Influence of Natural Landscape Fragmentation and Resource Availability on Distribution and Connectivity of Gray Wolves (*Canis lupus*) in the Archipelago of Coastal British Columbia, Canada

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Connectivity has emerged as an important ecological concept relating to how animals move among habitat patches in fragmented environments. Although connectivity is often considered landscape-and species-specific (Tischendorf and Fahrig 2000; Taylor et al. Chp. 2), fundamental ecological and physical processes influence movements of all species. Taylor et al. (1993) define connectivity as "the degree to which the landscape facilitates or impedes movement among resource patches". Most research, however, has centered on impediments to movement. For example, Tischendorf and Fahrig (2000) argue that landscape connectivity is "essentially equivalent to the inverse of patch isolation over the landscape". Herein we examine landscape and resource features that potentially impede (i.e., isolation) or facilitate (i.e., availability of food) movement of wolves (*Canis lupus*) using coastal islands in British Columbia (BC), Canada.

Investigations of oceanic archipelagos have revealed how island communities and species composition are related to area, isolation, and other island characteristics (e.g., MacArthur and Wilson 1967; Abbott, 1974; Kadmon and Pulliam 1993; Conroy et al., 1999). Biogeographic 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 and Wennergren, 1995; Dolman and Sutherland, 1997; Darimont et al. 2004). The equilibrium theory of island biogeography (MacArthur and Wilson 1967) and metapopulation theory (Levins 1976, Gilpin and Hanski 1991, Hanski and Gilpin 1996; Moilanen and Hanski Chp. 3) postulated several abiotic mechanisms explaining animal distribution and population persistence in patchy landscapes. Now, the original concept of a metapopulation as "a population of populations" has expanded to include other spatial population structures (Laurance and Cochrane 2001), including

mainland-island (Hanski and Gilpin 1991) and source-sink metapopulations (Pulliam 1996). Again, however, most studies focused on physiographic features thought to impede or limit movement and persistence of species, rather than biotic influences such as availability of food.

According to these theories, suitable habitat often is arranged across the landscape as island-like patches of various sizes (area) and distances from other patches (isolation). The occurrence of animals is thought to reflect direct responses of individuals to this physically varied environment (Kareiva 1990). The availability and productivity of these habitats likely influence animal movements, species composition, population dynamics, and community structure. On large spatial and temporal scales, area and isolation are the most important variables in predicting community structure in island biogeography theory (MacArthur and Wilson 1967) and population dynamics in metapopulation theory (Levins 1976). Collectively, these ideas provide much of the theoretical foundation for conservation biology.

To establish biological priorities for conservation, we need a firm understanding of how geography interacts with species to shape evolution, ecological relationships, and landscape processes. To that end, a long list of studies addressing birds, small mammals, and insects has contributed to the development of contemporary conservation theory (Ehrlich and Hanski 2004). Very few studies, however, have evaluated the response of large terrestrial predators to naturally fragmented landscapes or true island systems. In part, this is due to a lack of pristine sites to carry out such research. Moreover, large mammalian carnivores are rare on isolated or semi-isolated islands (Williamson 1981; Alcover and McMinn 1994). Nevertheless, elucidating the relationship between the geographic and ecological structure of true island systems and distribution of large mammals is a needed link between theory and application. Knowledge about large predators 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 and Ginsberg 1998), possibly resulting in mesopredator release and other ecosystem-wide consequences (Crooks and Soulé 1999; Terborgh et al. 2001). Consequently, archipelagos may provide model systems in which to predict the effects of size, isolation, resource availability, and other factors on predator persistence.

The archipelago of coastal British Columbia provides an opportunity to examine how a true island environment affects the distribution and abundance of wolves. The region is characterized by forested oceanic islands, mainland mountains, and island mountains that are potential barriers to movement, and diverse marine and terrestrial food resources. This remote and nearly pristine region is naturally fragmented, comprising numerous islands <100 m to >13 km apart (Fig. 1). Here, the wolf and black-tailed deer (*Odocoileus hemionus*) association forms the dominant mammalian predator-prey system, in which both animals can occupy many islands, at least ephemerally (Darimont and Paquet 2000, 2002). Documenting the response of wolves to true islands (i.e., surrounded by water) provides a reference for comparison with similar studies relating to connectivity in fragmented terrestrial landscapes (Harrision and Chapin 1998; Gaines et al. 2000; Carroll et al. 2004; Carroll Chp. 15).

This study evaluates and contributes to prevailing theories of metapopulation theory and predator-prey dynamics in fragmented landscapes. Herein, we examine the effects of island characteristics on distribution and spatial ecology of gray wolves. Specifically, we predict that geographic and resource characteristics of landmasses influence connectivity for this summit predator. We infer connectivity by documenting wolf presence on islands during a 5-year period. Our overarching research hypothesis is that distances among landmasses, juxtaposition of landmasses, geometry of landmasses, and prey availability influence wolf presence and persistence on islands. We predicted that wolves are more likely to be resident on islands that are largest, roundest, least isolated, and most productive.

