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Modelling Gray Wolf (*Canis lupus*) Distribution and Habitat in  
Coastal Temperate Rainforests of British Columbia, Canada

by

Patricia L. Swan

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled “Modelling Gray Wolf (*Canis lupus*) Distribution and Habitat in Coastal Temperate Rainforests of British Columbia, Canada” submitted by Patricia L. Swan in partial fulfillment of the requirements for the degree of Master of Science.

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Supervisor, Dr. Shelley M. Alexander, Geography

---

Dr. Paul C. Paquet, Environmental Design

---

Dr. Nigel M. Waters, Geography

---

Dr. Linda M. Fedigan, Anthropology

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Date

## **ABSTRACT**

Gray Wolves (*Canis lupus*) are a focal species for rare Temperate Rainforests located on the central coast of British Columbia, Canada. Characteristics of coastal wolf habitat are unknown. Wolf presence/absence data and spatial, physical and biological attributes of the coastal landscape were compiled in GIS and analysed with logistic regression.

Akaike's Information Criterion was used to select the best model describing wolf habitat. Island area and shape positively influenced wolf presence while distance to mainland, inter-island distance, and logged area negatively predicted wolf presence. Sub-island analysis showed positive effects on wolf occurrence from deer density and range of forest age, and a negative effect from mean forest age. Models had high classification accuracy evaluated with jackknife validation and Relative Operating Characteristic (ROC) curves. Identification of factors comprising coastal wolf habitat enhance understanding of the coastal ecosystem and are useful for conservation management and planning.

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## **1.0 INTRODUCTION AND RESEARCH OBJECTIVES**

The Central Pacific Coast of British Columbia, Canada is a unique area supporting Coastal Temperate Rainforest, which is an extremely rare ecosystem worldwide. The area is comprised of an island archipelago and is home to a diverse array of species. The landscape is nearly pristine because of minimal human development: this is exceedingly rare in the world today. Although biologically diverse, this area remains understudied due to its remoteness. Extensive logging proposals have prompted researchers to focus their efforts on understanding the coastal ecosystem to mitigate the negative effects of these planned disturbances. Species of importance to the coastal ecosystem have been identified as bear, wolf and salmon.

Research conducted to date on coastal wolves includes their general distribution (Darimont and Paquet 2002), interactions with salmon (Darimont et al. 2003) and foraging behaviour (Darimont et al. 2004). The relationship of wolves and coastal habitat, including physical, biological and spatial attributes is however, unknown. Identifying factors that affect wolf presence will enhance existing coastal wolf literature and provide insight into how wolves interact with a naturally fragmented landscape. The ability to predict areas of habitat importance for wolves will also assist in conservation planning.

Geographic Information Systems (GIS) are often used to model species habitat relationships as they can store and organize large amounts of data. GIS enables straightforward extraction of spatial landscape attributes, which often are difficult to

collect in the field. More importantly, GIS can be used to create predictive maps of species occurrence for conservation management and planning.

The objectives of this thesis were to:

- 1) Incorporate empirical and spatial data in a GIS to model wolf use of the coastal landscape;
- 2) Identify primary habitat factors that determine wolf presence and distribution; and
- 3) Create and validate a predictive model of habitat use by wolves, to assist in conservation initiatives.

This thesis is organized in the following manner: Chapter 2 outlines characteristics of the coastal study area in British Columbia, Canada. Chapter 3 discusses application of GIS to habitat modelling and statistical techniques, and Chapter 4 examines wolf life history. Methods and Results comprise Chapters 5 and 6 respectively, and Chapter 7 discusses the implications of the results. Chapter 8 summarizes the important conclusions from this research.

## **2.0 STUDY AREA**

Coastal Temperate Rainforest is an extremely rare habitat comprising only 2-3% of the world's temperate forests (Ecotrust 1995). Displaying the unique interaction of terrestrial and marine ecosystems, the habitat is characterised by the presence of ocean, coastal mountains, cool summers and high rainfall. They are extremely productive forests, storing between 500 and 2000 metric tons of organic matter (Ecotrust 1995). Historically,

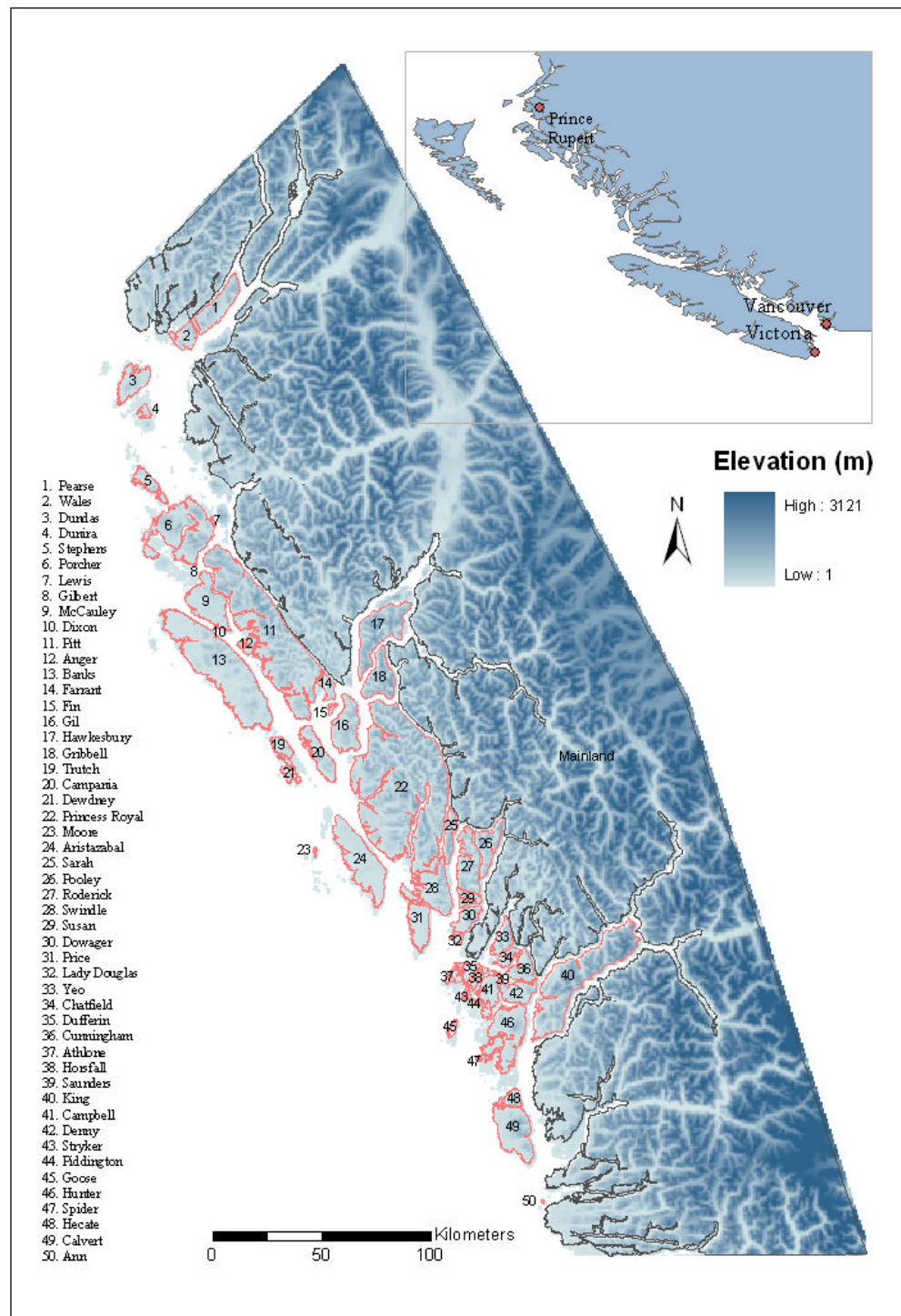
Coastal Temperate Rainforests extended from California north to Alaska, however only 56% of this range remains undeveloped. The Central Pacific Coast of British Columbia (BC), Canada, supports the most extensive remaining habitat of this type left in the world (MacDonald and Cook 1996). Combined with southeastern Alaska, the area supports the highest endemic species concentration for the Temperate Rainforest region of Pacific North America (Cook and MacDonald 2001).

The island archipelago ranging from the northern tip of Vancouver Island (51° 46' N, 127° 53' W) to Prince Rupert, BC (55° 37' N, 129° 48' W) forms 29 700 km<sup>2</sup> of study area of which 19 300 km<sup>2</sup> is land (Darimont and Paquet 2000) (Figure 1). Coastal Mountains bind the area to the east and the Pacific Ocean to the west. Temperate and wet climate dominates with most areas receiving more than 350cm of annual precipitation. Prominent tree species include Western Red Cedar (*Thuja plicata*), Western Hemlock (*Tsuga heterophylla*), Amabilis Fir (*Abies amabilis*) and Sitka Spruce (*Picea sitchensis*) (Darimont and Paquet 2000).

Access to this nearly roadless study area is limited to boat and plane travel. Development is minimal; few human settlements exist and consist primarily of First Nations people. The remoteness of this region has precluded major habitat disturbance however, mainland and island logging and salmon/shellfish farming exist. More extensive logging and oil/gas exploration are proposed for the immediate future. The threat of these developments has initiated a concerted effort to understand better the structure and function of the coastal system, so that the effects of further disturbance may be mitigated.

Ecologically, the region is understudied as it is remote and logistically challenging, however, bear (*Ursus arctos*), salmon (*Oncorhynchus* spp.) and wolf (*Canis lupus*) have been identified as focal species. Most focal species research conducted to date has studied coastal wolves.

**Figure 1:** Wolf study area: Central Pacific Coast, British Columbia, Canada. Islands included in analysis are shown outlined in pink.



## **2.1 COASTAL FOCAL SPECIES: WOLF**

Often conservation of habitat applies an ecosystem approach whereby the entire ecosystem is conserved to maintain system structure and function (Poiani et al. 2000).

One or more focal species are chosen to represent the ecosystem and provide a means to understand the structure and function of a much more complex community (Zacharias and Roff 2001). Four main types of focal species exist: indicator, keystone, umbrella and flagship (Simberloff 1998). Indicator species are sensitive to environmental change and gauge the health or quality of an ecosystem (Landres et al. 1988). Keystone species have a disproportionate effect in relation to their abundance and are integral to ecosystem function (Miller et al. 1998). Umbrella species are large ranging mammals and conservation of their habitat protects other animals within their range (Miller et al. 1998). Flagships are charismatic species used to gain public support for conservation issues (Zacharias and Roff 2001). Wolves are suitable focal species for the coastal study area as they display indicator, keystone, umbrella and to a limited degree, flagship species' attributes.

Large carnivores often are selected as indicators of ecosystem integrity. Because of shared life history characteristics including low population density, low fecundity, habitat specialization, and limited dispersal ability, large carnivores are considered sensitive to human modifications of the landscape (Carroll et al. 2000). Wolves in particular, are sensitive to human disturbance and avoid developed and high road-density areas (Fritts and Carbyn 1995, Mladenoff et al. 1995, Weaver et al. 1996, Theuerkauf et al. 2003). Coastal wolves display keystone species attributes as top predators exerting prey

population control, which indirectly affects system biodiversity (Terbough et al 1999). Coastal wolves feed primarily on Black-tailed deer; if wolves were removed from the system, escalating deer populations could result in the exclusion of deer competitors vying for the same resources (Darimont and Paquet 2000). Exclusion of a species can alter species assemblage and richness, and alter ecosystem structure. Coastal wolves are also keystone species because of their role in nutrient cycling. Wolves only ingest the head of spawning salmon leaving the remaining carcass on the forest floor (Darimont and Paquet 2000). Salmon remains are rich in phosphorus and nitrogen, and essential to the nutrient-deprived coastal system (Darimont et al. 2003).

Wolves are good umbrella focal species because they are good dispersers (Weaver et al. 1996) and use large home ranges (Carroll et al. 2000). Home range size varies from 500 to 2000 km<sup>2</sup> for Rocky Mountain wolves (Carroll et al. 2000). Protection of wolf habitat would protect habitat for a multitude of other species with smaller area requirements. Coastal wolves also play a limited role as flagship species; wolves are of conservation concern worldwide and portray an image of Canada's expansive wilderness.

### **3.0 GIS AND HABITAT MODELLING**

#### **3.1 GIS HABITAT MODELLING IN ECOLOGICAL RESEARCH**

To comprehend fully how a focal species interacts with its environment, habitat requirements must be identified in relation to landscape configuration. GIS and remote sensing (RS) applications are extremely useful tools to examine this relationship, and allow extraction of spatial attributes such as island area and isolation. Physical habitat

characteristics that are costly and time-consuming to collect in the field, can be easily extracted from RS imagery in conjunction with GIS. Landscape attributes can be combined with empirical data relating to species distribution and abundance, and modelled using GIS applications.

GIS can analyse systems that are very complex or difficult to study in a natural setting (Oreskes 2000). A greater advantage of GIS however, is the ability to make predictions. Models of species distribution and abundance can be used to delineate areas of conservation concern, and to identify and predict regions of biodiversity importance (Prasad et al. 1998, Debinski et al. 1999, Lenton et al. 2000). GIS and RS technologies are extremely useful modelling tools for conservation planning (Poiani et al. 2000). Yet conservation decisions often are based on interpretations of incomplete data extracted using GIS (Funk et al. 1999). Models are reflective of the quality of input data and should be interpreted with caution. Errors made in the initial stages of field sampling, measuring, or classification of RS imagery, can propagate throughout the modelling process and reduce confidence in the final predictions. If predictive models are to be used for conservation decisions, assumptions, limitations, and sources of error or bias, should be clearly stated.

### **3.1.1 Presence/Absence Habitat Models**

Despite limitations, GIS models that predict species presence are increasingly important tools for conservation and wildlife management (Pearce and Ferrier 2000). Species presence/absence data usually are collected in the field using a GPS to mark presence or



absence locations. These locations are directly transferred into GIS and used to extract corresponding habitat characteristics. Statistical analysis can be run and a predictive map created from the final statistical model. The predictive map shows probability of species occurrence throughout the study region based on the statistical model. Presence/absence GIS modelling has been conducted on a multitude of species including birds (Shriner et al. 2002), reptiles (Raxworthy et al., 2003), and mammals (Woolf et al. 2001).

### **3.2 LOGISTIC REGRESSION AND MODEL SELECTION**

#### **3.2.1 Logistic Regression**

Dettmers et al. (2002) found logistic regression to be a more fully developed statistical technique for general wildlife-habitat modelling. Logistic regression has advantages over linear and multiple regressions because it can accommodate dichotomous and categorical variables (Hosmer and Lemeshow 2000). Ecological data often are recorded as classes (e.g. vegetation) and in presence/absence binary form (e.g. species presence). Moreover, prediction of regular regression models results in negative probabilities, whereas logistic regression generates values confined between 0 and 1. Probabilities derived from logistic regression can be calculated as:

$$\text{Eq. 1} \quad p = 1/[1 + \exp(-1*(a + bX_1 + cX_2...))]$$

where  $p$  is the probability of interest,  $a$  is the intercept, and  $b$  and  $c$  are coefficients for independent variables,  $X_1$  and  $X_2$  (Logan 2003). Logistic regression is robust to violations of parametric assumptions (Trexler and Travis 1993) and does not assume normality of independent variables, although the power of analysis is increased with normality and linearity (Tabachnick and Fidell 2001). Consequently, logistic regression

is well suited to analyse ecological data, which often does not adhere to assumptions required for parametric regressions.

Logistic regression does however, maintain certain assumptions. It assumes that the model is well-fitted to the logistic function which can be examined with the Hosmer-Lemeshow chi-square test (Hosmer and Lemeshow 2000). Values approaching 1 are considered a good fit. Logistic regression also assumes the absence of multicollinearity amongst independent variables (Tabachnick and Fidell 2001). Correlated variables can increase standard error and weaken the analysis. Often correlations of 0.7 or greater are used as a cutoff to identify problem variables (Tabachnick and Fidell 2001). Removal of one or more of the correlated variables will eliminate multicollinearity. Assumptions of independent samples and removal of outliers also are necessary for logistic regression analysis. In particular, logistic regression assumes that the ratio of samples to independent variables is sufficient. Large parameter coefficients and standard errors, or complete failure of the model to derive a solution, may indicate that this assumption is violated (Hosmer and Lemeshow 2000, Tabachnick and Fidell 2001). For optimum confidence in analysis with logistic regression, data and assumptions should acquiesce.

When the previous assumptions are met, GIS habitat models using logistic regression and presence/absence data allow effective modelling of habitat (Boyce and MacDonald 1999). In fact, analyses of presence/absence data using logistic regression are prevalent (Boyce et al. 2002) and have been applied to songbirds (Boyce et al. 2002), grizzly bear (Apps et al. 2004), lynx (Schadt et al. 2002), and wolves (Ciucci et al. 2003).

### 3.2.2 Model Selection and Akaike's Information Criterion

In the past, habitat modellers (and scientists in general) have used null hypothesis testing to determine if the relationship between a species and specific habitat characteristics was significant. Traditional null hypothesis testing however, is rapidly being replaced with model selection techniques in ecology (Johnson and Omland 2004). The main advantage of a model selection technique is the absence of a probability threshold (i.e.  $p$ -value).

