

Influences of marine subsidies on coastal mammal ecology

by

Katie Davidson
B.Sc., Vancouver Island University, 2015

A Thesis Submitted in Partial Fulfillment
of the Requirements for the Degree of

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in the Department of Geography

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Abstract

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The marine ecosystem provides key resources to terrestrial organisms inhabiting oceanic islands. These subsidies of marine resources have the potential to affect species richness, ecology and productivity, especially on islands with high perimeter-area ratios. I investigated the impact and importance of marine subsidies on mammal diversity and diet on islands of British Columbia's Central Coast. Insular mammal species richness was significantly correlated with island area and quantity of marine subsidy (wrack). However, mink and river otter island occupancy was unaffected by island-level covariates, whereas small mammals were more likely to occupy islands closer together. Keen's mice and food items were subsidized directly (i.e., consumption) and indirectly (i.e., fertilization) by marine resources. Beach-dwelling arthropods composed 33% of mouse diets. Furthermore, mouse and terrestrial arthropod abundances and stable isotope signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of food items were depleted moving inland from the beach. Finally, reproductive male mice consumed up to twice the marine-derived prey as females. Collectively, this work demonstrates that insular mammalian richness, as mediated by island-level factors, may be complex due to variation within populations and the recipient ecosystem (e.g., prey biomass).

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Dedication

To my parents,

Jennifer and Allan,

who have significantly subsidized my life



1. General introduction

Research context

Allochthonous nutrient or resource subsidies – those produced in ‘donor habitats’ and transported to ‘recipient habitats’ – link adjacent ecosystems through the flow of energy and nutrients. Although allochthonous resources can be supplied to a recipient ecosystem through a variety of mechanisms and vectors, I focus on flows that are donor-controlled rather than the result of active foraging (*sensu* Richardson et al. 2010). An example of subsidy from active foraging is subtidal foraging by terrestrial mustelids; *Lontra canadensis* lives on land but forages subtidally for shellfish such as *Haliotis kamtschatkana*. In contrast, a donor-controlled subsidy is one where consumers have no direct influence on the rate of resource subsidy, but still benefit from the resource throughout its duration (Polis and Hurd 1996, Polis et al. 1997). For example, when terrestrial arthropods fall in streams, they are eaten by predatory fish and/or contribute to primary productivity through decomposition (Nakano et al. 1999).

Both indirect and direct pathways of subsidy may occur within the recipient habitat. These subsidies can be incorporated by consumers either through direct consumption or indirect augmentation of local resources (e.g., fertilization), ultimately resulting in higher densities of consumers (Polis et al. 1997). Numerical responses are often most prominent along ‘edge’ habitats (Pieczynska 1975, Marinelli and Millar 1989, Stapp and Polis 2003a). For example, the coastal fringes of islands and continents (where forest meets beach) are examples of recipient edge habitats. Here, marine subsidies can be temporally constrained or relatively continuous. Brief, intense nutrient pulses come from marine mammal carcasses washing-up on shore, or from seabirds depositing guano

at roost sites during the breeding season (Polis and Hurd 1996, Polis et al. 1997), while sea spray (Whipkey et al. 2000) and macroalgae deposition ('wrack') supply a relatively consistent year-round subsidy (Polis and Hurd 1996, Wickham 2018). These marine resources are incorporated by nearly all trophic levels, from plants to lizards and birds (Polis and Hurd 1995, Dugan et al. 2003, Spiller et al. 2010). The effects can be significant for the recipient ecosystem, particularly on small islands with high perimeter-area ratios (Polis and Hurd 1996, Polis et al. 1997) and beaches that are permeable to subsidy (Barrett et al. 2003).

Whether through wrack, seabird guano, or other sources, nutrient subsidies are ubiquitous across ecosystems – perhaps even influencing predictions of the foundational theory of island biogeography. Island biogeography theory (IBT; MacArthur and Wilson 1967) predicts that species immigration and extinction rates vary as a function of island size and distance from the mainland, with resultant diversity below the mainland source. Insular diversity is higher on large islands close to the mainland because they have higher immigration and possibly lower extinction rates compared to small, far islands. Revisions to IBT have been suggested (e.g., Brown and Lomolino 2000, Lomolino 2000a), particularly on very small islands ($< 3 \text{ km}^2$, the 'small island effect') that receive marine subsidies (Cody et al 1983, Polis and Hurd 1995, Lomolino 2000). As such, Anderson and Wait (2001) proposed a revised 'subsidized island biogeography hypothesis' (SIBH). SIBH integrates the species-area and productivity-diversity relationships, hypothesizing that marine nutrient subsidies are responsible for unexpected diversity patterns, particularly on small islands. Traditionally, (log) species-area relationships are positive and linear, with slope $\approx 1/4$. However, small islands (with high

perimeter-area ratios) have more resources per unit area when in-situ and allochthonous resources (that enter via island edges) are considered, in comparison to larger islands, and may exhibit higher or lower diversity than expected (Polis and Hurd 1996, Anderson and Wait 2001). The direction of the diversity response depends upon where the recipient taxa and habitat fall along the productivity-diversity curve: in some cases, subsidy may increase diversity due to lowered extinction rates, while in other cases it may decrease diversity through increased competitive dominance by a few species (Anderson and Wait 2001). This will result in small islands that fall either above or below the expected species-area line, and increasing or decreasing the slope of the line (respectively) (Anderson and Wait 2001). As islands increase in size, and decrease in relative edge, the influence of subsidy is reduced (Polis and Hurd 1996, Polis et al. 1997). Therefore, the SIBH only applies to small islands on the lower end of the species-area relationship (Anderson and Wait 2001).

Field studies testing the SIBH, and this 'small island effect' (SIE), have been limited. Barrett et al. (2003) found that SIE alone could not predict lizard diversity on islands in the Gulf of California. However, diversity was partially explained by SIBH, which may account for the lack of evidence for SIE (populations may be able to persist despite reduced terrestrial resources). Their analysis was sensitive to island size (statistically significant only when small islands were those $< 1 \text{ km}^2$), suggesting there may be a specific threshold for the effects of subsidies on island area. Expanding future studies to include more taxa across multiple guilds and trophic levels (including vegetation) may help to resolve patterns of diversity on very small ($< 1 \text{ km}^2$), subsidized islands.

As marine subsidies may influence whole island diversity, it is important to understand how far inland, and through which trophic levels, marine resources persist. On islands in the Gulf of California, carnivorous arthropods and mice are more abundant along coastlines than inland (Polis and Hurd 1995, Anderson and Polis 1998, Stapp and Polis 2003a), and arthropod tissues are more enriched with marine-derived nutrients near the coast than inland (Anderson and Polis 1998). However, on these islands terrestrial primary productivity is relatively low, and limited by rainfall (Polis et al. 1998). In this case, spatial patterns in subsidy from shorelines to island interiors are mostly driven by direct consumption of subsidized prey (e.g., littoral invertebrates), and the indirect effects of fertilization to terrestrial plants are negligible (but see Sanchez-Pinero and Polis 2000). Investigating spatial patterns (from shorelines to island interiors) in abundance and tissue enrichment of multiple trophic levels would provide clearer evidence as to whether marine subsidies permeate through the terrestrial environment through direct (i.e., consumption) or indirect (i.e., fertilization) pathways, and how far inland these patterns exist.

In addition to community-level responses, consumers can also respond to subsidies at the population and (or) individual levels. Whereas much work focuses on general consumer responses to subsidy (i.e., numerical responses; Polis and Hurd 1995, Anderson and Polis 1998, Stapp and Polis 2003b, Barrett et al. 2005), fewer studies have examined how subsidy effects might vary with the foraging strategies of consumers. In particular, omnivory introduces complexity and variability into a food web by spreading consumption across various trophic levels and resource pathways (Vadeboncoeur et al. 2005). In ‘multi-channel’ (or ‘multichain’, Vadeboncoeur et al. 2005) omnivory, an

omnivore consumes energy (indirectly or directly) from multiple channels outside of the 'focal' (or in-situ) food chain (Polis and Strong, 1996). When an omnivore is subsidized by an influx of 'non-normal' prey (e.g., a subsidy), its populations may temporarily increase, potentially depressing the numbers of in-situ 'normal' prey (Polis and Strong 1996). However, a diversified diet can maintain individuals and populations through unfavourable conditions of low prey availability (Polis and Strong 1996). Depending on in-situ resources and productivity, nutritional requirements, and extent of food-mixing behaviour, it is unclear whether omnivores would respond strongly or weakly to subsidy.

Intrapopulation variation among recipient consumers might influence the population's response to subsidy. While many studies treat consumer populations as a collection of ecologically equivalent individuals, this is seldom representative of actual systems (Bolnick et al. 2003, Araújo et al. 2011). Between-individual niche variation can account for most of the population's overall niche (Bolnick et al. 2003) and can be influenced by habitat heterogeneity and marine subsidy (Darimont et al. 2009). Intrapopulation variation might be most evident between sexes and breeding stages of adults. Females and males are often 'ecologically dimorphic' in the manner in which they forage, often due to the nutritional and energetic requirements of reproduction, particularly for females (Shine 1989, Polis 1991, Polis and Strong 1996, Hailey et al. 2001). However, these behavioural and physiological factors can vary among species and populations, depending upon reproductive strategies (e.g., extent of parental care), territoriality and aggression (Wolf and Batzli 2002, Ben-David et al. 2004, Rode et al. 2006, Adams et al. 2017).

Within populations, behaviour and physiology can vary at the individual level. Individuals trade-off risks (predation, aggression) and rewards (marine resources) associated with specific site characteristics (Lima and Dill 1990). Specifically, 'escape subcomponents' of foraging, where a resource in a risky habitat is adjacent to a preferred habitat (with 'escape' cover), have important implications for foraging (Lima and Dill 1990 and references within). For example, habitat edges are used frequently by predators and represent risky habitat (Wolf and Batzli 2002, 2004), yet supply abundant marine resources, whereas the adjacent forest provides shelter (Anderson et al. 2003, Anderson and Meikle 2006), but may have comparatively less resources. Trade-offs are often faced by omnivores, particularly smaller animals at lower trophic levels that must balance the relative risks (predation, aggression) and rewards (subsidized food) associated with foraging for marine resources.

Research contributions

Within this chapter I have identified some research gaps within the broad body of work pertaining to marine subsidies to terrestrial ecosystems. First, revisions to island biogeography theory have been posed for nearly 20 years (e.g., Lomolino 2000a, Anderson and Wait 2001). In particular, Lomolino (2000b) suggests that future work should focus on reporting deviations from the species-area relationship (rather than confirming it). Anderson and Wait (2001) propose that these deviations should be studied in the context of allochthonous marine resources, (the subsidized island biogeography hypothesis). However, field studies are rare, and including many taxa across multiple guilds and trophic levels may help to resolve patterns of diversity on very small (< 1 km²), subsidized islands.

To address these literature gaps, Chapter 2 of this thesis outlines my contribution to a large (10+ researchers), multi-year biodiversity project, *100 Islands*, investigating island biodiversity in relation to marine subsidies on the Central Coast of British Columbia, Canada. The islands in this region are subsidized by marine resources, primarily from macroalgal ('wrack') deposition (Wickham 2018). My objective was to document the presence and absence (i.e., incidence) of mammals across these islands. Using occupancy modeling, I have investigated how island area, distance from mainland, distance to the nearest island and quantity of marine subsidy (wrack biomass) may explain variation in island occupancy by common mammal groups (river otter, mink and small mammals), and statistically assessed the quality of the incidence data.

The second literature gap pertains to understanding how omnivores, with multiple channels of available resources, respond to marine subsidy. Most studies have focused on carnivores or obligate-insectivores (Polis and Hurd 1995, Dugan et al. 2003, Spiller et al. 2010). As well, these studies often occur in unproductive recipient terrestrial habitats (e.g., Stapp and Polis 2003a, Barrett et al. 2005, Lancaster et al. 2008). Omnivores, particularly those in productive terrestrial environments with diverse and abundant prey sources, may use and respond differently to such subsidies due to their flexible diets. Within omnivore populations, it is unclear whether individuals respond uniformly, or if individual variation can be attributed to site- or individual-level variables.

In Chapter 3, I addressed these gaps by studying a coastal omnivore, the Keen's mouse (*Peromyscus keeni*) and its food web on islands along the Central Coast of British Columbia. Among these islands a natural gradient of wrack subsidy occurs (Wickham 2018). I focused on two island regions at either end of this subsidy spectrum to maximize

variation in response to subsidy by mice and prey. Using environmental (e.g., food abundance) and individual (e.g., reproductive status) factors, I determined which aspects of the recipient habitat and population may explain variation in the extent of subsidy consumption by this abundant, insular omnivore.

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2. Mammal species richness and occupancy across a network of oceanic islands on the Central Coast of British Columbia

Abstract

Island biogeography theory provides a framework for understanding patterns of species richness on islands. However, island species richness may also be influenced by subsidies of marine resources, especially on small islands. I tested how island biogeography theory and marine subsidies (the biomass of macroalgal drift, or ‘wrack’ on an island) influence mammal species richness derived from presence-absence (i.e., incidence) data on 98 islands across the Central Coast of British Columbia, Canada. Log-species richness was positively related to log-island area (Linear regression, $t = 3.71$, $p < 0.001$, $r^2 = 0.12$) and wrack biomass ($t = 3.12$, $p = 0.002$, $r^2 = 0.09$). I also created individual single-season occupancy models for common mammalian taxa to determine if island-level covariates (island area, distance from mainland, distance to nearest island, and wrack biomass) influenced taxon-specific island occupancy. Models for river otter (*Lontra canadensis*) and mink (*Neovison vison*) indicated that island occupancy is unrelated to any island-level covariates, as the probability of island occupancy was equal across all islands. Small mammal (*Peromyscus keeni*, *Sorex spp.*, and *Microtus/Myodes spp.*) island occupancy was moderately explained by the distance to the nearest island (RVI = 0.39). Estimates for the probability of false absences were unaffected by island area, and declined considerably with increased sampling effort. While island area and quantity of wrack predicted overall species richness, there may be island-specific features influencing occupancy at the species-level. Future taxon-specific models should include more detailed habitat variables such as island shoreline slope, substrate or vegetation cover.

Introduction

For many organisms, the marine-terrestrial interface represents a habitat where both terrestrial and marine resources are available. On oceanic islands, marine resources are available through many pathways, including marine mammal carcass drift, seabird guano, fish spawn (e.g., Pacific herring), and macroalgal ('wrack') deposition (Polis and Hurd 1996, Polis et al. 1997, Rose and Polis 1998, Sanchez-Pinero and Polis 2000, Fox et al. 2014). These subsidies can increase plant growth rates and support high densities of consumers, particularly along shorelines (Rose and Polis 1998, Dugan et al. 2003, Spiller et al. 2010). However, such studies often focus on the numerical responses of consumers; whether marine subsidies influence island-level biodiversity across taxa is unexamined.

MacArthur and Wilson's (1967) theory of island biogeography (IBT) provides a framework for understanding patterns of species richness on islands. Species richness on islands is dependent upon immigration and extinction rates, which vary as a function of island size and distance from the mainland. Insular richness is higher on large islands close to the mainland, due to high immigration and low extinction rates, compared to small, far islands. However, deviations from expected richness patterns have been recorded on small ($< 3 \text{ km}^2$) oceanic islands (Cody et al 1983, Polis and Hurd 1995, Lomolino 2000b). Marine subsidies may influence small islands more than large ones due to high perimeter-area ratios, leaving them more exposed to subsidy (Polis and Hurd 1996).

Within the last two decades, theoretical models have been proposed to relate productivity (from marine subsidy) to diversity on small islands. In response to suggestions for a revision to classic island biogeography theory (IBT; e.g., Lomolino

2000a, 2000b), Anderson and Wait (2001) have proposed the ‘subsidized island biogeography’ hypothesis (SIBH). The two pillars of the SIBH are the species-area relationship (a major influence in IBT) and the productivity-diversity relationship. Together, these blend classic IBT with marine subsidies to explain diversity on small, subsidized islands (Anderson and Wait 2001). While this theory is not new, field tests are limited in number (e.g., Barrett et al. 2003).

The Central Coast of British Columbia, Canada includes thousands of islands where marine and terrestrial ecosystems frequently exchange nutrients and resources. While there are multiple types of marine subsidy occurring along this coastline, there is evidence that wrack deposition provides a continuous source of marine nutrients to the terrestrial environment, particularly on smaller, outer islands (Wickham 2018). However, the impact of wrack subsidy on island-level diversity is unknown. As part of a multi-year biodiversity study, I documented terrestrial mammal presence and absence (i.e., ‘incidence’) on 98 islands over three years to investigate island-level drivers of mammal species richness.

I investigated how island-level mammalian species richness ($n = 8$ species) correlated to four island variables: island area, distance from mainland, distance to the nearest island, and the quantity of marine subsidy deposited on each island (in this case, wrack biomass). I then developed single-season occupancy models for each of the three most commonly encountered taxa: river otter (*Lontra canadensis*), mink (*Neovison vison*) and a combined small mammal group (mostly *Peromyscus keeni*, but including *Sorex spp.* and *Microtus/Myodes spp.*). I modelled island use by each of these taxa as a function

of the island-level covariates of area, distance from mainland, distance to the nearest island, and wrack biomass.

Methods

Ethics statement

Research for this project operated out of the Hakai Institute (an extension of the Tula Foundation) on Calvert Island, and was conducted within Heiltsuk (“Heiltsuk Nation-Tula Foundation Protocol Agreement 2016”) and Wuikinuxv First Nations traditional territory and with permission and assistance from both tribal governments. It was also conducted within the Hakai Lúxvbálís Conservancy and the Calvert Island Conservancy, both British Columbia provincially protected parks. Research at the Hakai Institute research operates under BC Parks Permit #107190. In 2015, our project operated under University of Victoria (UVIC) Animal Use Permit (AUP) #2015-013(1). During 2016 we operated under renewed AUP #2015-013(1) and AUP #2016-012. Prior to field work using live traps, training was obtained from UVIC Animal Care Services (ACS), and field protocols for rodent handling and euthanasia followed UVIC ACS SOPs #AC2007 and #AC2023, respectively. In 2017 we operated under renewed AUPs #2015-013(1) and #2016-012.

Study area

The Central Coast spans the portion of the British Columbia coast stretching from approximately the northern tip of Vancouver Island to the southern tip of Haida Gwaii (Figure 2.1). It is the outer coast of the central portion of the Great Bear Rainforest, a temperate rainforest spanning 6.4 million hectares that is relatively untouched by

contemporary industrial development. The region is classified as a Coastal Western Hemlock biogeoclimatic zone, the very wet Hypermaritime coastal variant subzone (CWHvh2). The islands contain a combination of high and lower-productivity forests and various bog habitats (see Banner et al. 2005 for details). See Appendix I – Methods for island selection as part of the larger *100 Islands* study. We sampled a total of 98 islands over three summers (May – August) of 2015, 2016 and 2017.

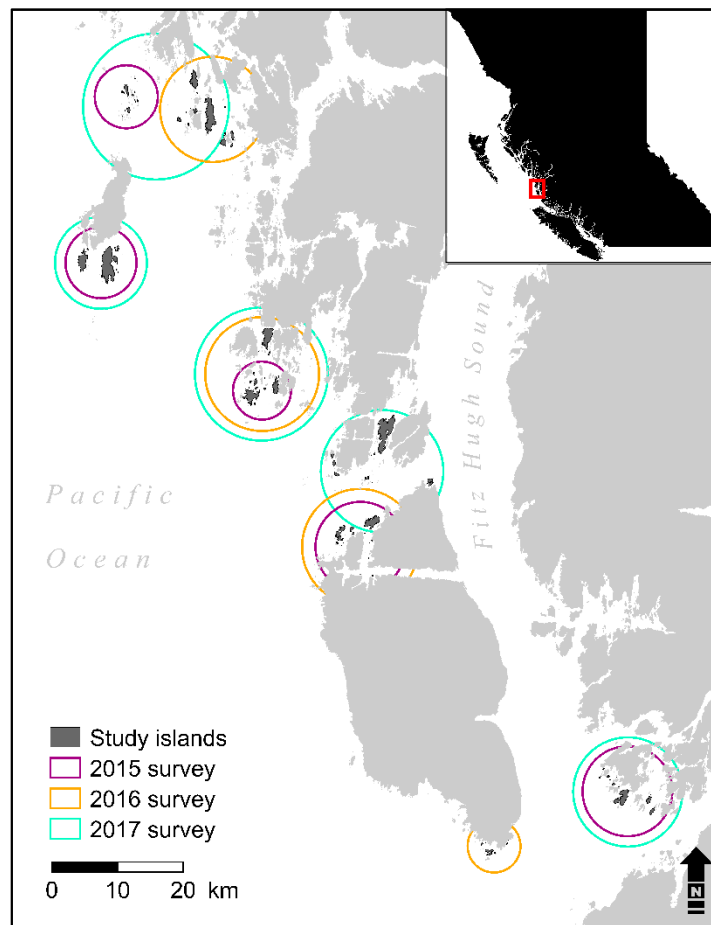


Figure 2.1. Island regions surveyed in 2015 (purple), 2016 (orange) and 2017 (teal) along the central coast of British Columbia (see inset).

