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Predators in natural fragments: foraging ecology of wolves in British Columbia's central and north coast archipelago

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ABSTRACT

Aim Predator–prey dynamics in fragmented areas may be influenced by spatial features of the landscape. Although little is known about these processes, an increasingly fragmented planet underscores the urgency to predict its consequences. Accordingly, our aim was to examine foraging behaviour of an apex mammalian predator, the wolf (*Canis lupus*), in an archipelago environment.

Location Mainland and adjacent archipelago of British Columbia, Canada; a largely pristine and naturally fragmented landscape with islands of variable size and isolation.

Methods We sampled 30 mainland watersheds and 29 islands for wolf faeces in summers 2000 and 2001 and identified prey remains. We examined broad geographical patterns and detailed biogeographical variables (area and isolation metrics) as they relate to prey consumed. For island data, we used Akaike Information Criteria to guide generalized linear regression model selection to predict probability of black-tailed deer (main prey; *Odocoileus hemionus*) in faeces.

Results Black-tailed deer was the most common item in occurrence per faeces (63%) and occurrence per item (53%) indices, representing about 63% of mammalian biomass. Wolves consumed more deer on islands near the mainland (65% occurrence per item) than on the mainland (39%) and outer islands (45%), where other ungulates (mainland only) and small mammals replaced deer. On islands, the probability of detecting deer was influenced primarily by island distance to mainland (not by area or inter-landmass distance), suggesting limited recolonization by deer from source populations as a causal mechanism.

Main conclusions Although sampling was limited in time, consistent patterns among islands suggest that population dynamics in isolated fragments are less stable and can result in depletion of prey. This may have important implications in understanding predator–prey communities in isolation, debate regarding wolf–deer systems and logging in temperate rain forests, and reserve design.

Keywords

Archipelago, British Columbia, black-tailed deer, *Canis lupus*, conservation, foraging, fragmentation, islands, *Odocoileus hemionus*, wolf.

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INTRODUCTION

Islands have been considered natural laboratories to study evolutionary and ecological process (Gorman, 1979; Williamson, 1981). Investigations of oceanic archipelagos have revealed

how island communities are related to area, isolation and other island characteristics (e.g. MacArthur & Wilson, 1967; Abbott, 1974; Kadmon & Pulliam, 1993; Conroy *et al.*, 1999). Biogeographical features, however, may also exert influence at the population level, including the mediation of predator–prey

dynamics on islands or in other fragmented systems (Kareiva, 1990; Kareiva & Wennergren, 1995; Dolman & Sutherland, 1997). A predator's niche breadth can be predicted by the diversity and abundance of potential prey species (MacArthur & Pianka, 1966), which may differ among islands. The limitations imposed by island geography, for example, may restrict prey species available to predators. For some consumers, however, foraging constraints on small or isolated oceanic islands may be mitigated by nutrient subsidies from the ocean, as recent investigations have revealed the coupled nature of marine-terrestrial ecosystems (Polis & Hurd, 1995; Rose & Polis, 1998; Reimchen, 2000).

The amplitude of predator and prey fluctuations reflect ecological conditions (Ricklefs, 1990), which may be unique in archipelagos or in other systems fragmented naturally or by humans. Predator-prey dynamics in isolation may be volatile, resulting in large amplitudes of predator and prey, or the extirpation of predator, prey, or both (Taylor, 1984). For example, the wolf-moose (*Canis lupus* – *Alces alces*) system on 540 km² Isle Royale, Michigan, is separated by 36 km to the mainland. There, wolves and moose have experienced extreme fluctuations in abundance that is at least partially associated with their interaction (Peterson *et al.*, 1984; Peterson & Page, 1988; Vucetich & Peterson, in press). Similar process has also been examined with smaller taxa in experimental designs. Populations of an herbivorous spider mite (*Tetranychus urticae*) and a predatory mite (*Phytoseiulus persimilis*) are highly unstable on isolated bean plants (*Phaseolus lunatus*) and can ultimately result in extinction of both (McCauley *et al.*, 2000).

Knowledge about predator-prey dynamics in patchy landscapes is valuable because the planet is becoming increasingly fragmented by human activities (Saunders *et al.*, 1991; Fahrig, 1997, 2003). Moreover, predators are more likely to decline or become extinct in fragments (Woodroffe & Ginsberg, 1998), possibly resulting in mesopredator release and other ecosystem-wide consequences (Crooks & Soulé, 1999; Terborgh *et al.*, 2001). Conversely, even the effects of native predators on endangered prey can be severe in fragmented environments (Schneider, 2001). Consequently, archipelagos may provide model systems in which to predict the effects of size and isolation on predator-prey dynamics.