Null hypothesis testing requires definition of a significance ( $p$ ) value to determine acceptance or rejection of the null hypothesis. Selection of the  $p$ -value often is arbitrary (usually 0.05 or 0.01) and may not reflect biological significance of the phenomena being tested (Burnham and Anderson 2002). Testing a null hypothesis also contributes little to the advancement of scientific information, because there is an expectation that it will be rejected. Alternatively, model selection techniques do not require an acceptance threshold, but rather select a model from a suite of potential models, that best describes the process of interest. Models can be ranked and weighted and those with similar weights can be averaged. Model selection is particularly beneficial for complex systems (e.g. ecosystems) that are difficult to test experimentally (Johnson and Omland 2004).

Model selection has philosophical differences to hypothesis testing. It is based on scientific *a priori* reasoning to develop a set of plausible candidate models that explain the process of interest. A best approximating model for the observed data is then selected from the set of candidate models (Burnham and Anderson 2002). Akaike's Information Criterion (AIC) and Bayesian Information Criteria (BIC) are model selection methods used to determine the best model according to model fit and complexity. However, the

strict assumptions of BIC that a true model exists, is present in the suite of models, and is equally as probable as the other candidate models before analysis, are often not met with empirical data (Johnson and Omland 2004).

AIC derives a measure of model fit using maximum-likelihood theory and Kullback-Leibler (K-L) information. K-L distance is the relative distance of each model in the set from an approximation of reality (Burnham and Anderson 2002). It is calculated as a negative loglikelihood (-2LL) score and actually measures the *lack* of fit of each model. Negative loglikelihood values between models in the set can be compared to determine which one best approximates the true process. AIC not only incorporates model fit when selecting a best model, but also accounts for model complexity. The Principle of Parsimony (i.e. Ockham's razor) is the balance of statistical bias and variance (Burnham and Anderson 2002). Models with too few parameters have highly biased parameter estimates and can underfit the data, leaving out important predicting factors. Models with too many parameters have high variance in parameter estimates and can overfit the data, which may inflate the importance of spurious factors (Burnham and Anderson 2002, Johnson and Omland 2004). In contrast, parsimonious models balance bias with variance. AIC applies the principle of parsimony by penalizing models with greater complexity (more parameters). AIC accounts for model fit and complexity according to:

$$\text{Eq. 2} \quad \text{AIC} = -2\text{LL} + 2K$$

where -2LL is the loglikelihood (representing lack of model fit), and K is the number of model parameters representing model complexity (Burnham and Anderson 2002). The best model will be that which minimizes K-L relative distance while maintaining

adequate complexity, and possesses the lowest AIC value. AIC however, can perform poorly if the number of parameters is too large relative to sample size,  $n$ . Specifically, when the ratio of sample size to parameters is less than 40, a corrected form of AIC (AICc) is used that accounts for sample size. This equation is calculated as:

$$\text{Eq 3.} \quad \text{AICc} = \text{AIC} + \frac{2K(K+1)}{n - K - 1} \quad (\text{Burnham and Anderson 2002})$$

The best model from the candidate set is selected using Akaike weights. Weight ( $w_i$ ) is the amount of evidence that a model is the best approximation of truth. To select the best model, AIC assumes that one of the models is a true description of the process (Burnham and Anderson 2002). Akaike weights are calculated for each model using the difference in AICc value between the lowest AICc model and each individual model. If a model is removed from the set, weights must be recalculated. The model with the greatest weight is the best approximating model.

The strength of AIC analysis lies in the comparison of several competing hypotheses and its ability to select the best model for the observed data. This strength assumes selection of candidate models is based on sound biologically-relevant reasoning (Burnham and Anderson 2002). A balance must be struck between having too few and too many models. Too few models may result in failure to include a potentially viable model and can result in a misleading outcome (Johnson and Omland 2004). Inclusion of every possible explanatory model is analogous to data dredging and counter to the philosophy of *a priori* reasoning (Burnham and Anderson 2002).

Although well developed in other fields (e.g. economics), AIC and model selection analysis is a relatively new approach to habitat modelling and represents a paradigm shift in ecological research. Model selection techniques have been used primarily to model habitat for birds (Boyce et al. 2002, Dettmers et al. 2002, Young and Hutto 2002) and less frequently in mammal research (Carroll et al. 1999, Apps et al. 2004). Model selection methods are however, expected to become more prevalent as time progresses.

### **3.3 MODEL VALIDATION**

Model selection techniques like AIC may select the best model for the data but offer no insight into predictive accuracy. Model evaluation is an important step in model development (Pearce and Ferrier 2000) but often is not applied. A good predictive model will be reliable and accurately predict the probability of species presence. It also will be discriminatory, correctly differentiating between species presence and absence irrespective of model reliability (Verbyla and Litvaitis 1989). Testing the model with independently collected data (not used to compile the model) is unquestionably the best way to determine model classification accuracy (Verbyla and Litvaitis 1989, Fielding and Bell 1997, Pearce and Ferrier 2000, Fielding 2002, and others). However, testing with independent data is not always possible due to the cost and time involved in data acquisition.

Several model validation methods exist that do not require independent data. These involve resampling of the original dataset and include resubstitution, cross-validation, jackknife and bootstrap methods (Fielding and Bell 1997). Resubstitution is simply

testing the model with the data it was derived from. However, this method is biased in prediction success and tends to overfit the model (Fielding 2002). Cross-validation is the division of the dataset into 2 subsets; one to compile the model and the other to test it. This method results in loss of degrees of freedom reducing model significance (Verbyla and Litvaitis 1989) and can be difficult to execute with a small sample size. Jackknife validation is much more precise than the previous two methods and tests the model through resampling without replacement: a single data record is withheld from the sample (of size  $n$ ) and a model is then compiled with the remaining  $(n-1)$  dataset. The withheld record is then used to test the model. This process is repeated for the entire sample resulting in  $n$  prediction and test values (Fielding and Bell 1997). Bootstrapping is similar to jackknifing but entails resampling *with* replacement and often is repeated 200-1000 times. Although bootstrapping is the most precise method of resampling validation, it requires the most computation time (Verbyla and Litvaitis 1989).

### **3.4 MODEL EVALUATION**

Misinterpretation of the predictive accuracy of a model could have devastating effects on a species, particularly if the model errs in predicting absence when a species is actually present (Fielding 2002). To illustrate, traditional model evaluation is calculated using a 2 X 2 confusion matrix, where species presence or absence is determined according to a probability threshold set by the researcher. Thus, if probabilities for a species presence range from 0 to 1, a species can be defined as present when the probability is 0.7 or greater, and absent when it is less than 0.7. The value of 0.7 is set by the researcher and is subjective. Four values are calculated in a confusion matrix: sensitivity, specificity,

false positive fraction and false negative fraction (Pearce and Ferrier 2000). Sensitivity is the percent of positive predictions that were actually present, and specificity is the percent of absence predictions that were actually absent. False positive and false negative fractions are calculated as the percent of observed values that were not accurately predicted by the model, and represent commission and omission error respectively. Commission error (false positive), occurs when a species is not present in a landscape but is predicted to be present by the model. Omission error, (false negative), occurs when a species is present in the landscape but not predicted by the model (Schaefer and Krohn 2002). Omission errors are more troublesome from a conservation perspective because they remain constant and become more precise with increased sample size. Commission error generally decreases with increased sample size (Karl et al. 2002). Thus, omission and commission errors can be weighted to reflect the severity of model mis-prediction by adjusting the probability threshold. Furthermore, if the dataset includes a small number of species presence points, overall model accuracy can be high, as it is based primarily on a high percent of correctly identified absences. The percent of correct and overall classifications is dependent on the presence threshold set by the researcher. Although this threshold can be adjusted to reflect species rarity and the severity of omission/commission error, it is still arbitrary in nature (Pearce and Ferrier 2000) and can bias the accuracy measure (Fielding and Bell 1997).

The use of Relative Operating Characteristic (ROC) curves eliminates the need to define a presence threshold and is a viable alternative to confusion matrices to evaluate model accuracy. ROC curves depict model discrimination between presence and absence over



the entire range of probability thresholds. Specifically, they plot model sensitivity (the proportion of true predictions that are present) on the y-axis against the false positive fraction values (1 - specificity) on the x-axis (Fielding 2002). A plot that results in a 45 degree line indicates the model has no discrimination ability and is no better than chance at predicting presence and absence. Discrimination ability is represented by AUC, the area under a ROC curve. An area of 1 represents perfect discrimination, or high classification accuracy. An area of 0.5 represents no discrimination ability and is represented by the 45 degree line (Fielding and Bell 1997). AUC is used as an index of model performance and allows comparison between models (Pearce and Ferrier 2000). ROC curves offer a viable technique to test model classification accuracy without the ambiguity of a probability threshold, as is required with traditional confusion matrices.

### **3.5 GIS HABITAT MODELLING OF COASTAL WOLVES IN THE STUDY AREA**

As discussed previously, GIS, logistic regression and AIC are extremely useful analytical tools to model and predict species presence. Habitat associations for coastal wolves are unknown and these methods allow exploration of habitat factors affecting coastal wolf presence. However, *a priori* hypotheses of what constitutes wolf habitat are required for AIC. Limited research is available on coastal wolves, yet there is an abundance of literature available on the ecology and life history of wolves located elsewhere in the world. Wolf life history traits can provide general insight into coastal wolf ecology. When combined with existing research on coastal wolves, life history characteristics can allow derivation of well-informed hypotheses describing coastal wolf habitat.

## 4.0 GRAY WOLF (*Canis lupus*) LIFE HISTORY

### 4.1 NATURAL HISTORY

Gray Wolf (*Canis lupus*) is the largest species of the carnivorous dog family, *Canidae*, which includes such mammals as foxes, coyotes and dogs. Wolves have thick black, gray, tan or white fur, are between 1.27 and 1.64m in length, and weigh between 20 and 80 kg (Paquet and Carbyn 2003). Wolves located in the coastal study area differ from interior wolves in size and fur colour; they are generally smaller and often exhibit a reddish-tinge coloured fur (Figure 2) (Darimont and Paquet 2000). Although all wolves are good swimmers (Mech 1970), coastal wolves are extremely adept at swimming and are able to swim distances as far as 13 km between islands (Darimont and Paquet 2002).

**Figure 2:** Coastal wolves (by permission, Raincoast Conservation Society).



## **4.2 DISTRIBUTION**

In North America, wolves were historically found in all habitats north of approximately 20° N latitude (Paquet and Carbyn 2003). Human persecution through trapping, hunting, poison, predator-control programs, and excessive prey hunting, has extirpated wolves from many habitats in North America. Wolves have been completely extirpated from the USA although reintroduction efforts in Yellowstone Park and surrounding areas have recolonized their populations (Smith et al. 2004). In Canada, wolves have been extirpated from southern BC, much of the prairies, southern Ontario and the Atlantic provinces (Theberge 1991). Canada however, continues to support the most widespread, unexploited population of wolves in the world, second only to the former Soviet Union where human persecution of wolves still exists (Theberge 1991). Coastal wolves once occupied the entire temperate rainforest range extending from California to Alaska. They are now isolated to central and northern BC and Alaska as a result of forestry practices and human development. Population of coastal wolves in the study area is estimated at 325-378 resident individuals (Darimont and Paquet 2000).

## **4.3 SOCIAL STRUCTURE AND REPRODUCTION**

Wolves are social animals, hunting and living in packs that defend territories. Alaskan coastal wolf pack size is estimated at 6.4 individuals (Person 2000) and is expected to be the same in the study area (Darimont and Paquet 2000). Packs are family-based consisting of a male, female, newborn and older pups, and occasionally adults from other packs (Mech 1970). The male and female parents guide the pack using a 'division-of-labour' structure where the female is responsible for the care and defense of pups, and the

male for hunting and providing food (Mech 1999). Wolves breed once a year between January and April at 2 to 3 years of age depending on pack structure (Mech 1970, Weaver et al 1996). Average litter size is 6 but ranges from 1 to 11 (Paquet and Carbyn 2003). Average litter size for coastal wolves is estimated at 3.3 pups (Darimont and Paquet 2000). Alaskan coastal wolves den under tree roots or fallen large logs in low elevation, old-growth forest near fresh water (Person 2000). B.C. coastal wolves are thought to have denning behaviour similar to Alaskan coastal wolves, but this has not been researched fully (Darimont and Paquet 2000). Rendez-vous sites usually are found in open, grassy areas and are used by pups to await the return of adults from hunting.

#### **4.4 PREY**

Wolves exhibit behavioural plasticity in food selection, substituting one prey for another according to availability (Weaver et al. 1996). They are prey generalists that hunt and scavenge a variety of species. A single or pair of wolves can take down young or old prey but often the entire pack is used to take down a fully mature adult. Coastal wolves feed primarily on Sitka black-tailed deer (*Odocoileus hemionus*) and prey more heavily on spawning chum and pink salmon (*Oncorhynchus* spp.) in the fall. Deer and salmon accounted for 84% and 9% respectively of coastal wolf diet in summer and for 68% and 24% in the fall (Darimont and Paquet 2000). Fishing for salmon is energetically less expensive than hunting for ungulates (Darimont et al. 2003) and the transition to salmon prey in the fall may improve pup survivorship during weaning (Person 2000).

A variety of other animals comprise the remaining small portion of coastal wolf diet. Other animals that have been identified in coastal wolf scat include moose (*Alces alces*), black bear (*Ursus americanus*), beaver (*Castor canadensis*), mountain goat (*Oreamnos americanus*), river otter (*Lutra canadensis*), marten (*Martes americana*), mustelids, beached marine mammals, birds and rodents (Darimont and Paquet 2000).

#### **4.5 COMPETITORS**

Interspecific competition of coastal wolves with other large carnivores is not fully understood but may reflect resource partitioning, where species co-exist by exploiting different resources (Smith 1996). Competitors of coastal wolves include large carnivores such as grizzly bear (*Ursus arctos horribilis*), black bear (*Ursus americanus*), wolverine (*Gulo gulo*), coyote (*Canis latrans*) and cougar (*Felis concolor*) (Darimont and Paquet 2000). Space and diet requirements of these species may overlap with that of coastal wolves and their presence may competitively exclude wolves from certain habitats.

#### **4.6 POPULATION FLUCTUATIONS**

Natural fluctuations in wolf populations can result from parasitism and disease, particularly Canine Parvovirus (CPV) and rabies (Mech 1970). CPV is a disease of domestic dogs, usually fatal in puppies. Although not documented in coastal wolves, CPV has been found to inversely affect pup proportion and percent annual population growth in Minnesota wolves, and is considered to be a potentially significant mortality factor in isolated, small populations (Mech and Goyal 1993). The rate of rabies in coastal wolves has not been recorded, but was responsible for 21% of mortalities (n = 52) in

northwest Alaska (Ballard and Krausman 1997) and was present in 12 of 51 cases of documented aggressive wolf-human encounters in Alaska and Canada (McNay 2002).

In populations relatively free of human disturbance, prey density is suggested to be the greatest limiting factor on wolf population (Fuller et al. 1992). The ability of wolves to control prey populations according to a predator-prey relationship is not very well understood and depends on numerous factors including the specific wolf population, prey size and weight, and the ratio of wolves to prey (Mech 1970, Bjorge and Gunson 1989). With undocumented disease rates, the presence of deer is likely the most important natural factor affecting coastal wolf populations.

#### **4.7 HABITAT**

Wolves exhibit habitat plasticity and can occupy any type of habitat that supports their prey (Mech 1995). Ungulate prey availability positively influenced wolf presence in northern Italy (Massolo and Meriggi 1998, Ciucci et al. 2003) and is thought to be the main factor contributing to viable wolf populations for the next 100 years (Carroll et al. 2000). Prey availability however is mediated by topographic characteristics such as slope, elevation and forest type, which can restrict wolf movement through a landscape. In the Central Canadian Rocky Mountains, elevations greater than 1850m, slopes greater than 30 degrees and SSW aspects were found to negatively affect wolf presence (Alexander et al. 1996). Ciucci et al. (2003) found wolves in northern Italy responded primarily to prey density but avoided high elevations, steep slopes and N-NE aspects during winter travels. Vegetation types are not usually indicative of wolf presence except

through provision of prey habitat (Carroll et al. 2000). However, forest provides denning and rendez-vous sites for wolves, as well as protection and concealment (Mech 1970, Theuerkauf et al. 2003).

Wolves are extremely efficient dispersers, observed to travel as far as 732 km in 9 months (Ballard et al. 1983). They require extensive areas and have large home ranges. Size of the home range depends on the specific pack location, and prey density and type (Paquet and Carbyn 2003). Although the home range size of coastal wolves is unknown, Alaskan coastal wolves are estimated to occupy areas of 260 km<sup>2</sup> (Person 2000).

Exact elements constituting coastal wolf habitat are unknown but likely reflect characteristics associated with deer habitat. The topographic complexity of the coastal region limits both deer and wolf movements through the landscape, forcing them to travel and habituate less steep, lower elevation valleys and estuaries. Old growth forest also is an important habitat characteristic, providing browse and winter habitat for deer, as well as sites important for wolf reproduction (dens and rendezvous sites).

#### **4.8 HUMAN EFFECTS AND FRAGMENTATION**

Historically, human-related activities have had the greatest influence on wolf presence in a landscape. In the last 200 years, wolf populations have been severely impacted by direct human persecution in the form of hunting, trapping and predator-control programs (Carbyn 1974, Kaye and Roulet 1979). Wolf mortalities from hunters in the study area are estimated to be 2.3% of the annual population (Darimont and Paquet 2000), however,

this rate would be expected to increase with more extensive human disturbance and presence.