Gray Wolves

The gray wolf is an elusive, low-density carnivore with an historical distribution comprising most of the Holarctic. The historic range of the species is the largest of any extant terrestrial mammal, with the possible exception of the African lion (*Panthera leo*) (Paquet and Carbyn 2003). Gray wolves occur in a variety of habitats, from dense forest to open grassland and from the Arctic tundra to extreme desert, avoiding only swamps and tropical rainforests. The gray wolf originally occupied all habitats in North America north of about 20° N latitude. On the mainland, wolves were found everywhere except the southeastern United States, California west of the Sierra Nevada, and the tropical and subtropical parts of Mexico. The species also occurred on large continental islands, such as Newfoundland, Vancouver Island, and smaller islands off coastal British Columbia and southeast Alaska, and throughout the Arctic Archipelago and Greenland, but was absent from Prince Edward Island, Anticosti, and the Queen Charlotte Islands (Paquet and Carbyn 2003).

Because wolves are not highly habitat-specific, move long distances, and require large home ranges, the species is regarded as a habitat generalist (Mech 1970, Fuller et al. 1992, Mladenoff et al. 1995). Populations, however, are adapted to local conditions and specialized concerning den-site use, foraging habitats, physiography, and prey selection (Fritts et al. 1995, Mladenoff et al. 1995, 1997, 1999; Paquet et al. 1996, Haight et al. 1998, Mladenoff and Sickley 1998, Callaghan 2002). Thus, wolves are better characterized as ecosystem generalists that are idiosyncratic concerning the surroundings in which they live (Paquet and Carbyn 2003).

The gray wolf is also the most vagile of all large terrestrial predators. Travel and dispersal distances of several hundred km are common and movements more than 1,000 km have been documented (Ballard et al. 1983, Fritts 1983; Boyd et al. 1995, Mech et al. 1995, Walton et al. 2001, Paquet and Carbyn 2003). The Canadian west coast wolf typifies this pattern of adaptability. Among regions still populated by wolves, the mainland coast of British Columbia and the associated archipelago of offshore islands are ecologically unique. This remote ocean archipelago hosts what is possibly North America's most pristine wolf population (Paquet et al. 2004-2005). There is, however, considerable conservation concern about future abundance and distribution in the area, given large scale and rapid industrial clearcut logging and associated effects (Darimont and Paquet 2000, 2002; Paquet et al. 2004-2005).

Wolves are widely distributed in the study area (Darimont and Paquet 2000, 2002). Although territorial behaviour is not well documented, coastal wolves in nearby southeast Alaska have average home ranges of about 230 km^2 (Person et al. 1996). Wolves can swim in open ocean between landmasses as distant as 13 km (Darimont and Paquet 2002). Movements, however, are thought to be limited by distance, wind, water temperature, and water currents (Darimont and Paquet 2002). Observations from our studies and southeast Alaska (Person et al. 1996; D. Person pers. comm.) confirm that some packs and individuals include a constellation of islands and mainland areas within their home range.

STUDY AREA
Our study area encompasses the island archipelago north of Vancouver Island (51˚ 46' N, 127˚ 53' W) to Prince Rupert, BC (55˚ 37'N, 129˚ 48'W). The region is approximately 29,700 km^2, of which 19,300 km^2 is land (Fig. 1). This wet, nearly roadless, and biologically productive area is isolated from continental North America by the Coast Mountain Range to the east and Pacific Ocean to the west, resulting in a unique ecological and evolutionary environment largely free from industrial development. The few human settlements consist primarily of First Nation's people.

Coastal temperate rainforest dominates the region (MacDonald and Cook 1996), constituting the largest remaining expanse of ancient temperate rainforest in the world (Schoonmaker et al. 1997). Most of the low elevation forest is within the Coastal Western Hemlock biogeoclimatic zone (Pojar and Mackinnon 1994). Climate is temperate and wet. Most areas receive more than 350 cm of annual precipitation (Environment Canada 1991).

Habitat heterogeneity in these temperate rainforests corresponds to landscape variability, which includes the following general regions: mountainous mainland, topographically complex inner islands, and flatter outer islands. The region's innumerable islands are separated by fiords, channels, other waterways, and open ocean. Islands we sampled ranged in size from 0.7 km² (Moore) to 2,295 km² (Princess Royal), distances (*sensu* Conroy et al. 1999) to mainland 250 m to 13.1 km, distances between islands 100 m to 13.0 km, and inter-landmass distances 50 m to 7.3 km. This complex physiography mediates the interaction of marine and terrestrial systems (see Talley et al. Chp. 5), creating many different kinds of environments in close proximity. The study region, combined with southeastern Alaska, supports the highest concentration of endemic species and populations for the temperate rainforest region of Pacific North America (Cook and MacDonald 2001).

The region is important to formerly wide-ranging species such as grizzly bears (*Ursus arctos*) and wolves now exterminated from most their former ranges (Paquet et al. 2004-2005). Genetically distinct populations of species such as Kermode black bear (*U. americanus kermodei*) are found on the Central Coast, providing a valuable opportunity for scientists studying evolutionary processes under natural conditions (e.g., Byun et al. 1997; Ritland et al. 2001; Marshall and Ritland 2002,). Basic ecological information, however, such as the distribution, density, and movements of large mammals, including gray wolves and their prey, is largely unknown.

Potential prey base for wolves is diverse, including Sitka black-tailed deer, moose (*Alces alces*), 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 and Paquet 2000, 2002; Darimont et al. 2003, 2004; in press).