Field sampling

Field methods were designed to capture a broad range of terrestrial mammal taxa.

However, due to logistical constraints we did not sample flying (e.g., bats) or arboreal (e.g., red or flying squirrels) mammals, although these are present on some Central Coast islands (Nagorsen 2002).

Track plates – I used track plates to non-invasively sample small mammals in the summers of 2015, 2016 and 2017. See Appendix I – Methods for details on track plate design and placement on islands. Track plates used non-toxic ink patches glued to paper strips which were housed within PVC piping and baited with peanut butter (Nams and Gillis 2003). Track plates were left for 2 – 4 nights. Animals leave behind tracks which are identified to the lowest taxonomic level possible. Keen’s mice are the only species of mouse on islands of the outer central coast (Nagorsen 2002), so tracks were identified to species level for mice (*Peromyscus keeni*). However, tracks could only be identified to broad groups for voles (*Microtus* and/or *Myodes* spp.) and shrews (*Sorex* sp.). Tracks were identified using known documentation in guide books (e.g., Elbroch, 2003) and a track guide created by Gillis and Nams (2002). As track plate analysis is difficult and subjective (Wiewel et al. 2007), I conducted multiple tests to confirm consistency in track identification (see Appendix I – Methods and Appendix I Table 2.6).

Live trapping – In 2016 we used Sherman live traps (Small Folding Aluminum) in conjunction with another study to confirm presence/absence of small mammals and obtain track confirmations. Live traps were placed in grids of either 24 (4 x 6) or 36 traps (6 x 6) for one night on each island. See Appendix I – Methods for live trapping details.

Remote cameras – One remote camera (Bushnell 6MP Trophy Cam Essential Trail Camera) was deployed per island with the goal of documenting large (e.g., wolves, black-tailed deer) and medium-sized (e.g., river otter, mink) mammals. Cameras were placed opportunistically to take advantage of game trails or other areas clearly used by animals (e.g., river otter latrines), and were baited with both 50 mL of fish fertilizer and peanut butter applied to a bait station of sticks and moss. Camera trap-nights varied from 2 to 9 nights depending on year and island.

Opportunistic documentation – Observations of recent animal activity (e.g., tracks, sign, anfaeces) were also recorded opportunistically. This method primarily obtained records for larger mammals (e.g., wolves, deer, mink and river otter), but occasionally sightings of smaller mammals were also used (e.g., shrews foraging in the intertidal area). These sightings were mostly used to confirm species records from the previous methods that might be unclear (e.g., blurry camera photo or smeared track on track plate).

Data analysis

I created a sample-based species accumulation curve to determine the total number of species recorded, as samples (i.e., islands) are added to the pool of previously observed samples (i.e., islands; Gotelli and Colwell 2001). I used the *rarefaction.sample* in the *rareNMtests* package (Cayuela and Gotelli (2014) in R (R Core Team 2017)). The accumulation curve for mammal species richness on islands reached a clear asymptote (Appendix I Figure 2.4), so I continued analyses with raw richness counts (Gotelli and Colwell 2001).

Cumulative richness data were obtained from track plates, live traps and remote cameras. I used log-transformed ‘raw’ (i.e., non-rarified) species richness ($S+1$ to account

for zeroes) to investigate univariate relationships between $\log(S+1)$ and four island covariates: log island area ('log area'), log island distance from mainland ('log D_{ML} '), island distance to nearest island ('log D_{NN} '), and log wrack biomass (mean g/m^2 per island, 'log(wrack+1)' to account for zeroes) obtained from Wickham (2018; Table 2.1). Wrack biomass also indicates the relative permeability of an island: wrack will accumulate more readily on islands with sloping beaches than on islands bordered by cliffs (Wickham 2018; Appendix I Figure 2.5). All log transformations are the natural logarithm.

Probability of island use by three focal mammal taxa

I created individual single-season occupancy models (McKenzie et al 2006) using incidence data for three common mammal taxa recorded on remote cameras. I pooled incidence data across 2015-2017. Although this sampling window spans multiple years, I did not re-sample any islands and so did not use a multi-year model (MacKenzie et al 2006). As occupancy modelling assumes that sites are closed to changes in occupancy within the sampling season (MacKenzie et al 2006), I assumed changes in occupancy did not occur within 2015-2017 (inclusive). As this is an unrealistic assumption for highly mobile mammals, I used the single-season single-species model with the assumption of occupancy closure relaxed to allow for random movement of species (MacKenzie et al 2006, Fisher et al. 2014). Therefore, results here should be interpreted as island usage (i.e., species is sometimes present), rather than the proportion of islands occupied by the species (i.e., species is always present). In addition, by modelling the probability of occupancy (ψ) as a function of four island-level covariates (Table 2.1 and Appendix I

Table 2.7), I will account for the assumption that the probability of occupancy is equal across all islands. I held the probability of detectability, p , constant across all models.

For each island, sampling periods were defined as a period of 24 hours from the time of camera set-up on ‘Day 1’ (usually around mid-day) until the same time on ‘Day 2’. Therefore, each interval captures one night, the time most mammals are active.

Mammal taxa used in occupancy modelling were: river otter (*Lontra canadensis*), mink (*Neovison vison*), and small mammals. Small mammals could not be distinguished to species on camera. However, Keen’s mice were the most common on track plates (87% of track plates) and in live traps (92% of live traps), which suggests they are more abundant than voles or shrews. Therefore, these models could be interpreted as an approximate indication of Keen’s mouse island use. For simplicity, these groups (river otter, mink and small mammals) will be referred to as mammal taxa throughout the occupancy analysis.

Occupancy models were created in *PRESENCE* software (v 12.7; Hines 2006). Occupancy models were not created for species with very low naïve detections (ψ_i ; wolves, deer and red squirrels) due to obstacles with model fitting and parameter estimates with sparse data ($\psi_i \leq 0.1$; Welsh et al 2013). I compared top models using Akaike’s Information Criterion (AIC; Burnham and Anderson 2002). Models were ranked based on Δ AIC scores and covariates were assessed based on Relative Variable Importance (i.e., \sum AIC weights).

Table 2.1. Covariates used in single-season, single-species occupancy models predicting mammal use of islands ($n = 91$). Continuous data (X) were standardized using the sample mean (μ) and standard deviation (σ).

Covariate	Description	Type	Form
area	<ul style="list-style-type: none"> Island land area (m^2) calculated based on vegetated land (the un-vegetated outside area and intertidal zone are excluded). Derived from WorldView2 satellite images (2m resolution) 	Continuous	Standardized $z = \frac{X - \mu}{2(\sigma)}$
D_{ML}	<ul style="list-style-type: none"> Distance (meters) from the island to the mainland over water using the least distance of water crossing 	Continuous	Standardized
D_{NN}	<ul style="list-style-type: none"> Distance (meters) to the nearest island 	Continuous	Standardized
wrack	<ul style="list-style-type: none"> Wrack biomass deposited on each island (g/m^2). See Wickham (2018) for methods. 	Continuous	Standardized

Probability of false absence

Conditional occupancy (Ψ_c) estimates the probability of a taxon's presence on an island given its detection history (where a taxon recorded 'present' scores $\Psi_c = 1.0$ and 'absent' is $\Psi_c < 1.0$). Therefore, it can be interpreted as a measure of reliability for recorded absences (i.e., zeroes) in the data. Island-level estimates of Ψ_c were obtained for each of the three taxa based on the top model predicting island use. I removed instances where $\Psi_c = 1.0$ to examine the probability that a taxon was present, given that it was not recorded, and tested it against two covariates: island area and length of sampling interval. Island area was of interest due to concern over unequal sampling effort, where large islands were not sampled as intensively as small ones. Likewise, some islands were only sampled for 2 nights, whereas some were sampled up to 9 nights. Finally, I created island-specific Ψ_c distribution maps for each taxon so that future spatial analyses can take into account the reliability of incidence data for each taxon on a given island.

Results

Patterns in species richness

Across the 98 islands sampled, 81% were occupied by at least one mammal species. Average species richness was 1.97 ± 1.37 species (coefficient of variation = 69.5%), with a maximum of 5 species ($n = 3$ islands). Keen's mice (*Peromyscus keeni*) were the most common mammal (naïve detection rate $\psi_i = 59\%$ of islands) followed by river otter (*Lontra canadensis*; $\psi_i = 42\%$ of islands) and mink (*Neovison vison*; $\psi_i = 41\%$ of islands; Table 2.2).

Table 2.2. Number of records ('n records') of each mammal species from track plates, remote cameras and opportunistic surveys on each island and associated overall naïve detection frequency (ψ_i). Based on all 98 islands ('n islands').

Species	n records	n islands	ψ_i
Red squirrel ¹	3	98	0.03
Deer	7	98	0.07
Wolf	9	98	0.09
Vole	11	98	0.11
Shrew	22	98	0.22
Mink	41	98	0.41
River otter	42	98	0.42
Mouse	58	98	0.59

¹ Although arboreal species were not targeted, red squirrels were caught on remote cameras on three islands

Island mammal species richness was positively related to island area (linear regression, $t = 3.71$, $p < 0.001$; Figure 2.2A). Although area only explained 12% of the variation in richness ($r^2 = 0.12$) and exhibited low slope ($z = 0.09 \pm 0.02$), the relationship was significant. Very small islands ($< 1 \text{ km}^2$) were depauperate (Figure 2.2A). Species richness was also positively related to wrack biomass, although the linear relationship was also weak ($r^2 = 0.09$, $t = 3.12$, $p = 0.002$; Figure 2.2B). There was no relationship

between species richness and distance from mainland (D_{ML} ; $t = 0.33$, $p = 0.75$; Figure 2.2C) or distance to the nearest island (D_{NN} ; $t = 0.31$, $p = 0.76$; Figure 2.2D).

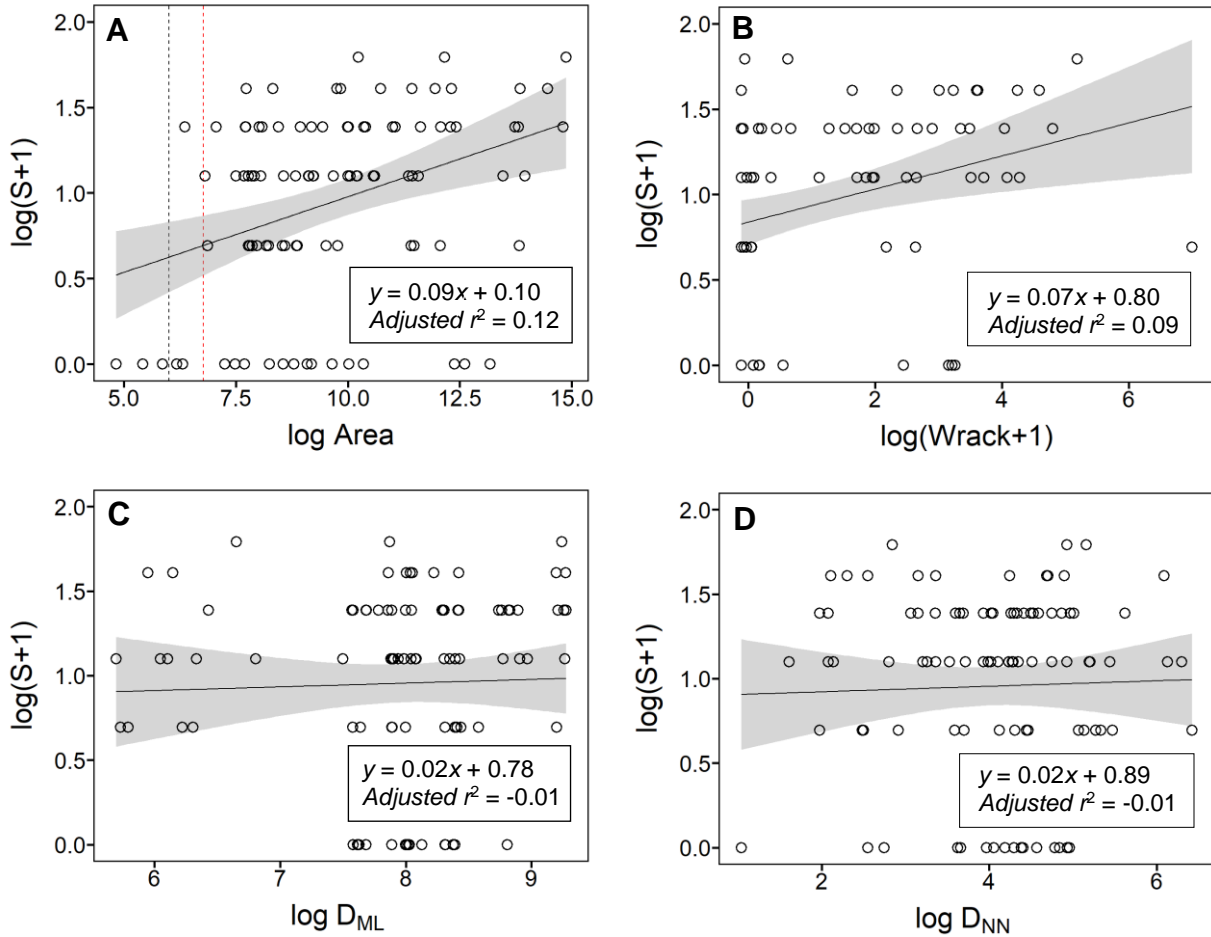


Figure 2.2. Relationships between species richness, $\log(S+1)$, and (A) log island area (red line = 3 km², black = 1 km²), (B) log wrack biomass, (C) log distance from mainland (D_{ML}), and (D) log distance from the nearest neighbouring island (D_{NN}). Note that $\log(S+1)$ and $\log(\text{wrack}+1)$ were used to allow for zeroes in the data. All log transformations are the natural log.

Probability of island use by three focal mammal groups

Remote camera footage was available to estimate mammal island use on 91 islands. Island use by river otters was not explained by island area ('area'), distance from mainland ('D_{ML}'), distance to the nearest island ('D_{NN}') or wrack biomass ('wrack'). The null occupancy model was almost 4 times as likely as the next model including area, D_{ML} and wrack (Evidence Ratio [ER] = 3.67; Table 2.3). Of the four island-level covariates, D_{ML} was best supported ($\sum AIC_w = 0.43$), followed by area ($\sum AIC_w = 0.33$), wrack ($\sum AIC_w = 0.30$) and D_{NN} ($\sum AIC_w = 0.18$). Based on constant ψ and p , the estimated probability of occupancy ($\Psi = 0.28 \pm 0.05$) was close to naïve occupancy ($\psi_i = 0.227$), suggesting the observed presence-absence data are representative (Appendix I Figure 2.6).

Table 2.3. Model results and modelled occupancy estimate ($\psi \pm$ standard error) for factors predicting river otter island use (n = 91 islands) based on standardized area ('area'), distance from mainland ('D_{ML}'), distance to the nearest island ('D_{NN}'), and wrack biomass ('wrack'). *Npar* = number of parameters estimated in model, $p(\cdot)$ = probability of detection (p) held constant. Akaike's Information Criterion weights (AIC_w) and delta values (ΔAIC) are given.

Model	NPar	AIC	ΔAIC	AIC_w	$\Psi \pm SE$
$\psi(\cdot)p(\cdot)$	2	275.52	0.00	0.4819	0.28 ± 0.05
$\psi(\text{area} + D_{ML} + \text{wrack})p(\cdot)$	4	278.12	2.60	0.1313	
$\psi(\text{area} + D_{ML})p(\cdot)$	3	278.17	2.65	0.1281	
$\psi(D_{NN} + \text{wrack})p(\cdot)$	3	279.90	4.38	0.0539	
$\psi(D_{ML} + \text{wrack})p(\cdot)$	3	279.90	4.38	0.0539	
$\psi(\text{area} + D_{ML} + D_{NN} + \text{wrack})p(\cdot)$	5	280.02	4.50	0.0508	
$\psi(\text{area} + D_{ML} + D_{NN})p(\cdot)$	4	280.09	4.57	0.0490	
$\psi(D_{ML})p(\cdot)$	2	282.34	6.82	0.0159	
$\psi(\text{area} + D_{NN})p(\cdot)$	3	283.20	7.68	0.0104	
$\psi(\text{area})p(\cdot)$	2	284.12	8.60	0.0065	
$\psi(D_{NN})p(\cdot)$	2	284.56	9.04	0.0052	
$\psi(\text{area} + D_{NN} + \text{wrack})p(\cdot)$	4	284.75	9.23	0.0048	
$\psi(D_{ML} + D_{NN})p(\cdot)$	3	285.46	9.94	0.0033	
$\psi(\text{area} + \text{wrack})p(\cdot)$	3	285.70	10.18	0.0030	
$\psi(\text{wrack})p(\cdot)$	2	286.78	11.26	0.0017	

Island use by mink was also not explained by island area, D_{ML} , D_{NN} , or wrack, as the null occupancy model was approximately 1.5 times as likely as the model including distance from mainland and wrack biomass (ER = 1.55; Table 2.4). Of the four island-level covariates, D_{ML} was most supported ($\sum AIC_w = 0.41$), followed by wrack ($\sum AIC_w = 0.35$), D_{NN} ($\sum AIC_w = 0.30$) and area ($\sum AIC_w = 0.17$).

Based on constant ψ and p , the estimated probability of occupancy ($\Psi = 0.33 \pm 0.06$) was close to naïve occupancy ($\psi_i = 0.253$), suggesting the presence-absence data are moderately representative (Appendix I Figure 2.6).

Table 2.4. Model results and modelled occupancy estimate ($\psi \pm$ standard error) for factors predicting mink island use (n = 91 islands) based on standardized area ('area'), distance from mainland (' D_{ML} '), distance to the nearest island (' D_{NN} '), and wrack biomass ('wrack'). $Npar$ = number of parameters estimated in model, $p(\cdot)$ = probability of detection (p) held constant. Akaike's Information Criterion weights (AIC_w) and delta values (ΔAIC) are given.

Model	<i>NPar</i>	AIC	ΔAIC	AIC_w	$\Psi \pm SE$
$\psi(\cdot)p(\cdot)$	2	251.47	0.00	0.3247	0.33 ± 0.06
$\psi(D_{ML} + wrack)p(\cdot)$	3	252.35	0.88	0.2091	
$\psi(D_{NN})p(\cdot)$	2	253.85	2.38	0.0988	
$\psi(D_{ML} + D_{NN})p(\cdot)$	3	254.79	3.32	0.0617	
$\psi(D_{ML})p(\cdot)$	2	255.00	3.53	0.0556	
$\psi(area + D_{NN})p(\cdot)$	3	255.13	3.66	0.0521	
$\psi(area)p(\cdot)$	2	256.00	4.53	0.0337	
$\psi(area + D_{ML})p(\cdot)$	3	256.36	4.89	0.0282	
$\psi(D_{ML} + D_{NN} + wrack)p(\cdot)$	4	256.40	4.93	0.0276	
$\psi(D_{NN} + wrack)p(\cdot)$	3	256.61	5.14	0.0249	
$\psi(wrack)p(\cdot)$	2	256.63	5.16	0.0246	
$\psi(area + D_{NN} + wrack)p(\cdot)$	4	257.08	5.61	0.0196	
$\psi(area + D_{ML} + D_{NN} + wrack)p(\cdot)$	5	257.66	6.19	0.0147	
$\psi(area + wrack)p(\cdot)$	3	257.96	6.49	0.0127	
$\psi(area + D_{ML} + wrack)p(\cdot)$	4	258.08	6.61	0.0119	

Variation in the probability of island use by small mammals was best explained by a negative relationship ($\Psi = -0.42 \pm 0.48$) with the distance to the nearest island (D_{NN} ; $ER = 1.20$, $\sum AIC_w = 0.39$). However, the weight of evidence was distributed relatively evenly over the other variables: D_{ML} ($\sum AIC_w = 0.35$), area ($\sum AIC_w = 0.32$), and wrack biomass ($\sum AIC_w = 0.31$), and the null model was also relatively well supported ($AIC_w = 0.12$; Table 2.5). Based on constant ψ and p , the modelled occupancy estimate ($\Psi = 0.46 \pm 0.06$) is close to naïve occupancy ($\psi_i = 0.429$), suggesting the presence-absence data are representative (Appendix I Figure 2.6).