Landscape modification by humans has played an indirect, yet extremely significant role in mediating wolf numbers through direct habitat and resource loss, but also fragmentation effects. Habitat fragmentation is the subdivision of a large contiguous habitat into smaller fragments and can be natural (ie disease, wildfire, storms, avalanches) or anthropogenic (ie logging, development, road creation) in origin. The effects of fragmentation and habitat loss are modified by landscape configuration, specifically the size, shape and layout of habitat fragments (Saunders et al. 1990). Larger, connected fragments provide more suitable habitat than smaller, isolated fragments (Diamond 1975). Isolated fragments impede species gene flow and genetic diversity that allow adaptation to environmental change (Britten and Baker 2002) and recolonization response to epidemics (Root 1998). Conservation and management of fragmented landscapes usually apply island biogeography and metapopulation theories to predict how species will respond to changes in their landscape. Island biogeography theory (IBT) maintains that species richness, as determined by the rate of immigration and extinction, is mediated by island area and isolation (MacArthur and Wilson 1967). A metapopulation is a collection of local or subpopulations, whose persistence is dependent on the interaction between colonization and extinction of subpopulations (Andren 1994); extinction of too many local populations will cause extinction of the metapopulation. The effects of fragmentation are complex but have three main consequences: habitat loss, reduction of existing habitat patch size, and isolation of remaining habitat fragments



(Andren 1994). The primary cause of modification affecting coastal wolves is clearcut logging and its effect on black-tailed deer populations. Coastal wolves are highly dependent on deer and the long-term carrying capacity of deer populations cannot be sustained with current logging practices (Darimont and Paquet 2000). Loss of habitat limits resource availability for both deer and wolves, and may force either species to relocate. Reduction of existing habitat from logging also increases the amount of edge relative to interior habitat available. Introduction of edge habitat can affect species functioning in a particular manner (Lidicker 1999) and alter the biotic community by exposing species to new competitors, predators or exotic species (Harrison and Bruna 1999). Road fragmentation from logging practices can directly affect wolf mortality rates through an increase in potential vehicle collisions or by providing previously non-existent access for hunters and poachers (Noss et al. 1996). Wolves avoid high traffic and high road density areas (Carroll et al. 2000, Ciucci et al. 2003, Theuerkauf et al. 2003, Jedrzejewski et al. 2004) and are considered sensitive to human disturbance (Weaver et al. 1996).

## **5.0 METHODS**

### **5.1 DEPENDENT VARIABLE**

Islands were surveyed for wolf presence during summer and fall from 2000 to 2003. Data were collected for 36 islands by C. Darimont and P. Paquet in 2000 and 2001 (Darimont and Paquet 2002). During 2002 and 2003, Darimont and Paquet surveyed 14 more islands and re-sampled several of the islands surveyed in 2000 and 2001 (Paquet et al. *in review*). I assisted in data collection for summer 2002. In total, 50 islands in the

archipelago were surveyed, ranging in size from 0.71 km<sup>2</sup> to 2290 km<sup>2</sup>. Sample sites on islands were selected non-randomly and limited to areas where safe moorage was possible. Surveys were initiated at beaches, estuaries and beach-flanked forests and followed wildlife trails, logging roads, forest ridgelines and the perimeters of wetlands and beaver ponds. Survey efforts did not extend further than 5 km inland. Wolf presence on an island was determined by the existence of scat, tracks, scrapings or direct observation (Darimont *pers. comm.*, Darimont and Paquet 2002). Howls or vocalizations also were considered indicative of wolf presence. Islands with wolf presence were given a value of 1; islands with no wolf presence were assigned a value of 0.

## 5.2 INDEPENDENT VARIABLES

### 5.2.1 Rationale

Based on wolf life history and Alaskan wolf attributes, coastal wolves are thought to prefer larger, less isolated islands that are not topographically complex, which may be a function of prey presence and density. Independent variables were selected to represent these factors affecting wolf presence (Table 1). Variables were further broken down into physical, spatial and biological categories (Table 2).

**Table 1:** Wolf presence factors and associated independent variables.

| <b>Factor</b>                                 | <b>Associated Independent Variables</b>                                       |
|---|---|
| Presence of prey                              | Deer density, mammal richness, prey richness, salmon richness, salmon biomass |
| Presence of Competitors                       | Competitor Richness   |
| Spatial Configuration of Islands and Mainland | Island area, shape index, distance to mainland, distance to nearest island    |
| Vegetation                                    | Vegetation index (greenness), old growth forest index (wetness, % old growth) |
| Topographic Complexity                        | Elevation, slope, aspect  |
| Human Disturbance                             | % Logged Area   |

**Table 2:** Physical, biological and spatial independent variables.

| <b>Physical</b> | <b>Spatial</b>                  | <b>Biological</b>    |
|-----------------|---------------------------------|----------------------|
| Elevation       | Island Area (km <sup>2</sup> )  | Deer Pellet Density  |
| Slope           | Island Shape Index              | % Old Growth Forest  |
| Aspect          | Distance to Mainland (km)       | Greenness            |
|                 | Distance to Nearest Island (km) | Wetness              |
|                 |                                 | Mammal Richness      |
|                 |                                 | Prey Richness        |
|                 |                                 | Competitor Richness  |
|                 |                                 | Salmon Richness      |
|                 |                                 | Total Salmon Biomass |
|                 |                                 | % Logged Area        |

Considering the strong relationship between wolves and ungulate prey, black-tailed deer presence is expected to be the most influential factor on coastal wolf occurrence.

However, landscape and biological characteristics also may predict wolf presence because of their importance to wolf reproductive ecology, or because they indicate deer habitat.

Physical influences on wolf presence include elevation, slope and aspect (Alexander et al. 1996). Topographic complexity of islands in the study region necessarily limits wolf and deer movements to low elevation and less steep terrain often located in valleys and estuaries. These areas can offer valuable deer habitat, denning sites, access to fresh water for pups and adults, and spawning salmon in the fall. Aspect may also influence wolf presence. South-facing slopes are warmer and drier than north slopes, and can support a completely different biotic community (Strahler and Strahler 2002). Deer may be attracted to a specific directional aspect because of vegetative associations, and wolves may respond to their presence.

The spatial relationship of wolves and deer likely is mediated by island configuration. An initial survey of islands in the study area found wolves on all islands with deer presence, except for small, isolated islands (Darimont and Paquet 2000). Island area, distance to mainland and distance to nearest island variables were selected to represent spatial aspects of the coastal landscape and to reflect IBT. Larger islands are expected to support deer and wolf because they have more habitat area. Islands that are closer to the mainland also may support deer and wolf because their close proximity to a population source allows efficient immigration. Closely clustered islands may effectively increase the total area available for wolves and deer. Islands with large distance to other islands are not expected to support wolves; wolves are capable of swimming between islands but are limited by island-to-island distance, wind, and water currents (Darimont and Paquet 2002). Shape index measures how convoluted the perimeter of an island is. Islands with a shape index approaching 1 maximize island area and according to IBT, increase the amount of potential deer and wolf habitat available.

Biological variables included vegetation characteristics, prey presence, competitor presence, and human disturbance. Forest provides habitat for deer and a multitude of other small mammals as well as denning and rendezvous sites for wolves. Greenness, a vegetation index derived from Landsat imagery using Tassel Cap Analysis (TCA), provides a measure of vegetation density, with higher values reflecting more vegetation. Wetness also is derived from TCA and is indicative of structural stages of old growth forest (Cohen and Spies 1992). Islands with a higher percentage of old growth forest were expected to attract deer and consequently wolves.

Wolves were found to consume more deer on islands close to the mainland than those further away, where small mammals replaced deer in wolf diet (Darimont et al. 2004). On more isolated islands, mammal and prey richness were expected to be more important factors affecting wolf presence than deer occurrence. Also, islands with more competitors may exclude wolves due to overlap of territories and competition for prey and other resources.

Second to deer, salmon comprise a substantial part of wolf diet (Darimont and Paquet 2000). Salmon richness and biomass are indicators of the number of salmon species present on an island, and the amount of salmon available for coastal wolves. High salmon richness and biomass were expected to positively influence wolf presence.

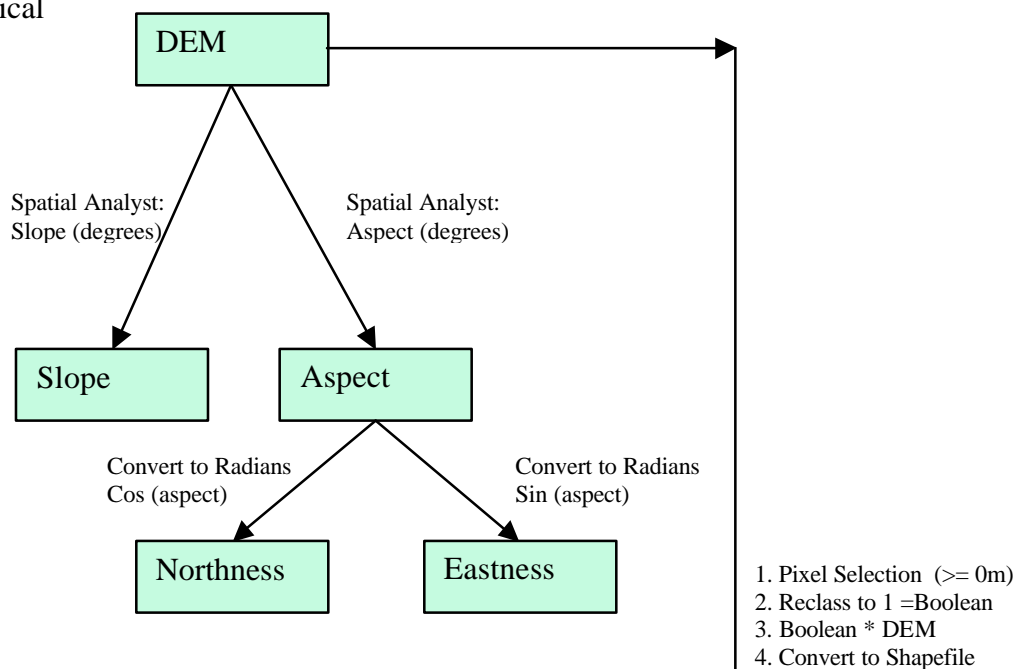
Presence of human disturbance in the form of logging is also thought to affect wolf presence (Darimont and Paquet 2000). Percent logged area represents the proportion of island area occupied by forestry activities including actual logged area, logging roads and logging camps. Islands with significant modification were expected to have lower probabilities of wolf presence.

### **5.2.2 Compilation**

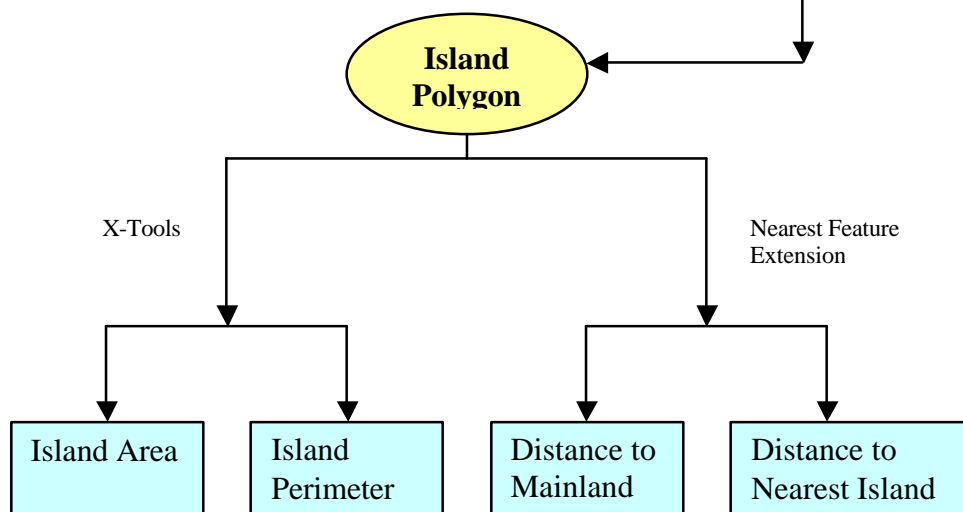
Predictive variables were created as GIS layers in ArcView 3.2 and ArcGIS 8.0 (ESRI 2000)(Figure 3). A 50m resolution Digital Elevation Model (DEM) was used to create an island polygon layer and its associated attribute table served as the final database, holding all variable data for each island.

**Figure 3:** Flow chart representing compilation of (a) physical, (b) spatial and (c) biological GIS data layers. Green boxes represent ArcGIS raster layers, yellow circles represent vector layers, blue boxes are data output and orange boxes, remotely sensed imagery.

a) Physical



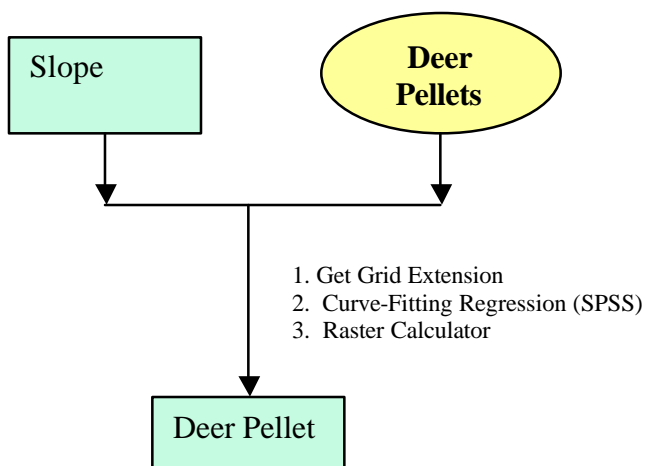
b) Spatial



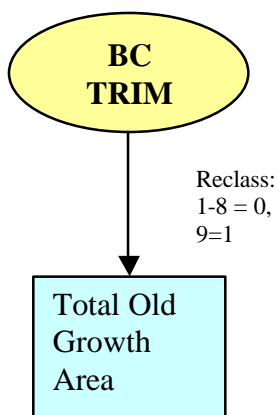
**Figure 3: cont.**

## c) Biological

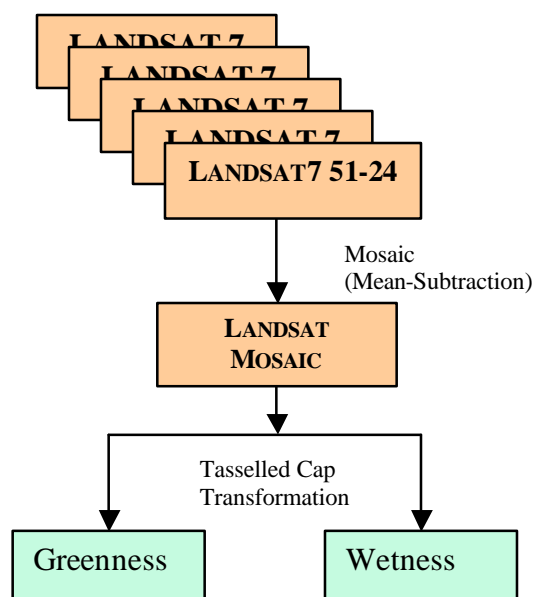
## Deer-Pellet Sub-model



## Old Growth



## TCA Variables



### ***Physical Variables***

Elevation data were extracted from the DEM. Slope and aspect layers were derived from the DEM using ArcGIS modules. Aspect was converted from degrees to radians using the formula:

$$\text{Radians} = \text{degrees} * \pi / 180 \text{ (where } \pi = 3.14159265\dots)$$

and subsequently transformed into northness and eastness layers to remove the circularity from the distribution (as per Clark et al. 1999). Northness represents a north-south gradient ( $\cos[\text{aspect}]$ ) and eastness an east-west gradient ( $\sin[\text{aspect}]$ ). Means and standard deviations were calculated per island for elevation, slope, northness and eastness layers using the island polygon layer and ArcGIS Spatial Analyst. This statistical extraction was necessary to quantify the raster-based layers for analysis.

### ***Spatial Variables***

Spatial variables included island area, distance to nearest island and to mainland and island shape index. Island area and perimeter were calculated with the X-Tools extension in ArcView3.2. Shape index was calculated as:

$$(0.25 * \text{Perimeter}) / \text{Square Root of Area}$$

as per Forman and Godron (1986) and McGarigal et al. (2002). Island distances to the mainland and to the nearest island were calculated using the Nearest Feature extension (ArcView3.2). This extension calculates the shortest distance between two designated polygons. It was assumed that wolves travel the shortest distance between islands or to the mainland.