The temperate rain forest archipelago of British Columbia (BC) is an ideal system in which to address the influence of area and isolation of fragments on predator-prey systems. This remote and nearly pristine region is naturally fragmented, comprised of dozens of islands < 0.1 to > 13 km apart (Fig. 1). Here, the wolf-black-tailed deer (*Odocoileus hemionus*) association forms the dominant mammalian predator-prey system, in which both animals can occupy all islands, at least ephemerally (Darimont & Paquet, 2000, 2002). Herein, we examine spatial variability of resource use during spring and summer by examining wolf faeces from BC's central and north coast mainland and 29 islands of the adjacent archipelago. Theory of predator-prey systems in fragments suggests that area and isolation effects can strongly influence population

dynamics, including processes associated with the depletion of prey (Kareiva, 1990; Kareiva & Wennergren, 1995; Dolman & Sutherland, 1997; McCauley *et al.*, 2000). Moreover, the marine-terrestrial interface and the heterogeneous landscape of our study area offer a broad potential niche to wolves. Accordingly, on smaller and/or more isolated islands, we predicted a departure from a diet dominated by their main prey (deer) to one that includes considerable use of alternative resources. Our objectives herein are to identify prey species consumed by wolves of British Columbia's archipelago during spring and summer and to examine variability in wolf foraging behaviour as it relates to area and isolation of islands.

METHODS

Study area

We collected wolf faeces on BC's coast between the Kshwan Valley (55°37' N, 129°48' W) in the north and the Koeve River (51°46' N, 127°53' W) in the south (Fig. 1). This large, nearly roadless, and mostly unsettled region is bounded by the Coast Mountain range and Pacific Ocean to the east and west, respectively. Most of the low elevation forest is within the Coastal Western Hemlock biogeoclimatic zone (Pojar & Mackinnon, 1994). Habitat heterogeneity in these temperate rain forests corresponds to landscape variability, which includes the following general regions: mountainous mainland, topographically complex inner islands, and flatter outer islands. Island sizes range from 5.0 km² (Moore) to 2295 km² (Princess Royal), distances to mainland 250 m to 13.05 km, and distances among landmasses 0.05–7.25 km (Fig. 1).

Potential prey base is diverse, including black-tailed deer, moose, mountain goat (*Oreamnos americanus*), beaver (*Castor canadensis*), black bear (*Ursus americanus*), river otter (*Lontra canadensis*), plus smaller mustelids, rodents and birds. Five species of spawning salmonids (*Onchorynchus* spp.), crustaceans, molluscs and marine mammals are also available to wolves (Darimont & Paquet, 2000, 2002), although salmon were not yet spawning widely when sampling occurred.

Faecal collection

During June and July 2000, and June and August 2001, we collected faeces in 30 mainland watersheds and on 29 islands (typically one to two sites per island). Sampling sites were selected non-randomly but were well distributed throughout the study area (Fig. 1). At each location, we surveyed beaches, estuaries and forests of the beach fringe, often on wildlife trails. We also surveyed logging roads when encountered, circumnavigated beaver ponds, and walked forest ridgelines. Surveys rarely extended > 5 km inland.

We stored faeces in plastic bags and froze them until analysis at the University of Victoria. Faeces can decompose rapidly in this wet environment (Wallmo *et al.*, 1962; C.T. Darimont unpublished data). Therefore, we assumed the samples represented late spring and summer diets of wolves.