Table 2.5. Model results and modelled occupancy estimate ($\psi \pm$ standard error) for factors predicting small mammal island use ($n = 91$ islands) based on standardized area ('area'), distance from mainland (' D_{ML} '), distance to the nearest island (' D_{NN} '), and wrack biomass ('wrack'). $Npar$ = number of parameters estimated in model, $p(\cdot)$ = probability of detection (p) held constant. Akaike's Information Criterion weights (AIC_w) and delta values (ΔAIC) are given.

Model	$NPar$	AIC	ΔAIC	AIC_w	$\Psi \pm SE$
$\psi(D_{NN})p(\cdot)$	2	418.10	0.00	0.1484	-0.42 ± 0.48
$\psi(\cdot)p(\cdot)$	2	418.46	0.36	0.1239	0.46 ± 0.06
$\psi(D_{ML})p(\cdot)$	2	418.58	0.48	0.1167	
$\psi(\text{area})p(\cdot)$	2	418.70	0.60	0.1099	
$\psi(\text{wrack})p(\cdot)$	2	418.76	0.66	0.1067	
$\psi(D_{ML} + D_{NN})p(\cdot)$	3	419.89	1.79	0.0606	
$\psi(\text{area} + D_{NN})p(\cdot)$	3	419.92	1.82	0.0597	
$\psi(D_{NN} + \text{wrack})p(\cdot)$	3	419.92	1.82	0.0597	
$\psi(\text{area} + D_{ML})p(\cdot)$	3	420.30	2.21	0.0491	
$\psi(\text{area} + \text{wrack})p(\cdot)$	3	420.49	2.39	0.0449	
$\psi(D_{ML} + \text{wrack})p(\cdot)$	3	420.54	2.44	0.0438	
$\psi(\text{area} + D_{ML} + D_{NN})p(\cdot)$	4	421.67	3.57	0.0249	
$\psi(D_{ML} + D_{NN} + \text{wrack})p(\cdot)$	4	421.81	3.71	0.0232	
$\psi(\text{area} + D_{ML} + \text{wrack})p(\cdot)$	4	422.24	4.14	0.0187	
$\psi(\text{area} + D_{ML} + D_{NN} + \text{wrack})p(\cdot)$	5	423.56	5.46	0.0097	

Probability of false absence

Conditional occupancy (Ψ_c) is the probability of presence, given the taxon was not recorded. There was no relationship between Ψ_c and log-area for river otter (linear regression, $r^2 = -0.005$, $p = 0.41$), mink ($r^2 = -0.009$, $p = 0.52$) or small mammals ($r^2 = -0.02$, $p = 0.83$; Figure 2.3A), although Ψ_c declined with increased sampling length (i.e., camera nights). Ψ_c approached zero around 8 nights for small mammals and river otter, while mink probabilities of presence were consistently highest with the most variability (Figure 2.3B).

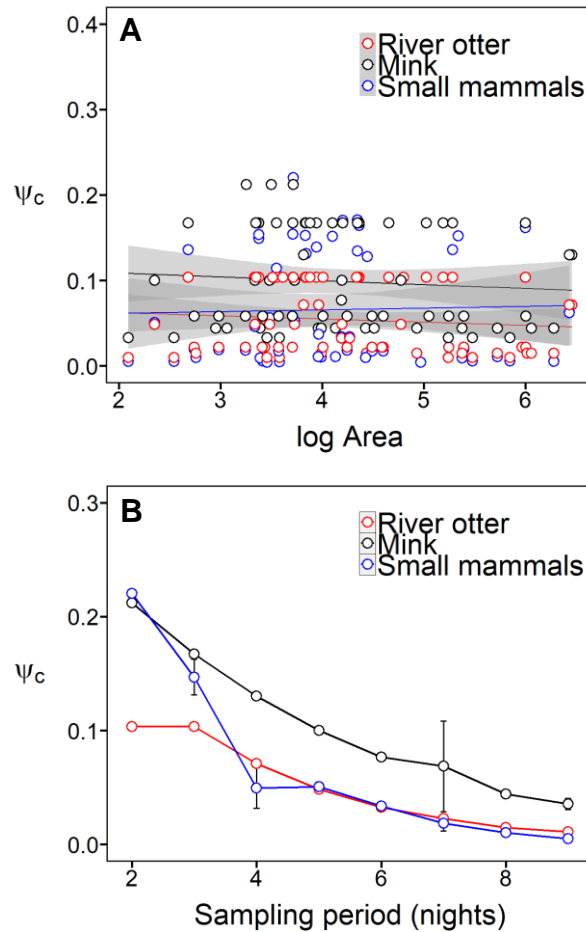


Figure 2.3. Relationships between the probability that an animal was present, given that it was not recorded (for $\Psi_c < 1.0$) and the relationship to **(A)** (natural) log island area, and **(B)** sampling period (camera nights) where Ψ_c values are $\bar{x} \pm \text{SD}$.

Discussion

There was a significant relationship between mammal species richness and quantity of marine subsidy (i.e., wrack biomass), as well as richness and area. Wrack subsidies may increase terrestrial productivity by enhancing vegetation growth rates and increasing arthropod abundances (Dugan et al. 2003, Spiller et al. 2010), which may provide high-quality forage for herbivores (e.g., deer and voles) and omnivores (e.g., mice and shrews). This may in turn attract predators such as mink and wolves. It is also possible that part of the species-wrack relationship was due to other island shoreline characteristics, such as substrate or slope (Wickham 2018). For example, the relationship between richness and island slope was negative (see Appendix I Figure 2.5), although non-significant, suggesting that islands with gradually sloping perimeters support higher mammalian species richness.

The relationship between richness and area was expected given the consistent correlation between species richness and area across ecosystems and habitats (Lomolino 2000b). However, the slope (z) of the (log) species-area relationship, which describes the rate of species accumulation with increasing island area, was much lower here ($z = 0.1$) than in other studies on insular mammal communities ($\sim 0.2-0.35$; Lomolino 1982, Russell et al. 2004). This is likely due to low variability in richness among islands, and low diversity overall. Even on some of the largest islands, I recorded zero species (possibly a product of low sampling effort), and most islands only supported ~ 2 species. Both factors would reduce the slope of the species-area relationship, resulting in slower accumulation of species per unit area increase. It is also important to note that other studies often discard sites with zero species (e.g., Lomolino 1982, Russell et al. 2004),

which can alter results and make comparisons difficult (Williams 1996). There also appeared to be a small-island effect, where islands $< \sim 2 \text{ km}^2$ had no mammals recorded. This is may be due to a lack of habitat and resources, which may increase extinction rates and decrease immigration rates. Most of the small islands had steep, rocky perimeters and inhospitable, dense salal (*Gaultheria shallon*) forests which provide poor habitat for mammals (McCabe and McTaggart-Cowan 1945), especially small mammals that prefer complex understory (Anderson et al. 2003, Anderson and Meikle 2006). Ultimately, it would seem these very small islands do not support viable populations of mammals, although may be used occasionally by large mobile mammals such as wolf or deer to ‘island hop’.

While patterns of overall species richness can provide insights into community assembly on islands, a criticism of island biogeography is that all species are considered equal, and all island habitats are homogeneous in all aspects other than area and isolation (Lomolino 2000a). That is, immigration and extinction rates are mediated only by island size and isolation, and do not account for habitat preference, resource requirements, or interspecific interactions (Lomolino 2000a). Creating taxon-specific models of island occupancy can provide insights into how these mammal communities assemble on islands. Occupancy models are preferable in this context to other multiple hypothesis tests (e.g., mixed-models) as they are robust to uneven sampling effort, missing observations for incidence data, and can incorporate multiple covariates to predict an approximation of abundance (i.e., ‘island use’) when only incidence data are available (MacKenzie et al 2006).

Overall, I found that island use by river otter and mink was uninfluenced by island size, distance from mainland (isolation), the distance to the nearest island, or the quantity of wrack biomass. Mink inhabiting coastal regions of Alaska selected shallow, tidal slopes composed of bedrock that were protected from wave action and bordered by more vegetation cover. Such sites provide access to intertidal forage despite the low swimming efficiency of mink, and protection from avian predators (Ben-David et al. 2016). In contrast, river otter selected sites with high wave exposure, likely due to their swimming ability, and high overstory cover which provides den sites (Ben-David et al. 2016). This niche partitioning suggests future analysis of mink and river otter island occupancy should include specific habitat variables such as island slope or vegetation cover. Furthermore, I found a positive relationship between mink and small mammal occupancy (preliminary data analysis not shown), indicating future models should consider species interactions when predicting island occupancy.

In contrast, small mammals were more likely to use islands that were closer together. Small mammals have relatively poor swimming ability compared to larger mammals, and may heavily rely upon 'island hopping' to colonize remote islands. Some of the study islands are connected at very low tides, which is the most likely method of island dispersal, as small mammals forage in the intertidal zone (Crowell 1973). In calm ocean conditions, mice (*Peromyscus* sp.) are able to swim 200 m or more, although endurance is limited to less than ½ hour (Sheppe 1965, Redfield 1976).

In addition to providing explanations for variation in island use, occupancy models can provide information on the reliability of observed occupancy patterns. For all three taxa, the modelled occupancy estimates were reasonably close to observed naïve

occupancy, particularly for small mammals. As well, the conditional probability of occupancy (Ψ_c , which estimates probability of presence, given an absence), was relatively low ($\Psi_c < 0.23$), especially for river otter ($\Psi_c < 0.11$). The probability of presence (given absence) was not related to (log) island area, despite concerns over unequal sampling effort. However, there was a clear relationship between the probability of presence (given absence) and the number of camera-nights, similar to that observed by Gu and Swihart (2004). This indicates that while island size did not impact the reliability of the incidence data, increasing camera-nights during 2016 and part of 2017 was valuable for retaining more accurate incidence data.

Coastal mammals are highly mobile and transient. On the Central Coast, larger mammals colonize and abandon islands within relatively short periods of time (e.g., Darimont and Paquet 2002). While my results indicate that island size and quantity of marine subsidy are correlated with overall insular richness, these covariates did not predict taxon-specific island use. Instead, island occupancy of mink and river otter was constant, while small mammals occupied islands closer together. Future models should consider the importance of specific habitat variables (e.g., shoreline slope, vegetation cover), as well as species interactions. In particular, predator-prey and competition/facilitation relationships can have an equally strong effect on species success (colonization) and failure (extinction) as the traditional island biogeography factors of area and isolation (Abbott 1983).

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Appendix I – Methods

Island selection and spatial analysis

Islands were selected as part of the larger *100 Islands* project and are not specific to this particular study. Islands were initially grouped using cluster analysis based on similar traits extracted from the BC ShoreZone dataset (Howes et al 1994) and refined further using WorldView-2 satellite imagery (DigitalGlobe Foundation, 2014). These traits included: area, perimeter to area ratio, exposure, shoreline type (e.g., cliff, sandy beach, etc.), distance from mainland, and proximity to other neighbouring islands. WorldView-2 allowed for higher resolution images where “true” island (i.e., vegetated land) could be distinguished from the shoreline (e.g., beach or barren rock) to obtain finer estimates of area, perimeter, etc. This method allowed for selection of islands representing the full range of features exhibited on the coast, and prevented the selection of many similar islands.

We further limited the range of island sizes to include islands large enough to support vegetation, but small enough to not support large bodies of freshwater year-round. Both of these requirements reflected the need to capture biodiversity of plant, terrestrial invertebrate, bird, and mammal diversity within a reasonable time frame and with reasonable effort and logistical complexity. The final output clustered islands into four groups: close to mainland and exposed, close to mainland and protected, far from mainland and exposed, and far from mainland and protected. We then identified key nodes (primarily based on existing island groups with adequate camp sites), which could be used as a base to sample the range of island types during the summers of 2015 (May –

June), 2016 (May – July) and 2017 (May – July; Figure 1). For full details on island selection and spatial analysis, refer to Reshitnyk et al (2015) and Ernst et al (2016).

Field sampling

Track plates – In 2015 I used two types of track plates: mesocarnivore (hereafter “MC”) track stations and small mammal (“SM”) track stations. MC stations were 11 x 11 x 32” white corrugated plastic (Plaskolite™) boxes anchored in the ground using metal tent pegs, wire, and tree branches (Gompper et al 2006, Iowa DNR 2006; Long et al 2008). Track plates within the housing were butcher paper with ink (3:1 heavy mineral oil and carbon black powder) applied to wax paper glued to the center of the track plate. These stations were baited with ~10mL of fish fertilizer (Alaska™ Fish Fertilizer) applied to a bundle of moss and sticks, along with a second bundle of peanut butter. MC stations were used to obtain tracks from medium-sized mammals such as mink (*Neovison vison*) or potentially larger rats (*Rattus norvegicus*). During 2015 I only recorded small mammal tracks at MC stations, so they were discontinued in subsequent years because they were bulky and difficult to transport. The number of SM track plates was subsequently increased.

SM track stations housings were 2 x 14” commercial PVC pipe with slits cut in the bottom to allow for water drainage (Nams and Gillis 2003). SM track plates also used ink (as above) applied to the waxy side of a 2 x 2” square of freezer paper glued to the center of a strip of standard printer paper (2.5 x 11”). SM stations were used to obtain tracks from small mammals including mice (*Peromyscus* spp.), voles (*Myodes* and/or *Microtus* spp.) and shrews (*Sorex* spp.).

Due to the highly variable sizes of islands surveyed, the number of track plates placed per island varied with island area. The minimum number of track plates on an island was 3, and was increased for progressively larger islands. During the summer of 2015 I was constrained to 50 SM stations and 20 MC stations per 6 islands. During the summer of 2016 I was constrained to 60 SM stations per ~8 islands.

Track plate placement on islands varied based on island accessibility and habitat. During summers 2015 and 2017, I placed track plates at approximate cardinal directions (North, South, East and West) to ensure plates were spread out, although this varied with terrain and accessibility. At each of the four cardinal directions, when possible, I stratified track plate placement by habitat type: track plates were spread from the edge of the island (often beach-forest transition zone or scrub), farther inland into the forest. On large islands, I also placed track plates in the interiors of the island.

During 2016, track plates were placed in the same locations as live trapping grids (details below) to reduce travel time. Grids were often located on beaches or accessible areas of the island. While variation in the number of track plates on islands of the same size across nodes occurred, I was only interested in presence/absence of mammals, so did not expect this to affect the results significantly. In all years, track plates were left out for 2-4 nights.

Live traps - The number of traps per island ranged from 3 to 36 depending on island size. Trapping grid size and placement approximately followed Stapp and Polis (2003a, 2003b), modified slightly. Trap lines were 15 m apart, with traps 25 m apart along each line. Rectangular grids extended from the supralittoral region (or forest edge where no littoral zone existed) and extended 125 m inland perpendicular to shore. On half

of the islands sampled in 2016 ($n = 20$), grids consisted of 24 traps (4 trap lines of 6 traps), although this was modified depending on island shape. On islands $> 1 \text{ km}^2$ ($n = 3$) grids consisted of 36 traps (6 lines of 6 traps; Stapp and Polis 2003a).

On small islands that could not support the 4 x 6 grid ($n = 13$ small islands), I scaled the number of traps on each island as a function of island area and the effective grid area in order to keep effort relatively consistent. Effective grid area is the total trappable area sampled by the trapping grid (Marinelli and Millar 1989). I determined the ‘effort’ afforded to islands receiving the 4x6 grid, and used that to determine how many traps smaller islands would receive. On these smaller islands, traps were distributed evenly across the island (rather than in a grid). Traps were supplemented with cotton nest material (LivingWorld® hamster bedding), carrots, mealworms and peanut butter for bait. They were set at dusk and collected the following morning (1 night of trapping per island).

Wrack biomass – Wrack biomass was collected from 2015 – 2017 and was shared as part of the *100 Islands* project (Wickham 2018).

Track plate confirmation tests

Identification of small mammal tracks on track plates is subjective and can be prone to identifier error (Wiewel et al. 2007). Over the three years of track plate collection (2015 – 2017 inclusive), two technicians identified tracks: User 1 (2015 and 2016) and User 2 (2017). I conducted three tests to determine the validity and give a measure of analyzer error: Accuracy, Intercoder and Precision tests. Approximately 5% ($n = 11$) of all track plates collected were used for Intercoder and Precision tests. All track plates collected from live-trapped mice were used for Accuracy tests ($n = 15$). A

third analyzer (User 3) was used for Agreement tests to determine how an identifier with no previous track identification experience would agree with Users 1 and 2 (User 3 did not identify any track plates used in data analyses). Descriptions of the tests and their results are given in Table 2.6.

Table 2.6 Track identification tests from track plates collected from 2015 – 2017. Tests (and relevant sample sizes) and descriptions are listed. Result percentages indicate the proportion of track plates which were correctly identified, or the proportion of track plates agreed upon by multiple analyzers. Interpretation summarizes the key results of each test.

Test	Description	Result	Interpretation
Accuracy (n = 15)	Analyzers were given track plates obtained from live-trapped mice (<i>P. keeni</i>). Therefore, the species was known (but not to the analyzers).	User 1: 100% User 2: 100%	Both users identified mouse tracks correctly 100% of the time. Note: only mice were live-trapped so Accuracy tests are only available for mice.
Intercoder	Measures the extent to which User 1 and User 2 agreed on track identification. Sub-divided by taxon: mice, voles and shrews.	Mice: Agreed on 9/11 (82%) Voles: Agreed on 8/11 (73%) Shrews: Agreed on 6/11 (55%)	User 1 and 2 agreed the most on mouse track identification, followed by voles. Users did not show consistent agreement on shrew track identification.
Precision (n = 11)	Extent to which users re-identified the same tracks a second time.	User 1: not available User 2: 100%	Data was not available for User 1. User 2 re-identified 100% of track plates the same a second time, for all taxa (mice, voles and shrews).
Agreement	Extent to which User 3 (no track identification experience) agreed with Users 1 and 2, subdivided by each taxon: mice, voles and shrews.	User 3-User 1: Mice: agreed on 18/20 (90%) Voles: agreed on 19/20 (95%) Shrews: agreed on 17/20 (85%) User 3-User 2: Mice: agreed on 7/10 (70%) Voles: agreed on 9/10 (90%) Shrews: agreed on 7/10 (70%)	There was variation in user agreement for mice and voles. Agreement among users was consistently lowest for shrew track identification.

Probability of island use by three focal taxa

Table 2.7 Candidate occupancy models with covariates predicted to influence island use by mammals ($n = 91$ islands), including standardized island area ('area'), standardized distance from mainland (D_{ML}), standardized distance to the nearest island (D_{NN}), and standardized wrack biomass. $p(\cdot)$ = probability of detection (p) is held constant in all models.

Model	Components
1	$\psi(\cdot)p(\cdot)$
2	$\psi(\text{area})p(\cdot)$
3	$\psi(D_{ML})p(\cdot)$
4	$\psi(D_{NN})p(\cdot)$
5	$\psi(\text{wrack})p(\cdot)$
6	$\psi(\text{area} + D_{ML})p(\cdot)$
7	$\psi(\text{area} + D_{NN})p(\cdot)$
8	$\psi(\text{area} + \text{wrack})p(\cdot)$
9	$\psi(D_{ML} + D_{NN})p(\cdot)$
10	$\psi(D_{ML} + \text{wrack})p(\cdot)$
11	$\psi(D_{NN} + \text{wrack})p(\cdot)$
12	$\psi(\text{area} + D_{ML} + D_{NN})p(\cdot)$
13	$\psi(\text{area} + D_{ML} + \text{wrack})p(\cdot)$
14	$\psi(D_{ML} + D_{NN} + \text{wrack})p(\cdot)$
15	$\psi(\text{area} + D_{ML} + D_{NN} + \text{wrack})p(\cdot)$

Appendix I – Results

Patterns in species richness

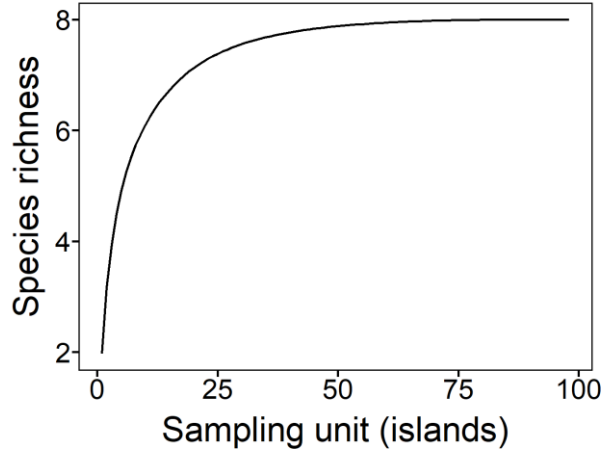


Figure 2.4. Sample-based species accumulation curve for mammal richness across 98 islands. The *rareNMtests* package in R automatically computes Hill numbers (Hill 1973), though in this case the Hill exponent (q), $q = 0$, is interpreted as species richness (Chao et al. 2014).