## ***Biological Variables***

### *Deer Sub-Model*

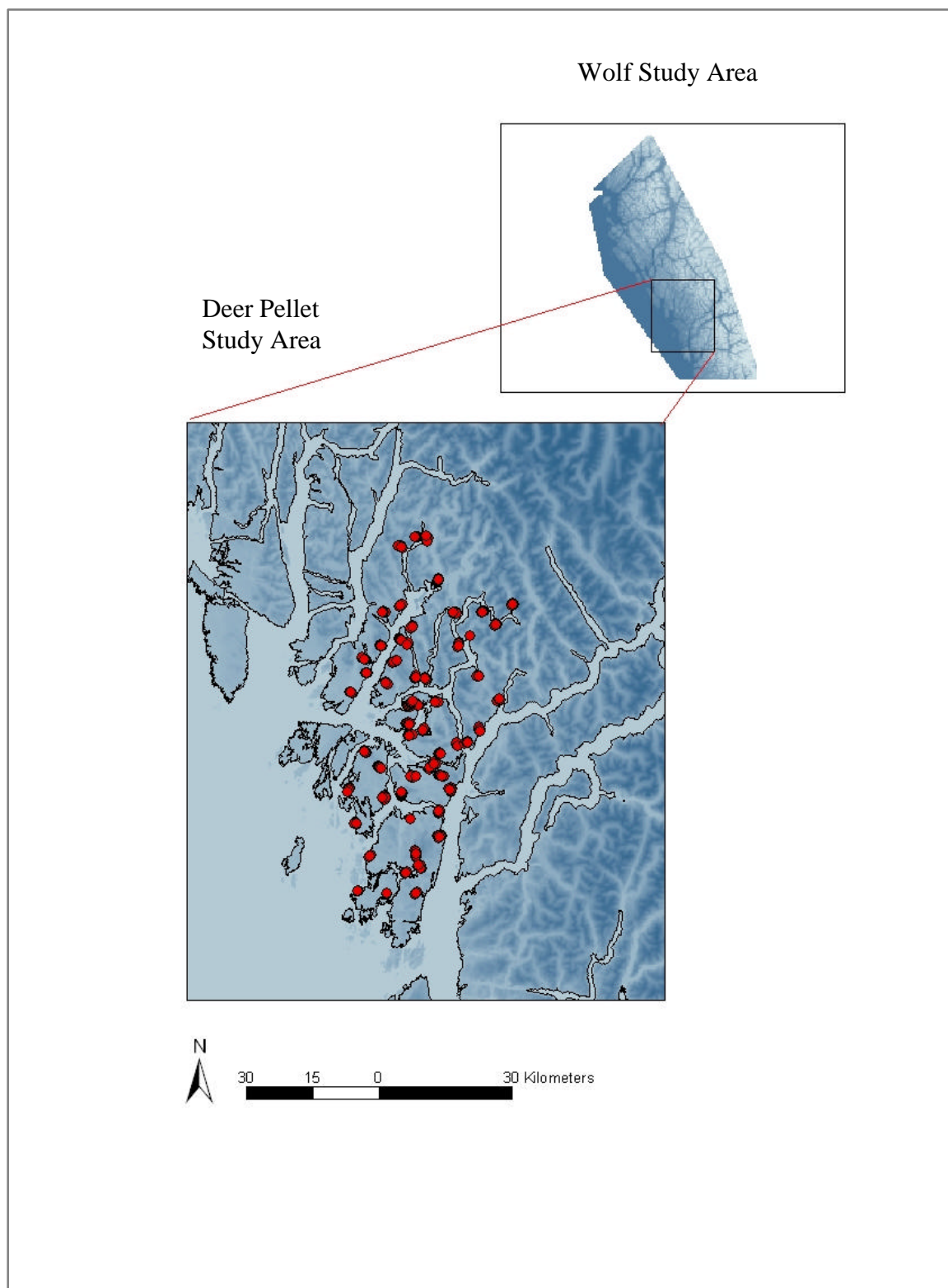
A deer sub-model was built to obtain deer probability values for each island. Deer pellet surveys were conducted in 2002-03 along 1km transects at 60 locations within a smaller 3000 km<sup>2</sup> study area (Figure 4). At least 200m apart, transects were paired and broken down into 1 by 20m plots (50 plots in total per transect). The number of deer pellets was recorded for each plot. GPS readings were taken at the beginning and end of each transect and at 100m intervals. These locations were then plotted as a point file in ArcGIS and the number of deer pellets up to and including the 100m interval point were tallied.

A deer pellet relationship was determined using logistic regression, relating deer pellet density with greenness and wetness layers. The analysis however, did not produce a significant model. Slope values for each pellet location were extracted using the Get Grid extension in ArcView and the DEM-derived slope layer. Curve-fitting regression in SPSS 10.0 (2000) quantified the relationship between deer pellet density and slope ( $r^2 = 0.924$ ) according to:

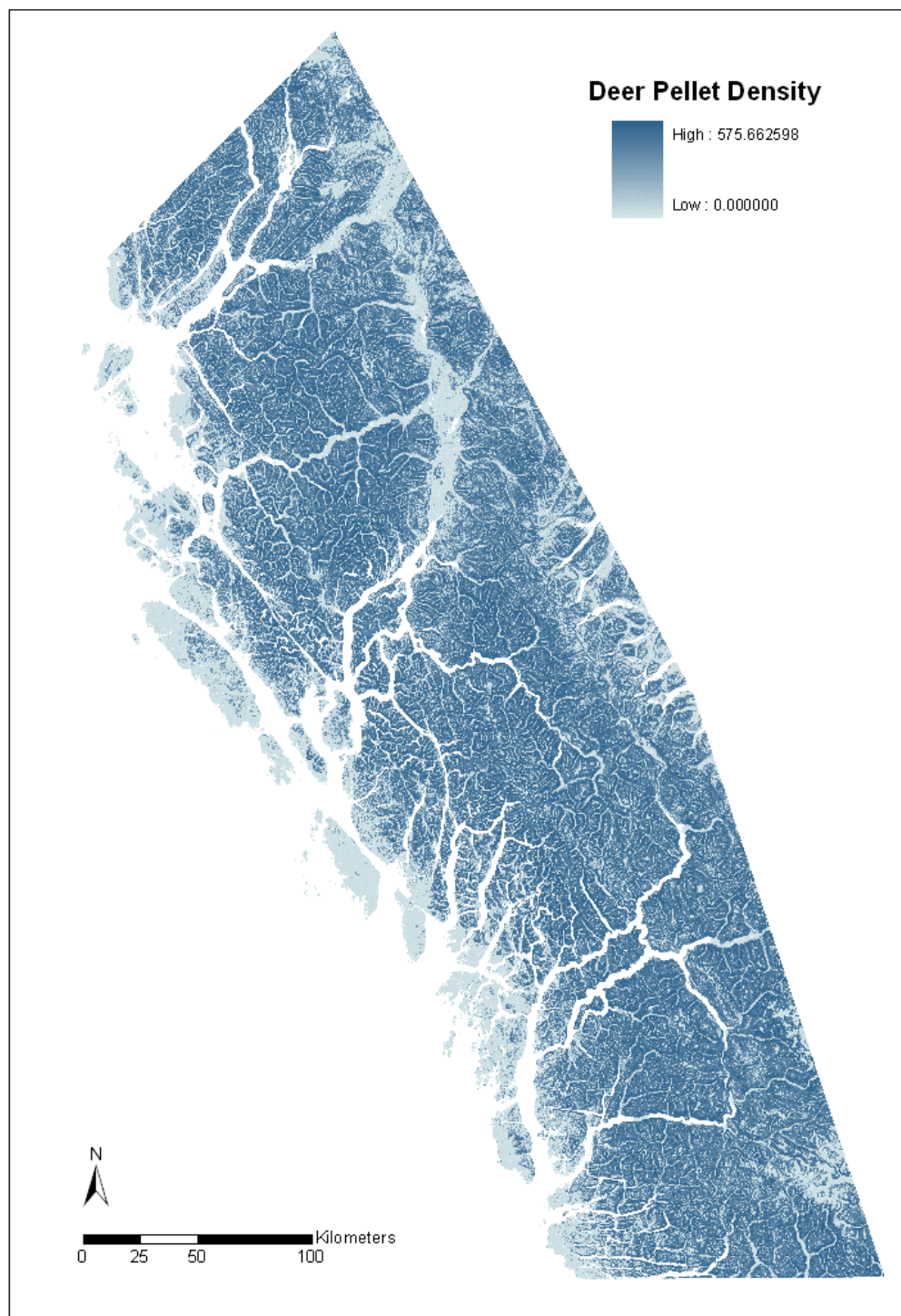
$$\text{Eq. 4: Pellet Density} = 0.0000094[\text{slope}^3] - 0.0009[\text{slope}^2] + 0.0231[\text{slope}] - 0.0022$$

Equation 4 was extrapolated to the entire study area using ArcGIS Raster Calculator, which created a deer pellet density layer (Figure 5). From this layer, mean and standard deviations were extracted per island. Pellets were assumed to represent deer presence; more pellets indicated higher deer density.

**Figure 4:** Study area for deer pellet surveys. Transects are marked in red.



**Figure 5:** Deer pellet density layer.



### *Remaining Biological Variables*

Percentage old growth forest per island was obtained from BC TRIM polygon data (Raincoast Conservation Society 2003). Old growth areas were selected as forests >200 years old (TRIM Class 9) and calculated as:

$$(\text{Total old growth area} / \text{total island area}) \times 100\%$$

Five Landsat 7 ETM+ images were used to derive surrogate layers of vegetation density (greenness) and structural complexity (wetness). Landsat ETM imagery is acquired by satellite Enhanced Thematic Mapper (ETM) sensors that record earth surface reflectance of solar electromagnetic radiation. The imagery is comprised of 7 bands that measure visible (Bands 1-3), infrared (Bands 4-5, 7) and infrared thermal (Band 6) spectral responses of features in a landscape (Lillesand and Kiefer 2000). Using control points (known coordinates of surface features such as road intersections), images are often orthorectified by matching the corresponding location on the image to the control points. This process increases overall image accuracy (Government of Canada, GeoGratis 2003).

Tasseled Cap Transformation (TCT) is a type of remote sensing analysis that is used on Landsat TM/ETM imagery to create a vegetation index. Tasseled Cap analysis applies a linear transformation to 6 of the spectral bands (Bands 1-5 and 7) to reduce them to 3 vegetation measures: greenness, wetness and brightness (Crist and Ciccone 1984, Jensen 1996). This transformation reduces TM/ETM imagery into more manageable components that account for most of the variance in the original bands, and which correlate with physical landscape characteristics (Crist and Ciccone 1984). Specifically,

the index measures the amount of green vegetation (greenness), moisture in the canopy and soil (wetness), and soil reflectance (brightness) (Lillesand and Kiefer 2000).

Greenness is often used as a surrogate of vegetation where higher values represent more biomass. Wetness has been linked to structural complexity and old growth forest, where low values represent clearcut areas and high values, young, closed-canopy forest (Cohen and Spies 1992). Brightness often is used as an indicator of human development where higher values represent urbanized areas (Seto et al. 2002).

Orthorectified Landsat 7 ETM+ images were acquired from Government of Canada GeoGratis (2003) and were taken between 1999 and 2001 in July and October. Although ideal, Landsat images taken at one point in time were not attainable for this study. The time discrepancy between wolf surveys in 2002/2003 and the Landsat imagery was assumed to be negligible as the study area has not been significantly altered in the intervening years. Images were atmospherically-corrected and then mosaiced in ENVI (RSI 2001) using a mean-subtraction method, whereby individual pixel values in one image were subtracted from the mean of all pixel values in a second image. Mean-subtraction was determined to be the best method to reduce the time discrepancy between images. Other mosaic methods blend only the edges of images leaving interior pixel values unaltered (Cheng *pers. comm.*). TCT analysis was then run in ENVI to produce greenness and wetness layers. Brightness was not used in this analysis, as human development in the study area is minimal. Means and standard deviations for greenness and wetness were calculated per island using Spatial Analyst and the island polygon layer.

Island mammal, prey and competitor richness values were derived from 3 pre-1990 island surveys (Craig 1990) and augmented with data from surveys conducted from 1999 to 2003 (Darimont *pers. comm.*). Mammal presence was determined by scat, tracks, direct observation or calls where appropriate. Mammal richness included all mammals present on an island. Mammal parts found in wolf scat analysis or known prey of coastal wolves were tallied as prey richness (Darimont *pers. comm.*). Competitor richness included mammals that prey on similar species or are known to occupy similar habitat as coastal wolves (Darimont *pers. comm.*). Species included in each variable are listed in Appendix 1.

Pink, Coho, Chinook and Sockeye salmon presence data were obtained from Government of Canada, Department of Fisheries and Oceans FISS inventory data (2003). Salmon richness was a tally of the number of species present in island streams. An escapement rate database (Raincoast Conservation Society 2004) was used to determine salmon biomass per island. Escapement rates for 1999 and 2000 were averaged and multiplied against the weight of the species (Table 3). Male and female were assumed to be of equal mass. All species were then summed to give an overall biomass per island. Of the 50 islands included in the sample, biomass data was only available for 20.

**Table 3:** Salmon species and mass (Margolis and Groot 1991).

| Species | Mass (kg) |
|---------|-----------|
| Chum    | 4.16      |
| Coho    | 3.22      |
| Pink    | 1.87      |
| Sockeye | 2.56      |

Percentage of logged area per island was obtained from raster data (Raincoast Conservation Society) and calculated according to:

$$(\text{Total logged area} / \text{total island area}) \times 100\%$$

### 5.3 ANALYSIS

All statistical analyses were conducted in SPSS 10.0 (2000). Assumptions of parametric analysis were tested on independent variables using the Descriptive Statistics module. Variables were not normally distributed and were tested using Spearman's rho, a non-parametric correlation analysis. Inclusion of highly correlated variables in regression analysis can lead to multicollinearity, weakening the analysis by inflating coefficient error (Tabachnick and Fidell 2001). Highly correlated variables, defined by rho greater than or equal to 0.7 (Tabachnick and Fidell 2001) were examined to determine which variable to remove from further analysis. The variable with higher significance for predicting wolf presence in univariate logistic regression, was retained.

Previous analysis of data showed island area to have an overwhelming effect on wolf presence (Paquet et al. *in review*). Variables were therefore, separated into island and sub-island (resource) levels for separate analysis. A global logistic regression model (including all variables) was run before each AIC analysis. Global models are used to determine overall model goodness of fit; if the global model fits the data well, then empirically, sub-models of the global model will also have good fit (Burnham and Anderson 2002). If the global model is not a good fit, an alternative statistical method must be found that will fit the data. The Hosmer-Lemeshow test was used to evaluate

model fit where a nonsignificant chi-square indicated good fit (Tabachnick and Fidell 2001).

A suite of candidate models was created for island and sub-island level analyses using different combinations of independent variables. Combinations of variables in each potential model were based on *a priori* ecological reasoning. Burnham and Anderson (2002) emphasized the importance of compiling candidate models that are scientifically (in this case, ecologically) justified to maximize the usefulness of AIC analysis. Candidate models constructed using *a priori* reasoning also discourage data dredging. The choice of how many models to include must be weighed against the chance of omitting an important model (Burnham and Anderson 2002). Twenty candidate models based on ecological reasoning were chosen for island and sub-island analyses.

A logistic regression was run on each candidate model using wolf presence as the dependent variable. The log-likelihood (-2LL) and number of predictors (K) were used to calculate an AIC value for each model (see Equations 2 and 3). Burnham and Anderson (2002) recommend using AICc values when the ratio of sample size to maximum number of model parameters is less than 40. AICc calculations were used to determine the best approximating model at the island and sub-island levels.

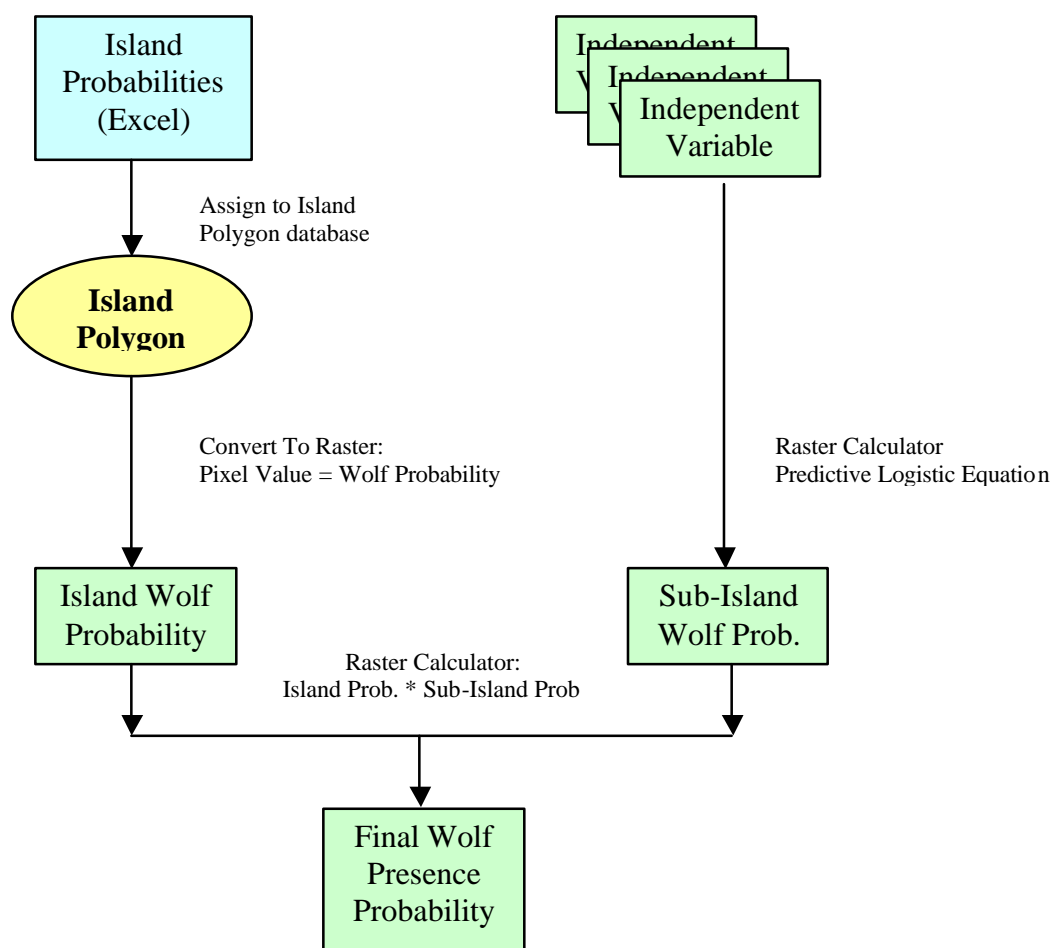
#### **5.4 PROBABILITY SURFACES**

Probability surfaces of wolf presence were created for island and sub-island level analyses (Figure 6). Probabilities were calculated manually in Microsoft Excel for the



island top model and assigned accordingly to the island polygon layer. The polygon layer was then converted to a raster format using wolf probability as the pixel value; all individual pixels within an island displayed the island probability value. Probabilities at the sub-island level were calculated for the top model in ArcGIS Raster Calculator, and manually per island in Excel. Island and sub-island probability surfaces were then multiplied together in Raster Calculator to create a final probability surface of wolf presence. Final island probabilities were also calculated manually in Excel.