METHODS
Distributional Data
        We assembled the ecological and geographic information used in our analyses from a variety of sources. During summer and fall 2000 to 2004, we surveyed islands in the study area for the presence of wolves and other mammals (Fig. 1). During summers 2000 and 2001, we surveyed 36 islands and 42 mainland watersheds for wolves (Darimont and Paquet 2002). We surveyed 14 additional islands during 2002 to 2004 and re-sampled many of islands visited in 2000 and 2001. In total, 50 islands were surveyed, ranging in size from $0.71 km^2$ to $2,295 km^2$.
        Sampling sites on islands were selected non-randomly but influenced by our knowledge of the area and its resources. Local First Nations colleagues and the traditional ecological knowledge they shared (Huntington 2000; Pierotti and Wildcat 2000; Turner et al. 2000) also guided us. 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 more than 5 km inland. Presence of wolves was determined by occurrence of wolf feaces, tracks, scrapings, vocalizations, or direct observations (Darimont and Paquet 2002). All data were imported into GIS for analyses.

Landscape Data
        Using a Geographic Information System (ArcView3.2 and ArcMap), we extracted landscape configuration metrics from LANDSAT-7 and a digital elevation model (DEM). Landsat 7 images were taken from 1999 through 2001 between the months of July and October. Mean-subtraction was used to mosaic the images, whereby the pixel value of 1 image was subtracted from the mean of all pixel values of a second image. This smoothed pixel values and accounted for time discrepancy between images.
        A 50 m resolution Digital Elevation Model (DEM) provided the basis for an island/mainland polygon layer. We calculated area of islands and shape indices from a digital map derived from the DEM using the X-Tools extension in ArcView3.2. Shape index was calculated as (0.25*Perimeter)/sqrt(Area), where 0.25 accounts for square pixel shape. Smaller shape index values represent rounder islands. An index of 0.099 is perfectly round. Island distance to nearest island and island distance to mainland (c.f. Conroy et al. 1999) were calculated using the Nearest Feature extension for ArcView3.2.

Prey Resource Availability

        Deer and salmon are the primary prey of wolves in this region (Darimont et al. 2004), so we expected that the relative abundance of these resources among islands could predict occurrence of wolves. Accordingly, we conducted deer pellet surveys within a 3,000 km^2 portion of our study area using 1-km paired transects at 60 locations. Paired transects were at least 200-m apart and consisted of 50 continuous 1 X 20 m belt plots. We recorded the number of pellet groups in each plot (Kirchhoff and Pitcher 1988; Kirchhoff 1990). We used hand-held GPS to locate the beginning and end of transects, as well as each 100-m interval. All GPS locations were input into GIS to obtain a spatial map of deer pellet locations.

        We obtained information on distribution of chum (*O. keta*), pink (*O. gorbuscha*), coho (*O. kisutch*), chinook (*O. tschawytscha*), and sockeye (*O. nerka*) salmon from Department of Fisheries and Oceans FISS (Government of Canada, Fisheries Information Summary System) inventory data (ftp://gis.luco.gov.bc.ca/pub/coastal/aquaculture/; http://www.bcfisheries.gov.bc.ca/fishinv/db/default.asp). Abundance of salmon fluctuates among years owing to ecological variability and exploitation by humans (Groot and Margulis 1991; National Resources Council 1996). Moreover, the reliability of spawning salmon enumerations by government inventories has not been rigorously assessed, nor have all potential salmon-bearing watersheds been inventoried (Thomson and MacDuffee 2002). Therefore, we used salmon richness or the number of known salmon species per island, as a proxy for availability and abundance. Because each species spawns at different peak times and in different riparian habitat, richness reflects the temporal and spatial breadth of this resource for island wolves.

Deer Sub-Model

        We created a sub-model to estimate the relative abundance of deer on each island. Using our field data on pellet-groups, we derived an equation that predicts the relative distribution (Loft and Kie 1988, Edge and Marcum 1989, Weckerly and Ricca 2000) and density (Rowland et al. 1984, Patterson et al. 2002, c.f. Fuller 1992, White 1992) of deer based on topographic slope. We assumed a linear positive relationship between numbers of pellet groups and numbers of deer. Observed pellet-group densities were normalized to account for representation of available slopes and sampling bias. Using a curve-fitting regression method (SPSS 11.0, SPSS Inc., Chicago, USA), we generated a curvilinear function describing the relationship between mean pellet-group density and slope that was highly predictive ($R^2 = 0.92$). This was then converted to a spatial probability layer in ArcView using the following equation:

        Relative pellet-group density = 0.0000094[slope^3] - 0.0009[slope^2] + 0.0231[slope] – 0.0022

Statistical Analyses

We used an information theoretic approach to evaluate which models and parameters best explain observed patterns in our field data (Burnham & Anderson 1998; Anderson et al. 2001). We formed exploratory *a priori* hypotheses to explain how biogeographic features and availability of prey affect the presence of wolves on coastal islands. These hypotheses were based on our knowledge of the area, previous studies, ecological theory, and discussions with First Nations colleagues. Specifically, we postulated that wolves are most likely to occur on the most productive, largest, and roundest islands that are closest to the mainland or other islands. From these hypotheses, we developed a set of candidate logistic regression models (Hosmer & Lemeshow 1989) to predict the probability of wolves being either present or absent on islands during our surveys. These were restricted to combinations of 1 to 6 of the identified (and untransformed) parameters (Table 1), and 2-way interaction terms we felt were useful based on theory and our previous empirical work (AREA x MAIN, DEER x MAIN, and DEER x AREA; MacArthur and Wilson 1967; Darimont et al. 2004). In addition, we assessed the potential bias of our survey effort by including the number of visits to each island as a parameter (SURVEFFORT). A Hosmer-Lemeshow goodness-of-fit statistic based on the global model showed the data did not depart from a logistic-regression model ($P = 0.871$). Multicollinearity diagnostics suggested only weak interdependencies among predictor variables (Variance Inflation Factors range: 1.3 to 2.3).