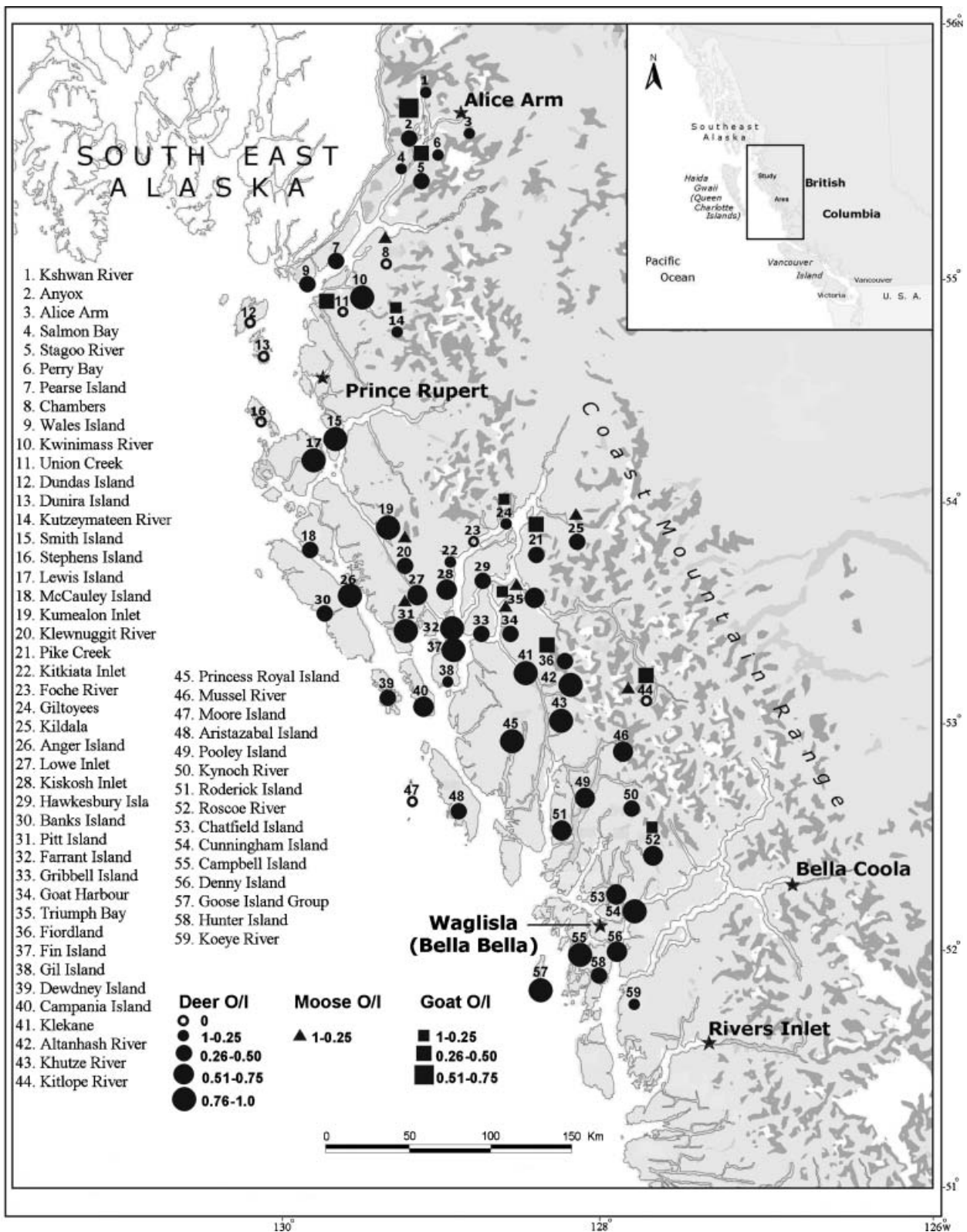


Figure 1 Study area where wolf (*Canis lupus*) faeces were collected in coastal British Columbia, Canada, during summers 2000 and 2001. Fifty-nine sampled islands and mainland watersheds numbered. Sampling extended from the Kshwan River (1) in the north to the Koye River (59) in the south. Also shown are symbols denoting occurrence per item data for ungulates consumed (deer, *Odocoileus hemionus*; moose, *Alces alces* and goat, *Oreamnos americanus*).

Prey item identification and reporting

Identification of prey followed Ciucci *et al.* (1996) and Kohira & Rexstad (1997). Samples were autoclaved, then soaked and rinsed in a 1 mm mesh sieve until only hair, bone fragments and other macroscopic components remained. Mammalian prey was identified by comparing hair in faeces with voucher samples and use of dichotomous keys and dissecting microscope (magnification 20–40×; Mathiak, 1938; Mayer, 1952; Stains, 1958). When identification was uncertain ($n = 60$ scats), scale imprints from a few guard hairs melted in acetate were examined using a compound microscope (magnification 40–400×). Non-mammal prey, such as fish, bird, and marine invertebrates, were identified by bones, teeth, feathers and shell fragments. Birds and small rodents (i.e. rodents smaller than beaver) were not identified further than class and order respectively. To eliminate inter-observer bias, only one person identified prey remains (MP) and only after a lengthy training period (c. 40 h). We estimated precision by re-sampling approximately 10% of samples ($n = 59$), in which prey remains were consistently identified in 58 cases (98%).

We report occurrence per faeces (O/F) index for comparison with published literature but use the occurrence per item (O/I) index in statistical tests as the former can be problematic because it exceeds unity when summed (Kohira & Rexstad, 1997). These two metrics are important when faeces often contain more than one item (see Results). O/F is the frequency by which an item occurs in faecal samples, whereas O/I is the item's frequency among all items identified in all faeces combined. We also estimated mammalian biomass consumed using a regression equation estimated by Weaver (1993): $Y = 0.439 + 0.008X$, where Y is the estimated biomass of prey consumed per faecal sample and X is the mass of prey. Although masses may differ among age and sex classes, and wolves may kill unequal ratios of these classes, we used mean masses of adults reported in Cowen & Guiguet (1975) and assumed a 1 : 1 sex ratio. For deer, however, we distinguished between adults and fawns for biomass calculations using diagnostic hair diameter and colour characters, which are useful until the autumn (Scott, 1979). By necessity, biomass estimates excluded non-mammalian prey ($n = 124$ of 705 items identified).

Statistical analyses

General geographical patterns in foraging ecology

We tested for general geographical patterns in foraging ecology among three areas that are associated with general habitat differences: mainland, inner islands, and outer islands. We defined inner islands as those directly adjacent to the mainland and outer islands as those that are not, irrespective of distance to mainland. This classification is consistent with mainland, southern inner island, and southern outer island biogeographical sub-regions defined in southeast Alaska, which are based on presence of endemic species and unique combinations of

native taxa (MacDonald & Cook, 1996). We compared O/I indices for deer, other ungulates (moose, goat), and small mammals among these areas using ANOVA or Kruskal–Wallis tests. We repeated these tests with indices relating to the proportion of total biomass represented by these taxa.