**Figure 6:** Flow chart depicting compilation of wolf presence probability surfaces. Colour and shape codes are identical to those in Figure 3.



## 5.5 VALIDATION

Model testing with independent data is ideal (Fielding 2002, Fielding and Bell 1997) but was not fiscally possible for this analysis. Jackknife validation was used as it was found to be a superior evaluation tool for habitat models (Etherington and Lieske *in review*) and is less cumbersome to compute than bootstrapping (Verbyla and Litvaitis 1989). The process of jackknife validation employed for top models at the island and sub-island levels, is outlined in Table 4. A single island record was withheld and analysis run on the

remaining island records using only the variables found in the top AIC model. The resulting logistic regression model was then used to predict the outcome of the withheld record. The process was repeated for all islands in the sample, creating a set of predicted presence/absence values to evaluate against actual presence/absence values. Evaluation of the accuracy of the models was conducted with a ROC curve.

**Table 4:** Jackknife validation procedure.

| Islands Included in Analysis (Island #s) | Withheld Island # for Testing |
|--|-------------------------------|
| 2 – 50                                   | 1                             |
| 1, 3-50                                  | 2                             |
| 1,2, 4-50                                | 3                             |
| Etc                                      | ...                           |
| 1-49                                     | 50                            |

Final island probabilities were derived by multiplying island and sub-island probabilities. Final probabilities were then tested against observed presence/absence using a ROC curve.

## 6.0 RESULTS

Coastal wolves were present on 42 of the 50 islands surveyed. Independent variables were considered highly correlated if Spearman's rho values were 0.7 or greater (Tabachnick and Fidell 2001). Correlated variables were assessed individually using univariate logistic regression and the more significant variable was retained for further analysis. Island and sub-island level Spearman's rho correlation and univariate logistic regression results are shown in Appendices 2 and 3. Correlated variables removed from island and sub-island level analyses are shown in Table 5.

**Table 5:** Variables included and removed from further analysis based on Spearman's rho correlation tests.  $\mu$  represents statistical mean and S, standard deviation. Asterisks denote which variables were correlated within each level of analysis.

| Island                     |                   | Sub-island          |                        |
|----------------------------|-------------------|---------------------|------------------------|
| Final Variables            | Removed           | Final Variables     | Removed                |
| Island Area*               | Mammal Richness** | Greenness ( $\mu$ ) | Elevation ( $\mu$ )*   |
| Island Shape Index         | Salmon Richness*  | Greenness (S)       | Elevation (S)*         |
| Distance to Mainland       | Salmon Biomass*   | Wetness ( $\mu$ )   | Slope (S)*             |
| Distance to Nearest Island |                   | Wetness (S)         | Northness (S)**        |
| % Logged Area              |                   | Slope ( $\mu$ )*    | Deer Pellet ( $\mu$ )* |
| % Old Growth Area          |                   | Northness ( $\mu$ ) | Deer Pellet (S)*       |
| Competitor Richness        |                   | Eastness ( $\mu$ )  |                        |
| Prey Richness**            |                   | Eastness (S)**      |                        |

## 6.1 ISLAND LEVEL

Salmon richness and biomass were correlated highly with island area ( $r^2 = 0.817$  and  $r^2 = 0.737$  respectively) and were removed from further analysis. Salmon however, are an important prey species of coastal wolves. To represent salmon in analysis, the less correlated salmon variable (salmon biomass) was included in several candidate models. All models that included salmon biomass excluded island area to prevent multicollinearity. As a result, two global logistic regression models were run; one with salmon biomass and the other with island area substituted for salmon biomass. Both global models were highly significant (Omnibus  $p = 0.00$ ). The global model including salmon biomass produced a Hosmer-Lemeshow value of 0.97 indicating good model fit. The island area global model showed a perfect fit of data (Hosmer-Lemeshow = 1.0) indicating a likely overfit of the model. Burnham and Anderson (2002) suggested a model can overfit data when a small sample size is used and further, that a global model is not always necessary depending on the dataset used.

In the absence of a reliable island area global model, Hosmer-Lemeshow and Omnibus values were recorded for each model in the AIC suite of models. This inclusion allowed assessment of goodness of fit and model significance for each model in the set. These values, as well as AIC calculations and ecological justification for each model, are listed in Table 6. Top AIC models were defined as any model with an AICc value less than 2 units from the lowest AICc model (Burnham and Anderson 2002). Top models are displayed in Table 7. All top models were significant overall (Omnibus  $p = 0.00$ ) and had good fit (Hosmer Lemeshow  $> 0.87$ ). Top model variables and coefficients are shown in Table 8.

**Table 6:** Island AIC candidate models with ecological reasoning and AICc calculations. **Omn.** represents Omnibus model significance, **H-L** the Hosmer-Lemeshow value, **-2LL** the log-likelihood, **K** the number of model parameters, **change i** the difference between AICc and the smallest AICc in the model set, and **wi** the model weight. Model rank is based on model weight. Sample size (n) for all models is 50. Top models are in gray.

| Model | Variables                          | Justification   | Omn. | H-L  | -2LL  | K | AIC   | AICc  | change i | wi     | RANK |
|-------|------------------------------------|---|------|------|-------|---|-------|-------|----------|--------|------|
| 1     | All with SalmonMass                | global model with SalmonMass  | 0.00 | 0.97 | 7.58  | 9 | 25.58 | 30.08 | 11.38    | 0.0012 | 9    |
| 2     | Area, SI, Near, Main               | spatial variables only  | 0.00 | 0.94 | 8.15  | 5 | 18.15 | 19.51 | 0.81     | 0.2361 | 2    |
| 3     | Prey, Competitor, %Log, Area, Main | IBT theory, prey availability, competition and human disturbance        | 0.00 | 0.98 | 6.69  | 6 | 18.69 | 20.65 | 1.95     | 0.1338 | 3    |
| 4     | Area                               | Island area effect  | 0.00 | 0.96 | 16.91 | 2 | 20.91 | 21.17 | 2.47     | 0.1032 | 4    |
| 5     | Area, Main                         | IBT area-distance model   | 0.02 | 0.15 | 16.03 | 3 | 22.03 | 22.55 | 3.85     | 0.0517 | 6    |
| 6     | Area, Main, Prey                   | IBT, prey availability  | 0.04 | 0.46 | 14.95 | 4 | 22.95 | 23.84 | 5.14     | 0.0271 | 8    |
| 7     | Prey, Competitor, SalmMass, %Log   | prey availability, human disturbance and competition                    | 0.03 | 0.21 | 20.31 | 5 | 30.31 | 31.67 | 12.97    | 0.0005 | 15   |
| 8     | %OldG, Prey, SalmMass              | old growth and prey   | 0.14 | 0.22 | 21.78 | 4 | 29.78 | 30.67 | 11.96    | 0.0009 | 11   |
| 9     | Competitor, Prey, SalmMass         | competition and available prey  | 0.14 | 0.23 | 21.28 | 4 | 29.28 | 30.17 | 11.47    | 0.0011 | 10   |
| 10    | Main, Area, %OldG                  | IBT, old growth   | 0.00 | 1.00 | 14.39 | 4 | 22.39 | 23.28 | 4.58     | 0.0358 | 7    |
| 11    | Prey                               | prey only   | 0.00 | 0.88 | 26.97 | 2 | 30.97 | 31.23 | 12.53    | 0.0007 | 13   |
| 12    | Prey, SalmMass                     | prey and salmon   | 0.00 | 1.00 | 24.99 | 3 | 30.99 | 31.51 | 12.81    | 0.0006 | 14   |
| 13    | SalmMass                           | salmon only   | 0.00 | 0.95 | 35.41 | 2 | 39.41 | 39.67 | 20.97    | 0.0000 | 17   |
| 14    | %Log, Prey, SalmMass               | islands with prey regardless of disturbance                             | 0.00 | 1.00 | 24.03 | 4 | 32.03 | 32.92 | 14.22    | 0.0003 | 16   |
| 15    | %OldG                              | old growth only   | 0.07 | 0.47 | 41.76 | 2 | 45.76 | 46.02 | 27.31    | 0.0000 | 19   |
| 16    | Main, Near                         | IBT   | 0.00 | 0.74 | 37.98 | 3 | 43.98 | 44.50 | 25.80    | 0.0000 | 18   |
| 17    | Main, Near, Prey, Competitor       | stepping stone greater opportunity for prey and competitors to colonize | 0.00 | 0.94 | 19.54 | 5 | 29.54 | 30.90 | 12.20    | 0.0008 | 12   |
| 18    | %Log                               | human disturbance   | 0.00 | 0.84 | 41.79 | 2 | 45.79 | 46.04 | 27.34    | 0.0000 | 20   |
| 19    | Prey, Area                         | prey and island area  | 0.00 | 1.00 | 16.01 | 3 | 22.01 | 22.53 | 3.83     | 0.0522 | 5    |
| 20    | %Log, Area, Main, Near, SI         | human disturbance and spatial   | 0.00 | 0.88 | 4.75  | 6 | 16.75 | 18.70 | 0.00     | 0.3540 | 1    |

**Table 7:** Top island logistic regression models based on AIC analysis of 20 candidate models. **K** represents the number of parameters in the model, **change i** the difference between AICc value of the model and the lowest AICc model, and **wi** the model weight.

| Rank | Variables  | Omnibus | Hosmer-Lemeshow | K | AICc  | change i | wi   |
|------|--|---------|-----------------|---|-------|----------|------|
| 1    | %Logged, IslArea, Dist.Main, Dist.Near, ShapeIndex | 0.00    | 0.88            | 6 | 18.70 | 0.00     | 0.35 |
| 2    | IslArea, Dist.Main, Dist.Near, ShapeIndex          | 0.00    | 0.94            | 5 | 19.51 | 0.81     | 0.24 |
| 3    | %Logged, IslArea, Dist.Main, PreyRich, CompRich    | 0.00    | 0.98            | 6 | 20.65 | 1.95     | 0.13 |

**Table 8:** Top island logistic regression models with variables, coefficients (B) and standard errors (SE).

|                         | Model 1 |       | Model 2 |       | Model 3 |         |
|-------------------------|---------|-------|---------|-------|---------|---------|
| Variable                | B       | S.E.  | B       | S.E.  | B       | S.E.    |
| %Logged Area            | -2.65   | 2.87  |         |       | -9.18   | 25.21   |
| Island Area             | 0.24    | 0.24  | 0.20    | 0.30  | 0.55    | 0.53    |
| Distance Mainland       | -0.13   | 0.19  | -0.04   | 0.13  | -0.76   | 0.80    |
| Dist. to Nearest Island | -0.69   | 1.03  | -1.48   | 2.51  |         |         |
| Island Shape Index      | 6.89    | 6.79  | 10.11   | 14.90 |         |         |
| Prey Richness           |         |       |         |       | 1.94    | 2.08    |
| Competitor Richness     |         |       |         |       | 9.33    | 2726.96 |
| Constant                | -13.25  | 14.04 | -21.96  | 34.17 | -9.21   | 9.89    |

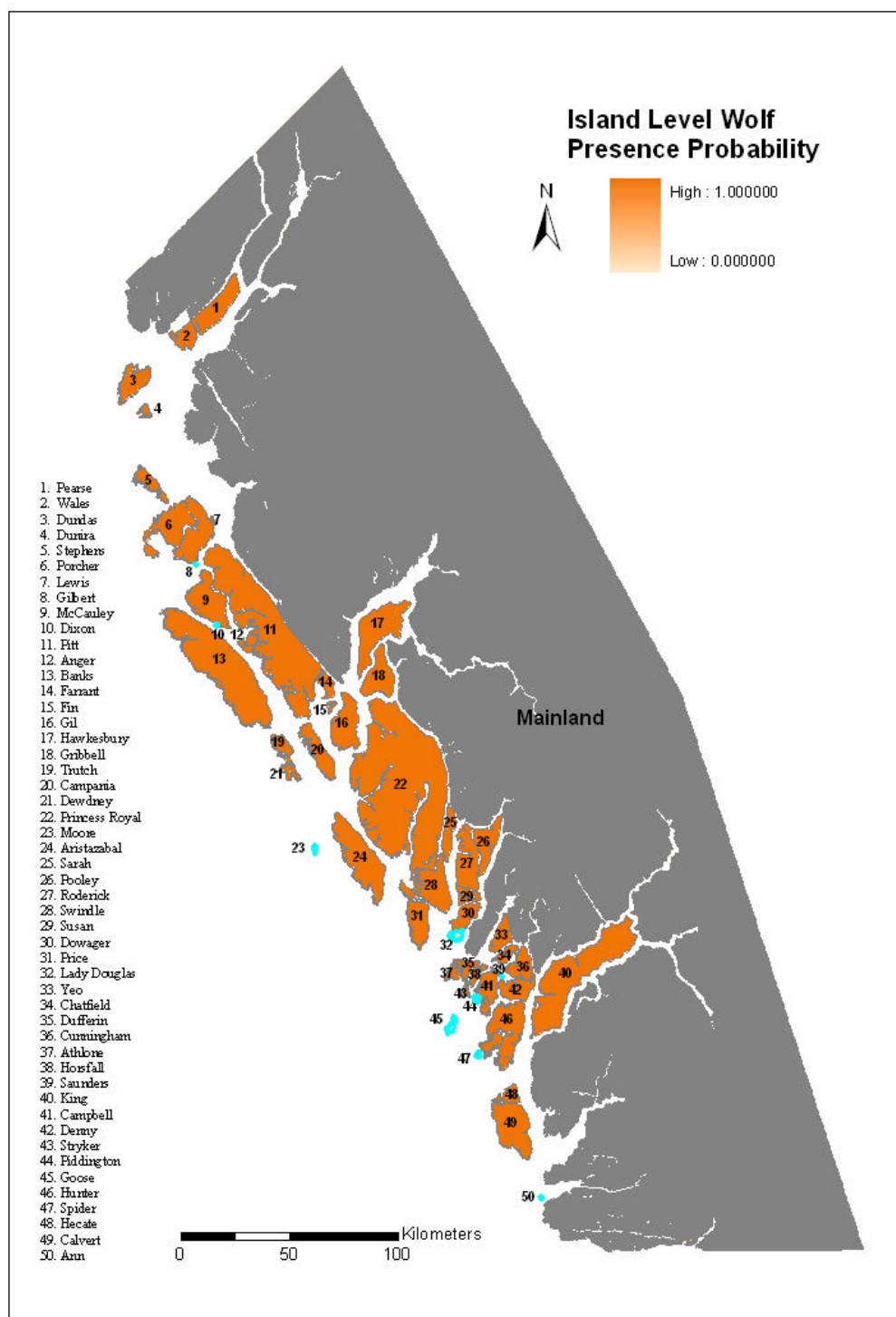
Island physiognomy and human disturbance (logging) were the primary factors affecting coastal wolf presence at an island level. Percent logged area, island area, distance to mainland, distance to nearest island, and island shape index variables comprised the top model and accounted for 35% of data variability. Island area and shape index positively predicted wolf presence while percent logged area, island distance to mainland, and

distance to nearest island variables negatively related to wolf presence. Island area and distance to mainland variables were present in all three top models. The third ranked model also showed a negative relationship to percent logged area and a positive response of wolves to prey and competitor richness. Constants for all models were negative. Although Salmon Biomass was included in several AIC models, it did not appear in the top 3 models. The univariate regression of salmon biomass with wolf presence however, indicated a non-significant relationship (coefficient significance = 0.757).

Wolf presence probabilities were calculated manually in Excel for the top model and are listed in Appendix 4. Spatial application of the probabilities is shown in Figure 7. Forty-one islands showed wolf presence probabilities greater than 0.89 and nine islands predicted absence ( $p < 0.70$ ): Gilbert, Dixon, Moore, Lady Douglas, Saunders, Piddington, Goose, Spider and Ann. Islands predicting no presence were extremely small in area and isolated from the mainland and other islands (Figure 7).



**Figure 7:** Wolf presence probabilities for the top model at the island level. The mainland is shaded in gray and was not included in analysis. Islands with no wolves present are highlighted in blue.



## 6.2 SUB-ISLAND LEVEL

Six variables were removed from sub-island level analysis (Table 5) including deer pellet mean and standard deviation, mean and standard deviation elevation, standard deviation of slope and standard deviation of northness. Deer pellet mean and standard deviation were correlated highly with slope mean, at  $r^2 = 0.979$  and  $r^2 = 0.964$  respectively (Appendix 3). Black-tailed deer however, are the primary prey of coastal wolves and were therefore, included in several models that excluded slope mean. The global model that included slope mean showed good fit (Hosmer-Lemeshow = 0.71) and high significance (Omnibus  $p = 0.00$ ). The global model including deer pellet mean showed model overfit (Hosmer-Lemeshow = 1.0). Omnibus and Hosmer-Lemeshow values were recorded for all candidate models as in island level analysis. Model fit, significance, ecological reasoning and AIC calculations for all models are shown in Table 9. Top AIC sub-island models (Table 10) were highly significant (Omnibus = 0.00) and fit the logistic regression model (Hosmer-Lemeshow > 0.89). Equations for the top 2 models are shown in Table 11.

