the distribution of nitrogen isotopes
1006 in animals. Geochimica et Cosmochimica Acta, 45(3), 341–351.

1007 Ellers, J., Toby Kiers, E., Currie, C. R., McDonald, B. R., & Visser, B. (2012). Ecological
1008 interactions drive evolutionary loss of traits. Ecology Letters, 15(10), 1071–1082.

1009 Elton, C. (1927). Animal ecology. 207 pp. Sidgwick & Jackson, LTD. London.

1010 Engelstoft, C. (2001). Effects of Sitka Black-tailed Deer (Odocoileus Hemionus Sitkensis) on
1011 Understory in Old Growth Forest on Haida Gwaii (Queen Charlotte Islands), British Columbia.
1012 University of Victoria.

1013 Engelstoft, C., Kirchhoff, M. D., & Eastman, D. (2008). Herbivory and the missing understory
1014 on Haida Gwaii. In Lessons from the Islands: Introduced Species and What They Tell Us About
1015 How Ecosystems Work. (pp. 78–86). Canadian Wildlife Service, Environment Canada,
1016 Ottawa.

1017 Estes, J. A., Brashares, J. S., & Power, M. E. (2013). Predicting and detecting reciprocity
1018 between indirect ecological interactions and evolution. The American Naturalist, 181(S1),
1019 S76–S99.

1020 Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S.
1021 R., Essington, T. E., Holt, R. D., Jackson, J. B. C., Marquis, R. J., Oksanen, L., Oksanen, T.,
1022 Paine, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., …
1023 Wardle, D. A. (2011). Trophic Downgrading of Planet Earth. Science, 333(6040), 301–306.

1024 Gaston, A. J., Stockton, S. A., & Smith, J. L. (2006). Species-area relationships and the impact
1025 of deer-browse in the complex phytogeography of the Haida Gwaii archipelago (Queen
1026 Charlotte Islands), British Columbia. Écoscience, 13(4), 511–522.
1027 https://doi.org/10.2980/1195-6860(2006)13[511:SRATIO]2.0.CO;2

1028 Gaynor, K. M., Brown, J. S., Middleton, A. D., Power, M. E., & Brashares, J. S. (2019).
1029 Landscapes of fear: Spatial patterns of risk perception and response. Trends in Ecology &
1030 Evolution, 34(4), 355–368.

1031 Golumbia, T., Bland, L., Moore, K., & Bartier, P. (2008). History and current status of
1032 introduced vertebrates on Haida Gwaii. In Lessons from the islands: Introduced species and
1033 what they tell us about how ecosystems work (pp. 8–31). Canadian Wildlife Service,
1034 Envionment Canada, Ottawa.

1035 Greenberg, R., & Mettke-Hofmann, C. (2001). Ecological aspects of neophobia and neophilia
1036 in birds. Current Ornithology, 119–178.

1037 Haeckel, E. (1866). Generelle Morphologie der Organismen. Allgemeine Grundzüge der
1038 organischen Formen-Wissenschaft, mechanisch begründet durch die von C. Darwin reformirte
1039 Descendenz-Theorie. Allgemeine Entwicklungsgeschichte. (Vol. 2). De Gruyter.

1040 Janzen, D. H. (1974). The deflowering of central america. Natural History Magazine, 83(4),
1041 48–51.

1042 Jolly, C. J., Webb, J. K., & Phillips, B. L. (2018). The perils of paradise: An endangered species
1043 conserved on an island loses antipredator behaviours within 13 generations. Biology Letters,
1044 14(6), 20180222. https://doi.org/10.1098/rsbl.2018.0222

1045 Kelly, J. F. (2000). Stable isotopes of carbon and nitrogen in the study of avian and mammalian
1046 trophic ecology. Canadian Journal of Zoology, 78(1), 1–27.

1047 Klein, D. R. (1995). The introduction, increase, and demise of wolves on Coronation Island,
1048 Alaska. Ecology and Conservation of Wolves in a Changing World, 275, 280.

1049 Kuijper, D. P. J., Sahlén, E., Elmhagen, B., Chamaillé-Jammes, S., Sand, H., Lone, K., &
1050 Cromsigt, J. (2016). Paws without claws? Ecological effects of large carnivores in
1051 anthropogenic landscapes. Proc. R. Soc. B, 283. http://dx.doi.org/10.1098/rspb.2016.162

1052 Lack, D. L. (1968). Ecological adaptations for breeding in birds. Methuen.

1053 Le Saout, S., Chollet, S., Chamaillé-Jammes, S., Blanc, L., Padié, S., Verchere, T., Gaston, A.
1054 J., Gillingham, M. P., Gimenez, O., Parker, K. L., Picot, Verheyden, & Martin, J.-L. (2014).
1055 Understanding the paradox of deer persisting at high abundance in heavily browsed habitats.
1056 Wildlife Biology, 20(3), 122–135.