Examining area and isolation effects on islands

General geographical patterns, although informative, cannot adequately address the influence of area and isolation on predator–prey dynamics. For example, an inner island, next to the mainland, may be more isolated from other landmasses by water barriers compared with a collection of nearby outer islands. Thus we examined how biogeographical parameters, area (AREA), distance to mainland (MDIST), and inter-landmass distance (LDIST) affected the probability of deer occurring in faecal remains on islands. We used these two isolation metrics to disentangle the possible influences of distance from the mainland, which may be the ultimate source for prey colonization, and distance to other landmasses, which likely provide the most available sources for prey colonization.

We measured MDIST as the shortest island-to-mainland distance or sum of island-to-island distances to mainland excluding distances across islands, whichever was shorter (Conroy *et al.*, 1999). LDIST was the minimum distance to landmasses $> 75 \text{ km}^2$ (either mainland or island), roughly the size of Coronation Island, in nearby southeast Alaska, on which a small population of wolves existed for 8 years (Klein, 1996). All geographical parameters were estimated using marine charts (Canadian Hydrographic Service, Ottawa, Ontario) and Geographic Information Systems (Darimont & Paquet, 2002).

We formed exploratory *a priori* hypotheses to explain how these biogeographical features would affect the probability of deer occurring in wolf faeces on islands, which were based on our knowledge of the area and ecological theory described above. From these hypotheses, we developed a set of candidate generalized linear regression models (binary logistic form). These were restricted to combinations of one to three of the identified (and untransformed) parameters and two-way interaction terms. We considered islands as the experimental unit, with the number of faeces containing deer as events and the total number of faeces as trials. A Hosmer–Lemeshow goodness-of-fit statistic based on the global model showed the data did not depart from a logistic-regression model ($P = 0.475$). Multicollinearity diagnostics suggested only weak interdependencies among predictor variables (Variance Inflation Factors range: 1.076–1.709). For each model, we calculated Akaike Information Criteria, adjusted for small sample sizes (AIC_c), following the formula: $AIC_c = -2(\log \text{likelihood}) + 2K + 2K(K + 1)/(n - K - 1)$, where K is the number of parameters and n the number of sampled islands. We then evaluated ΔAIC_c to select best approximating model(s) and make appropriate inference, using $\Delta AIC_c < 2$ to describe the top model set (offering substantial level of empirical support). Finally, we summed Akaike weights (ω_i) across the top model

set for each variable to rank them by importance (Burnham & Anderson, 1998; Anderson *et al.*, 2001). Tests were performed using SPSS 11.0 (SPSS Inc., Chicago, IL, USA) and SAS 8 (SAS Inc., Cary, NC, USA).

RESULTS

Coastal wolves showed a wide dietary niche across the heterogeneous landscape (Table 1). We collected a mean of 8.77 samples at mainland sites (range 1–36; SD = 1.65; $n = 263$) and 11.45 at island sites (range 1–64; SD = 3.24; $n = 332$). Of 705 food items identified, black-tailed deer was the most common item in both occurrence/faeces and occurrence/item indices, followed by salmon, mountain goat, bird, mustelids, intertidal organisms, black bear, beaver, mink, moose and small mammals (Table 1). Biomass estimates demonstrated a different order of occurrence, with ungulates (deer, goat, moose) representing a combined 82.3% of mammal biomass consumed (Table 1). Grizzly bear (*Ursus arctos*), fisher (*Martes pennanti*), harbour seal (*Phoca vitulina*) and wolf each occurred once. We could not identify six items.

Foraging patterns of wolves differed among areas. Fifteen species occurred in mainland samples and 13 in island samples. Mountain goat, grizzly bear and fisher were found exclusively at mainland locations, whereas the sample containing seal was collected on an island. Goat remains were restricted to areas in or near rocky inlets, whereas moose remains, although near inlets, had a greater distribution, including on one island (Fig. 1).

Differences we observed in detection of deer and non-deer prey provide evidence of major changes in predation regime among geographical areas. Generally, deer dominated the diet on inner islands whereas other ungulates (goat, moose) and small mammals collectively occurred approximately as often as deer at mainland and outer island sites. Differences in occurrence/item among mainland, island, and outer island sites for deer approached significance (ANOVA; $F_{2,56} = 2.967$, $P = 0.060$) and was highest on inner islands, but differed little between mainland and outer islands (Fig. 2a). Similarly, proportion of total mammalian biomass represented by deer also was highest on inner islands and varied little between mainland and outer islands sites (ANOVA; $F_{2,56} = 6.972$, $P = 0.002$; Fig. 2b). Other ungulates (moose, goat) represented significantly higher occurrence/item (Kruskal–Wallis H -test; $\chi^2 = 14.961$; $P = 0.001$; Fig. 2a) and proportion of mammalian biomass (Kruskal–Wallis H -test; $\chi^2 = 14.885$; $P = 0.001$; Fig. 2b) on mainland sites compared with extremely low or nil values on inner and outer islands respectively. In place of deer, wolves also foraged on small mammals, which generally occurred more frequently at mainland and outer island sites compared with inner islands (Fig. 2a,b), but this difference was not significant in occurrence/item (Kruskal–Wallis H -test; $\chi^2 = 1.775$; $P = 0.412$) or proportion of total mammalian biomass (Kruskal–Wallis H -test; $\chi^2 = 1.120$; $P = 0.571$).