There was a negative ($r^2 = 0.02$), but non-significant relationship between richness and mean island slope (linear regression, $t = -1.67$, $p = 0.10$).

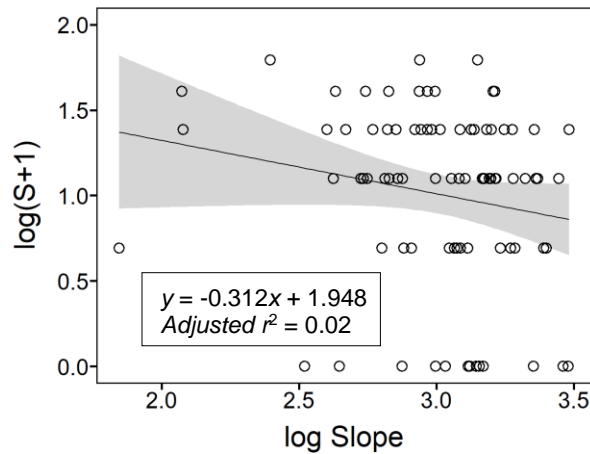


Figure 2.5. Relationship between (natural) log species richness (natural) log mean island slope (degrees). Note that $\log(S+1)$ was used to allow for zeroes in the data.

Probability of island use by three focal taxa

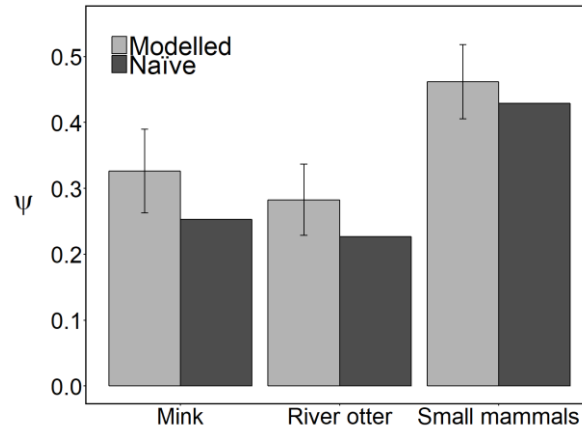


Figure 2.6. Estimates of modelled ($\Psi \pm SE$) and observed naïve (Ψ_i) occupancy (or island use) for the three most common taxa recorded on remote cameras across 91 islands. Modelled estimates are based on the null model $\Psi(\cdot)p(\cdot)$.

Conditional occupancy (Ψ_c)

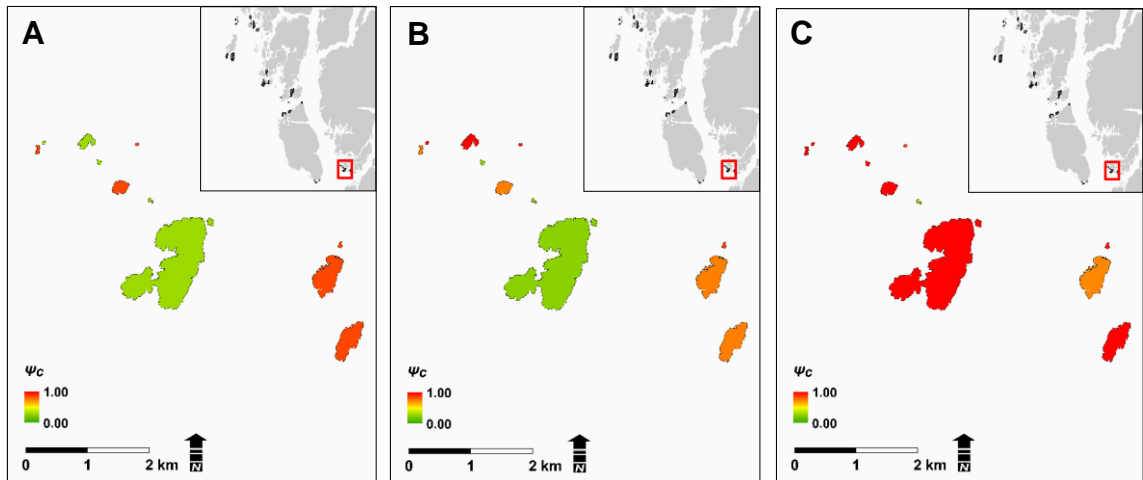


Figure 2.7. Example of distribution maps using conditional occupancy (probability of presence given detection history, Ψ_c , where ‘presence’ scores $\Psi_c = 1.0$ and ‘absence’ scores $\Psi_c < 1.0$) for (A) river otter, (B) mink and (C) small mammals. Islands pictured here are from the Penrose group near Rivers Inlet, BC (study islands outlined dark).

3. Marine subsidies to island food webs drive spatial patterns and intrapopulation variation in diet in an omnivore, the Keen's mouse (*Peromyscus keeni*) in coastal British Columbia

Abstract

Marine subsidies can influence multiple trophic levels in terrestrial food webs, but influences on omnivore consumers, particularly in terrestrial environments with multiple resource pathways, are not well understood. I sampled mice (*Peromyscus keeni*) and their food items from islands on the Central Coast of British Columbia, Canada. Using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotopes in mouse hair and faeces, arthropods and vegetation, along with biomass and mouse capture frequencies, I examined the potential direct and indirect routes of subsidy to the terrestrial food web. Mouse captures and terrestrial arthropod biomass were highest at the beach and declined inland. These patterns were mirrored in the stable isotope signatures, particularly $\delta^{15}\text{N}$, in plants, terrestrial arthropods and mouse faeces, which were enriched by up to 6‰ at the beach compared to inland. An isotope mixing model indicated that approximately one-third (~33%, range 2.5 – 42%) of mouse diets are composed of beach-dwelling arthropods. Variation among individual diets was best explained by the combined gender and reproductive status (RVI = 0.80-0.99). Reproductive males had more enriched signatures and consumed up to twice as much marine prey than females. Although the biomass of beach-dwelling arthropods was positively associated with the proportion of beach-dwelling arthropods in mouse diets, it was less important than gender-reproductive status (RVI = 0.44 – 0.70). These results indicate that the effects of marine subsidies cascade inland through multiple trophic levels, and provide direct and indirect benefits to higher trophic levels. Furthermore,

intrapopulation differences explain the variation in marine resource use more than variation in subsidized prey abundance.

Introduction

The flow of nutrients across ecosystem boundaries can have wide-reaching effects on recipient populations and communities. Along the coastal margin, marine nutrients are available to terrestrial organisms in several ways. Some are temporally constrained ('pulsed'), e.g., marine mammal carcass drift (Rose and Polis 1998) and seabird guano deposition (Polis et al. 1997, Barrett et al. 2005). Others are relatively consistent and year-round, e.g., beach-cast seaweed ('wrack') (Polis and Hurd 1996, Polis et al. 1997, Spiller et al. 2010). Through direct and (or) indirect pathways, marine subsidies cascade through terrestrial ecosystems and may cause increases in terrestrial primary productivity (Polis and Hurd 1996, Spiller et al. 2010) and numerical responses by low and high trophic level consumers (Polis and Hurd 1995, Dugan et al. 2003, Barrett et al. 2005, Spiller et al. 2010). However, most studies occur in regions with very low in-situ (terrestrial) productivity (e.g., Baja, California), where it is likely that a relatively small input of allochthonous resources will cause a pronounced response within the recipient ecosystem.

On islands with low terrestrial primary productivity, wrack deposited on shorelines provides the main primary productivity resource and supports high quantities of beach-dwelling arthropods. As a result, more consumers aggregate along shorelines to exploit this prey (Polis and Hurd 1995, Stapp and Polis 2003a), and their diets contain more marine-derived nutrients than inland conspecifics (Anderson and Polis 1998). However, it is unclear if these trends would be replicated in a terrestrial environment

where in-situ primary productivity is relatively higher than these environments. As marine subsidies are hypothesized to influence whole-island communities (Polis and Hurd 1996, Anderson and Wait 2001), it is important to understand how far inland these resources penetrate and which trophic levels or populations might be vectors for transfer. Understanding the extent of these patterns (both abundance and enrichment) across space and among trophic levels will also help resolve whether coastal subsidies are present in the terrestrial environment through direct or indirect pathways, especially to high-level consumers with multiple resource pathways.

Consumer responses to subsidy are likely mediated by trophic patterns in diet. Omnivory introduces complexity and variability into food webs when individuals forage across trophic levels and resource pathways (Vadeboncoeur et al. 2005). As omnivores have access to multiple channels of energy acquisition (Polis and Strong 1996), their responses to subsidy may depend largely on the conditions (i.e., productivity) of the recipient ecosystem (Stapp and Polis 2003a, 2003b, Lancaster et al. 2008). If a subsidy is consistent and in-situ productivity is relatively high, it is unclear whether omnivores would respond as strongly as specialist or carnivorous consumers.

Individuals within populations may respond differently to a subsidy, which can lead to intrapopulation variation in diet and population niche width (Bolnick et al. 2003, Darimont et al. 2009, Araújo et al. 2011). These intrapopulation differences may arise due to behavioural or physiological traits that mediate how individuals respond to resource subsidies. Reproductive individuals, particularly females, may consume more high-quality food due to the energetic and nutritional requirements of reproduction (Shine 1989, Polis 1991, Polis and Strong 1996, Hailey et al. 2001), but dominant males may

monopolize resources through territorial or aggressive behaviour (Wolf and Batzli 2002, Ben-david et al. 2004, Rode et al. 2006, Adams et al. 2017). The location within the recipient habitat in which these subsidies occur, and associated risk of predation (e.g., Wolf and Batzli 2002, 2004) may also alter foraging strategies. Ultimately, individual perception of risks (predation, aggression) and rewards (marine resources) interact with habitat and may mediate foraging decisions (Lima and Dill 1990).

I studied a ubiquitous coastal omnivore, the Keen's mouse (*Peromyscus keeni*) and its associated food web on oceanic islands along the Central Coast of British Columbia, Canada. There is evidence that coastal mice benefit from shoreline subsidies in the Pacific Northwest, although most records are anecdotal (McCabe and McTaggart-Cowan 1945, Thomas 1971, Marinelli and Millar 1989). Along the Central Coast, islands vary in the quantity of wrack deposited along shorelines (Wickham 2018). I focused on two island systems at either end of this subsidy gradient to capture the widest potential range of mouse responses to subsidy (Wickham 2018). Using abundances and stable isotopes of mice and their food items, I determined whether spatial trends in subsidy were evident from island shorelines to interiors, and whether direct or indirect pathways of subsidy influence mouse diets. I also used individual- and site-level variables to determine whether landscape and (or) intrapopulation factors could predict variation among individual diets.

Methods

Ethics statement

Small mammal trapping was approved under University of Victoria (UVIC) Animal Use Permit (AUP) #2016-012(1) in accordance with Canadian Council on

Animal Care guidelines, and followed UVIC SOPs #AC2007 and #AC2023. Field work was conducted out of the Hakai Institute on Calvert Island, BC, within the Hakai Lúxvbálís Conservancy area under a long-term operation BC Parks Use Permit No. 107190. Trapping and survey methods comply with the BC RISC Standards for Inventory Methods for Small Mammals (Ministry of Environment, Lands and Parks Resources Inventory Branch Report No. 31, Version 2.0, 1998). All field researchers completed animal handling training sessions through the University of Victoria Animal Care Services. Field work was conducted with permission from the Heiltsuk and Wuikinuxv First Nations in whose traditional territories we worked.

Study area

Islands along the Central Coast of British Columbia are within the Coastal Western Hemlock biogeoclimatic zone, Very Wet Hypermaritime subzone (CWHvh2) of the Coast Forest Region (Banner et al. 2005). Sampling occurred at five sites across two regions, the Goose Island archipelago and Calvert island (Figure 3.1A). Three sites were on Calvert Island (CV): North Beach (NB), Grief Bay (GF) and Indian Paintbrush beach (IP). Two sites were in the Goose archipelago (GS): one on Gosling Island (GOS) and another on Goose Island (GS-S; Figure 3.1A). All sites were predominantly sandy or sand-pebble beaches. Sampling occurred in late May (GF and IP), mid July (NB), late August (GOS) and early September (GS-S) of 2016.

The Goose Group and Calvert Island differ in their exposure to marine subsidies. Preliminary data suggest the Goose Group has more wrack deposition along beaches than Calvert (Wickham 2018). However, some of these data were collected in years prior to this study, and the quantity of wrack deposited can vary by site characteristics or among

years (Orr et al. 2008, Barreiro et al. 2011, Wickham 2018). Additionally, a pilot study using mouse specimens (Royal BC Museum) collected from GS (n = 11) and CV (n = 62; c. 1930-1950) indicated that GS mouse diets were more enriched with marine-derived nutrients than CV. Isotope analysis of fur and preliminary diet modelling indicated GS mice consumed over twice the proportion of marine arthropods (~88%) as Calvert mice (~33%, unpubl. data).

It is also potentially important to note that the Goose archipelago also differs in its lack of understory canopy due to grazing pressure from deer (*Odocoileus hemionus sitkensis*), which appear to have colonized this isolated archipelago sometime after the 1950s, and lived there without non-human predators until 2007 when coastal wolves (*Canis lupus*) began to occupy the archipelago (Darimont and Paquet 2002). Understory vegetation structure may influence aspects of small mammal ecology (e.g., Anderson and Meikle 2006) that are not accounted for here.

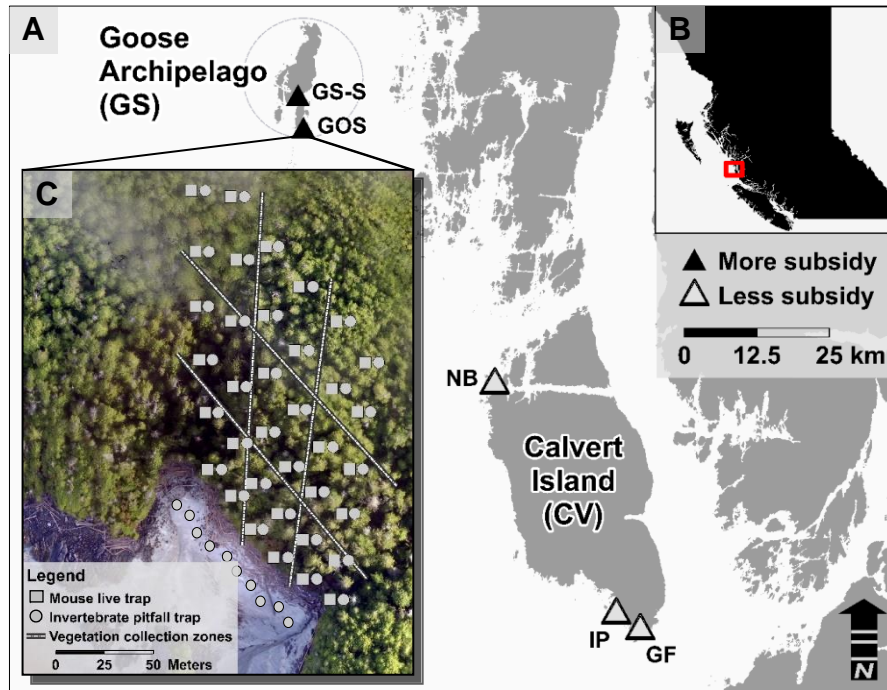


Figure 3.1. (A) Study map of high (GS-S, GOS, collectively ‘GS’) and low (NB, IP, GF, collectively ‘CV’) subsidy sites on the (B) Central Coast of British Columbia, Canada, with (C) example sampling grid at GOS showing approximate vegetation collection zones, mouse live traps (squares) and arthropod pitfall traps (circles).

Field sampling

Trapping grids – At each site in 2016 I laid a grid of trap stations extending from the beach into the forest, where one trap station included one mouse live trap and one forest arthropod pitfall trap (Figure 3.1C). Stations were set in a grid resembling the layout used by Stapp and Polis (2003a, b; see Figure 3.1C). Grids extended 125 m – 200 m inland depending on site (Appendix II – Methods). I transferred mice from traps to Ziploc® bags to take weights, hind foot measurements, record gender, breeding status, and age (adult or sub-adult), and to obtain hair samples. See Appendix II – Methods for sampling details and Tables 3.4 and 3.5 for species collected.

I used track plates (Nams and Gillis 2003) to passively collect faecal samples in 2015 (GOS) and 2017 (NB). Track stations were arrayed in a grid the same as live traps

(Figure 3.1C), although at some sites only 3 trap lines were placed. Faecal samples were obtained from track plates after approximately three nights and stored in 75% ethanol for 1-3 months until lab processing could occur. Additional track plate design details can be found in Appendix II – Methods.

Vegetation – Within each grid I also collected vegetation from nine zones for stable isotope analysis (Figure 3.1C). Due to timing of collection and logistics, vegetation samples were not collected from GF and IP, but were collected at NB, GS-S and GOS. Plant matter was stored in 75% ethanol for 1-3 months before lab processing. See Appendix II Tables 3.4 and 3.5 for species collected.

Normalized Differentiated Vegetation Index (NDVI) data were obtained from the Worldview2 sensor at 2-m resolution for GOS and GS-S 14-August-2014, for NB 4-August-2014, and for GF and IP 4-June-2015. NDVI captures infrared wavelengths re-emitted by leaves (typically of the upper canopy) during photosynthesis, giving an indication of photosynthetically active biomass and consequently productivity (ranging from -1.0 to 1.0, low to high photosynthetic activity, respectively). I used this as a proxy for terrestrial primary productivity within predictive models to represent available plant foods at each site, as ground-based estimates of plant biomass were not available. NDVI may be able to predict fruit yields (Li et al. 2010), and its fine-scale resolution makes it ideal for use in modelling. However, NDVI is representative of the upper canopy and not the shrub layer, where many fruits are produced (e.g., salal or huckleberry plants).

Beach arthropods – Beach pitfall traps (n = 25 per site) were the same as those used for terrestrial arthropods. Traps were distributed ~1-2 m above the recent highest wrack line, extending along the front of the trapping grid to catch beach-dwelling

arthropods adjacent to wrack piles. Traps were left out for 1 night. I collected beach arthropods from all five sites during summer 2016. Arthropods were stored in 75% ethanol for 1-3 months before lab processing. See Appendix II Tables 3.4 and 3.5 for species collected.

Stable isotope sample and data analyses

Food items (vegetation, and beach and forest arthropods), mouse hair, and faecal samples were analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotopes (see Appendix II – Methods for details). I corrected $\delta^{13}\text{C}$ signatures for faecal matter using equations given in Post et al. (2007) due to high lipid content in samples (>75%). I did not correct for lipid content in any other tissues because consumers typically eat prey whole and consume all lipid content. Comparisons of regional differences in isotopic signatures of mouse tissues and food items were done using Wilcoxon (Mann-Whitney) tests (R Core Team 2017).

I determined the relative contribution of food items to mouse diets using an isotopic mixing model, MixSIAR in the *MixSIAR* package (v 3.0, Moore and Semmens 2008) in R. I used region-specific models due to regional differences in isotope signatures of five food groups: vegetation (berries, fruit, seeds), terrestrial arthropod herbivores, terrestrial arthropod carnivores, beach arthropod herbivores, and beach arthropod carnivores (see Appendix II Tables 3.5, 3.6 and 3.9). I used the mean and standard deviation $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for each of the five food groups with individual mouse hair signatures to estimate the relative proportion of each food group to individual diets. I used trophic fractionation values of +3.3‰ for $\delta^{15}\text{N}$, and +1‰ and +2‰ for $\delta^{13}\text{C}$ for arthropod and plant tissue, respectively (Drever et al. 2000). Mixing models were run

with both ‘region’ and ‘individual’ as fixed effects to obtain regional and individual diet proportions. All diet proportions presented are medians with 95% confidence intervals.

Data analysis of spatial patterns in abundance and stable isotopes

I calculated the average (\pm standard error) proportion of mice caught at each distance class from the beach back into the forest (0-25, 50-75, 100-125, 150-200 m) similar to Stapp and Polis (2003a), where the proportion caught per 100 trap-nights took into account varied sampling effort and misfired traps (i.e., CPUE; Nelson and Clark 1973, Beauvais and Buskirk 1999). Details on CPUE calculations by site can be found in Appendix II – Methods. I compared capture proportions at distance classes using a one-Way ANOVA and Tukey post-hoc tests (R Core Team 2017), ensuring assumptions of normality and variance were met.