**Table 9:** Sub-island AIC candidate models with ecological reasoning and AICc calculations. **Omn.** represents Omnibus model significance, **H-L** the Hosmer-Lemeshow value, **-2LL** the log-likelihood, **K** the number of model parameters, **change i** the difference between AICc and the smallest AICc in the model set, and **wi** the model weight. Model rank is based on model weight. Sample size (n) for all models is 50. Top models are in gray.

| Model | Variables                                      | Justification  | OMN. | H-L  | -2LL  | K | AIC   | AICc  | change i | wi     | RANK |
|-------|--|--|------|------|-------|---|-------|-------|----------|--------|------|
| 1     | All  | Global with Slope                                      | 0.00 | 0.71 | 12.90 | 9 | 30.90 | 35.40 | 12.64    | 0.0007 | 15   |
| 2     | GreenSTD                                       | Vegetation diversity                                   | 0.55 | 0.16 | 43.61 | 2 | 47.61 | 47.87 | 25.11    | 0.0000 | 20   |
| 3     | WetnessM                                       | old growth   | 0.00 | 0.80 | 34.73 | 2 | 38.73 | 38.98 | 16.22    | 0.0001 | 17   |
| 4     | SlopeM   | Topography   | 0.00 | 0.80 | 29.67 | 2 | 33.67 | 33.93 | 11.17    | 0.0014 | 14   |
| 5     | NorthM   | higher productivity on southern slopes                 | 0.00 | 0.57 | 26.75 | 2 | 30.75 | 31.00 | 8.24     | 0.0062 | 13   |
| 6     | WetM, SlopeM, NorthM                           | southern aspect, topography and old growth             | 0.00 | 0.89 | 17.89 | 4 | 25.89 | 26.78 | 4.02     | 0.0516 | 4    |
| 7     | WetM, SlopeM                                   | old growth and topography                              | 0.00 | 0.99 | 20.48 | 3 | 26.48 | 27.00 | 4.24     | 0.0461 | 5    |
| 8     | SlopeM, NorthM                                 | southern aspect and topography                         | 0.00 | 0.87 | 22.40 | 3 | 28.40 | 28.92 | 6.16     | 0.0177 | 9    |
| 9     | GreenM, WetM                                   | old growth and dense vegetation                        | 0.01 | 0.26 | 33.46 | 3 | 39.46 | 39.98 | 17.22    | 0.0001 | 18   |
| 10    | GreenM, WetM, SlopeM, NorthM                   | dense vegetation, old growth, southern and topography  | 0.00 | 0.86 | 17.77 | 5 | 27.77 | 29.14 | 6.38     | 0.0159 | 10   |
| 11    | GreenM, GreenSTD, WetM, WetSTD                 | vegetation only  | 0.02 | 0.22 | 32.39 | 5 | 42.39 | 43.75 | 20.99    | 0.0000 | 19   |
| 12    | DeerM  | deer (prey) only                                       | 0.00 | 0.42 | 22.77 | 2 | 26.77 | 27.03 | 4.27     | 0.0456 | 6    |
| 13    | WetM, WetSTD, DeerM                            | old growth, structural diversity and deer              | 0.00 | 0.96 | 13.87 | 4 | 21.87 | 22.76 | 0.00     | 0.3846 | 1    |
| 14    | NorthM, EastM, EastSTD                         | Aspect only  | 0.00 | 0.28 | 26.56 | 4 | 34.56 | 35.45 | 12.69    | 0.0007 | 16   |
| 15    | NorthM, DeerM                                  | southern aspect and deer                               | 0.00 | 0.60 | 19.04 | 3 | 25.04 | 25.56 | 2.80     | 0.0950 | 3    |
| 16    | NorthM, DeerM, WetM                            | southern aspect , deer and old growth                  | 0.00 | 0.90 | 14.71 | 4 | 22.71 | 23.60 | 0.84     | 0.2528 | 2    |
| 17    | NorthM, DeerM, GreenM                          | southern aspect, deer and dense vegetation             | 0.00 | 0.63 | 18.59 | 4 | 26.59 | 27.48 | 4.72     | 0.0364 | 7    |
| 18    | DeerM, GreenSTD                                | deer and vegetation diversity                          | 0.00 | 0.90 | 22.65 | 3 | 28.65 | 29.17 | 6.41     | 0.0156 | 11   |
| 19    | GreenM, GreenSTD, WetM, WetSTD, NorthM, SlopeM | vegetation, southern aspect and topography             | 0.00 | 0.99 | 14.29 | 7 | 28.29 | 30.96 | 8.20     | 0.0064 | 12   |
| 20    | GreenM, GreenSTD, WetM, NorthM, DeerM          | High veg, veg diversity, old growth, southern and deer | 0.00 | 0.85 | 14.42 | 6 | 26.42 | 28.37 | 5.61     | 0.0232 | 8    |

**Table 10:** Top sub-island logistic regression models based on AIC analysis of 20 candidate models. **K** represents the number of parameters in the model, **change i** the difference between AICc value of the model and the lowest AICc model, and **wi** the model weight.

| Rank | Variables  | Omnibus | Hosmer-Lemeshow | K | AICc  | change i | wi   |
|------|--|---------|-----------------|---|-------|----------|------|
| 1    | Wetness Mean, Wetness Standard Deviation, Deer Pellet Mean | 0.00    | 0.96            | 4 | 22.76 | 0.00     | 0.38 |
| 2    | Wetness Mean, Deer Pellet Mean, Northness Mean             | 0.00    | 0.90            | 4 | 23.60 | 0.84     | 0.25 |

**Table 11:** Top sub-island logistic regression models with variables, coefficients (B) and standard errors (SE).

|                            | Model 1 |       | Model 2 |       |
|----------------------------|---------|-------|---------|-------|
| Variable                   | B       | S.E.  | B       | S.E.  |
| Wetness Mean               | -4.60   | 2.677 | -2.59   | 2.04  |
| Wetness Standard Deviation | 1.82    | 1.39  |         |       |
| Deer Pellet Mean           | 10.72   | 6.82  | 6.29    | 4.49  |
| Northness Mean             |         |       | 13.00   | 13.14 |
| Constant                   | -11.92  | 6.71  | -4.83   | 3.99  |

Wolf presence at the sub-island (resource) level was influenced by forest structure and deer presence. Mean and standard deviation of wetness and mean deer pellet variables appeared in the top model compromising 38% of data variability. Mean wetness was negatively related to wolf presence while wetness standard deviation and mean deer density variables positively predicted wolf presence. Mean wetness and deer density were found in both top models and the second rank model also included a positive response with mean northness. Both models showed negative constants.

Wolf presence probabilities were calculated for the top model using ArcGIS Raster Calculator and the predictive form of the logistic regression equation (Equation 1). The original greenness and deer-density layers were used to represent mean variables. A wetness standard deviation layer was created for inclusion in the predictive surface: the island polygon layer was converted into a raster format and assigned the corresponding wetness standard deviation values to all pixels within an island. Probabilities ranged between 0 and 1 and visually showed lower probabilities on Fin, Moore, Goose and Ann islands as well as those in the Hunter/Campbell region, specifically, Spider, Hunter, Piddington and Campbell (Figure 8). When calculated at the island level using means and standard deviations however, Athlone, Ann, Gilbert, Goose, Lady Douglas, Moore, Piddington, Saunders, Spider and Stryker islands predicted wolf absence ( $p < 0.56$ )(Appendix 4). The following islands predicted absence in both island and sub-island analyses: Ann, Gilbert, Goose, Lady Douglas, Moore, Piddington, Saunders and Spider. Stryker and Athlone islands were predicted present at the island level, but absent in sub-island analysis. Dixon island was predicted absent at the island level but present in sub-island analysis.

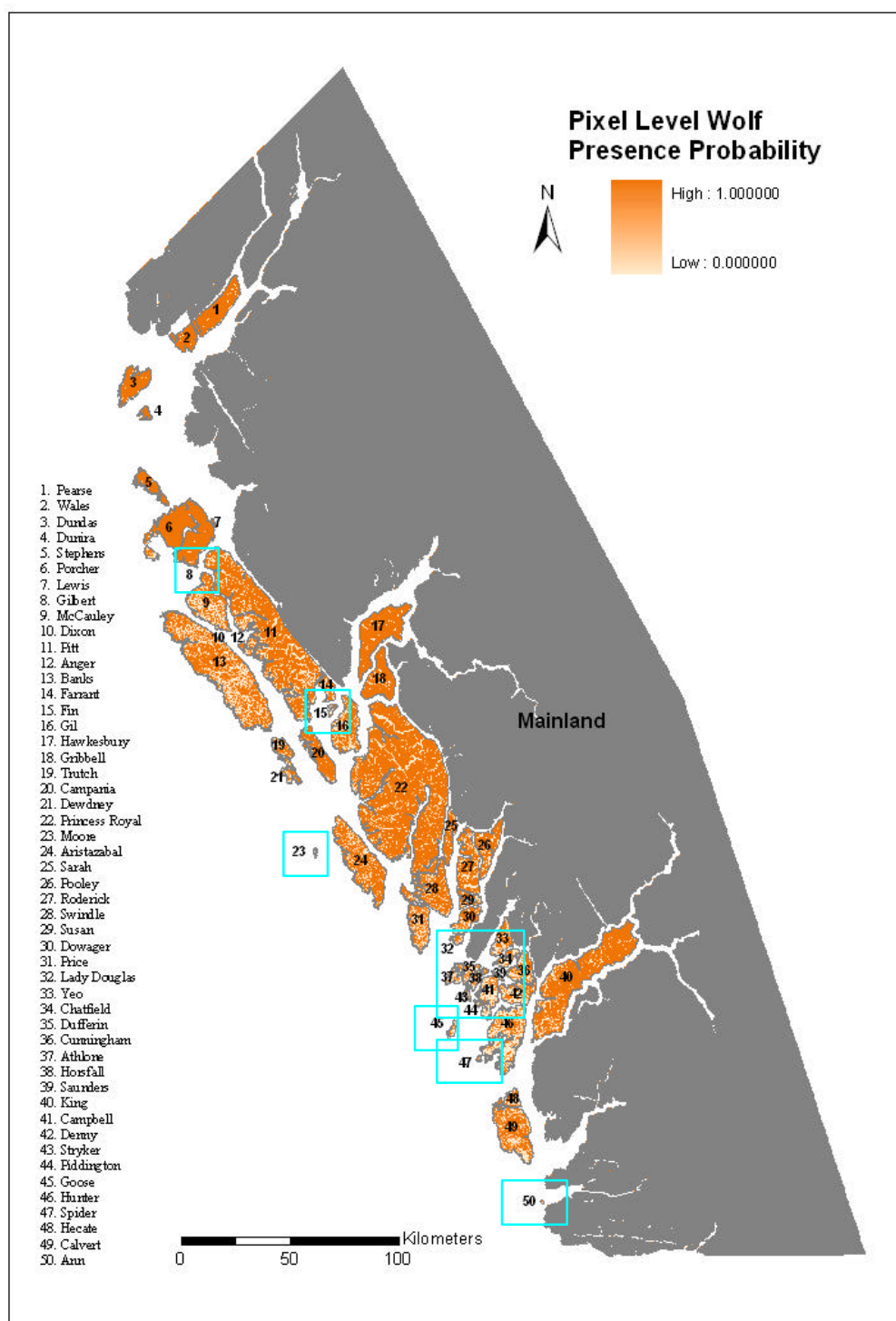
### **6.3 COMBINED ISLAND AND SUB-ISLAND ANALYSIS**

Island and sub-island probability layers were multiplied in Raster Calculator to create a final predictive surface. All islands predicted wolf presence ( $p > 0.88$ ) except Ann, Athlone, Dixon, Gilbert, Goose, Lady Douglas, Moore, Piddington, Saunders, Spider and Stryker ( $p < 0.49$ )(Figure 9). Island and sub-island probabilities were multiplied together to give final island probability values (Appendix 4).

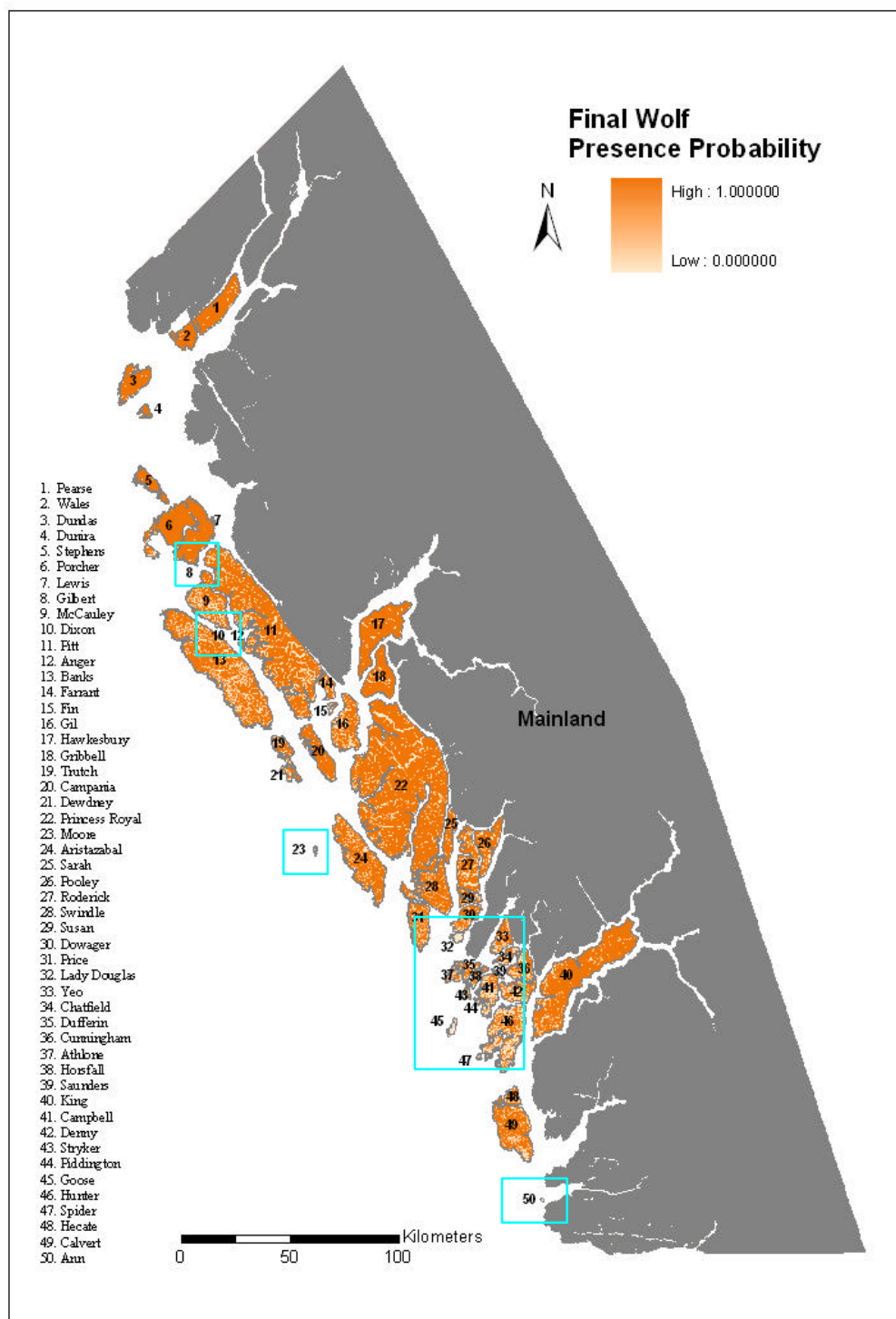
## **6.4 VALIDATION**

Model discrimination was high for all island and sub-island models, as well as final island probabilities (Figure 10). Area under the ROC curves indicated 80% and 91% presence classification accuracy for island and sub-island jackknife validations respectively, and 94% accuracy for final island probabilities (Table 12).

**Figure 8:** Wolf presence probabilities for the top model at the sub-island level. The mainland is shaded in gray and was not included in analysis. Blue squares indicate areas with islands that had lower probabilities.



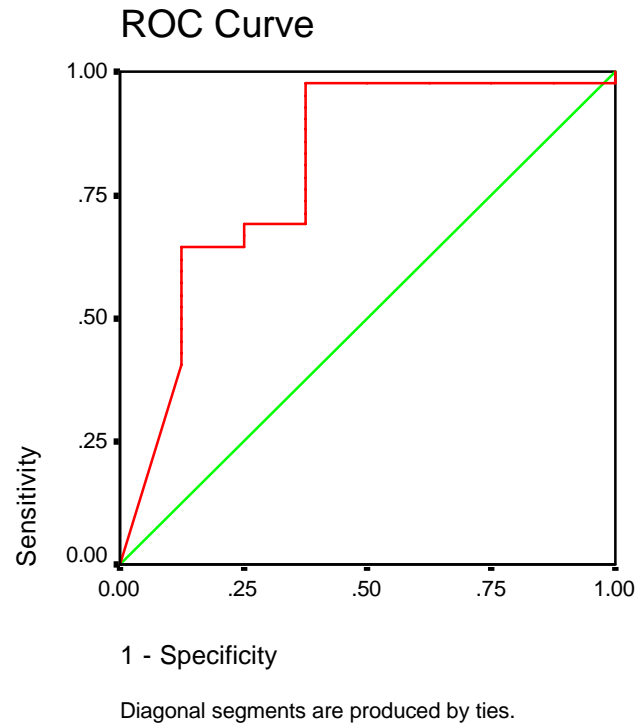
**Figure 9:** Final predictive surface (island \* sub-island). The mainland is shaded in gray and was not included in analysis. Blue squares indicate areas with islands that predicted wolf absence.