Model selection and multimodel inference suggest that among island sites, isolation was more important than area in predicting departure from a diet dominated by deer.

Table 1 Prey items identified in 595 wolf (*Canis lupus*) faeces collected summers 2000 and 2001 on the mainland and archipelago of coastal British Columbia

Prey taxa	Mainland sites			Island sites			All sites combined			Biomass (%)
	<i>n</i>	O/F (%)	O/I (%)	<i>n</i>	O/F (%)	O/I (%)	<i>n</i>	O/F (%)	O/I (%)	
<i>Odocoileus hemionus</i> (deer)	124	47.1	39.5	250	75.3	63.9	374	62.7	53.0	64.6
<i>Onchorynchus</i> spp. (salmon)	21	8.0	6.7	25	7.5	6.4	46	7.7	6.5	N/A
<i>Oreamnos americanus</i> (goat)	37	14.1	11.8	0	0.0	0.0	37	6.2	5.3	9.1
Aves (birds)	15	5.7	4.8	22	6.6	5.6	37	6.2	5.3	N/A
<i>Martes americana</i> (marten)	20	7.6	6.4	14	4.2	3.6	34	5.7	4.8	2.9
<i>Mustela erminea</i> (ermine)	25	9.5	8.0	8	2.4	2.1	33	5.5	4.7	2.7
<i>Lontra canadensis</i> (otter)	10	3.8	3.2	15	4.5	3.8	25	4.2	3.6	2.1
Intertidal organisms	13	4.9	4.1	12	3.6	3.1	25	4.2	3.6	N/A
<i>Ursus americanus</i> (bear)	9	3.4	2.9	9	2.7	2.3	18	3.0	2.6	5.8
<i>Castor canadensis</i> (beaver)	6	2.3	1.9	10	3.0	3.0	16	2.7	2.3	2.1
<i>Mustela vison</i> (mink)	4	1.5	1.3	12	3.6	3.1	16	2.7	2.3	1.3
<i>Alces alces</i> (moose)	11	4.2	3.5	1	0.0	0.0	12	2.0	1.7	8.6
Small rodents	5	1.9	1.6	3	0.9	0.8	8	1.3	1.1	0.7
Vegetation	9	3.4	2.9	5	1.5	1.3	14	2.4	2.2	N/A
Other*	5	1.9	1.6	5	1.5	1.3	10	1.7	1.4	N/A
Total	314	119	100	391	117	100	705	118	100	100

*Other represents single occurrence of brown bear (*Ursus arctos*), wolf, seal (*Phoca vitulina*) and fisher (*Martes pennanti*), plus six unidentified remains.

n, Number of items; O/F, occurrence/faeces; O/I, occurrence/item.

Biomass estimates are proportion of total mammalian biomass. Taxa organised by decreasing O/F and O/I for all sites combined.

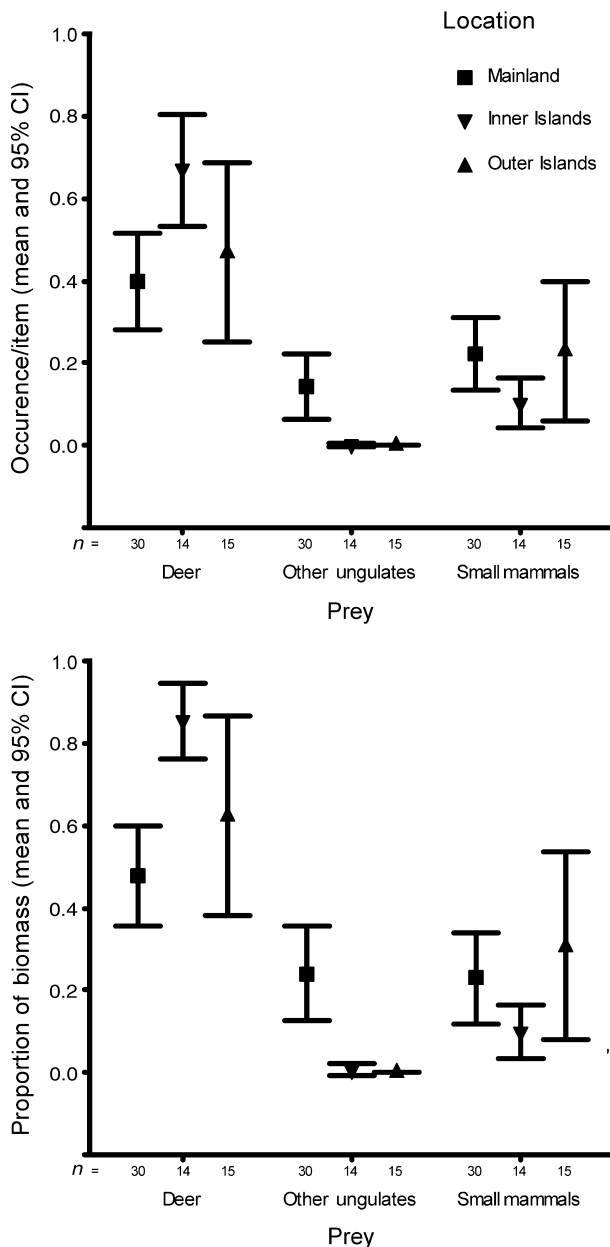


Figure 2 (a) Mean occurrence per item and (b) mean proportion of total mammalian biomass of prey detected in 595 wolf (*Canis lupus*) faeces from 59 sampling locations on the islands and mainland coast of British Columbia, Canada, summers 2000 and 2001. ‘Small mammals’ included river otter (*Lontra canadensis*), marten (*Martes americanus*), ermine (*Mustela ermina*), mink (*Mustela vison*), and rodent (*Rodentia* spp.). ‘Other ungulates’ were goat (*Oreamnos americanus*) and moose (*Alces alces*). Deer are *Odocoileus hemionus*.