Terrestrial arthropod biomass was analyzed in a similar manner, with mean (\pm standard error) biomass (corrected for sampling effort) estimated for each distance interval. Biomass data were log (base 10) transformed and compared using one-way ANOVA and Tukey post-hoc tests (as above). Spatial patterns by guild were analyzed with a two-way ANOVA. See Appendix II – Methods for details.

Stable isotope signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) were also examined along a spatial gradient from the beach into the forest for mouse faeces, terrestrial arthropods, and plants. Signatures were compared overall using Kruskal-Wallis tests.

I examined variation in marine subsidy consumption and stable isotope signatures (in hair) among sexes and reproductive statuses of mice across all sites, and compared multiple groups using Kruskal-Wallis tests with either post-hoc pairwise Wilcoxon Rank Sum (R Core Team 2017) or Dunn’s tests when ties could not be computed (*dunn.test*

package, Dinno 2017). As well, I visually compared the relative proportions of male and female captures along the above spatial gradient to determine if there was evidence of spatial segregation between sexes that might explain dietary variation.

Modelling variation among individual diets

I used a similar method to Service et al. (2017) to model how ecological, behavioural and physiological predictors may influence marine resource consumption in mice. I tested my hypotheses (Appendix II – Methods, Table 3.7 and below) on three model sets each with different response variables: a derived estimate of the proportion of beach-dwelling arthropods (P_{BA}) in individual diets (from MixSIAR results) and individual mouse hair $\delta^{13}C$ and $\delta^{15}N$ signatures. To obtain P_{BA} , I extracted the median proportions of beach arthropod herbivores and carnivores from the posterior distributions of diet proportions for each individual mouse. I then summed them together for a total estimate of the proportion of beach-dwelling arthropods (P_{BA}) in individual diets.

I used the following four variables to predict each response: beach arthropod biomass (AB_B), terrestrial arthropod biomass (AB_T), NDVI, and a combined reproductive-gender status of each individual mouse (Table 1). AB_T and NDVI were analyzed at the site- and trap-level to account for the different scales at which these predictor variables might act upon mouse diets (Table 3.1).

Table 3.1. Hypothesized relationships between predictor and response variables used in a GLMM to explain variation among individual mouse diets (P_{BA}) and hair signatures ($\delta^{13}C$, $\delta^{15}N$). For gender-reproductive status (gen-rep), ‘+♀♀’ indicates reproductive females should have the highest P_{BA} and more enriched tissues. See Appendix II – Methods for details.

Variable	Description	Level	Relationship to responses
AB_B	Average beach-dwelling arthropod biomass	Site	$P_{BA} +$ $\delta^{13}C +$ $\delta^{15}N +$
AB_T¹	Average terrestrial arthropod biomass	Site (AB _{T-S})	$P_{BA} +/-$ $\delta^{13}C +$ $\delta^{15}N +$
	Average terrestrial arthropod biomass of trap location + all adjacent traps	Trap (AB _{T-T})	$P_{BA} +/-$ $\delta^{13}C +$ $\delta^{15}N +$
NDVI	Average NDVI value	Site (NDVI _S)	$P_{BA} -$ $\delta^{13}C +$ $\delta^{15}N +$
	Average NDVI values within 5-m buffer around trap + all adjacent trap buffers	Trap (NDVI _T)	$P_{BA} -$ $\delta^{13}C +$ $\delta^{15}N +$
gen-rep	Combined gender-reproductive status (4 levels)	Individual	$P_{BA} + \text{♀♀}$ $\delta^{13}C + \text{♀♀}$ $\delta^{15}N + \text{♀♀}$

¹Data not available from IP, so mouse samples from this site were excluded from models

I standardized continuous predictors by subtracting the sample mean and dividing by two times the sample standard deviation. I included ‘site’ as a random effect, although this could be problematic for two reasons. First, in some candidate models, site-level variation is taken up by the site-level predictors (AB_B, AB_{T-S} and NDVI_S). Second, ‘site’ only has 4 levels, which is considered low. However, Gelman and Hill (2007) suggest random effects have little risk for mixed-models and are important for understanding variation among underlying groups.

I investigated collinearity of predictor variables using regression plots and Variance Inflation Factors (VIF, *car* package v2.1-5 in R), reporting GVIF ($GVIF^{1/2*df}$) values for correlated covariates. Correlation analysis revealed that NDVI and AB_T were strongly negatively correlated at the site ($r = -0.92$) and trap-level ($r = -0.69$), as was site-level AB_T and AB_B ($r = -0.65$). However, GVIF values for predictors were all < 2 . Therefore, I did not include any levels of NDVI or AB_T in the same model, nor did I include site-level AB_T and AB_B in the same models (Appendix II Table 3.7). I did not drop any variables as $GVIF < 2$ is considered a conservative cut-off for multicollinearity, and did not want to lose important ecological information (Graham 2003).

I assumed the P_{BA} response variable to be beta-distributed and used a logit link function, while $\delta^{13}C$ and $\delta^{15}N$ signatures were normally distributed. I created a candidate set of models (Appendix II Table 3.7), and fit beta-GLMMs with the *glmmADMB* package v 0.8.3.3 (Fournier et al 2012; Skaug et al 2016) and normal-GLMs with the *lmer* function from the *lme4* package (v 1.1-13, Bates et al 2015). I compared top models using Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002) with the *AICcmodavg* package (Mazerolle 2017). Models were ranked based on $\Delta AICc$ scores and top models were those accounting for $\geq 95\%$ of the total model weight. I used the *MuMIn* package (Bartón 2016) to calculate relative variable importance (RVI) scores (by summing the weights for the parameters across full model sets) and determine model-averaged predictions from the top model set.

Results

Spatial patterns in the nearshore food web

I found a significant effect of distance on the proportion of mice caught excluding recaptures (One-way ANOVA, $F = 4.90$, $df = 3$, $p = 0.02$; Figure 3.2), with significantly more mice caught at the beach-forest fringe (0-25 m) than back in the forest (150-200 m; Tukey post-hoc, $p = 0.03$; Figure 3.2). These results were consistent when all recaptures of all mice were included. However, data from recaptures of 7 mice suggested that some individuals were able to travel up to 2793 m² (approximately 125 m inland) in 4-5 nights (Appendix II Table 3.7 and Figure 3.9). I captured 56 mice across 5 sites.

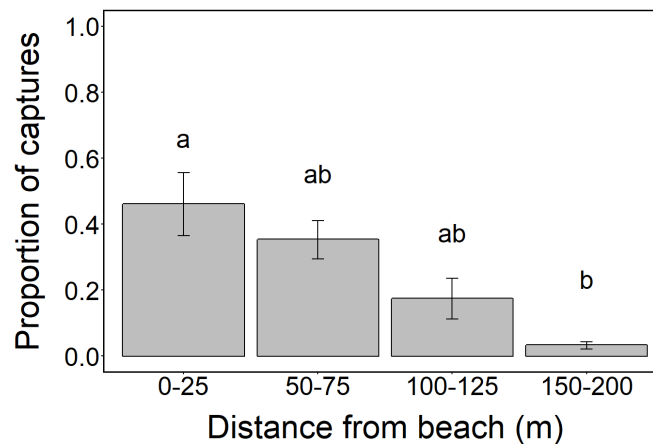


Figure 3.2. Average (± 1 SE) proportion of mice caught at each distance interval from the beach back to the forest, excluding recaptures. Proportions were obtained from catch per unit effort (Appendix II Equation 1). Distance classes with the same letters are not statistically significant from each other (Tukey multiple comparison tests, $p > 0.05$). Sample sizes were $n = 5$ sites for 0-125m, and $n = 2$ sites (GF and IP) for 150-200m.

While terrestrial arthropod biomass (AB_T) declined in a similar way as mouse capture rates, the relationship was not significant overall (Two-way ANOVA, $F = 1.56$, $df = 3$, $p = 0.20$; Figure 3.3A). There was a significant difference among guild biomass ($F = 22.05$, $df = 2$, $p < 0.001$) due to exceptionally low detritivore biomass (Figure 3.3B). There was no difference in biomass between herbivores and carnivores ($p = 0.60$; Figure 3.3B). See Appendix II Figure 3.10 and Table 3.8 for site-specific arthropod biomass.

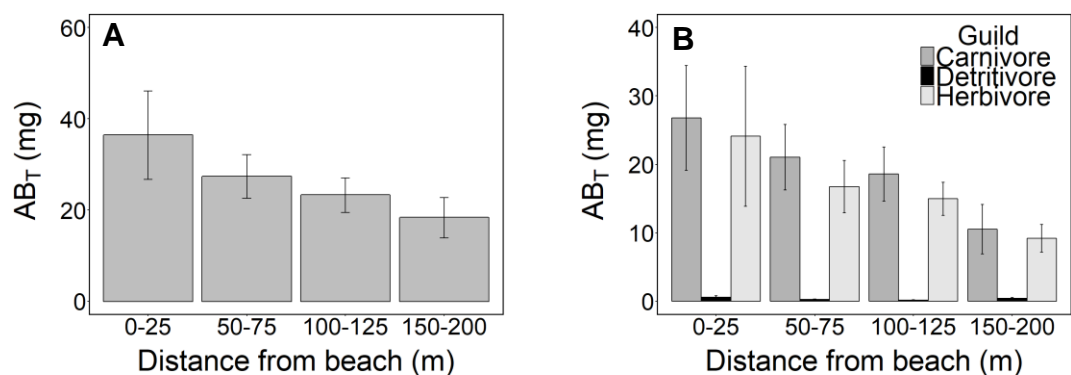


Figure 3.3. Average (± 1 SE) biomass of terrestrial arthropods (AB_T) per trap (A) overall and (B) by guild from all sites caught at each distance interval from the beach back to the forest. There were no significant differences in biomass (Tukey multiple comparison tests, $p > 0.05$). Sample sizes were $n = 4$ sites for 0-125m, and $n = 1$ site (GF) for 150-200m.

Mouse faecal $\delta^{15}N$ stable isotope signatures decreased significantly with increasing distance from shore (Kruskal-Wallis test; $\chi^2 = 17.45$, $df = 8$, $p = 0.03$; Figure 3.4A). Lipid-corrected faecal $\delta^{13}C$ depletion was more variable and exhibited overall depletion of only 1.21‰ that was not significant ($\chi^2 = 10.03$, $df = 8$, $p = 0.26$; Figure 3.4B).

$\delta^{15}N$ signatures in all three food groups declined from the beach into the forest (Figure 3.4C). Ground beetles were significantly depleted (-2.06‰; $\chi^2 = 11.55$, $df = 2$, $p = 0.009$; Figure 3.4C), as were salal berries (-5.48‰; $\chi^2 = 19.43$, $df = 2$, $p < 0.001$; Figure

3.4C). There was no significant change in $\delta^{15}\text{N}$ in weevils ($\chi^2 = 3.01$, $df = 1$, $p = 0.08$; Figure 3.4C).

Spatial patterns in $\delta^{13}\text{C}$ signatures of food items were less apparent (Figure 3.4D). Ground beetles showed almost no change from the beach to forest ($\chi^2 = 1.39$, $df = 2$, $p = 0.71$; Figure 3.4D), nor did weevils ($\chi^2 = 0.83$, $df = 1$, $p = 0.36$; Figure 3.4D). In contrast, salal exhibited pronounced depletion in $\delta^{13}\text{C}$ (1.19‰; $\chi^2 = 6.97$, $df = 2$, $p = 0.03$; Figure 3.4D).

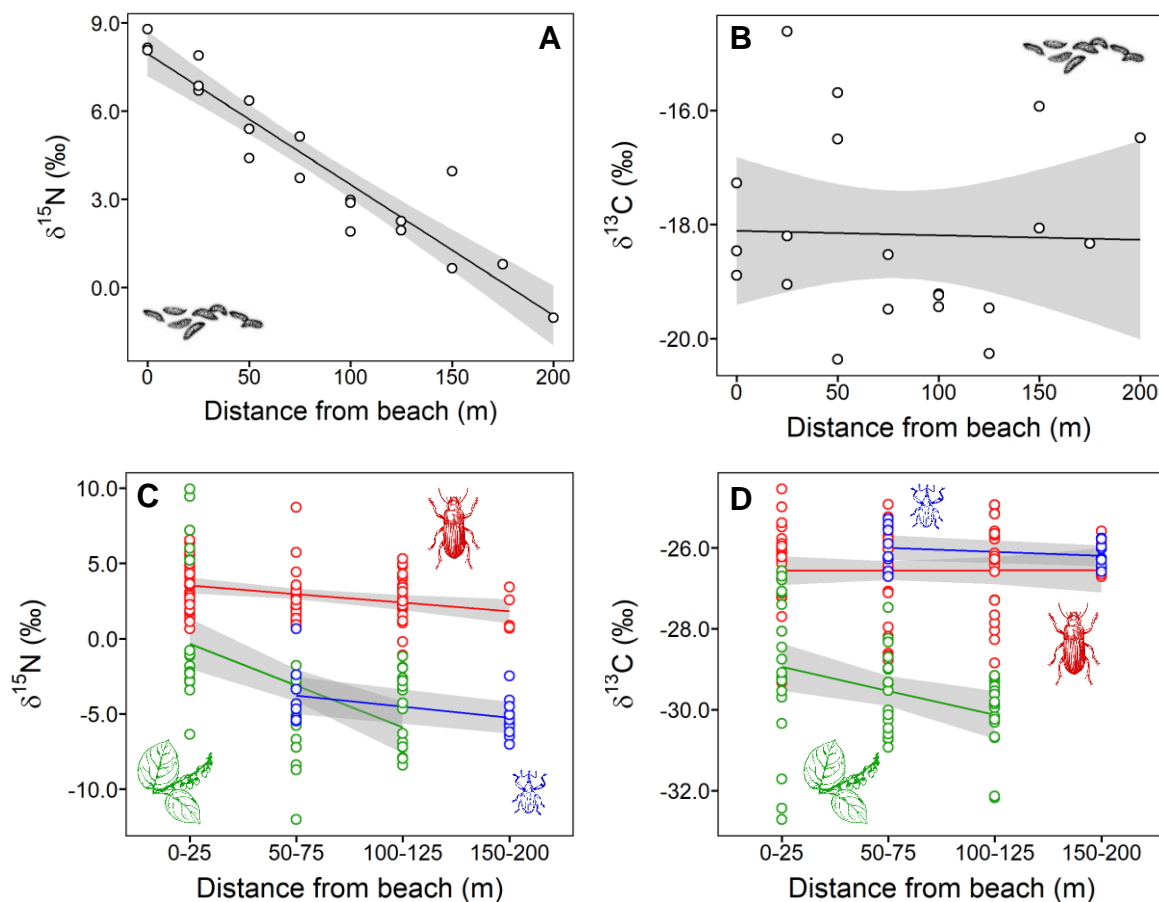


Figure 3.4. Spatial patterns in mean (\pm SE) stable isotope signatures of (A) mouse faecal $\delta^{15}\text{N}$, (B) mouse faecal lipid-corrected $\delta^{13}\text{C}$ signatures, and (C) $\delta^{15}\text{N}$ and (D) $\delta^{13}\text{C}$ in ground beetles (red), weevils (blue), and salal berries (green) from the beach into the forest. Weevils displayed here represent samples pooled across 0-75m and 100-200m. Values are raw isotope signatures without fractionation.

Mouse diet reconstruction

I created region-specific mixing models to estimate contributions to mouse diets because food items from Goose (GS) were consistently more enriched than those from Calvert (CV; Appendix II Table 3.9). Candidate food groups used in MixSIAR were pooled into five food groups (Figure 3.5A and B). Mice from GS consumed less plant-based food than mice from CV (9.6% versus 29.6%, respectively), and their diets were more evenly-spread across beach (27.4%) and forest (24.1%) arthropod carnivores (Figure 3.5A). Mice from GS consumed more animal-derived food, with 45.3% of diets composed of terrestrial arthropod carnivores, followed by 22.4% beach arthropod carnivores (Figure 3.5B).

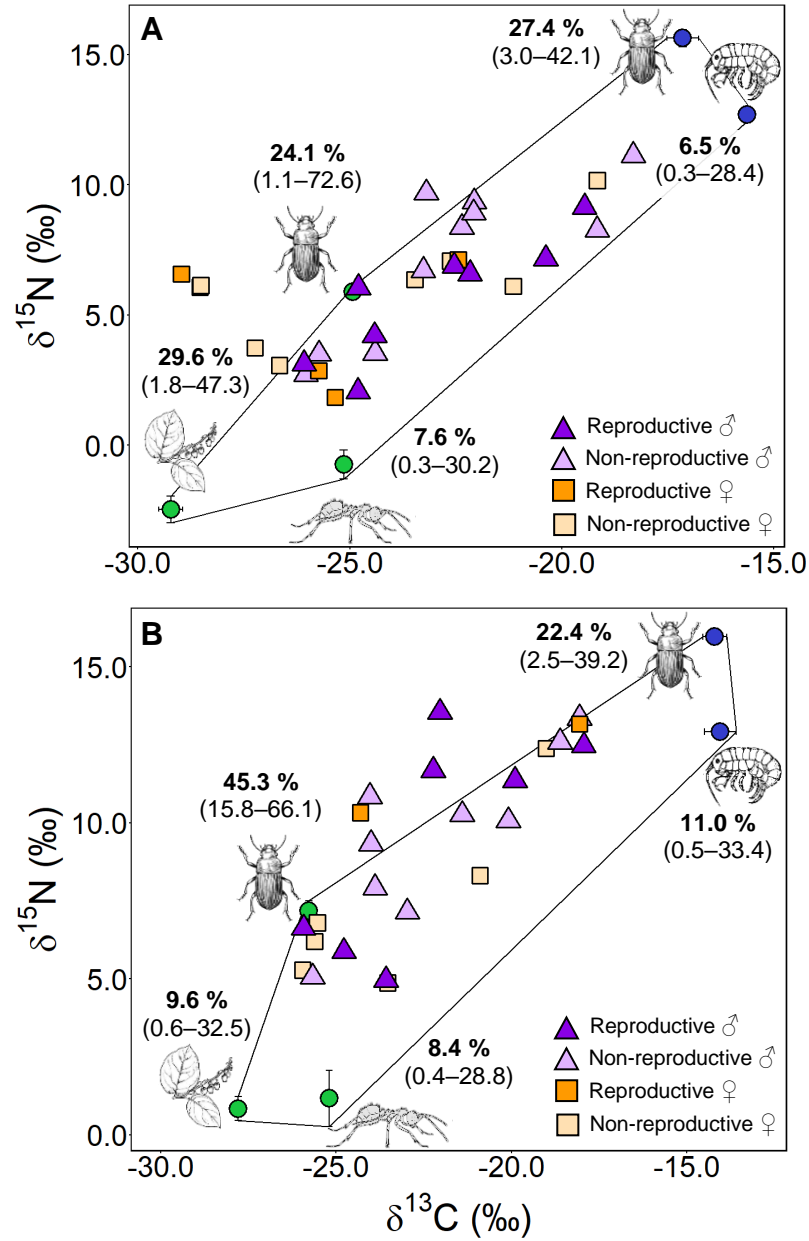


Figure 3.5. Mixing polygons from (A) CV and (B) GS representing food sources used in region-specific MixSIAR diet models with respective proportions of diet (95% CI). Food values are mean \pm SE (green = terrestrial, blue = beach) with overlaid individual consumer stable isotope signatures. Trophic fractionation values of +3.3‰ $\delta^{15}\text{N}$, and +1‰ and +2‰ $\delta^{13}\text{C}$ for arthropod and plant material (respectively) have been applied.

Intrapopulation diet variation

There was a significant effect of gender-reproductive status on the proportion of beach arthropods in diet (P_{BA} ; Kruskal-Wallis $\chi^2 = 10.16$, $df = 3$, $p = 0.02$; Figure 3.6A). Males (both reproductive and non-reproductive) consumed almost twice the proportion of beach arthropods compared to females (Dunn post-hoc $p = 0.03$; Figure 3.6A).

There was moderately significant effect of gender-reproductive status on $\delta^{13}C$ signatures (Kruskal-Wallis $\chi^2 = 7.76$, $df = 3$, $p = 0.05$; Figure 3.6B). Reproductive males were slightly more enriched than non-reproductive females (Dunn post-hoc $p = 0.05$; Figure 3.6B). There were no significant differences in $\delta^{15}N$ signatures among gender-reproductive statuses of mice ($\chi^2 = 4.80$, $df = 3$, $p = 0.19$; Figure 3.6C).