1057 Le Saout, S., Martin, J.-L., Blanchard, P., Cebe, N., Mark Hewison, A. J., Rames, J.-L., &
1058 Chamaillé-Jammes, S. (2015). Seeing a ghost? Vigilance and its drivers in a predator-free
1059 world. Ethology, 121(7), 651–660.

1060 Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A
1061 review and prospectus. Canadian Journal of Zoology, 68(4), 619–640.

Maillard, M., Martin, J.-L., Chollet, S., Catomeris, C., Simon, L., & Grayston, S. J. (2021). Belowground effects of deer in a temperate forest are time-dependent. Forest Ecology and Management, 493, 119228.

Martin, J.-L., & Baltzinger, C. (2002). Interaction among deer browsing, hunting, and tree regeneration. Canadian Journal of Forest Research, 32(7), 1254–1264. https://doi.org/10.1139/x02-043

Martin, J.-L., Chamaillé-Jammes, S., & Waller, D. M. (2020). Deer, wolves, and people: Costs, benefits and challenges of living together. Biological Reviews, 93(3), 782–801.

Martin, J.-L., Gaston, A. J., & Hitier, S. (1995). The effect of island size and isolation on old growth forest habitat and bird diversity in Gwaii Haanas (Queen Charlotte Islands, Canada). Oikos, 115–131.

Martin, J.-L., Stockton, S. A., Allombert, S., & Gaston, A. J. (2010). Top-down and bottom-up consequences of unchecked ungulate browsing on plant and animal diversity in temperate forests: Lessons from a deer introduction. Biological Invasions, 12(2), 353–371. https://doi.org/10.1007/s10530-009-9628-8

Martin, T. G., Arcese, P., & Scheerder, N. (2011). Browsing down our natural heritage: Deer impacts on vegetation structure and songbird populations across an island archipelago. Biological Conservation, 144(1), 459–469.

Mathews, N. E., & Porter, W. F. (1988). Black bear predation of white-tailed deer neonates in the central Adirondacks. Canadian Journal of Zoology, 66(5), 1241–1242.

Monestier, C., Morellet, N., Verheyden, H., Gaillard, J.-M., Bideau, E., Denailhac, A., Lourtet, B., Cebe, N., Picot, D., & Rames, J.-L. (2017). Neophobia is linked to behavioural and haematological indicators of stress in captive roe deer. Animal Behaviour, 126, 135–143.

Moseby, K. E., Blumstein, D. T., & Letnic, M. (2016). Harnessing natural selection to tackle the problem of prey naïveté. Evolutionary Applications, 9(2), 334–343.

Moseby, K. E., Carthey, A., & Schroeder, T. (2015). The influence of predators and prey naivety on reintroduction success: Current and future directions. Advances in Reintroduction Biology of Australian and New Zealand Fauna, 29–42.

Moseby, K., Van der Weyde, L., Letnic, M., Blumstein, D. T., West, R., & Bannister, H. (2023). Addressing prey naivety in native mammals by accelerating selection for antipredator traits. Ecological Applications, 33(2), e2780.

Paine, R. T. (1966). Food web complexity and species diversity. The American Naturalist, 100(910), 65–75.

Paine, R. T. (1969). A Note on Trophic Complexity and Community Stability. The American Naturalist, 103(929), 91–93.

Palmer, M. S., Gaynor, K. M., Becker, J. A., Abraham, J. O., Mumma, M. A., & Pringle, R. M. (2022). Dynamic landscapes of fear: Understanding spatiotemporal risk. Trends in Ecology & Evolution, 37(10). https://doi.org/10.1016/j.tree.2022.06.007

Pojar, J. (1999). The effects of deer browsing on the plant life of Haida Gwaii. Proceedings of the Cedar Symposium: Growing Western Redcedar and Yellowcypress on the Queen Charlotte Islands/Haida Gwaii. BC Ministry of Forests/Canada–British Columbia South Moresby Forest Replacement Account, Victoria, BC, 90–97.

Racine, J. S. (2012). RStudio: A platform-independent IDE for R and Sweave. JSTOR.

Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P.-O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. Philosophical Transactions of the Royal Society B: Biological Sciences, 365(1560), 4051–4063.

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. Biological Reviews, 82(2), 291–318.

Richards, M. P., Fuller, B. T., & Molleson, T. I. (2006). Stable isotope palaeodietary study of humans and fauna from the multi-period (Iron Age, Viking and Late Medieval) site of Newark Bay, Orkney. Journal of Archaeological Science, 33(1), 122–131.