Specifically, the probability of wolves foraging on deer declined primarily with increased island isolation from the mainland, but less so with isolation from other landmasses and smaller island area (Table 2; Fig. 3). All five models in the top model set (0–2 Δ AIC_c) contained MDIST. Considerable ambiguity,

however, existed among top models, which had similar Akaike weights ($\omega_{i=1 \text{ to } 5} = 0.21$ to 0.08; Table 2). Moreover, these top models explained a similar proportion of the variance (Nagelkerke R^2 range = 0.218–0.242; note that pseudo R^2 values for logistic regression are lower than would be expected in a linear model; Table 2). In cases when the data do not strongly support a single best model, however, the one with fewest parameters is often worth most consideration, following the rule of parsimony (Burnham & Anderson, 1998). Accordingly, we consider model 4, containing only the intercept and MDIST, as a preferred model (Table 2).

The top model set can still make robust multimodel inference (Burnham & Anderson, 1998); summing the Akaike weights across top models ranked the variable MDIST ($\Sigma\omega_i = 0.74$) higher than LDIST and AREA ($\Sigma\omega_i = 0.35$ and 0.27) by factors of 2.11 and 2.74 respectively. Moreover, the strength of coefficients associated with isolation metrics was much higher than those for area, which approached zero (Table 2). Interaction terms MDIST \times LDIST ($\Sigma\omega_i = 0.20$) and AREA \times MDIST ($\Sigma\omega_i = 0.20$) were less important.

DISCUSSION

Islands provide ideal model systems for studying predator–prey interactions (e.g. Peterson *et al.*, 1984). Often, however, isolated islands lack predators and even on less isolated islands mammalian carnivores are relatively rare (Williamson, 1981; Alcover & McMinn, 1994). Consequently, our knowledge of predator–prey dynamics in isolated systems is limited. Moreover, our ecological knowledge of coastal temperate rain forests of North America is in its infancy (MacDonald & Cook, 1996). Herein we examine the foraging ecology of BC’s coastal wolves and provide additional insight into predator–prey dynamics in fragmented landscapes. Specifically, we partitioned the variability we observed to spatial features of the landscape, both on a gross geographical scale (mainland, inner and outer islands) and with finer resolution by disentangling the effects of area and isolation.

Across their holarctic distribution, wolves hunt a diverse suite of animals (Paquet & Carbyn, 2003; Peterson & Ciucci, 2003). Here we show high trophic diversity and variability among wolves within a single biome. On BC’s coast, we observed a minimum of 14 terrestrial mammals, a marine mammal, salmon, birds and marine invertebrates in diet. We did not detect any ‘species richness’ effects (narrower dietary niche for wolves on isolated islands), perhaps because these prey taxa are not as sensitive as others to biogeographical effects of isolation. Prey detected across this landscape greatly exceeds the number of items identified in earlier studies in the same biome [Scott & Shackleton, 1980 (Vancouver Island; 3 items); Milne *et al.*, 1989 (Vancouver Island; 4 items); Kohira & Rexstad, 1997 (Southeast Alaska; 11 items)]. This difference may reflect our greater geographical span of sampling and a more rigorous laboratory protocol.

Table 2 Top generalized linear regression model set to predict the probability of deer remains occurring in wolf faeces collected on islands of British Columbia ($n = 29$ islands), with model structure, deviance, and corresponding ΔAIC_c and Akaike weight (ω_i). MDIST is island distance to mainland, LDIST is island distance to another landmass $> 75 \text{ km}^2$, and AREA is area of island. Shown also are parameter coefficients, their standard errors, and model Nagelkerke R^2

Model form	Deviance	ΔAIC_c	ω_i	β_0	SE	β_1	SE	β_2	SE	β_3	SE	β_4	SE	Nagelkerke R^2
$\beta_0 + \beta_1(\text{MDIST}) + \beta_2(\text{LDIST}) + \beta_3(\text{MDIST} \times \text{LDIST})$	312.107	0.000	0.21	2.156**	0.244	-0.444**	0.109	-0.616*	0.242	0.075*	0.032	-	-	0.242
$\beta_0 + \beta_1(\text{MDIST}) + \beta_2(\text{AREA}) + \beta_3(\text{MDIST} \times \text{AREA})$	312.184	0.077	0.20	1.593**	0.243	-0.317**	0.104	0.001*	0.000	-0.001*	0.000	-	-	0.242
$\beta_0 + \beta_1(\text{MDIST}) + \beta_2(\text{LDIST})$	315.514	0.700	0.14	1.988**	0.202	-0.363**	0.106	-0.351	0.204	-	-	-	-	0.229
$\beta_0 + \beta_1(\text{MDIST})$	318.384	1.072	0.12	1.915**	0.197	-0.494**	0.093	-	-	-	-	-	-	0.218
$\beta_0 + \beta_1(\text{MDIST}) + \beta_2(\text{AREA})$	311.862	1.960	0.08	1.716**	0.246	-0.469**	0.094	-0.001	0.000	-	-	-	-	0.225

* $P < 0.05$, ** $P < 0.01$.