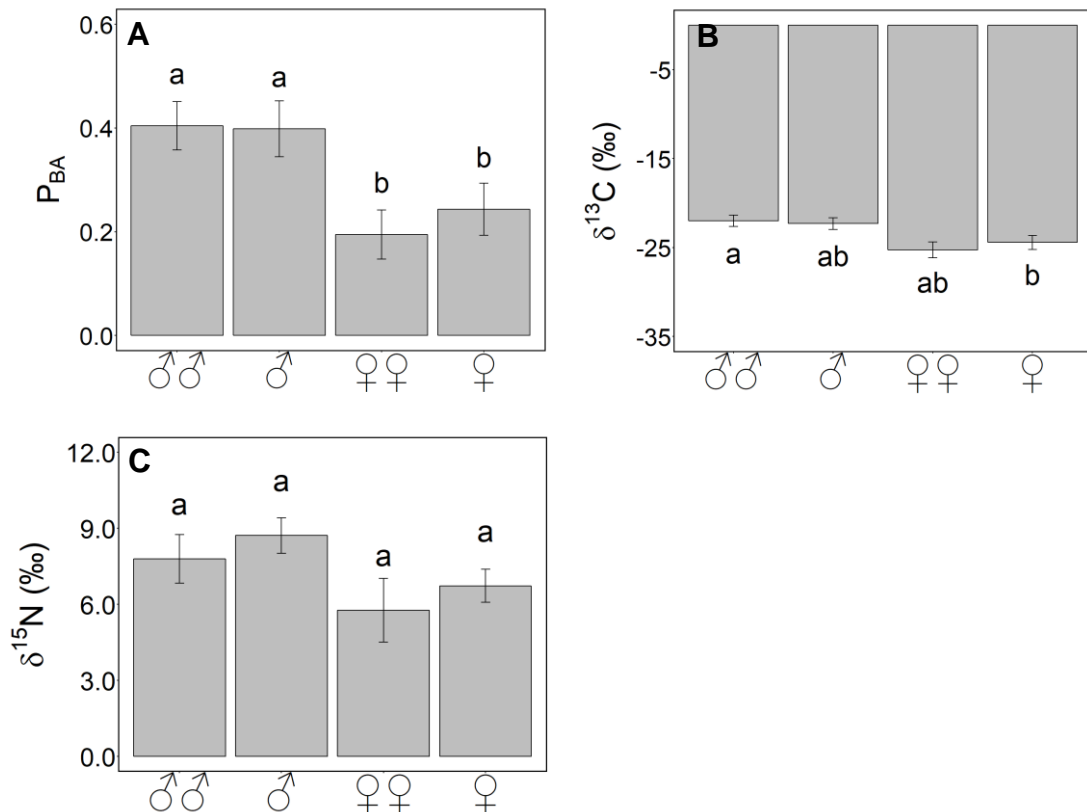


Figure 3.6. Variation in (A) P_{BA} , (B) $\delta^{13}C$ and (C) $\delta^{15}N$ among the gender-reproductive statuses of mice. Double symbols indicate reproductive condition. Values are mean \pm SE. Series with the same letters are not statistically significant ($p \geq 0.05$).

Based on the proportion of total captures, males seem to be more concentrated near the beach (no male mice were caught past 125 m), but overall fewer females were caught (Figure 3.7).

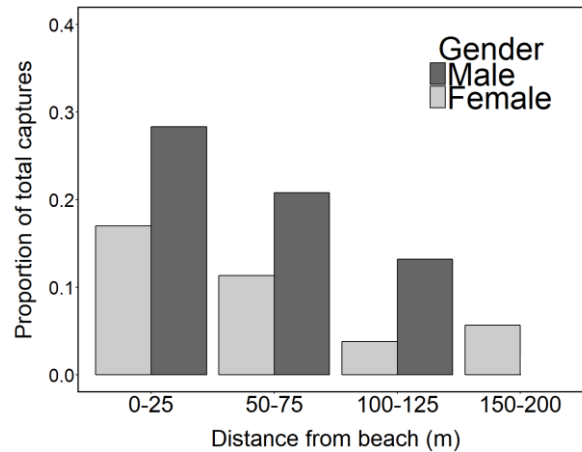


Figure 3.7. Proportion of total captures ($n = 53$) of male (dark) and female (light) mice at distance classes from the beach into the forest.

Modelling variation among individual diets

The top model predicting the proportion of beach arthropods (P_{BA}) in diet included gender-reproductive status and beach arthropod biomass (AB_B) ($AIC_{Cw} = 0.40$; $ER = 3.3$; Table 3.2). The best-supported models included gender-reproductive status of the mouse ($RVI = 0.92$), where reproductive males had the highest proportion of beach arthropods in their diet (Table 3.3). The biomass of beach arthropods also explained much of the variation in the proportion of beach arthropods in diet ($RVI = 0.70$, Table 3.3) and both variables were positively correlated (Table 3.3; Figure 3.8). There was relatively little support for NDVI at the site- ($NDVI_S$) or trap-level ($NDVI_T$), or the biomass of terrestrial arthropods at the site- (AB_{T-S}) or trap-level (AB_{T-T}) (Tables 3.2 and 3.3).

Table 3.2. Top models ($\geq 95\%$ model weight) predicting variation in proportion of beach-dwelling arthropods (P_{BA}). Genrep: gender-reproductive status, AB_T : terrestrial arthropod biomass (S: site, T: trap-level), AB_B : beach arthropod biomass, and NDVI (S: site, T: trap-level).

Response	Models	df	AICc	$\Delta AICc$	$AICc_w$
P_{BA}	genrep + AB_B	7	-29.00	0.00	0.40
	genrep	6	-26.56	2.44	0.12
	NDVI _T + genrep + AB_B	8	-26.10	2.90	0.09
	genrep + AB_B + NDVI _S	8	-26.06	2.94	0.09
	genrep + AB_B + AB_{T-T}	8	-26.00	3.00	0.09
	genrep + AB_{T-S}	7	-25.24	3.76	0.06
	AB_B	4	-24.51	4.49	0.04
	genrep + NDVI _S	7	-24.27	4.73	0.04
	NDVI _T + genrep	7	-24.22	4.78	0.04
	AB_{T-S}	4	-23.17	5.83	0.02
AB_B + NDVI _S	5	-22.60	6.40	0.02	

Table 3.3. Full model-averaged parameter estimates and RVI scores for factors predicting variation in proportion of beach-dwelling arthropods (P_{BA}). Genrep: gender-reproductive status (where a double symbol indicates reproductive classes), AB_T : terrestrial arthropod biomass (S: site, T: trap-level), AB_B : beach arthropod biomass, and NDVI (S: site, T: trap-level).

Response	Predictor variable	Parameter estimate	SE	RVI
P_{BA}	Genrep			0.92
	♂	0.75	0.37	
	♂♂	0.98	0.42	
	♀♀	0.21	0.40	
	AB_B	0.38	0.32	0.70
	NDVI _S	0.02	0.11	0.14
	AB_{T-T}	-0.01	0.11	0.13
	NDVI _T	0.01	0.10	0.12
AB_{T-S}	-0.03	0.12	0.08	

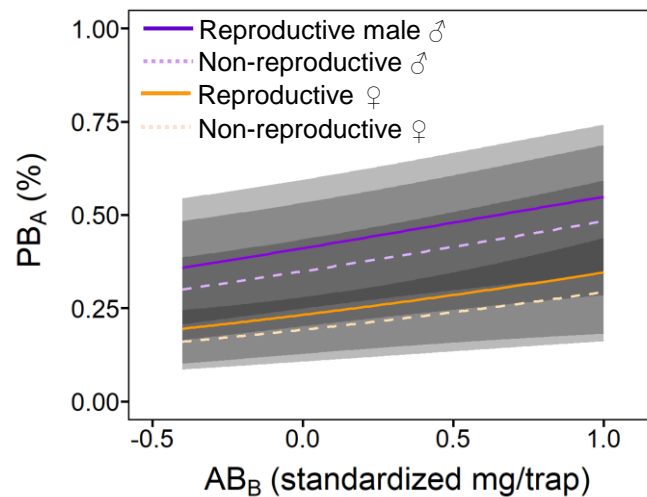


Figure 3.8 Beach-dwelling amphipod biomass (AB_B) and gender-reproductive status mediate the proportion of beach arthropods (P_{BA}) in mouse diets. Predictions are based on top model parameter estimates.

The top model explaining individual variation in $\delta^{13}\text{C}$ hair signatures included gender-reproductive status, AB_B and $NDVI_S$ ($AICc_w = 0.22$; $ER = 1.2$; Appendix II Table 3.10). However, the weight of evidence was spread relatively evenly across the top four models (Appendix II Table 3.10). The best supported models all included the gender-reproductive status of the mouse ($RVI = 0.99$) and revealed that reproductive males are more enriched in $\delta^{13}\text{C}$ (Table 3.11). AB_B was moderately important ($RVI = 0.44$) and positively related to enriched $\delta^{13}\text{C}$ (Appendix II Table 3.11). There was little support for $NDVI_S$, $NDVI_T$, AB_{T-T} and AB_{T-S} (Appendix II Table 3.10 and 3.11).

Model results for $\delta^{15}\text{N}$ were similar, with the top two models the same as $\delta^{13}\text{C}$ (Appendix II – Table 3.12). However, the top model, including gender-reproductive status, AB_B and $NDVI_S$ accounted for more of the model weights ($AICc_w = 0.31$, $ER = 1.8$, Appendix II Table 3.12). Again, the gender-reproductive status of a mouse best

explained trends in $\delta^{15}\text{N}$ (RVI = 0.81), where reproductive males were more enriched (Appendix II Table 3.13). AB_B explained some variation (RVI = 0.67), although was negatively related to $\delta^{15}\text{N}$ enrichment (Appendix II Table 3.13). Finally, NDVI_S also explained some variation in $\delta^{15}\text{N}$ (RVI = 0.60, Appendix II Table 3.13) and was positively related to more enriched signatures. There was little evidence for $\text{AB}_\text{T-T}$, $\text{AB}_\text{T-S}$ and NDVI_T (Appendix II Table 3.12 and 3.13).

Discussion

Marine-derived diets of coastal mice

Using evidence from mouse ecology, stable isotopes, and statistical modelling, I determined the influence of marine subsidies on insular mouse populations inhabiting a coastal temperate rainforest. Given that the majority of marine-derived food items available are arthropods that consume wrack (or eat those that do), inference suggests that wrack deposition is important.

Mice consumed approximately 66-87% animal-derived prey, of which up to half (~33% of total) were beach-dwelling arthropods inhabiting wrack piles. CV mice exhibited a broader dietary niche, spreading consumption equally across vegetation, beach and terrestrial sources, whereas GS mice consumed relatively little vegetation, with a narrow focus on animal prey. These results are consistent with other studies of coastal mice (e.g., Thomas 1971, Drever et al. 2000, Stapp and Polis 2003a, 2003b), which consistently consume more animal-derived protein than their inland conspecifics (e.g., Bomford 1987, Selva et al. 2012).

Spatial patterns in food web components

I trapped approximately 50% of mice within 25m of the beach. Similar capture frequencies have been noted on arid islands of southern California (Stapp and Polis 2003a), and these patterns have been considered evidence of marine resource use. Terrestrial arthropod biomass also declined moving inland which was consistent for both herbivores and carnivores. Herbivores may benefit from increased foliar growth rates and nitrogen content (Spiller et al. 2010), while carnivores may benefit from increases in both beach-dwelling and terrestrial arthropod prey (Polis and Hurd 1995, Spiller et al. 2010). It is that possible arthropod biomass patterns also partially explain mouse distributions. If prey biomass is abundant near shorelines, consumers may spend more time in this region to capitalize on abundant high-quality food.

It is important to consider these spatial patterns in consumers and prey abundance in the context of 'edge effects'. Edge habitats, particularly forest edges, can have sparser canopy, lower soil moisture, and higher plant species richness compared to interiors (Saunders et al. 1991, Murcia 1995, Gehlhausen et al. 2000). It has been hypothesized these edge habitats facilitate higher densities of mice through increased structural diversity and food supply (both plant and arthropod sources). However, results are contrasting for invertebrates (Magura 2002, Wolf and Batzli 2004) and mice. Previous studies have found more mice near edges (Cummings and Vessey 1994, Anderson et al. 2003), no differences between edge and interior abundances (Nupp and Swihart 1996), and even lower densities at habitat edges (Wolf and Batzli 2002, 2004). As well, vegetation edge effects cannot explain similar spatial patterns in mouse densities along shorelines in low-productivity ecosystems with sparse vegetation cover and no canopy

(Stapp and Polis 2003a). These results suggest the spatial patterns in abundance of mice and terrestrial arthropods may indicate a response to shoreline subsidies.

Stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) exhibited similar spatial patterns, where isotope signatures of several terrestrial consumers were depleted moving inland. Plants, terrestrial arthropod herbivores and carnivores, and mouse faecal matter all exhibited considerable $\delta^{15}\text{N}$ enrichment near the beach (+1.5-5.5‰), while $\delta^{13}\text{C}$ was variable and uninfluenced by distance from the beach. Fruits and berries near the beach were $\delta^{13}\text{C}$ -enriched (+1.2‰), although this is likely due to water stress, as carbon is not indicative of marine subsidy in plants (Farquhar and Richards 1984, Gehlhausen et al. 2000, Dercon et al. 2006). Preliminary data from islands within our study region support this, as soil moisture content is higher in the interiors of islands compared to shorelines (O. Fitzpatrick, pers. comm.).

Both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ also provide insight into direct and indirect pathways of subsidy from wrack to mice, although these pathways are not mutually exclusive. Direct consumption of marine resources should increase both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures in terrestrial animal tissues, while indirect pathways (e.g., fertilization of terrestrial plants which cascades up the food chain) should only lead to increased $\delta^{15}\text{N}$ signatures in animals, as plant $\delta^{13}\text{C}$ signature are not related to marine subsidy (Hocking and Reimchen 2002). My results indicated that nearshore vegetation is marine subsidized due to high $\delta^{15}\text{N}$ near the beach. Terrestrial arthropods are enriched by the effect of fertilization, rather than directly consuming shoreline resources (e.g., wrack or Talitrid amphipods), as evident in depleted $\delta^{15}\text{N}$ but consistent $\delta^{13}\text{C}$ over space. However, subsidy may be reaching mice both directly and indirectly, as faecal signatures indicated

considerable depletion in both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ moving away from the beach (although $\delta^{13}\text{C}$ was more variable). It is likely faecal $\delta^{15}\text{N}$ trends are partially due to consuming food with similar trends (i.e., indirect pathway), but the eventual decline in faecal $\delta^{13}\text{C}$ may suggest predation upon shoreline marine resources. If faecal $\delta^{13}\text{C}$ trends were due to consumption of terrestrial vegetation, I would expect to see similar declines in $\delta^{13}\text{C}$ in arthropod herbivores and carnivores over space, which are not evident.

Factors mediating intrapopulation subsidy use

Spatial patterns in habitat use and diet (both direct and indirect pathways) indicate evidence of marine subsidy to mice. However, this assumes landscapes, populations, and particularly individuals, are equivalent in subsidy response. Using environmental and behavioural-physiological variables within a predictive model, I determined that variation in individual resource use was best explained by the gender of the individuals. While I hypothesized that reproductive individuals (Polis 1991, Polis and Strong 1996), particularly females (Shine 1989, Hailey et al. 2001), would have more enriched signatures and more marine resources in their diets due to the energetic demands of reproduction, my results indicate that reproductive males consume more marine resources and have more enriched diets overall.

Monopolization of resources by males may be due to territoriality and (or) competitive exclusion. Male grizzly bears (*Ursus arctos*) consume more marine subsidy (salmon, *Onchorhynchus sp.*) than females, likely due to competitive exclusion and (or) female avoidance of aggressive males (Ben-David et al. 2004, Rode et al. 2006, Adams et al. 2017). In mice, dominant reproductive males are known to hold territories in higher-quality edge habitats (Wolf and Batzli 2002) and are known to have larger home ranges

than females (Blair 1942, Wolff 1985, Attuquayefio et al. 1986), presumably to increase access to resources (Shine 1989). Therefore, males may trade-off high-quality forage with predation risk, as edge habitats are frequently used by mammalian and avian predators and may represent risky habitat (Wolf and Batzli 2002, 2004).

In contrast, females may be more risk-averse, spending more time foraging in complex understory (which confers less predation risk; Anderson et al. 2003, Anderson and Meikle 2006). While sample sizes were low, females were the only sex found > 150 m away from the beach. Females are usually the ‘limiting resource’ within a population due to reproductive requirements, yet do not seem to consume as much marine-derived resources. Therefore, variation in quantity of subsidy may not result in strong numerical responses as would be expected based on other studies where pulsed resources cause numerical responses in mice (Hansen and Batzli 1979, Stapp and Polis 2003b).

Conclusion

Mice inhabiting coastal temperate islands consume shoreline-subsidized prey through direct and indirect food sources. There were consistent spatial patterns that suggested the terrestrial food web is subsidized by wrack deposition on beaches. First, the frequency of mouse captures and terrestrial arthropod biomass were highest at the beach and declined in the forest. Second, terrestrial vegetation, arthropods, and mouse faecal matter exhibited enriched stable isotope signatures (particularly $\delta^{15}\text{N}$) near the beach, which were depleted farther into the forest. This suggests coastal habitat to be of higher quality for arthropods and mice, likely due to marine subsidy. Much of the variation among individual diets was explained by the gender and reproductive status of mice, with reproductive males consuming more marine prey and having more enriched tissues. This

‘ecological dimorphism’ (Shine 1989) in the context of marine subsidy may provide important implications for the regulation of coastal rodent populations. Males may trade-off predation risk with food rewards, and the modest female response may suggest limited numerical fluctuations as subsidy biomass changes.

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Appendix II – Methods

Field sampling

Mice – At each site a grid of traps was laid extending from the beach into the forest. At early sites (GF, IP) 4 transects of 9 stations were set at the beach extending into the forest, with transects 15 m apart and each successive trap station spaced at 25 m intervals (extending a total of 200 m inland). This design was changed due to logistical constraints for later sites (NB, GS-S, GOS), and was instead 6 transects each of 6 traps (extending a total of 125 m inland) with same transect and inter-station spacing as above (Figure 1c).

Mice were trapped using Sherman small folding aluminum live traps baited with peanut butter. I also supplied traps with approximately 2 g of high-quality cotton nest material (LivingWorld® FLUFF Hamster Bedding) which did not absorb as much moisture as standard cotton batting, approximately 4 g of mealworms (Garden Chic Dried Mealworms) for protein, and approximately 2 g of carrot chunks for a water source. Mealworms were primarily to reduce stress and probability of mortality for shrew by-catch, which depend upon frequent protein ingestion (Do et al. 2013). At each site, traps were opened at dusk and closed in the morning, on average open for approximately 10 hours. Live trapping was not conducted during rain due to mortality risk, so traps were set for 1-5 nights, depending on the site.

Once transferred to Ziploc bag (Ziploc® Double Zipper Large Produce Bags), weights (Pesola spring scale, 0.5 g precision), hind foot measurements (4” and 6” Blindman’s Fractional Electronic Calipers, accurate to 0.01 mm), and gender, breeding status, and age (adult or sub-adult) were recorded. Gender was assessed using anal-

genital distance and (or) breeding traits, e.g., scrotal testes. Reproductive status was assessed for males by the presence of scrotal testes, and for females by the colour and shape of the vaginal opening, the presence of a copulatory plug, and (or) bare patches around nipples indicating nursing offspring. I marked animals uniquely at the base of their tail using Stoelting animal markers to gain rough estimates of home range sizes and movement (at GF and IP only). Fur tufts were obtained by cutting hairs using dissection-grade scissors from the dorsal surface, towards the rump.

Track plates were housed within approximately 5 x 35 cm commercial PVC pipe with slits cut in the bottom to allow for water drainage (Nams and Gillis 2003). Track plates were strips of standard printer paper (approximately 6 x 28 cm) and recorded tracks as small mammals walked through ink (3:1 heavy mineral oil and carbon black powder) applied to wax paper glued to the center of the paper slip. Track plates were baited with a small amount of peanut butter applied to the roof of the PVC tube to increase mouse visitations and ensure mice remained in the tube long enough to deposit fecal matter. All equipment that touched animals directly was sterilized with 95% ethanol between individuals. All trapping equipment was sterilized with 10% bleach between sites.