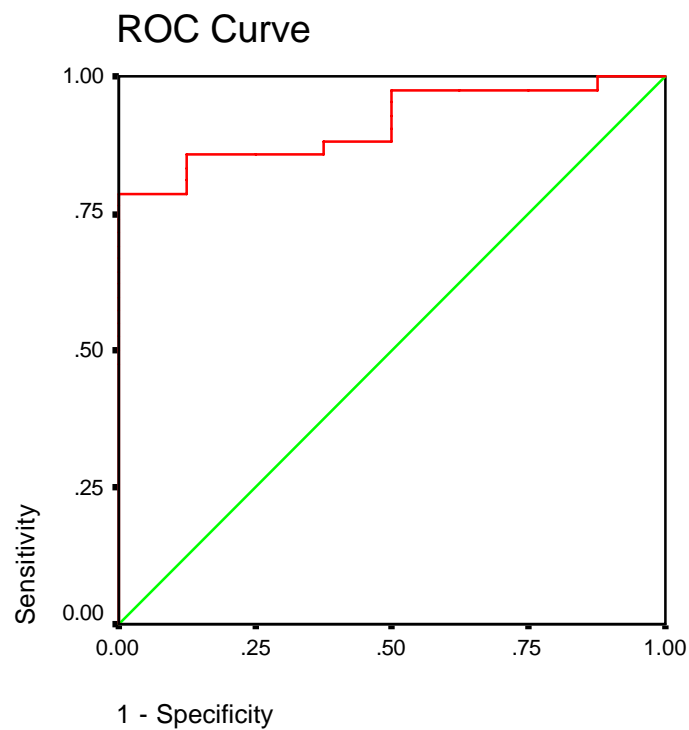


**Figure 10:** ROC curves for island jackknife validation (a), sub-island jackknife validation (b) and validation of final island probabilities (c).

a) Island Jackknife Validation

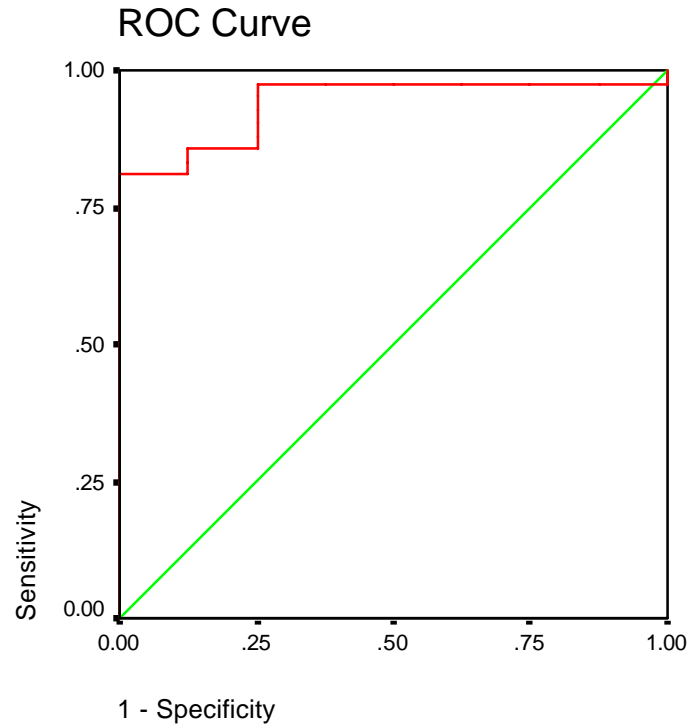


b) Sub-island Jackknife Validation



**Figure 10: cont.**

c) Final Island Probabilities

**Table 12:** Area under ROC curves for island and sub-island jackknife validation, and final island probabilities.

|                                 | <b>AREA UNDER ROC CURVE</b> |
|---------------------------------|-----------------------------|
| Island Jackknife Validation     | 0.802                       |
| Sub-island Jackknife Validation | 0.914                       |
| Final Island Probabilities      | 0.940                       |

## 7.0 DISCUSSION

### 7.1 WOLF PRESENCE AT THE ISLAND LEVEL

Island area, isolation (distance to mainland and nearest island), shape, and degree of logging determined coastal wolf occurrence on islands. Specifically, larger islands with more complex shapes, situated closer to the mainland and closer to other islands, were more likely to support wolves. This reflected the general tenants of Island Biogeography

Theory (IBT). In addition, islands with fewer logged areas were more likely to support wolves, which reflected the sensitivity of coastal wolves to human disturbance.

### **7.1.1 Island Biogeographic Influences: Island Area, Shape, and Isolation**

#### ***Area and Shape***

According to IBT, islands with larger area provide more resources and can support higher species richness (MacArthur and Wilson 1967). However, habitat quality is not directly related to size. As such, island area can be misleading as a predictor of a single species presence because the quality of the area will depend on specific habitat requirements. Large islands however, are more likely to support a greater diversity of habitat, increasing the potential that a focal species habitat will be present. Hence, area effects include response of a species to island area itself, to greater habitat diversity, and the interaction of these two responses (Triantis et al. 2003). Wolves tend to be habitat generalists that thrive in nearly any type of habitat that supports their prey (Mech 1995). Consequently, wolves may respond first to island area, then to habitat diversity. The large home range required by wolves supports a positive response to larger islands that can encompass their area needs.

Island shape also can affect species occurrence and the amount of secure habitat available. Island shape index (SI) calculates the amount of area relative to perimeter; SI values approaching 1 indicate that island area is maximized. Coastal wolves responded positively to larger islands with more extensive perimeters. This response suggests that wolves selected islands with convoluted, perhaps dendritic shapes that may provide more

points of contact for wolves travelling between islands. In theory, more access points should minimize travel distance and decrease energy expenditure when moving between islands. Islands with high shape index values also may have more beach line, which often is used by wolves for foraging and travel (Paquet et al. *in review*).

### ***Isolation***

The effects of isolation are difficult to separate from island area effects. In IBT, island area and isolation have an interactive effect on species occurrence. The degree of a species response is based on life history traits, particularly immigration ability and vulnerability to extinction. Occupation of isolated islands by species with high immigration abilities relative to extinction rates is mediated by island area (Lomolino 1986). That is, if an island is not large enough to meet a species' requirements, isolation may be more influential on species presence.

Wolves are extremely good dispersers (Paquet and Carbyn 2003) but also require large home ranges (Carroll et al. 2000). Hence, the potential for high immigration rates for wolves is limited by their area requirements. Coastal wolves are no exception; they are competent swimmers, able to move between islands that are as far apart as 13 km (Darimont and Paquet 2002), but require approximately 260 km<sup>2</sup> for territory (Person 2000). Maximum inter-island distance in this study was 9.4 km for Goose Island, a distance that can be travelled by coastal wolves. However, Goose Island had no wolf presence recorded and with an area of 18.6 km<sup>2</sup>, was too small for coastal wolves to establish territory. Maximum island distance to mainland was approximately 65 km for

Moore Island. This island also had no wolves present and was extremely small (area of  $4.2 \text{ km}^2$ ). The nearest island to Moore was Aristazabal situated 8.9 km away.

Aristazabal is a large island with recorded wolf presence and an area of  $443 \text{ km}^2$ , large enough to sustain coastal wolf area requirements and well above average island area of  $223 \text{ km}^2$ . Hence, wolves are capable of travelling to isolated islands but may not do so if island area is not large enough to sustain their habitat requirements. This interaction between island area and isolation makes it difficult to determine an optimum area that will maintain a viable coastal wolf population, unless immigration is irrelevant to wolf population dynamics (Lomolino 1986).

Species with poor dispersal abilities may not reflect this area-isolation relationship seen with coastal wolves. Nagorsen and Keddie (2000) examined 13 large islands from the Alexander Archipelago in Alaska, south to Vancouver Island, and found isolation to be the primary factor affecting mountain goat presence on coastal islands (Nagorsen and Keddie 2000). Coastal mountain goats are poor dispersers and consequently would have low immigration rates, which could be compensated for by occupying islands closer to a source of immigrants (the mainland). Conroy et al. (1999) also found isolation to be a better predictor of terrestrial mammal richness in the Alexander Archipelago, but found isolation to be correlated with island area. Conroy et al. hypothesized that the relationship between mammal richness, area and isolation, reflected post-glacial movement of species. The system may not yet have been at equilibrium and was still driven primarily by colonization events. The coastal ecosystem in this study is assumed to be at equilibrium, however considering the results of Conroy et al., this may not be the

case. Furthermore, equilibrium of the coastal ecosystem may be in the midst of a shift in response to human disturbance, primarily in the form of logging. Russell et al. (2004) found large mammal richness was influenced most greatly by the level of anthropogenic activity on offshore islands of New Zealand. Anthropogenic activity can reduce the amount of area available to a species on an island, and may interact with island area to determine species presence. The appearance of the logging variable in the top model of this study supports the results obtained in New Zealand, and indicates wolves responded to increased anthropogenic activity. This response may have resulted from sensitivity to human disturbance, but also from a decrease in available habitat from logging activities.

#### **7.1.2 Human Disturbance: Logging**

Wolves responded negatively to logged areas. Coastal wolves often den in the roots of old growth trees (Darimont and Paquet 2000, Person 2000) and even-aged stands that have replaced logged old growth forests, would not be expected to provide the same quantity or quality of potential sites. It is possible that wolves reacted more negatively to logging of a particular tree species, but this response was not discernible in this analysis. The negative response of coastal wolves to logging more likely reflected intolerance of human presence. Sensitivity of wolves to human disturbance has been well documented (Mladenoff et al. 1995, Weaver et al. 1996, Massolo and Meriggi 1998, Theuerkauf et al. 2003, Jedrzejewski et al. 2004) although the magnitude of response varies between individuals, packs, and populations, and depends on ecological conditions (Paquet and Carbyn 2003). Wolves are particularly sensitive to road density (Mladenoff et al. 1995, Alexander et al. 1996, Ciucci et al. 2003) and the introduction of logging roads allows

access for hunters and poachers to enter previously undisturbed landscape. The creation of logging roads can result in more wolf-human encounters and as hunting and poaching are the primary factors of unnatural coastal wolf mortality, they are reason for concern.

## **7.2 WOLF PRESENCE AT THE SUB-ISLAND LEVEL**

Wolf presence at the sub-island or resource level was influenced most strongly by structural complexity (wetness) of forest stands and prey presence. Structural complexity is associated with old growth forest and forest-age diversity. Wetness standard deviation and deer pellet density positively predicted wolf presence, while mean wetness had a negative effect. The positive relationship of deer to wolf presence was expected as deer comprise the majority of coastal wolf diet.

### **7.2.1 Structural Complexity – Old Growth Forest**

The negative response of wolves to mean island wetness indicated selection for islands with lower mean structural complexity. However, interpretation of this result is dependent on the correlation of wetness to structural complexity. Wetness was actually found to be better described as ‘maturity’ because of its correspondence with the stages of forest stand succession (Cohen and Spies 1992). Wetness values are lowest for bare ground and clearcut areas, and highest for young, closed canopy stands. Wetness values for fully mature, old growth forest however, are not high as would be expected, but rather mid-range because of its spectral response. When forests begin to age, trees begin to die and the amount of woody debris and lichen growth increases. Bark, dead wood and lichen all produce lower wetness values than green foliage (Cohen and Spies 1992). As a

result of higher proportions of woody materials, old growth forests have lower wetness values than young, closed canopy forest. Hence, wolf selection for islands with lower mean wetness values may have reflected selection for islands with old growth forest.

Lower mean wetness values may also reflect however, that wolves selected for islands with more bare ground or clearcut areas that would lower mean wetness values.

Considering deer response to logging is initially positive, the response of wolves to islands with lower mean wetness was more likely a result of bare ground and clearcut areas.

The positive relationship of wolves to wetness standard deviation also reflected deer response to logging. Greater standard deviation of wetness may have indicated a wide range of different-aged forest on an island, including clearcut/bare ground, old growth forest, and young, closed, canopy stands. Islands that have been logged previously would exhibit high standard deviations as a result of the different stages of tree succession. Wolf presence may be related to higher wetness standard deviation because of deer response to logging. Although the long-term carrying capacity of deer cannot be sustained by current clearcut logging practices, deer initially react positively to the abundance of new browse (Darimont and Paquet 2000). Hence, this result may be reflective of the temporal limitations of this study. Deer, and consequently wolves, initially are attracted to islands with a variety of forest stand ages. However examination of this same system 15 – 30 years from now, when canopy growth of recolonizing areas begins to limit forage for deer (Darimont and Paquet 2000), may generate different



results. Specifically, wolves may avoid islands with a large range of wetness values in response to deer avoidance of these same islands.

### **7.2.2 Prey – Black-tailed Deer Density**

A positive response of wolves to deer density was expected. Although wolves exhibit behavioural plasticity and are able to exploit food resources according to availability (Weaver et al. 1996), black-tailed deer remain the primary prey for coastal wolves. Dietary analysis showed deer was the most common food item in coastal wolf scat (Darimont et al. 2004) and the importance of ungulate prey to wolf populations is well documented (Bjorge and Gunson 1989, Fuller et al. 1992, Fritts and Carbyn 1995, Messier 1995, Massolo and Meriggi 1998, Ciucci et al. 2003). The existence or nature of a regulatory relationship of wolf on ungulate populations however, appears to depend on the location of the study and the density and diversity of prey available. Black-tailed deer are the most common ungulate prey available to coastal wolves; moose and mountain goat are found in the study area but are primarily limited to the mainland (Darimont and Paquet 2002). Less deer remains were found in wolf scat on the mainland, possibly reflecting a switch in wolf predation from deer, to moose and mountain goat (Darimont et al. 2004). On islands however, deer would be more readily available prey than moose and mountain goat. Consequently, islands with higher densities of deer would be more likely to attract wolves.

### **7.3 COMBINED EFFECTS OF ISLAND AND SUB-ISLAND LEVEL TOP MODELS**

The disproportionate number of islands with wolf presence (84% - 42 of 50) indicated that wolves were well distributed throughout the study area. The final predictive map (Figure 9) shows the probability of wolf presence based on the integration of significant factors identified at island and sub-island levels. Larger, less isolated islands with more convoluted shapes and less logged area had higher probabilities of wolf presence. Islands with greater forest-age diversity and higher deer densities also had high wolf probabilities.

The complexity of the coastal system precipitates interaction amongst island and sub-island variables, although no statistical correlations were found. Previous research on coastal wolves hypothesized that the presence and abundance of deer and protection from human activities, determine the persistence of wolves on any given island (Darimont and Paquet 2002). Although island residency of wolves was not examined, results presented here supported this hypothesis and showed the mediating effect of island configuration on deer-wolf dynamics. However, the spatial effects that determined wolf presence may not solely have been a function of deer density. Darimont et al. (2004) showed small mammals replaced deer as the primary component in wolf scat on islands that were further away from the mainland. Probability of detecting deer remains in wolf scat was related negatively with distance to mainland, rather than island area and inter-island distance. Wolves occurred more frequently on islands that were situated closer to the mainland, but also on islands in close proximity to other islands. Swimming and dispersal ability of wolves would facilitate access to isolated islands, which suggests

wolves may only access these distant islands if deer are present. Wolves are more likely to minimize energetic costs and remain on islands or island groups, close to the mainland that support high deer densities and allow for deer recolonization.

Higher occurrence of forest-age diversity and deer density predicted wolf presence on islands. As habitat generalists, wolves usually are not associated with a vegetation type but rather with prey response to vegetation types (Carroll et al. 2000). Wolves are attracted to islands with lower overall stand maturity and higher forest age diversity. This response was likely related to deer attraction for younger stands produced from clearcut logging. Hence, wolves were sensitive to the amount of logging at an island level, but attracted to islands with more logging at the sub-island level because of the presence of deer. A more detailed resource-level analysis may be necessary to understand fully the interaction of deer, forest stand age, old growth forest, logging and coastal wolf distribution. However, at an island level, wolves clearly selected larger islands that were not isolated and that retained low levels of logging disturbance.

## **7.4 MODEL ASSUMPTIONS AND LIMITATIONS**

### **7.4.1 Assumptions**

The relationship of wolves to island and sub-island level variables was based on a variety of assumptions which limit model applicability. First and foremost was that wolf sign was indicative of wolf presence. Moreover, wolf sign did not reflect density or residency of wolves on islands but indicated a wolf was present on the island at one time.

Assigning wolf presence to islands may have been a product of sampling effort and

assumed that wolf signs were correctly identified. It is possible that signs were missed on islands designated with wolf absence. Incorrect identification of wolf tracks and scat was considered negligible; wolf tracks are considerably larger than coyote (Darimont and Paquet 2002) and consist primarily of hair.

Datasets of independent variables were assumed to be accurate and complete. However, due to sampling constraints, salmon and deer variables may have been inaccurate.

Salmon and deer comprise the majority of wolf diet (Darimont and Paquet 2000) yet data on density and distribution of these species is incomplete and dated. Salmon richness was derived from DFO FISS database whose surveys to obtain salmon presence data were not extensive. Similarly, salmon biomass was based on escapement rates measured per island and was only available for a subset of the islands included in this analysis.

Salmon have been observed on islands that did not have biomass values (Darimont *pers.comm.*), however data did not exist to quantify their presence. Salmon are an important part of coastal wolf diet and the absence of salmon richness and biomass variables in the top models may be a reflection of the limited data they were represented by.