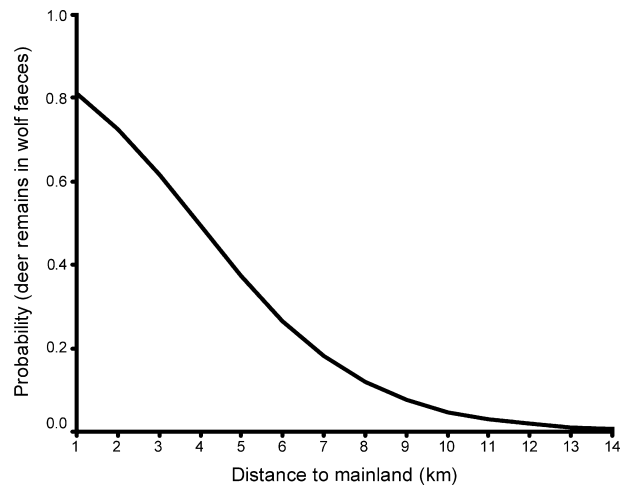


Figure 3 Probability of deer (*Odocoileus hemionus*) remains occurring in wolf (*Canis lupus*) faeces on islands as a function of their distance to the mainland (MDIST). Samples collected in coastal British Columbia, summers 2000 and 2001. Equation: $Y = 1.915 - 0.494 \times \text{MDIST}$, which forms the simplest model in our top model set based on Akaike Information Criteria ranking.

Additional spatial and temporal aspects of our sampling may explain differences with previous studies. Sampling within 5 km of shoreline may explain the abundance of smaller prey consumed. For example, marine invertebrates accounted for approximately 4% of prey items we detected. In addition, river otter and mink, which accounted for a combined 5.9%, are primarily occupants of the beach fringe. Moreover, we detected beaver in $< 3\%$ of scats, which differs greatly from other North American studies in which they occurred much more commonly (Voigt *et al.*, 1976; Fuller, 1989; Thurber & Peterson, 1993). This too may reflect our sampling bias of omitting much of the inland area, and/or a naturally low abundance of beaver in this conifer-dominated landscape (McCabe, 1948). Also, because faecal samples represented late spring and summer diet, more than half a year of dietary information was excluded. Early runs of spawning salmon accounted for the second highest proportion of prey consumed by wolves (6.5%) and recent stable isotope and behavioural evidence suggest that salmon runs during late summer and autumn support a major seasonal shift in the foraging of coastal wolves (Szepanski *et al.*, 1999; Darimont & Reimchen, 2002; Darimont *et al.*, 2003).

Major changes in the predation regime occurred across broad geographical categories, possibly because of associated habitat differences. Wolves consume less deer in rocky mainland areas compared with nearby but less mountainous inner islands (Figs 1 & 2). This may relate to low deer biomass per area on the mainland where elevations $> 1100 \text{ m}$ are common, altitudes at which deer in nearby southeast Alaska are known not to occur (Schoen & Kirchhoff, 1985). Although no similar data exist for BC's coast, deer densities in southeast Alaska are lower on the mainland coast compared with adjacent inner islands (Kirchhoff, 1996). Alternatively or

concomitantly, the lower observed frequency of deer in wolf diet on the mainland can be attributed to a more species-rich prey assemblage in mainland watersheds. For example, mountain goat and moose are two large terrestrial mammals that predominantly occupy mainland habitats and provided an additional food resource.

Predator–prey dynamics in fragmented landscapes may be determined by area of fragments, their isolation, and system-specific factors, which in coastal BC may include carrying capacity for deer. Similar to mainland areas, habitat on outer islands may support fewer deer. Thus, the lower frequency of this item in wolf diet may reflect lower availability. We consider this unlikely to serve as the full explanation. Similar outer islands, but those lacking wolves, in southeast Alaska and Haida Gwaii, BC, support (or supported before wolf introduction) high populations of deer (Reimchen *et al.*, in press; Kirchhoff, 1994, 1996; Klein, 1996). Likewise, on a recent survey of the Goose Group of islands (*c.* 25 km²), an outer archipelago at least 7 km from the nearest habitable island, we noted an absence of wolves and severe over browsing of vegetation by deer, suggesting high deer densities (Darimont & Paquet, 2000, 2002). Deer density data for islands in this archipelago would aid in evaluating this hypothesis.