Table 1. Metric type, data source, derived variables, and parameter names used in logistic regression analyses to predict the presence of wolves on the islands of the British Columbia's coastal archipelago, 2000 to 2004. See methods for detailed description of variables and data sources.

Metric	Source	Derivative	Parameter
Biogeographic	Digital Elevation Models	Island Area[a]	AREA
	LANDSAT 7	Dist. to Mainland	MAIN
		Dist. to Island > 75 km^2 [a,b]	NEAR
		Island Shape	SHAPE
Food Resource	Field Data	Deer Abundance Model	DEER
	Government Database	Salmon Species Richness	SALMONRICH
Analytical	Field Data	Survey Effort	SURVEFFORT

a)   see Conroy et al. 1999 for details regarding the measurement of distances
b)   see Darimont et al. 2004 for details regarding the 75 km^2 threshold

For each model, we calculated Akaike Information Criteria, adjusted for small sample sizes (AIC_c), following the formula: AIC_c = -2(log likelihood) + 2K + 2K(K + 1)/(n - K - 1), where K is the number of parameters and n the numbered of sampled islands. We then evaluated ΔAIC_c to select best approximating model(s) and make appropriate inference, using $\Delta AIC_c < 4$ to describe the top model set (offering substantial level of empirical support; Burnham and Anderson 1998). 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). We ran models in SPSS 11.0 (SPSS Inc., Chicago, USA).

RESULTS

Over 5 field seasons, we observed wolves or sign of wolves on 42 of 50 islands surveyed. The maximum distance between landmasses where wolves were recorded was 13 km (on the most isolated of islands). Based on continuous monitoring and visual re-identification of conspicuous individuals, some packs occupied constellations of islands.

Biogeographic and food resource parameters contributed to highly predictive models to explain the presence of wolves on islands. Moreover, relationships among parameters and island occupancy by wolves were in the direction predicted by theory and our *a priori* hypotheses (except for island shape; Tables 2, 3). Although both were important, biogeographic parameters were more useful than food resources in predicting occupancy by wolves. Specifically, model selection and multimodel inference suggest that AREA was clearly the most important parameter influencing detection of wolves, whereas other biogeographic features (isolation and shape) and food resources were less important.

Six of 8 models in the top model set contained AREA (Table 2). The leading model (Akaike weight or $\omega_i = 0.28$) predicted wolf distribution as a function of island size (and intercept) alone. The 8 leading models accounted for a collective Akaike weight of 0.71. Remaining models had very little support in the data. Some ambiguity, however, existed among top models, among which Akaike weights were not particularly widely distributed ($\omega_{i=1\ to\ 8} = 0.28$ to 0.04; Table 2). The top model, containing AREA and the intercept only, was roughly 3 times more informative than the next leading model ($\omega_i = 0.28$ vs. 0.10 respectively). Moreover, these top models explained a similar proportion of the variance (Nagelkerke R^2 range = 0.654 to 0.717; Table 2). In cases when the data do not strongly support a single best model, the model with fewest parameters is often worth most consideration, following the rule of parsimony (Burnham and Anderson 1998). Accordingly, we consider model 1, containing only intercept and AREA, as a preferred model (Table 2). The probability of wolf occupancy on islands declined with smaller island area.

Table 2. Top logistic regression model set to predict the probability of wolf occupancy on islands (n = 50) of British Columbia's archipelago. Shown is model structure, deviance, and corresponding ΔAICc, Akaike weight (ω_i), and model Nagelkerke R^2. AREA is island area, SURVEFFORT is the number of occasions we surveyed an island, SHAPE is island shape, DEER is estimated deer abundance from a model we generated from field data, NEAR is island distance to another landmass > 75 km², and SALMONRICH is the number of salmon species present on the island.

Model Form	Deviance	ΔAIC$_c$	ω_i	Nagelkerke R^2
AREA	20.657	0.00	0.28	0.654
AREA, SURVEFFORT	18.358	2.01	0.10	0.717
AREA, SHAPE	18.952	2.61	0.08	0.706
DEER, SHAPE	19.557	3.21	0.06	0.695
AREA, DEER	19.630	3.29	0.05	0.693
AREA, NEAR	19.970	3.63	0.05	0.687
DEER, SALMONRICH	20.108	3.76	0.04	0.684
AREA, SALMONRICH	20.302	3.96	0.04	0.680

The top model set can still make robust multimodel inference (Burnham and Anderson, 1998); summing the Akaike weights for each parameter across top models (Table 3) ranked the variable AREA ($\sum\omega_i = 0.61$) roughly 4 and 15 times higher than other biogeographic parameters SHAPE and NEAR ($\sum\omega_i = 0.16$ and 0.05 respectively). Collectively, food resources also appear important in attracting wolves to islands. The estimated abundance of deer (DEER) and salmon richness (SALMONRICH) occurred multiple times in top models (Table 2). Deer abundance was twice as valuable as salmon richness ($\sum\omega$ of 0.16 vs. 0.08 respectively; Table 3).