Terrestrial arthropods – At each trap station a plastic cup (~10 cm wide and deep) was dug into the ground and filled with 3:1 propylene glycol and water, with a small amount of Tritin X detergent to break surface tension. Each pitfall trap was placed approximately 2 metres from a mouse live trap (Figure 1c). Terrestrial arthropods were collected at four of five sites (IP not sampled) and stored in 75% ethanol for 1-3 months before lab processing. See Appendix II Tables 3.4 – 3.6 for species collected.

Wrack – To assess the quantity of marine subsidy available to the terrestrial environment, I surveyed wrack biomass in approximately the same temporal period as mouse trapping and arthropod collection occurred. I surveyed wrack at IP (6-May-2016), GF (9-May-2016), NB (1-July-2016), GSS (7- and 8-Aug-2016) and GOS (8-Aug-2016). At each site, I used 100-m transects along the most recent high wrack line and the spring high tide line to randomly place three 1-m² quadrats on each transect (6 total). On beaches longer than 100 m, multiple surveys were conducted (up to 5 on one beach), with each survey separated by 100 m.

Within each quadrat, I identified wrack to lowest taxonomic level. Each taxon was then assigned to a decomposition state (from 1 to 3), and weights were obtained (nearest gram) for each decomposition state: 1 = desiccated from sun/air exposure, 2 = partially dried, but still retaining minimal water content, 3 = freshly deposited with full water content (Wickham 2018). Wrack registering less than 0.5 g was recorded as “trace”, but was later removed from quantitative analysis. I then used conversion factors supplied by Wickham (2018) to convert wet to dry mass (for each decomposition state). All biomass estimates from here on are reported as dry weights.

Stable isotope analysis

I rinsed samples stored in ethanol (plants, arthropods and fecal matter) three times in deionized water, dried them at 60°C for 24-48 hrs (large-bodied arthropods, e.g., slugs and ground beetles, were dried longer), and ground them in a ball mill grinder (Retsch Mixer Mill MM200). For berries and fruits, I homogenized 3-10 individuals per sample, depending on size. The number of arthropods per sample varied based on body size, ranging from one individual per sample for large arthropods (e.g., Carabid ground

beetles) to 60-80 individuals per sample (e.g., Collembola). All faecal matter collected from a track plate was pooled into one sample. I rinsed and cleaned mouse hair samples in 2:1 chloroform-methanol to remove surface oils and dirt, and dried samples overnight in a fume hood.

Samples were encapsulated in tin capsules at average sample weights of 1.23 ± 0.13 mg, 3.44 ± 0.53 mg, 1.21 ± 0.09 mg, and 1.27 ± 0.06 mg for arthropod, plant, hair, and fecal tissue, respectively, using a microbalance (Mettler-Toledo MX5, accurate to 0.001 mg). Samples were sent to the University of California Davis Stable Isotope Facility (see <http://stableisotopefacility.ucdavis.edu/13cand15n.html> for details). The long term standard deviation for the UC Davis Stable Isotope Facility's lab is 0.2 permil (‰) for ^{13}C and 0.3 permil (‰) for ^{15}N . The final delta values, $\delta^{13}\text{C}$ (e.g., Equation 1) and $\delta^{15}\text{N}$, are expressed relative to international standards V-PDB (Vienna PeeDee Belemnite) and air for carbon and nitrogen, respectively.

$$\delta^{13}\text{C} = \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \cdot 1000\text{‰} \quad (1)$$

Where R is the ratio of the heavy to light isotope within a sample or standard material.

Additional mouse parameters

Mouse body condition was estimated using a regression of body mass versus hind foot length and extracting the residuals for non-reproductive adult mice. Positive residual values indicate a mouse with a good body condition, whereas negative values indicate poor body condition (Schulte-Hostedde et al. 2001). Residuals were then compared with a one-way ANOVA.

Approximate home range areas were only estimated for 7 individuals as I required a minimum of three recapture events to estimate a polygon. I created convex hull polygons around trap locations using the Minimum Bounding Geometry tool in ESRI ArcMap (v 10.2).

Spatial gradients in food web items

To estimate capture proportions along a spatial gradient from beach to forest, I used Equation 1 (Nelson and Clark 1973) to calculate the number of individuals (excluding recaptures) captured per 100 trap-nights, controlling for our varied trapping effort at each site (number of trap-nights x number of traps) and corrected for misfired traps (e.g., traps sprung by environment or non-target species) to account for the reduction in cumulative trapping ability at the site (Beauvais and Buskirk 1999). CPUE (Equation 2) is catch per unit effort expressed as animals caught per 100-trapping-units, and A = the number of animals captured at a given distance class, P = number of trapping intervals (in our case, 1-5 nights depending on site), I = length of trapping interval (in our case, only 1 night), N = number of traps (collectively PIN = number of trapping-units), and S = total number of misfires. I calculated CPUE for each distance class at each site. For GF and IP sites, I calculated CPUE for each distance class over individual nights due to early differences in trapping effort between nights. I summed these per-night CPUE values for an overall CPUE for each distance class at each site. I then divided these values by the site total, calculating the proportion of captures at each distance class for each site.

$$CPUE = A \cdot \frac{100}{(P \cdot I \cdot N) - \frac{I \cdot S}{2}} \quad (2)$$

I estimated beach and terrestrial arthropod biomass by randomly selecting up to 30 individuals from the most common taxa (~ 95% of identified counted taxa sampled, Appendix II Table 2.6). Individuals were dried for 24-48 h (depending on body size and moisture content) at 60°C and weighed on a microbalance (model as above). Based on these weights, an average weight per individual for each taxon was obtained and used to convert the remaining count data to biomass data (Table 2.6). Some species exhibiting major body size variation within taxa were binned into two size classes representing small and large morphs and 30 individuals from each size class were sampled: spiders were binned into ≤ 3 mm and > 3 mm in length, and Staphylinid beetles and Talitrid amphipods into ≤ 5 mm and > 5 mm in length. I did not include any strictly aerial insects (e.g., adult forms of flies, bees or wasps) in our calculations as they are unlikely to be consumed by rodents. I also omitted un-identifiable or very rare individuals from which I did not obtain weights. I summed the total arthropod dry biomass in each trap, correcting for varied trap effort (1-6 nights depending on location and transect), averaged values across each distance interval (\pm standard error). These data were analyzed along a spatial gradient from the beach back ~200m into the forest to determine if there was evidence of subsidy in biomass patterns.

I summed total dry wrack biomass per quadrat and averaged across all quadrats for a measure of average biomass/m² (\pm one standard error) at each site. I compared log-transformed biomass among sites using a One-Way ANOVA.

Modelling variation among individual diets

Detailed derivation and justification for each variable using in predictive modelling:

AB_B – I obtained site-level beach arthropod biomass (AB_B) by summing the biomass of each beach trap and taking an average of the trap biomasses at each site ($n \approx 25$ traps per site). I hypothesized that the proportion of beach-dwelling arthropods (P_{BA}) in mouse diets, and the enrichment within hair, would be positively related to AB_B . Increased availability of beach arthropod prey may result in a greater representation (i.e., higher proportion) within mouse diets, and would subsequently enrich hair $\delta^{13}C$ and $\delta^{15}N$ signatures.

AB_T – I obtained site-level terrestrial arthropod biomass (AB_{T-S}) by summing the biomass of each forest trap and taking an average of the trap biomasses at each site ($n \approx 36$ traps per site). I estimated trap-level biomass (AB_{T-T}) by considering the pitfall trap at the first location of capture for each mouse, plus a buffer of all adjacent pitfall traps (*adjI*). Biomass of each trap was summed and an average of those sums was attributed as that mouse's available terrestrial arthropod prey biomass. I assume that the *adjI*-location where I caught the mouse represents an area where it spends most of its time, which allowed for a range of possible terrestrial arthropod prey biomasses to each mouse.

I hypothesized that the proportion of beach-dwelling arthropods (P_{BA}) in mouse diets, and the enrichment within hair, may be negatively or positively related to AB_T . Increased AB_T may provide an alternative, less risky prey than beach-dwelling arthropods, thus reducing the P_{BA} in diets. As well, adequate terrestrial prey may encourage mice to avoid risk associated with open beach habitat (e.g., Wolf and Batzli

2002, 2004). Conversely, increased AB_B may increase AB_T (Spiller et al. 2010). As stated above, I hypothesized that higher AB_B would increase P_{BA} . Therefore, P_{BA} and AB_T may be positively related through this ‘indirect’ effect, depending on how mice choose to forage.

However, if mice exhibit preference for animal-derived protein and consume terrestrial arthropods more readily than vegetation, AB_T and stable isotope signatures in fur may exhibit a positive relationship. As well, if terrestrial arthropods are subsidized by marine resources (and therefore increase numerically), they may also have more enriched tissues (through consumption of marine-derived foods), further adding to the positive relationship between AB_T and hair enrichment. Overall, I would expect both AB_T and (or) AB_B availability to explain a large amount of variation in mouse diets due to their regulation of protein intake (Sørensen et al. 2008) and frequent consumption of animal-derived protein in coastal systems (Thomas 1971, Drever et al. 2000).

NDVI – I estimated site- and trap-level NDVI values in a similar way as AB_T . I created a 5-m buffer around each trap location and averaged NDVI values within that buffer for a trap-level NDVI value ($NDVI_T$). I then used the same *adjl* method as above to average across adjacent NDVI buffers to apply an individual estimate for each mouse. Site-level NDVI ($NDVI_S$) was obtained by averaging all of the NDVI pixel values across the trapping grid area.

Using NDVI as a proxy for terrestrial primary productivity, I would expect that mice inhabiting a highly productive terrestrial environment may not consume as much subsidized prey, either because alternative prey is abundant (e.g., AB_T or vegetation), or to avoid risk presented by open beach areas. Therefore, the relationship between NDVI

and P_{BA} , and isotope signatures, should be negative. However, it is possible that an increase in subsidy will not only increase AB_B , but may also fertilize nearshore terrestrial vegetation. As subsidy can increase foliar growth rates (Spiller et al. 2010), this may influence site- or trap-level NDVI signatures. As stated above, higher AB_B should increase P_{BA} . Therefore, the relationship between P_{BA} and NDVI may be positive if this indirect subsidy pathway occurs. As with AB_T , the scale of this predictor may depend upon the home range and movement ability of a mouse, and could be occurring at the trap (i.e., assumed home range) or site level.

Genrep – The gender-reproductive status of mice was a categorical variable with four levels: reproductive female and males, and non-reproductive females and male. I hypothesized that reproductive individuals, particularly females, should consume more enriched prey due to energetic and nutritional reproductive requirements (Gittleman and Thompson 1988, Polis and Strong 1996, Hailey et al. 2001). Low food availability can decrease female fecundity (Merson and Kirkpatrick 1981, Gittleman and Thompson 1988), and female mice on low-protein diets mature later and are less likely to produce litters than those on high-protein diets (Vandenbergh et al. 1972). Therefore, I would expect reproductive females to have higher P_{BA} in their diets and more enriched stable isotope signatures than reproductive males, and especially non-reproductive individuals.

Table 3.4. Species composing each food group used in stable isotope analysis and MixSIAR modelling for the low subsidy region (CV).

Region	Food group	Species	Tissue	N (samples)	Individuals per sample
CV	Vegetation	Red huckleberry (<i>Vaccinium parvifolium</i>)	Berry	16	10-12
		Salal (<i>Gaultheria shallon</i>)	Berry	3	10
	Terrestrial arthropod herbivores/detritivores	Weevil (<i>Steremnius carinatus</i>)	Whole body	11	5-7
		Springtails (O. Entomobryomorpha, Poduromorpha, Symphyleona)	Whole body	4	>100
		Isopod (O. Isopoda)	Whole body	1	5-10
	Terrestrial arthropod carnivores	Centipede (<i>Scolopocryptops spinicaudus</i>)	Whole body	1	5
		Carabid ground beetles (<i>Scaphinotus angusticollis</i> , <i>Pterostichus lama</i> , <i>Zactous matthewsii</i> , <i>Cychrus tuberculatus</i>)	Whole body	42	1-10
		Spiders (F. Linyphiidae, Lycosidae)	Whole body	6	~30*
	Beach arthropod herbivores	Amphipods (<i>Traskorchestia traskiana</i> , <i>Megalorchestia columbiana</i>)	Whole body	30	10
		Spiders (F. Linyphiidae, Lycosidae)	Whole body	3	~30*
	Beach arthropod carnivores	Rove beetle (F. Staphylinidae)	Whole body	8	5
		Carabid ground beetle (<i>Bembidion</i> sp.)	Whole body	4	10
		Rove beetle (<i>Thinopinus pictus</i>)	Whole body	2	15-30
	Consumer	Mice (<i>Peromyscus keeni</i>)	Hair	30	1

* Varied depending on Family and body size

Table 3.5. Species composing each food group used in stable isotope analysis and MixSIAR modelling for the high subsidy region (GS).

Region	Food group	Species	Tissue	N (samples)	Individuals per sample
GS	Vegetation	Red huckleberry (<i>Vaccinium parvifolium</i>)	Berry	30	10-12
		Salal (<i>Gaultheria shallon</i>)	Berry	51	10
	Terrestrial arthropod herbivores/detritivores	Pacific crab apple (<i>Malus fusca</i>)	Fruit	18	3-5
		Crowberry (<i>Empetrum nigrum</i>)	Berry	6	10
	Terrestrial arthropod herbivores/detritivores	Weevil (<i>Steremnius carinatus</i>)	Whole body	8	5-7
		Springtails (O. Entomobryomorpha, Poduromorpha, Symphyleona)	Whole body	3	> 100
		Isopod (O. Isopoda)	Whole body	1	5-10
		Centipede (<i>Scolopocryptops spinicaudus</i>)	Whole body	1	5
	Terrestrial arthropod carnivores	Carabid ground beetles (<i>Scaphinotus angusticollis</i> , <i>Pterostichus lama</i> , <i>Zactous matthewsii</i> , <i>Cychrus tuberculatus</i>)	Whole body	45	1-10
		Spiders (F. Linyphiidae, Lycosidae)	Whole body	6	~30*
		Amphipods (<i>Traskorchestia traskiana</i> , <i>Megalorchestia columbiana</i>)	Whole body	20	10
	Beach arthropod herbivores	Weevils (<i>Steremnius carinatus</i>)	Whole body	11	5-7
		Ants (F. Formicidae)	Whole body	1	20-30
	Beach arthropod carnivores	Spiders (F. Linyphiidae, Lycosidae)	Whole body	9	~30*
Rove beetle (F. Staphylinidae)		Whole body	12	5	
Consumer	Rove beetle (<i>Thinopius pictus</i>)	Whole body	1	15-30	
	Mice (<i>Peromyscus keeni</i>)	Hair	24	1	

* Varied depending on Family and body size

Table 3.6. Candidate models developed with *a priori* biological hypotheses for use in a Generalized Linear Mixed Model (GLMM). Response variables are measures of individual-level proportions of beach arthropods (P_{BA}) from MixSIAR output, raw $\delta^{13}C$ and $\delta^{15}N$ signatures in mouse hair.

Response	Model	Fixed effects	Random effect
a) P_{BA}	1	Null	site
b) $\delta^{13}C$	2	AB_B	site
c) $\delta^{15}N$	3	AB_{T-S}	site
	4	AB_{T-T}	site
	5	$NDVI_S$	site
	6	$NDVI_T$	site
	7	genrep	site
	8	$AB_B + AB_{T-T}$	site
	9	$AB_B + NDVI_S$	site
	10	$AB_B + NDVI_T$	site
	11	$AB_B + \text{genrep}$	site
	12	$AB_{T-S} + \text{genrep}$	site
	13	$AB_{T-T} + \text{genrep}$	site
	14	$NDVI_S + \text{genrep}$	site
	15	$NDVI_T + \text{genrep}$	site
	16	$AB_B + AB_{T-T} + \text{genrep}$	site
	17	$AB_B + NDVI_T + \text{genrep}$	site
	18	$AB_B + NDVI_S + \text{genrep}$	site
	19	$AB_B + NDVI_T + AB_{F-T}$	site

Limitations with stable isotopes and models

While environmental variables (AB_F , AB_B , NDVI) did not predict much of the variation in mouse diets in this analysis, they are likely still important drivers over time and space. Seasonal variation in fruit and seed yield within and among years may have important influence on mouse diets. Mice switch between plant and animal tissue seasonally to capitalize on high vegetation or arthropod yields when available in the habitat. On a sub-Antarctic island beach, the importance of plant material in mouse diets spiked during summer months, but was augmented on either side by targeting emerging

arthropod prey (Smith et al, 2002). Similarly, mice inhabiting coastal New Zealand exhibit diet shifts between invertebrate life stages (e.g., larvae to adults) and tree seeds when available (Badan 1986). My window of sampling represents a very brief snap-shot and does not incorporate seasonality or even variation within a season at a site.

Diet inferences based on stable isotopes are restricted to the turnover rate of the focal tissue. The moult patterns of mice have not been studied in depth, although evidence suggests they moult in the non-breeding season, peaking in August to October but maintaining low levels of moult throughout the year (Collins 1919, 1923, Tabacaru et al. 2011). There may also be an early moult in some populations (Brown 1963), which is hypothesized to be due to early surges of resources in favourable climates (Tabacaru et al. 2011). Hair samples used in this analysis were collected in May, July, mid-August and early September. If mouse populations on the BC Central Coast only undergo one moult in the early fall, hair samples may represent up to 10 months of integrated diet. However, if an early spring moult occurred, hair samples may only represent 1-4 months of integrated diet. Wrack, vegetation and arthropods exhibit seasonal cycles of abundance, and the degree to which those food sources are incorporated in diet may depend on the lag time to incorporate prey isotopic signatures into hair. For example, amphipod reproduction peaks in early summer (April/May, Koch 1990). Depending on the specifics of the amphipod life cycle during the summer of 2016, mice sampled in early summer may not have integrated as much marine-derived prey as those sampled at the end of summer (GOS, GS-S).

Appendix II – Results

General mouse ecology

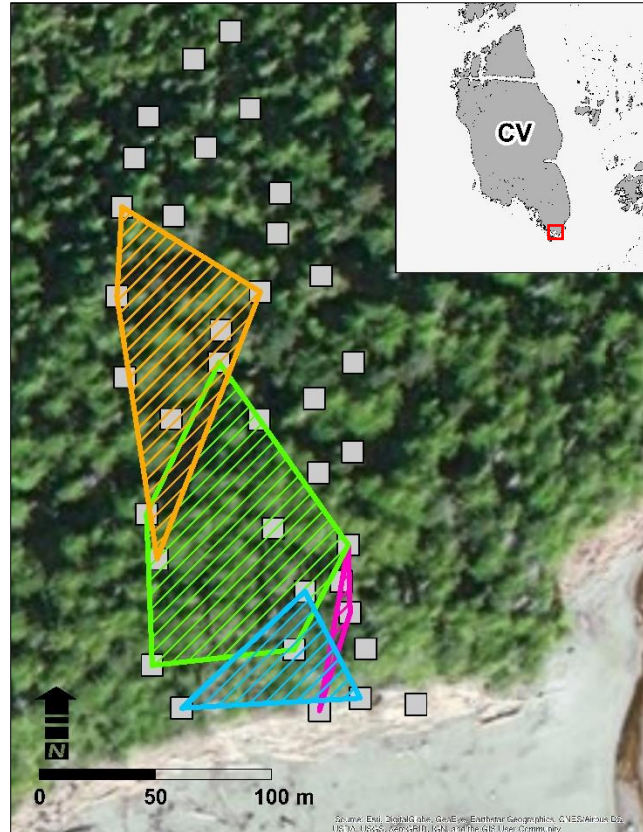


Figure 3.9. Home range estimates for four mice from Grief Bay (GF) on Calvert Island (CV). Polygons represent minimum convex polygons created in ArcMap. Estimates are from 5 nights of trapping.

There was no significant difference in mouse body condition indices (i.e., residuals) at the site ($F = 2.44$, $df = 4$, $p = 0.07$) or region levels ($F = 0.632$, $df = 1$, $p = 0.43$; Appendix II Table 3.7). Body mass was not significantly different at the region level ($F = 2.11$, $df = 1$, $p = 0.16$), but exhibited significant differences at the site level ($F = 3.53$, $df = 4$, $p = 0.02$), where GOS mice were significantly smaller than GF ($p = 0.036$) and GS-S ($p = 0.039$) mice (Table 3.7).

Table 3.7. Estimates of sex and age class proportions, masses and abundances from five sites from high (GS) and low (CV) subsidy regions. Values are means \pm standard error, and relevant sample sizes are given in parentheses, where applicable.