Among biogeographical parameters to predict the occurrence of deer in wolf faeces, we found isolation, specifically distance to mainland, to be more important than area, likely because it influences dispersal. Regardless of carrying capacity, predators may deplete resources in isolated fragments if colonization by prey is limited. We consider this a plausible hypothesis for wolf–deer systems on isolated islands of coastal BC. We postulate that greater distances to mainland reduce immigration rates by deer, predisposing island populations to sustained predation by wolves. Neither area nor the interaction between isolation and area was very important, perhaps because the ecological conditions we deduce from our one-time sampling represent a steady state: over time wolves regulate deer on isolated islands to low abundance, regardless of island size.

Deer are excellent dispersers, however, capable of swimming across water bodies with intense and frequent wave and tidal action (Wallmo, 1981). Reimchen *et al.* (in press) examined deer colonization rates to offshore islands of Haida Gwaii, BC, using microsatellite markers. These authors made a conservative estimate of persistent dispersal of about one deer per year to Skaang Gwaii and Reef Islands, isolated by 2 and 6 km respectively. If colonization rates are similar in BC, our data suggest this is too infrequent to prevent depletion of deer prey on isolated islands. Mainland distance may have been more important than our inter-landmass metric because it estimates distance from the probable ultimate source populations for deer prey.

Our single sampling of this archipelago revealed a pattern of decreased occurrence of deer as prey with isolation, to which we attribute top–down effects coupled with limited recolonization by deer. To be certain, one must sample islands before

and after wolf colonization and estimate deer abundance and wolf foraging ecology over time. In the 1960s, a small experiment addressed these parameters by introducing four wolves to the 73 km² Coronation Island, southeast Alaska, 900-m from another landmass (Klein, 1996). After reaching a peak of 13 wolves in 4 years, the population fell to one, having apparently reduced deer numbers significantly. During this time, wolves foraged extensively on smaller mammals, seals and intertidal organisms (Klein, 1996). The last wolf was shot in the late 1960s, ending the experiment, and the deer population has since rebounded (Person *et al.*, 1996).

Others have demonstrated the consequences of insularity on mammalian predator–prey communities on islands but the dynamics of these systems vary. On Isle Royale, fluctuations of wolves and moose have been extreme but this system has persisted for over 50 years (Peterson *et al.*, 1984; Peterson & Page, 1988; Vucetich & Peterson *in press*). In contrast, Kauhala & Auniola (2001) suggested that raccoon dogs (*Nyctereutes procyonoides*) can extirpate frog populations on some islands in the Finnish Archipelago, as they are easy prey to capture and occur frequently in mainland diet. Migration by predators among landmasses may also be important; by switching between islands and mainland areas from winter to summer, foxes can stabilize fluctuations in hare numbers on Swedish islands, but the effect depends on how often ice permits foxes to recolonize islands and numerical response by predators (Angerbjörn, 1989).

Wolves may persist on isolated islands because alternate prey are available. When deer are scarce (and other large mammals like goat and moose absent), smaller prey such as mink, river otter and bird, appear to be important dietary items (Table 1; Fig. 2). Many of these taxa are either aquatic or volant and not likely as affected by isolation that may limit migration by larger, terrestrial prey.

Future studies in BC's archipelago, combining stable isotope and faecal analyses and occurring over several seasons, may provide better insight into predator–prey dynamics in this fragmented marine landscape. Notably, if combined with microsatellite genetic markers, we may learn how food resources influence presence, movements and demographical fates of individuals over time and assess how water barriers among islands may affect metapopulation dynamics (Hanski & Gilpin, 1991; Hanski, 1991); such frameworks for other large mammals in habitat patches have recently been developed (e.g. Elmhagen & Angerbjörn, 2001). Notably, although water barriers may constrain dispersal of predator and prey, this study suggests the ocean also provides food. In this respect, for wolves and likely other animals, BC's islands are not fragments within a totally inhospitable matrix, to which other islands have been likened (Brotons *et al.*, 2003; see also Dunning *et al.*, 1992; Fahrig, 1997).

This study has implications for conservation of predator–prey systems regionally and beyond. Deer constitute the majority of diet for BC's coastal wolves and salmon is an important seasonal resource (this study; Kohira & Rexstad, 1997; Szepanski *et al.*, 1999; Darimont & Reimchen, 2002;

Darimont *et al.*, 2003). Mounting evidence, however, suggests that carrying capacity for deer is reduced by clearcut logging in west coast temperate rain forests (Wallmo & Schoen, 1980; Alaback, 1982; Rose, 1982; Schoen *et al.*, 1984, 1988; Van Horne *et al.*, 1988). Likewise, many Pacific Northwest salmon stocks have declined dramatically because of the modification of spawning habitat by logging and over-exploitation by the fishing industry (National Resources Council, 1996). If current planning processes aim to preserve this remnant population of wolves in its current form (Darimont & Paquet, 2002), we suggest that plans include significant protection of critical habitat for deer and salmon, especially on islands. Moreover, in any ecosystem, a system of reserves must have appropriate connectivity to permit gene flow (Soulé & Simberloff, 1986). Our data suggest that connectivity should also be considered to accommodate fluctuations in population structure to prevent predator–prey disequilibria, to which fragments may already be predisposed.

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