Table 3. Sum of Akaike weights ($\sum \omega_i$) for each parameter included in the top model set (0 – 4ΔAIC$_c$). AIC$_c$ values calculated from logistic regression models to predict the presence of wolves on islands of British Columbia's archipelago, 2000 to 2004. Shown also is association between parameter and presence of wolves on islands (i.e., direction).

Parameter	$\sum \omega_I$	Association
AREA	0.61	+
DEER	0.16	+
SHAPE	0.13	+
SURVEFFORT	0.10	+
SALMONRICH	0.08	+
NEAR	0.05	-

Some parameters were not important in predicting island occupancy by wolves. We infer that the interactive properties we examined are not important, as no interaction terms were included in the top model. Likewise, MAIN, or isolation from the mainland, appeared to be of little importance in determining the presence of wolves on islands.

DISCUSSION
Consumers often forage in spatially complex environments where resources are distributed unevenly among patches that differ in productivity, size, isolation, and other physical traits. Therefore, resource acquisition, and ultimately fitness, can depend on patch choice and the ease in which animals are able to move among patches (i.e., connectivity). From an optimal foraging perspective (Stepehns and Krebs 1986), "patch choice" is an important aspect of foraging ecology because it is the first decision relating to patch use (Kevan and Greco 2001). Yet, the influence of patch choice and food resources on connectivity has received far less attention than other components of foraging ecology, such as residence and departure times (Kevan and Greco 2001). Moreover, most connectivity and meta-population models assume that patches of habitat are embedded in a matrix that has little value for the species considered, even though the surrounding matrix may be of varying quality (Taylor et al. Chp. 2).
Herein, we address some of these potential limitations. Specifically, we demonstrate that both physical features and patch quality of fragments are important aspects of connectivity for island dwelling wolves. We inferred patch quality from estimates of prey resource availability. With the proper caveats, these preliminary findings are relevant to understanding the effects of isolation and fragmentation in other ecosystems. We caution that our analytical design may have influenced our results. For

example, one reasonable model suggested the probability of detecting wolves increased with survey effort.

Well adapted to the marine environment, many coastal wolves are island dwellers whose territories can include groups of islands. Consequently, movement within territories requires traveling on land and among landmasses, which means swimming in open ocean (Darimont and Paquet 2002). Dispersing and traveling animals also need to cross expanses of inhospitable terrestrial habitat. Moreover, many of the prey upon which wolves depend for their survival and other carnivores with which they compete (e.g., black bears, grizzly bears), are influenced similarly. We expected, therefore, that isolation, island size, and availability of prey would govern the many potential influences that combine to determine accessibility and use of coastal islands by wolves. Our assessment suggests that island size is the overwhelmingly dominant influence in determining wolf presence, followed by availability of primary prey (deer and salmon), and island shape. In comparison, isolation, expressed as island-to-island distance and island-to-mainland distance, seems unimportant.

SIZE MATTERS

Island area is clearly the dominant factor in determining wolf residency. In nearby southeast Alaska, wolves also are typically absent on small islands. Wolf scat or wolf-killed deer were observed on only 6 of 97 islands surveyed repeatedly between 1989 and 1993. These very small islands ranged in size from 0.2 to 134 hectares (Kirchhoff 1994; Emlen et al. 2003).

We believe island size influences the quantity and quality of resources available to wolves. For example, larger islands, likely have greater food resources overall, and those prey populations are probably more stable (Burkey 1995, Newmark 1995). Thus, wolves can maintain longer residency times on these islands, which would increase the probability of their detection during our surveys. Moreover, owing to topographic features, a larger island may have disproportionately more habitat than predicted by 2-dimensional area calculations alone.

ISOLATION

The effects of isolation are important for consumers with high resource demands because they relate to the economics of time and energy. Giving up on a site (Kareiva et al. 1989) and moving to another imposes time and energetic costs (Stephens and Krebs 1986; Ritchie 1998). Swimming in marine environments probably carries considerably more energetic costs than travel on land and may impose costs on fitness (e.g., drowning). Moreover, the influences of currents, which vary between landmasses, may be as important as straight-line distances in affecting dispersal (Cameron 1958; Williamson 1981). Sightability may affect orientation (MacArthur and Wilson 1967) and influence which islands wolves select, especially during foggy periods. Finally, in any landscape, animals run a risk that the new patch is less productive than the current one. Therefore, in an environment where patches are unevenly distributed, foragers might prefer to occupy less isolated patches.