	CV			GS			
	GF	IP	NB	Region	GOS	GS-S	Region
Females (%)	0.30	0.27	0.42	0.33 \pm 0.04	0.44	0.29	0.37 \pm 0.08
Adults (%)	1.0	1.0	1.0	1.0	0.83	0.86	0.85 \pm 0.01
Breeding (%)	0.40	0.27	0.67	0.45 \pm 0.11	0.33	0.29	0.31 \pm 0.02
Body mass (g) ¹	29.3 \pm 1.17	27.0 \pm 1.65	25.9 \pm 2.70	27.6 \pm 1.01	23.1 \pm 1.36	30.3 \pm 1.52	25.3 \pm 1.40
Density ²	57.4 (5)	41.3 (4)	34.3 (1)	—	55.6 (2)	16.7 (1)	—
Home range (m ²) ³	1354.6 \pm 601.0 (4)	619.1 \pm 227.8 (3)	—	—	—	—	—

¹ Excludes sub-adult and reproductive individuals

² Number per 0.01 km². Calculated per 100-trap-nights using equation 2 in Nelson and Clark (1973), excluding subadults. Number of trap nights in parentheses.

³ Home ranges calculated for ≥ 3 recaptures of an individual mouse. Number of mice informing home range estimate in parentheses.

Biomass of food web components

Despite previous evidence suggesting that the Goose Archipelago received more wrack subsidy (Wickham 2018), I found that there was no significant difference in overall wrack biomass between the offshore Goose Archipelago and nearshore Calvert Island (ANOVA, $F = 0.438$, $df = 1$, $p = 0.51$; Figure 3.10A). At the site level, wrack biomass varied significantly (ANOVA, $F = 0.6.77$, $df = 4$, $p < 0.001$), ranging from 45.6 ± 18.3 (GF) to 405.1 ± 80.7 g/m² (NB; Figure 3.10A).

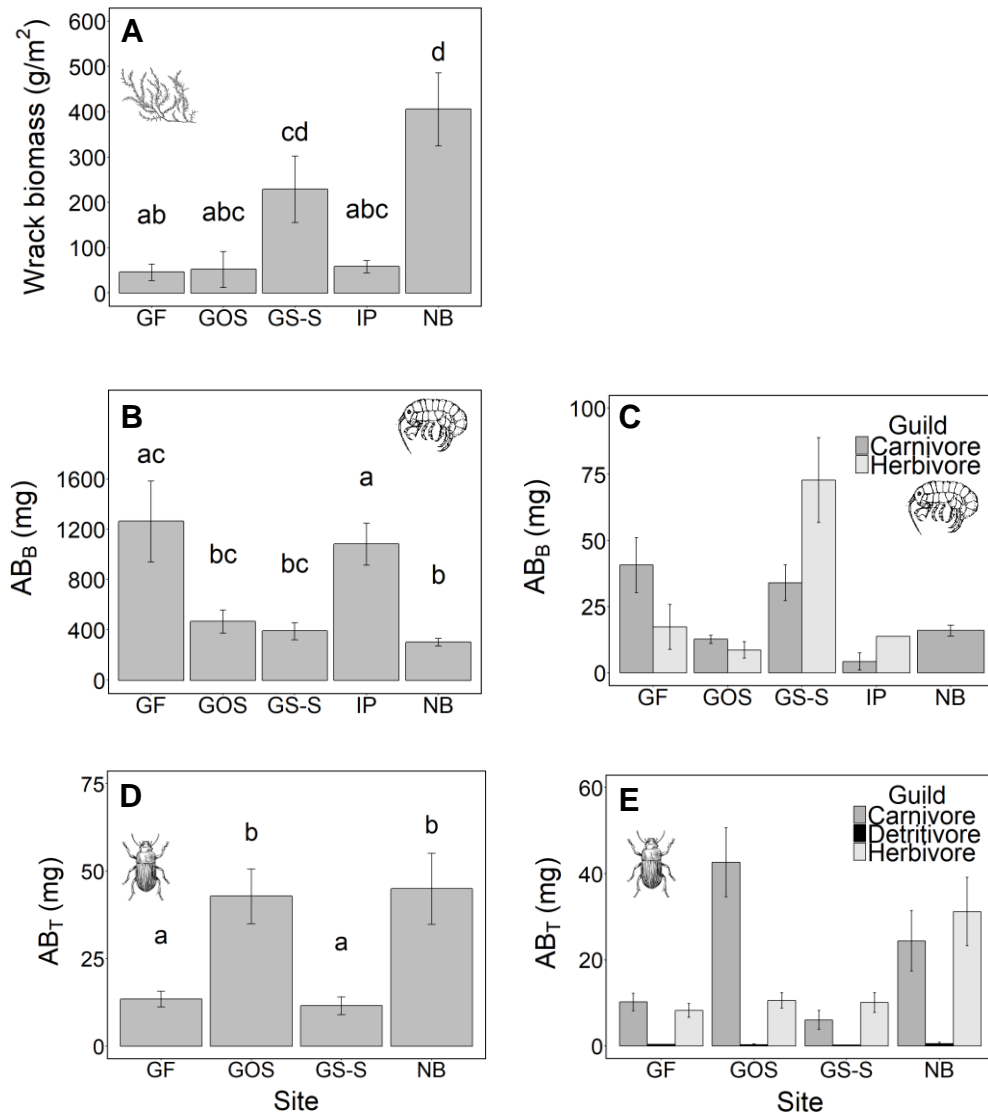


Figure 3.10. Average (± 1 SE) biomass of (A) wrack (g/m²), (B) overall beach arthropod biomass (AB_B, mg), (C) AB_B by guild, (D) overall terrestrial arthropod biomass (AB_T, mg), and (E) AB_F by guild at sites from low (CV: GF, IP, NB) and high (GS: GOS, GS-S) subsidy regions. Means with the same letters are not statistically significant.

Amphipods accounted for the majority of arthropods caught in beach pitfall traps (Appendix II Table 3.8). When analyzed individually, there were significant differences among sites (One-way ANOVA, $F = 6.92$, $df = 4$, $p < 0.001$) and between high and low subsidy regions, with low (CV) subsidy regions having significantly more amphipods than high (One-way ANOVA, $F = 9.558$, $df = 1$, $p = 0.003$; Table 3.8). When all beach arthropod taxa biomasses were pooled (AB_B), there were significant differences across sites (One-way ANOVA, $F = 4.62$, $df = 4$, $p = 0.002$; Appendix II Figure 3.10B). However, there was no significant difference between overall regions (One-Way ANOVA, $F = 3.265$, $df = 1$, $p = 0.07$; Table 3.8).

There were significant differences in terrestrial arthropod biomass (AB_T) across four sites (One-Way ANOVA, $F = 13.29$, $df = 3$, $p < 0.001$; Figure 3.10D), a pattern related to high abundance of carnivores at GOS and carnivores and herbivores at NB (Figure 3.10B). Overall, however, there was no difference in AB_T between regions (One-Way ANOVA, $F = 0.32$, $df = 1$, $p = 0.57$; Appendix II Table 3.8).

Table 3.8. Wrack, beach-dwelling arthropod biomass (AB_B) and terrestrial arthropod biomass (AB_T) (d/w) from five sites from high (GS) and low (CV) subsidy regions. Values are average \pm standard error.

	CV				GS			
	GF	IP	NB	Region	GOS	GS-S	Region	Region
Wrack biomass (g/m ²)	45.6 \pm 18.33	57.9 \pm 13.40	405.1 \pm 80.7	147.5 \pm 32.30	51.6 \pm 40.0	228.4 \pm 73.21	198.1 \pm 61.88	198.1 \pm 61.88
AB _B (mg/trap)	1261.6 \pm 321.75	1081.6 \pm 167.52	300.6 \pm 31.72	839.6 \pm 119.80	464.4 \pm 91.51	388.9 \pm 68.56	427.5 \pm 57.18	427.5 \pm 57.18
Amphipod (%) ¹	89.8 \pm 4.49	95.3 \pm 4.15	83.8 \pm 5.83		90.5 \pm 4.43	73.2 \pm 3.52		
AB _T (mg/trap)	13.4 \pm 2.24	–	45.0 \pm 10.2	29.0 \pm 5.45	42.8 \pm 7.83	11.5 \pm 2.55	27.2 \pm 4.53	27.2 \pm 4.53

¹ Of beach pitfall traps

$\delta^{15}\text{N}$ in mouse hair was also depleted moving away from the beach, although also less pronounced, with an overall depletion of 2.18‰ that was not significant (Wilcoxon test, $W = 15$, $p = 0.93$; Appendix II Figure 3.11A). $\delta^{13}\text{C}$ signatures in mouse hair were slightly enriched from the beach back into the forest, with an overall enrichment of 0.18‰ which was also not a significant difference (Wilcoxon test, $W = 19$, $p = 0.5$; Figure 3.11B).

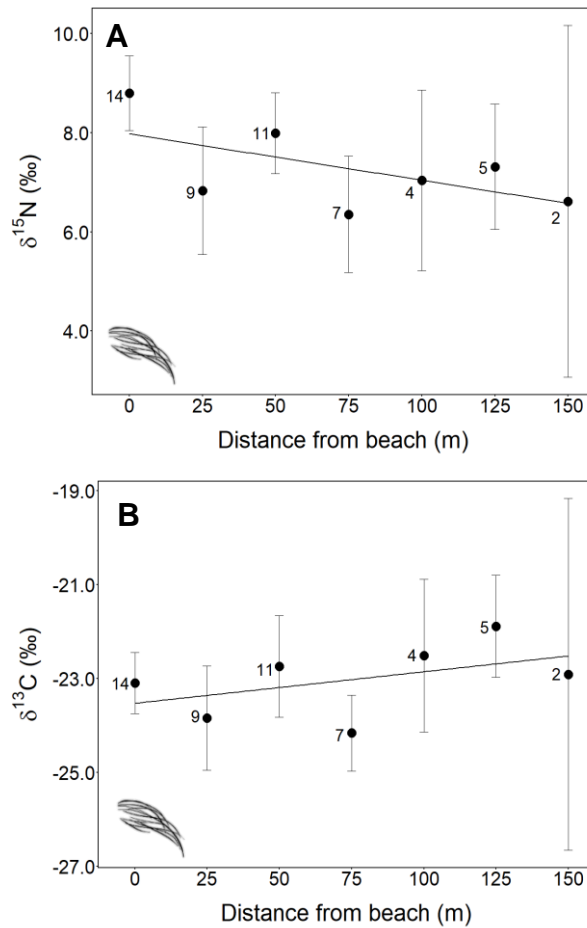


Figure 3.11. Spatial patterns in mean (\pm SE) (A) $\delta^{15}\text{N}$ and (B) $\delta^{13}\text{C}$ in mice hair from the beach into the forest. Numbers indicate sample sizes per data point.

Regional differences in stable isotopes of food items

Beach arthropod herbivores and carnivores were not significantly different in $\delta^{15}\text{N}$ signatures between regions, but both guilds were significantly more enriched in $\delta^{13}\text{C}$ at GS (Appendix Table 3.9). Terrestrial arthropod carnivores and vegetation were both significantly more enriched in $\delta^{15}\text{N}$ at GS, but the terrestrial arthropod carnivores were significantly depleted in $\delta^{13}\text{C}$ at GS (Table 3.9). Terrestrial arthropod herbivores were not significantly different in $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ between regions (Table 3.9). Mice from the high subsidy region (GS) were significantly more enriched in $\delta^{15}\text{N}$ than those from the lower subsidy region (CV), but exhibited no significant differences in $\delta^{13}\text{C}$ signatures (Table 3.9).

Table 3.9. Wilcoxon (Mann-Whitney) tests for regional comparisons of food items. *W*-statistic, *p*-values, average (\pm one SE) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values with samples sizes in parentheses. No trophic fractionation applied to food items. Bolded values indicate the more enriched region in pairwise comparisons, and the asterisk indicates significant differences

Food group	$\delta^{13}\text{C}$				$\delta^{15}\text{N}$			
	CV	GS	W	<i>p</i>	CV	GS	W	<i>p</i>
Mice (<i>P. keeni</i>)	-23.58 \pm 0.51 (31)	-22.56 \pm 0.54 (25)	308	0.26	6.37 \pm 0.45 (31)	8.88 \pm 0.64 (25)	220	0.009*
Beach arthropod herbivores	-16.63 \pm 0.18 (30)	-15.04 \pm 0.45 (32)	309.5	0.02*	9.40 \pm 0.09 (30)	9.62 \pm 0.10 (32)	356	0.08
Beach arthropod carnivores	-18.15 \pm 0.37 (17)	-15.20 \pm 0.34 (22)	49	< 0.001*	12.32 \pm 0.34 (17)	12.67 \pm 0.14 (22)	180	0.86
Forest arthropod herbivores	-26.71 \pm 0.20 (27)	-26.18 \pm 0.15 (16)	143	0.07	-2.55 \pm 0.50 (27)	-0.89 \pm 0.88 (16)	145	0.08
Forest arthropod carnivores	-25.93 \pm 0.10 (49)	-26.78 \pm 0.18 (52)	1853.5	< 0.001*	2.58 \pm 0.19 (49)	3.88 \pm 0.31 (52)	850	0.004*
Vegetation ¹	-31.22 \pm 0.28 (19)	-30.54 \pm 0.20 (81)	594.5	0.13	-5.76 \pm 0.52 (19)	-2.66 \pm 0.44 (81)	360	< 0.001*

¹ Only includes salal and huckleberry as these were the only two species collected in both regions

Table 3.10. Top models ($\geq 95\%$ model weight) predicting variation in $\delta^{13}\text{C}$ signatures in hair. Genrep: gender-reproductive status, AB_T : terrestrial arthropod biomass (s: site, T: trap-level), AB_B : beach arthropod biomass, and NDVI (s: site, T: trap-level).

Response	Models	df	AICc	ΔAICc	AICc_w
$\delta^{13}\text{C}$	genrep + AB_B + NDVI_S	8	206.63	0.00	0.22
	genrep + NDVI_S	7	206.90	0.27	0.19
	genrep + AB_{T-S}	7	207.11	0.48	0.17
	genrep + AB_B	7	207.43	0.80	0.15
	genrep	6	208.19	1.56	0.10
	genrep + NDVI_S + AB_{T-T}	8	208.35	1.72	0.09
	NDVI_T + genrep + AB_B	8	208.90	2.27	0.07

Table 3.11. Full model-averaged parameter estimates and RVI scores for factors predicting $\delta^{13}\text{C}$ mouse hair signatures. Genrep: gender-reproductive status (where a double symbol indicates reproductive classes), AB_T : terrestrial arthropod biomass (s: site, T: trap-level), AB_B : beach arthropod biomass, and NDVI (s: site, T: trap-level).

Response	Predictor variable	Parameter estimate	SE	RVI
$\delta^{13}\text{C}$	Genrep			0.99
	♂	2.84	0.95	
	♂♂	3.64	0.97	
	♀♀	1.11	1.19	
	NDVI_S	0.65	1.40	0.50
	AB_B	0.58	1.44	0.44
	AB_{T-S}	-0.28	0.92	0.17
	AB_{T-T}	-0.11	0.47	0.09
NDVI_T	0.02	0.22	0.07	

Table 3.12. Top models ($\geq 95\%$ model weight) predicting variation in $\delta^{15}\text{N}$ signatures in hair. Genrep: gender-reproductive status, AB_T : terrestrial arthropod biomass (s: site, T: trap-level), AB_B : beach arthropod biomass, and NDVI (s: site, T: trap-level).

Response	Models	df	AICc	ΔAICc	AICc_w
$\delta^{15}\text{N}$	genrep + AB_B + NDVI_S	8	218.68	0.00	0.31
	genrep + NDVI_S	7	219.94	1.26	0.17
	genrep + AB_B + AB_{T-T}	8	221.11	1.43	0.15
	AB_B + NDVI_S	5	221.12	2.44	0.09
	genrep + AB_{T-S}	7	221.58	2.90	0.07
	genrep + AB_B	7	222.41	3.73	0.05
	NDVI_T + genrep + AB_B	8	222.77	4.09	0.04
	NDVI_S	4	223.17	4.49	0.03
	genrep	6	223.23	4.55	0.03
	AB_B + AB_{T-T}	5	223.42	4.74	0.03
NDVI_T + genrep	7	223.55	4.87	0.03	

Table 3.13. Full model-averaged parameter estimates and RVI scores for factors predicting $\delta^{15}\text{N}$ mouse hair signatures. Genrep: gender-reproductive status (where a double symbol indicates reproductive classes), AB_T : terrestrial arthropod biomass (s: site, T: trap-level), AB_B : beach arthropod biomass, and NDVI (s: site, T: trap-level).

Response	Predictor variable	Parameter estimate	SE	RVI
$\delta^{15}\text{N}$	Genrep			0.81
	♂	1.64	1.64	
	♂♂	2.03	2.02	
	♀♀	0.38	0.38	
	AB_B	-0.70	2.02	0.67
	NDVI_S	2.07	2.10	0.60
	AB_{T-T}	0.53	1.09	0.18
	AB_{T-S}	-0.15	0.81	0.07
	NDVI_T	-0.06	0.32	0.07

4. General discussion

The flow of nutrients from the marine to terrestrial environment represents an important source of food and nutrients for many coastal organisms. This is especially apparent on islands where perimeter-area ratios are high and subsidies can be supplied continually (Polis and Hurd 1996, Polis et al. 1997). These subsidies may even interact with traditional island biogeography theory to explain patterns of species richness on oceanic islands (Anderson and Wait 2001). In Chapter 2 I demonstrated that, while insular mammal species richness was significantly correlated with island area, the quantity of wrack biomass also explained richness patterns. Despite these patterns, the probability of island use by both mink and river otter is unaffected by any island-level covariates (at least, those tested here). The probability of island use by small mammals is affected by the connectivity between islands, where small mammals are more likely to use islands than they are closer to other neighbouring islands. It is possible this may represent differences in colonizing abilities of mammals based on body size, where larger mammals (i.e., mink and river otter) are less limited by water barriers than smaller animals (Russell et al. 2004).

The results from Chapter 2 will be used within the larger *100 Islands* project to investigate relationships between biodiversity (including terrestrial invertebrates, plants, and songbirds) and marine subsidy, in particular on the small, outer islands of the Central Coast. As such, in Chapter 2 I also presented statistical analyses of the reliability of the mammal incidence data for future use. These data can not only be useful for *100 Islands*, but also demonstrate how occupancy modelling in particular can be valuable for

analyzing large datasets collected over several years with multiple sampling crews and variable effort.

In Chapter 3, I looked closer at the site-specific factors influencing marine subsidy use by terrestrial consumers. Using omnivorous Keen's mice (*Peromyscus keeni*) as a focal species, as well as its food web, I ultimately determined that mice are subsidized both directly and indirectly by marine resources. One-third of their diets are composed of beach-dwelling arthropods, and the remainder is sourced from terrestrial foods that are subsidized through consumption or fertilization. Furthermore, spatial patterns in both mice and terrestrial arthropods reflected spatial patterns in enrichment, indicating that the beach-forest fringe habitat supports high abundances of enriched terrestrial organisms. Within these productive habitats, reproductive male mice consume up to twice the marine-derived prey that females do, which may suggest males hold territories that allow them to access these resources more readily, but they may also have to trade-off predation risk with subsidy reward (Wolf and Batzli 2002, 2004).

Collectively, these chapters demonstrate that insular mammalian richness, and the interactions between physical island characteristics and marine subsidy, may be more complex than previously considered due to heterogeneity within the recipient environment (e.g., biomass of available prey) and intrapopulation variation. In future, this work could be expanded upon in several ways. In terms of the overall mammalian richness trends, increasing sampling to obtain more observations for rare species (e.g., deer and wolf) would allow for the creation of occupancy models. In particular, multi-species models could be constructed to investigate whether patterns of island use are driven more by

species interactions (e.g., competition, predation or facilitation) than by physical island characteristics (Abbott 1983).

Experimental field work manipulating the quantity of marine subsidy (e.g., wrack) and monitoring the numerical and stable isotope responses of consumers and plants would help to identify specific mechanisms for subsidy transfer within the terrestrial environment. In the context of the mouse subsidy work, investigating whether specific factors are limiting marine resource consumption (e.g., predation or competition) would provide important insights into how coastal rodent diets are regulated. As well, expanding to include multiple sites would help to refine the modelling process. It is likely that site-level factors are more important, or equally as important, as individual ones, but my low sample size of 4 sites limited my ability to investigate site-level impacts on diets.

Documenting overall insular mammal species richness, modelling the importance of island-level covariations on species and group-specific island use, and presenting in detail how one coastal omnivore utilizes marine resources has provided considerable insight into the relationship between the marine and terrestrial realm for coastal mammals.

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