Rodriguez-Prieto, I., Fernández-Juricic, E., Martín, J., & Regis, Y. (2009). Antipredator behavior in blackbirds: Habituation complements risk allocation. Behavioral Ecology, 20(2), 371–377.

Roffler, G. H., Eriksson, C. E., Allen, J. M., & Levi, T. (2023). Recovery of a marine keystone predator transforms terrestrial predator–prey dynamics. Proceedings of the National Academy of Sciences, 120(5), e2209037120.

Salomon, A. K., Shears, N. T., Langlois, T. J., & Babcock, R. C. (2008). Cascading effects of fishing can alter carbon flow through a temperate coastal ecosystem. Ecological Applications, 18(8), 1874–1887.

Schulting, R. J., Blockley, S. M., Bocherens, H., Drucker, D., & Richards, M. (2008). Stable carbon and nitrogen isotope analysis on human remains from the Early Mesolithic site of La Vergne (Charente-Maritime, France). Journal of Archaeological Science, 35(3), 763–772.

Schuttler, S. G., Parsons, A. W., Forrester, T. D., Baker, M. C., McShea, W. J., Costello, R., & Kays, R. (2017). Deer on the lookout: How hunting, hiking and coyotes affect white-tailed deer vigilance. Journal of Zoology, 301(4), 320–327.

Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: An ecological and evolutionary overview. Trends in Ecology & Evolution, 19(7), 372–378.

1131 Sih, A., Cote, J., Evans, M., Fogarty, S., & Pruitt, J. (2012). Ecological implications of
1132 behavioural syndromes. Ecology Letters, 15(3), 278–289.

1133 Soulé, M. E., Estes, J. A., Berger, J., & Del Rio, C. M. (2003). Ecological effectiveness:
1134 Conservation goals for interactive species. Conservation Biology, 17(5), 1238–1250.

1135 Stankowich, T. (2008). Ungulate flight responses to human disturbance: A review and meta-
1136 analysis. Biological Conservation, 141(9), 2159–2173.

1137 Stankowich, T., & Coss, R. G. (2006). Effects of predator behavior and proximity on risk
1138 assessment by Columbian black-tailed deer. Behavioral Ecology, 17(2), 246–254.

1139 Stankowich, T., & Coss, R. G. (2007). Effects of risk assessment, predator behavior, and
1140 habitat on escape behavior in Columbian black-tailed deer. Behavioral Ecology, 18(2), 358–
1141 367.

1142 Stock, B. C., Jackson, A. L., Ward, E. J., Parnell, A. C., Phillips, D. L., & Semmens, B. X.
1143 (2018). Analyzing mixing systems using a new generation of Bayesian tracer mixing models.
1144 PeerJ, 6, e5096.

1145 Stock, B., Semmens, B., Ward, E., Parnell, A., Jackson, A., & Phillips, D. (2018). Package
1146 'MixSIAR.' Bayesian Mixing Model s in R, Version, 3(10).

1147 Stockton, S. A., Allombert, S., Gaston, A. J., & Martin, J.-L. (2005). A natural experiment on
1148 the effects of high deer densities on the native flora of coastal temperate rain forests. Biological
1149 Conservation, 126(1), 118–128. https://doi.org/10.1016/j.biocon.2005.06.006

1150 Taylor, W. P. (1956). The Deer of North America. Stackpole Company and Wildlife
1151 Management Institute, Washington.

1152 Team, R. C. (2018). R: A language and environment for statistical computing; 2018.

1153 Valiente-Banuet, A., Aizen, M. A., Alcántara, J. M., Arroyo, J., Cocucci, A., Galetti, M.,
1154 García, M. B., García, D., Gómez, J. M., & Jordano, P. (2015). Beyond species loss: The
1155 extinction of ecological interactions in a changing world. Functional Ecology, 29(3), 299–307.

1156 Vila, B., Torre, F., Guibal, F., & Martin, J.-L. (2004). Can we reconstruct browsing history and
1157 how far back? Lessons from Vaccinium parvifolium Smith in Rees. Forest Ecology and
1158 Management, 201(2), 171–185.

1159 Waller, D. M., & Reo, N. J. (2018). First stewards: Ecological outcomes of forest and wildlife
1160 stewardship by indigenous peoples of Wisconsin, USA. Ecology and Society, 23(1), 45.
1161 https://doi.org/10.5751/ES-09865-230145

1162 Williams, S. C., DeNicola, A. J., & Ortega, I. M. (2008). Behavioral responses of white-tailed
1163 deer subjected to lethal management. Canadian Journal of Zoology, 86(12), 1358–1366.

Ydenberg, R. C., & Dill, L. M. (1986). The economics of fleeing from predators. Advances in the Study of Behavior, 16, 229–249.