Although few in number, other studies carried out in coastal BC and Alaska found isolation on islands to be an important factor affecting species presence and diversity

(Craig 1990, MacDonald and Cook 1996; Conroy et al. 1999). We expected wolf presence to be related to island isolation because water poses a considerable barrier to movement for most terrestrial species. Surprisingly, wolves were not limited by island isolation as inferred from distance among landmasses. Likely, however, a threshold exists where isolation does limit or preclude movements. We believe the excellent swimming ability of wolves allows them to move unrestricted among all landmasses within our study area. For example, 1 pack colonized a 240-km² cluster of islands 13 km from the nearest landmass (Darimont and Paquet 2002), which is the most isolated landmass in the study area. Apparently, these wolves first arrived in 1996 (Tshimsian Nation family, pers comm.). Moreover, we continue to monitor 3 packs that move frequently among multiple landmasses. Notably, we rarely observe evidence of these wolves on the smallest of nearby islands. We believe the costs wolves incur travelling among islands are outweighed by the benefits accrued exploiting the most productive sites (Stephens and Krebs 1986).

Although not addressed by our study, connectivity for all coastal mammals that travel through water corridors can be adversely affected by human disturbances such as boat traffic. These disturbances are analogous with the adverse influences associated with roads, railways, and other infrastructure (Paquet et al. 1996, Clevenger and Waltho 2000, Duke et al. 2001, Clevenger et al. 2002, Alexander et al. 2004; Clevenger and Wierzchowski Chp. 20). Human presence and boat wash can stress and disturb swimming animals. In addition, humans occasionally harass and kill deer, bear, and wolves as these animals travel between landmasses (C. Darimont unpublished data, P. Paquet per. observation). Ocean channels, coastlines, and river systems provide humans access to remote areas and opportunities for disrupting connectivity via disturbance. In southeastern Alaska, for example, humans who gained access by boat to areas otherwise secure were responsible for more than 50% of all wolves killed by hunters and trappers (Person et al. 1996). Moreover, predation by non-humans may occur, if only rarely. Killer whales (*Orcinus orca*), for example, are known to prey on moose and deer swimming between islands in the study area (Ford and Ellis 1999).

ISLAND SHAPE

In theory, narrower islands should pose greater risk for wildlife than rounder islands of similar size. Rounder islands provide more security because interiors are more difficult to reach, and compared with narrow islands, proportionately less coastline is exposed. Thus, we expected that wolves, being security conscious, would be less likely to occupy islands with more exposed edge (Woodroffe and Ginsburg 1998). We found, however, a positive association between narrow islands and occupancy (Table 3). This could reflect survey bias related to our failure to detect wolves using the interior of rounder islands, but we consider this unlikely for the following reasons. First, wolves in this area are only lightly persecuted. We estimated annual human-caused mortality at 2-5% (Darimont and Paquet 2000). Because this danger is concentrated primarily around human settlements, it is unlikely to repel wolves from using island edges.

Second, our foraging data suggest wolves spend considerable time along island edges, which could make narrower islands more attractive to them. A high percentage of

the diet of coastal wolves is composed of foods that occur on the beach fringe (Darimont et al. 2004). Therefore, we postulate that narrower islands may have food resource benefits greater than rounder islands of similar size. Other canids are known to capitalize on marine food along seashores. The diet of coastal coyotes (*C. latrans*) in Baja, California includes a significant proportion of marine food (Rose and Polis 1998; Talley et al. Chp. 5). Likewise, Angerbjörn et al. (1999) found significantly enriched marine isotope values in coastal compared with interior arctic foxes (*Alopex lagopus*), suggesting substantial use of marine resources.

Finally, the orientation of islands relative to the mainland and other islands might interact with shape to influence the presence of wolves. It seems reasonable that longer islands are more likely to be intercepted by swimming wolves because they are more visible, appear larger, or make a larger target to a wolf if the major axis (simplifying the shape of the island to an ellipse) is perpendicular to the wolf's line of sight. Assuming that movement patterns of wolves are mediated by their awareness of geography (Peters and Mech 1975, 1978), then the ability of wolves to detect and cognitively map landmasses might be an important factor determining presence of wolves on islands. Accordingly, a wolf's perceptual range would vary with the animal's physical position relative to sea level and wind direction. We are uncertain, however, whether the maximum distances between islands classified as occupied in our study exceeded the perceptual range of wolves.

FOOD RESOURCES

Results of our study suggest strongly that physical characteristics of islands, particularly area, are more important than availability of food in influencing occurrence of wolves on islands and travel among islands. This, however, needs to be considered in the proper context. Specifically, we emphasize that in most of our top models, deer and to a lesser extent salmon, occur as variables that predict the presence of wolves on islands. For large carnivores such as wolves, energetic needs are substantial, particularly while raising young (Paquet and Carbyn 2003; Mech and Boitani 2003). Although moderated by the physical landscape, demands for food likely motivate the island hopping behaviour of wolves in our study area. In short, food may facilitate connectivity but not as much as biogeographic factors such as water barriers impede it. In any case, we suggest the physical landscape, food productivity, and food availability are inextricably linked.