Assumptions also were made for statistical analysis. Logistic regression assumes absence of multicollinearity, independence of sample cases, removal of outliers and anomalies, and a sufficient sample size with enough positive and negative cases (Tabachnick and Fidell 2001). All variables were tested for multicollinearity before analysis and were accounted for if correlations were greater than or equal to Spearman's rho of 0.7.

Independence of samples for logistic regression was not specifically tested, but assumed due to the nature of the intervening matrix between islands. Although wolves are capable swimmers, the energetic cost of inter-island travel was assumed to render the islands independent cases. Sample size may be a limiting factor in application of the predictive model particularly as larger sample size increases statistical power of analysis (Tabachnick and Fidell 2001). Furthermore, it is the number of positive and negative events rather than total sample size, that affects model performance when using logistic regression (Hosmer and Lemeshow 2000). In particular, the proportion of presence and absence events and the number of predictor variables can lead to a violation of the logistic regression assumption that the ratio of predictors to events is sufficient. In this study, 8 islands of wolf absence likely were not sufficient. As a result, prediction of wolf presence using the derived model may not be justified. Testing the models with more islands that do not support wolves may improve model reliability and classification accuracy. Alternatively, the small sample size and lack of absence points may warrant analysis with statistical approaches that do not require absence data, in particular, presence-only techniques (eg Hirzel et al. 2002) or distance from optimum habitat measures such as the Mahalanobis statistic (Corsi et al. 1999).

#### **7.4.2 Limitations**

As discussed above, the small sample size used here may have limited the power of logistic regression and consequently, the predictive power of island and sub-island models. However, the ROC curve validation of the top models showed high classification accuracy. Testing with independent data could reveal model variables to be

limited in their range of application and would be expected in such a large study area. Identification of these ranges would assist in determining where the model is actually valid (Van Horne 2002). Both models were limited by the spatial resolution of the imagery used to derive independent variables. Prediction can only be accurate to 50 m, based on the largest data pixel size derived from the DEM. Spatial data and layers also introduce error into models that can be accounted for by ground-truthing. Testing the spatial data however, was not logistically or financially possible for this study.

Sampling for wolf presence only occurred in summer and fall and hence, application of the final models is constrained to these seasons. During winter and spring, wolves may select islands according to different factors particularly because of winter storms, which can be severe on the coast.

Model selection with AIC was limited by the models comprising the test group.

Candidate models are selected by the researcher based on what they deem to be relevant hypotheses driving the process of interest. AIC selects the best model of a group of models, and if the model that is the true representation of the process is not included, it cannot be selected. AIC still selects a best model from a group of poor models. Here, efforts were made to include all possible hypotheses to describe wolf habitat, and to base them on sound *a priori* reasoning.

Island and sub-island predictive models would benefit from larger sample size, specifically the inclusion of more islands with wolf absence. Further testing of the models

with a more rigorous resampling approach (i.e. bootstrap) or with independent data, is recommended. As presented, the models show high classification accuracy and are useful to identify factors affecting wolf presence in the landscape.

## **8.0 CONCLUSIONS**

The models created here yield accurate habitat relationships that are important to wolves in the coastal landscape. Knowledge of these relationships may be used as a basis for further habitat modelling and enhances our understanding of coastal wolf ecology. The efficacy of GIS in habitat modelling has also been evident. GIS technology made it possible to analyse quickly spatial characteristics of the extremely large study area, and allowed extraction and effective management of a correspondingly large dataset.

The results of this research underscored the importance of sample size and the need for extensive empirical data collection. Most importantly, improved deer and salmon species presence data is recommended. Wolf density data collection also may improve the model, as would the inclusion of variables such as habitat diversity, water characteristics such as channel depth, temperature and speed, and wolf use of island groups. Exploration of directional (N,E,S,W) and seasonal effects on wolf distribution may also be informative.

Wolves are focal species for the coastal ecosystem and understanding their relationship to landscape attributes can help guide management actions and conserve ecosystem structure and function. However, the role of focal species in effective conservation

planning is dependent on the ecosystem of study (Fleishman et al. 2000). If wolves are used for conservation planning, their role should be explicitly defined and assessment goals and possible shortcomings, clearly identified (Landres et al. 1988). The status of wolves and their habitat requirements should not be the sole means by which conservation decisions are made, but should be used in conjunction with research relevant to other coastal focal species, specifically grizzly bear and salmon. Responses of focal species should only be considered as insight into the integrity of the larger ecosystem (Noon and Dale 2002) and used accordingly.

The central coast of British Columbia, Canada, supports rare Coastal Temperate Rainforest and is extremely worthy of research and conservation efforts. Understanding the unique interactions of focal species with the coastal ecosystem will help to conserve what remains of this habitat, and contribute to a scientific base that ensures ecosystem integrity in the future.



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## APPENDICES

**APPENDIX 1:** Species list of mammals comprising predator and prey richness variables. Mammal richness was the sum of all mammals per island.

|                          | Prey | Predator |                              | Prey | Predator |
|--------------------------|------|----------|------------------------------|------|----------|
| Shrew                    | x    |          | Cougar                       |      | x        |
| Masked Shrew             | x    |          | Wolverine                    |      | x        |
| Northern Water Shrew     | x    |          | Nutria                       |      |          |
| Vole                     | x    |          | Dama Gazelle                 |      |          |
| Deer Mouse               | x    |          | Mink                         | x    |          |
| Southern Red-Backed Vole | x    |          | River Otter                  | x    |          |
| Mouse                    | x    |          | Sea Otter                    | x    |          |
| Red Squirrel             | x    |          | Norway Rat                   | x    |          |
| Northern Flying Squirrel | x    |          | Black Rat                    | x    |          |
| Marmot                   |      |          | House Mouse                  | x    |          |
| Muskrat                  |      |          | Rabbit                       |      |          |
| Beaver                   | x    |          | Dog                          | x    | x        |
| Raccoon                  | x    |          | Northern Sea Lion (Stellers) | x    |          |
| Black-tailed deer        | x    |          | California Sea Lion          | x    |          |
| Elk                      |      |          | Harbour Seal                 | x    |          |
| Dawson Caribou           |      |          | Northern Elephant Seal       | x    |          |
| Mountain Goat            | x    |          | Northern Fur Seal            | x    |          |
| Marten                   | x    |          | Fisher                       | x    |          |
| Ermine                   | x    |          | Reithrodontomys sumichrasti  | x    |          |
| Black Bear               | x    | x        | Moose                        | x    |          |
| Coyote                   |      | x        | Brown Bear                   |      | x        |

**APPENDIX 2:** Spearman's rho correlation (A) and univariate logistic regression results (B) for island level analysis. Variables with significant correlations ( $r^2 \geq 0.7$ ) or significant regressions ( $p < 0.05$ ) are highlighted.

A) Island Spearman's rho results. \*Significant correlations at  $p = 0.05$  (2-tailed). \*\*Significant correlations at  $p = 0.01$  (2-tailed).

| Variable          | MAMM RICH | PREY RICH | COMP RICH | AREA     | SHAPE INDEX | DIST NEAREST | DIST MAIN | LOG%      | % OLD GROWTH | SALM RICH | SALM BIOMASS |
|-------------------|-----------|-----------|-----------|----------|-------------|--------------|-----------|-----------|--------------|-----------|--------------|
| MAMMAL RICHNESS   | 1.000     | .979(**)  | .531(**)  | .661(**) | .332(*)     | -.174        | -.286(*)  | .465(**)  | -.001        | .611(**)  | .553(**)     |
| PREY RICHNESS     | .979(**)  | 1.000     | .479(**)  | .626(**) | .339(*)     | -.130        | -.213     | .421(**)  | .011         | .555(**)  | .553(**)     |
| COMP RICHNESS     | .531(**)  | .479(**)  | 1.000     | .539(**) | .042        | -.255        | -.514(**) | .560(**)  | -.115        | .623(**)  | .590(**)     |
| ISLAND AREA       | .661(**)  | .626(**)  | .539(**)  | 1.000    | .231        | -.036        | -.296(*)  | .528(**)  | -.080        | .817(**)  | .737(**)     |
| SHAPE INDEX       | .332(*)   | .339(*)   | .042      | .231     | 1.000       | .007         | .333(*)   | -.168     | -.285(*)     | .147      | .003         |
| DISTANC E NEAREST | -.174     | -.130     | -.255     | -.036    | .007        | 1.000        | .455(**)  | -.318(*)  | -.184        | -.128     | -.061        |
| DISTANC E MAIN    | -.286(*)  | -.213     | -.514(**) | -.296(*) | .333(*)     | .455(**)     | 1.000     | -.582(**) | -.311(*)     | -.305(*)  | -.294(*)     |
| % LOGGED          | .465(**)  | .421(**)  | .560(**)  | .528(**) | -.168       | -.318(*)     | -.582(**) | 1.000     | .207         | .571(**)  | .539(**)     |
| OLD GROWTH %      | -.001     | .011      | -.115     | -.080    | -.285(*)    | -.184        | -.311(*)  | .207      | 1.000        | -.063     | -.024        |
| SALMON RICHNESS   | .611(**)  | .555(**)  | .623(**)  | .817(**) | .147        | -.128        | -.305(*)  | .571(**)  | -.063        | 1.000     | .755(**)     |
| SALMON BIOMASS    | .553(**)  | .553(**)  | .590(**)  | .737(**) | .003        | -.061        | -.294(*)  | .539(**)  | -.024        | .755(**)  | 1.000        |

**APPENDIX 2:** cont.

B) Island univariate logistic regression results

| <b>Island Variable</b>  | <b>Coefficient Significance (p)</b> |
|-------------------------|-------------------------------------|
| Mammal Richness         | 0.003                               |
| Prey Richness           | 0.003                               |
| Competitor Richness     | 0.804                               |
| Island Area             | 0.030                               |
| Island Shape Index      | 0.054                               |
| Distance Nearest Island | 0.042                               |
| Distance Mainland       | 0.036                               |
| % Logged                | 0.258                               |
| % Old Growth            | 0.146                               |
| Salmon Richness         | 0.851                               |
| Salmon Biomass          | 0.757                               |

**APPENDIX 3:** Spearman's rho correlation (A) and univariate logistic regression results (B) for sub-island level analysis. Variables with significant correlations ( $r^2 \geq 0.7$ ) or significant regressions ( $p < 0.05$ ) are highlighted.

A) Sub-island Spearman's rho results. \*Significant correlations at  $p = 0.05$  (2-tailed). \*\*Significant correlations at  $p = 0.01$  (2-tailed).

|              | GREEN<br>M | GREEN<br>STD | WETM    | WET<br>STD | ELEV<br>M | ELEV<br>STD | SLOPE<br>M | SLOPE<br>STD | NORTH<br>M | NORTH<br>STD | EASTM  | EAST<br>STD | DEER M | DEER<br>STD |
|--------------|------------|--------------|---------|------------|-----------|-------------|------------|--------------|------------|--------------|--------|-------------|--------|-------------|
| GREEN<br>M   | 1.000      | .614**       | -.122   | .354*      | -.056     | -.081       | -.005      | -.101        | -.083      | -.067        | .297*  | .020        | -.067  | -.089       |
| GREEN<br>STD | .614**     | 1.000        | -.205   | .667**     | .118      | .137        | .187       | .140         | .151       | .098         | .345*  | -.113       | .150   | .154        |
| WET M        | -.122      | -.205        | 1.000   | -.503**    | -.081     | -.123       | .118       | .051         | -.074      | -.056        | .048   | .082        | .034   | .010        |
| WET<br>STD   | .354*      | .667**       | -.503** | 1.000      | .222      | .242        | .131       | .146         | .083       | -.015        | .004   | -.004       | .156   | .159        |
| ELEV M       | -.056      | .118         | -.081   | .222       | 1.000     | .982**      | .927**     | .933**       | .617**     | .210         | -.253  | -.192       | .948** | .948**      |
| ELEV<br>STD  | -.081      | .137         | -.123   | .242       | .982**    | 1.000       | .913**     | .936**       | .587**     | .203         | -.236  | -.183       | .946** | .947**      |
| SLOPE<br>M   | -.005      | .187         | .118    | .131       | .927**    | .913**      | 1.000      | .963**       | .564**     | .228         | -.102  | -.209       | .979** | .964**      |
| SLOPE<br>STD | -.101      | .140         | .051    | .146       | .933**    | .936**      | .963**     | 1.000        | .581**     | .257         | -.192  | -.235       | .985** | .983**      |
| NORTH<br>M   | -.083      | .151         | -.074   | .083       | .617**    | .587**      | .564**     | .581**       | 1.000      | .220         | -.171  | -.196       | .616** | .631**      |
| NORTH<br>STD | -.067      | .098         | -.056   | -.015      | .210      | .203        | .228       | .257         | .220       | 1.000        | -.302* | -.995**     | .217   | .222        |
| EAST M       | .297*      | .345*        | .048    | .004       | -.253     | -.236       | -.102      | -.192        | -.171      | -.302*       | 1.000  | .287*       | -.144  | -.150       |
| EAST<br>STD  | .020       | -.113        | .082    | -.004      | -.192     | -.183       | -.209      | -.235        | -.196      | -.995**      | .287*  | 1.000       | -.196  | -.200       |
| DEER M       | -.067      | .150         | .034    | .156       | .948**    | .946**      | .979**     | .985**       | .616**     | .217         | -.144  | -.196       | 1.000  | .994**      |
| DEER<br>STD  | -.089      | .154         | .010    | .159       | .948**    | .947**      | .964**     | .983**       | .631**     | .222         | -.150  | -.200       | .994** | 1.000       |

**APPENDIX 3:** cont.

B) Sub-island univariate logistic regression.

| <b>Sub-island<br/>Variable</b> | <b>Coefficient Significance (p)</b> |
|--------------------------------|-------------------------------------|
| Greenness M                    | 0.471                               |
| Greenness STD                  | 0.569                               |
| Wetness M                      | 0.036                               |
| Wetness STD                    | 0.384                               |
| Elevation M                    | 0.035                               |
| Elevation STD                  | 0.058                               |
| Slope M                        | 0.013                               |
| Slope STD                      | 0.017                               |
| Northness M                    | 0.004                               |
| Northness STD                  | 0.979                               |
| Eastness M                     | 0.833                               |
| Eastness STD                   | 0.483                               |
| Deer Pellet M                  | 0.080                               |
| Deer Pellet STD                | 0.053                               |

**APPENDIX 4:** Manually calculated wolf presence probabilities per island for island and sub-island AIC top models. Probabilities are also listed for the final surface (sub-island\*island). Islands in dark gray were predicted absent in island and sub-island analyses (present being  $p \geq 0.7$ ). Islands in light gray showed discrepancies between the two analyses.

| Name        | Island | Sub-island | Combined | Name         | Island | Sub-island | Combined | Name           | Island | Sub-island | Combined |
|-------------|--------|------------|----------|--------------|--------|------------|----------|----------------|--------|------------|----------|
| Anger       | 1      | 1          | 1        | Fin          | 0.9497 | 0.9972     | 0.9470   | Porcher        | 1      | 1          | 1        |
| Ann         | 0.0036 | 0.1616     | 0.0006   | Gil          | 1      | 1          | 1        | Price          | 1      | 1          | 1        |
| Aristazabal | 1      | 1          | 1        | Gilbert      | 0.0065 | 0.0222     | 0.0001   | Princess Royal | 1      | 1          | 1        |
| Athlone     | 1      | 0          | 0        | Goose        | 0.0102 | 0.1790     | 0.0018   | Roderick       | 1      | 1          | 1        |
| Banks       | 1      | 1          | 1        | Gribbell     | 1      | 1          | 1        | Sarah          | 1      | 1          | 1        |
| Calvert     | 1      | 1          | 1        | Hawkesbury   | 1      | 1          | 1        | Saunders       | 0.0003 | 0.1474     | 0.0000   |
| Campania    | 1      | 1          | 1        | Hecate       | 0.9990 | 1.0000     | 0.9990   | Spider         | 0.4011 | 0.4826     | 0.1936   |
| Campbell    | 1      | 1          | 1        | Horsfall     | 0.9885 | 0.9961     | 0.9846   | Stephens       | 1      | 1          | 1        |
| Chatfield   | 1      | 1          | 1        | Hunter       | 1      | 1          | 1        | Stryker        | 0.9992 | 0.4885     | 0.4881   |
| Cunningham  | 1      | 1          | 1        | King         | 1      | 1          | 1        | Susan          | 0.9989 | 1.0000     | 0.9989   |
| Denny       | 1      | 1          | 1        | Lady Douglas | 0.0255 | 0.5596     | 0.0142   | Swindle        | 1      | 1          | 1        |
| Dewdney     | 1      | 1          | 1        | Lewis        | 0.8992 | 1.0000     | 0.8992   | Trutch         | 1      | 1          | 1        |
| Dixon       | 0.0003 | 0.7504     | 0.0002   | McCauley     | 1      | 1          | 1        | Wales          | 1      | 1          | 1        |
| Dowager     | 1      | 1          | 1        | Moore        | 0.0353 | 0.0053     | 0.0002   | Yeo            | 0.9972 | 1.0000     | 0.9972   |
| Dufferin    | 1      | 1          | 1        | Pearse       | 1      | 1          | 1        |                |        |            |          |
| Dundas      | 1      | 1          | 1        | Piddington   | 0.6967 | 0.5170     | 0.3602   |                |        |            |          |
| Dunira      | 0.9991 | 1.0000     | 0.9991   | Pitt         | 1      | 1          | 1        |                |        |            |          |
| Farrant     | 0.9914 | 1.0000     | 0.9914   | Pooley       | 1      | 1          | 1        |                |        |            |          |