We believe the relationship between use of food resources and connectivity is important but poorly understood. Island ecosystems may impose unique constraints on activities of predator and prey (Peterson and Page 1998; Peterson et al. 1998). Our analysis of wolf foraging behaviour on coastal islands could provide helpful insights (Darimont et al. 2004). Specifically, isolation (as measured by distance between landmasses) seems to affect wolf-prey dynamics. The probability that wolves forage for deer on islands is determined primarily by distance to the mainland. Wolves are more likely to consume deer on islands close to the mainland rather than islands that are more distant (Fig. 2, from Darimont et al 2004). Thus, we believe that predator-prey dynamics on isolated islands are potentially less stable, characterized by frequent declines in prey populations (Darimont et al. 2004)

We suspect deer cannot reproduce or immigrate fast enough to remote islands to replace those killed by wolves (Darimont et al. 2004). Because connectivity for deer is restricted, these islands may become temporary mortality sinks, resulting in ephemeral populations of deer and wolves. Without wolves, deer slowly recolonize isolated islands and the cycle of depletion repeats when wolves return. Consequently, (and contrary to predictions based on abiotic factors alone, which would suggest reduced movement with isolation), we suspect that coastal wolves are compelled to move frequently among isolated landmasses, assessing the potential of islands to support them while exploiting those that can.

We note that wolves might persist on some isolated islands when deer and other large mammals like goat and moose are scarce or absent by relying on smaller prey such as mink (*Mustela vison*), river otter, and birds (Darimont et al. 2004). Many of these taxa are either aquatic or volant and not likely as affected by isolation that limits migration of larger, terrestrial prey. In addition, recent investigations have revealed the coupled nature of marine-terrestrial ecosystems (Polis and Hurd 1995; Rose and Polis 1998; Reimchen 2000; Talley et al. Chp. 5). For some consumers, foraging constraints on small or isolated oceanic islands can be moderated by nutrient subsidies from the ocean. Our research suggests the ocean augments food available to wolves inhabiting islands (Darimont and Reimchen 2002; Darimont et al. 2003; Darimont et al. 2004). In this respect, many coastal islands are not impoverished fragments, as some oceanic islands have been described (Brotons et al. 2003; see also Dunning et al. 1992; Fahrig 1997). For example, coastal wolves feed on mollusks, crustaceans, and marine carrion such as beached mammals (e.g. *Phoca vitulina*) and whales (e.g. *Megaptera novaeangliae*). In the fall spawning salmon, having traveled thousands of km in ocean corridors, return to rivers and creeks of the islands of coastal BC, and constitute a considerable part of the diet of coastal and even interior wolves (Szepanski et al. 1999; Darimont and Reimchen 2002; Darimont et al. 2003, 2004). Notably, these are the same rivers and creeks used by wolves, bears, and other terrestrial species to travel among estuaries and access inland forests. Like bears and river otters (Reimchen 2000; Ben-David et al. 1998), wolves act as vectors by transporting marine nutrients from waterways along networks of intersecting trails into the regions' ancient forests. Abandoned salmon carcasses, faeces and urine feed a diversity of users and become important fertilizers in nutrient-limited coastal ecosystems (Reimchen 2000, 2002; Darimont et al. 2003).

In addition, data constraints in our analysis might have underestimated the importance of food relative to physical factors. Using GIS and satellite imagery, we were able to measure accurately landscape features of islands. Conversely, the availability of food resources was estimated using gross proxies. Specifically, we employed a habitat model for deer using indices of relative abundance, and used species richness for salmon. In addition, we did not account for how islands may differ in availability of other foods regularly consumed by coastal wolves such as beach carrion, marine mammals, and small terrestrial animals (Darimont et al. 2004).

CONCLUSIONS AND FUTURE DIRECTIONS

Our earlier research showed deer are the primary prey of coastal wolves and the probability that wolves eat deer on islands is negatively related to isolation as measured by distance between landmasses (Darimont et al. 2004). We postulated that was because deer occupying remote islands cannot immigrate and reproduce fast enough to compensate for mortality. Here we conclude the time wolves spend on islands depends primarily on size of the islands, which we argue is linked inextricably to availability of prey. Therefore, the movement and distribution of island wolves are not significantly affected by what we expected was poor connectivity (Darimont and Paquet 2002), at least within the geographic confines of our study area. The time between population recovery by deer following predation by wolves in isolated fragments, the island's subsequent re-colonization by wolves, plus the availability and seasonality of salmon and other marine resources, define a unique predator-prey system with different dynamics than most terrestrial systems.

In addition to spatial influences and food availability, we believe use of islands by wolves reflects, in part, evolved behaviours and life-history traits that confer a rare ability to adapt to environmental diversity at various temporal and spatial scales (Weaver et al. 1996). In contrast, coastal islands support only a subset of the adjacent mainland's mammalian carnivores, likely biased towards fecund species adept at crossing large expanses of water. For example, grizzly bears, black bears, and cougars (*Felis concolor*) occur on far fewer islands than wolves, and usually close to the mainland (P. Paquet and C. Darimont unpublished data). In addition, we expect that physiography, vegetation, and human disturbance alter the amount of habitat available to wolves on islands and the mainland. Finally, characteristics of water channels (e.g., tides, depth, water temperature, and currents) separating landmasses may influence species movement through the landscape.

Ongoing studies combining stable isotope and faecal analyses, and occurring over several seasons, might provide better insight into connectivity and predator-prey dynamics in marine archipelagos. Notably, if combined with microsatellite genetic markers, we may learn how food resources influence presence, movements, and fates of individuals and populations over time, and assess how water barriers affect metapopulation dynamics (Hanski 1991; Hanski and Gilpin 1991). Similar frameworks for other large mammals in habitat patches have recently been developed (e.g., Elmhagen and Angerbjörn 2001).

We have presented several working hypotheses and charted a course for future research. As one of the few remaining large blocks of comparatively unmodified landscapes on Earth, we consider the Great Bear Rainforest, to which the area is commonly referred, a precious academic, aesthetic, and spiritual resource (Paquet et al. 2004-2005). The Great Bear harbours one of humankind's last opportunities for studying the outcome of long-term evolution on a geographic scale, and observing highly specialized and coevolved interactions that are being replaced elsewhere with invasive species or managed landscapes (McKinney and Lockwood 1999; Crooks and Suarez Chp. 18). No amount of money or efforts in restoration ecology can recapture the geographic mosaics of these long-term experiments in evolution. Sadly, the rate of human-induced environmental change is happening so rapidly in the Great Bear (Moola et al. 2004) that many species must be tracking their changing environment with a noticeable lag. Consequently,

connectivity for wolves and other inhabitants of these ancient temperate rainforests will likely emerge as a more pressing concern.

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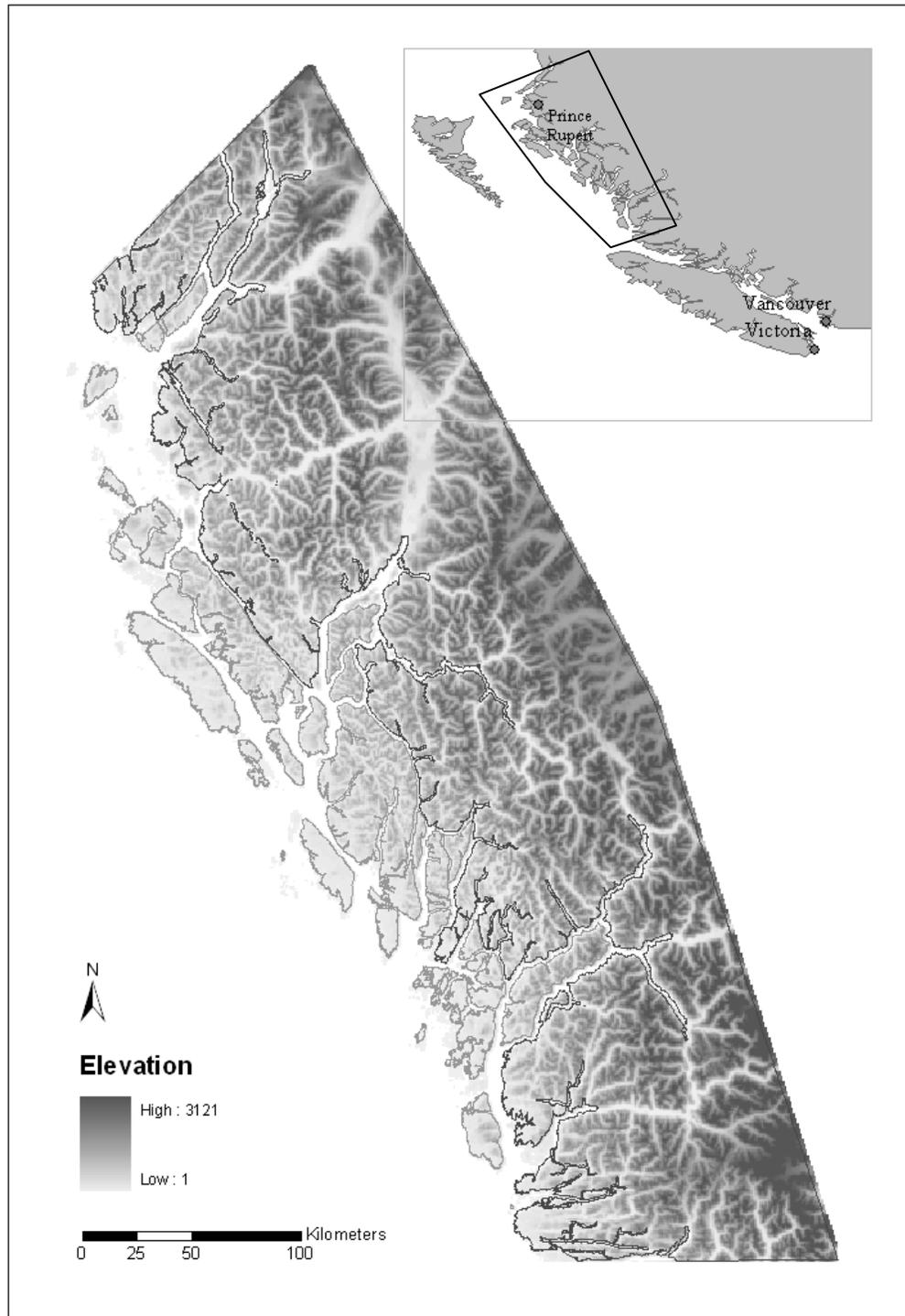Figure 1: Study area: Pacific coast of British Columbia, Canada (Darimont and Paquet 2002).

Figure 2. Probability of deer remains occurring in wolf faeces on islands as a function of their distance to the mainland. Samples collected in coastal British Columbia, summers 2000 and 2001. Reproduced from Darimont et al. (2004) with permission from Blackwell.