

APPROVAL

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Can They Indicate Estuaries in British Columbia for
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ABSTRACT

In response to increasing threats, habitat loss, and degradation of British Columbian (BC) estuaries, the Pacific Estuary Conservation Program (PECP) protects estuaries through land acquisition and stewardship programs. To assist the PECP in prioritizing BC estuaries, I develop a conservation tool that exclusively considers estuarine significance within a reserve network for migrating waterfowl. Using a dynamic state variable (DSV) optimization model, I predict estuary stopovers used by Dusky Canada Geese (*Branta canadensis occidentalis*) during spring migration. The DSV model predicts that only geese beginning migration in poor condition with respect to fat deposition use estuaries to maximize expected fitness. Numerous versions of the DSV model identify the Fraser River Estuary as an important stopover for geese of initially lower energy reserves. Introducing the assumption of density-dependence increases the total number of estuaries used as stopovers. Postulated scenarios of estuarine habitat losses decrease expected fitness more than scenarios of population increases.

Keywords: estuaries; waterfowl migration; Dusky Canada Goose; *Branta canadensis occidentalis*; dynamic state variable model; conservation planning

DEDICATION

To my mother and father, Waltraud and Gyula Kereki, for their steady support all these

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ecological process, i.e., bird migration (Chave and Wiegand 2002, Cabeza and Moilanen 2003, Nikolakaki and Dunnett 2005).

Using dynamic state variable modelling, estuary importance is predicted from the perspective of a waterfowl (*Anseriforms*) species, the Dusky Canada Goose (*Branta canadensis occidentalis*) as it migrates to its northern breeding grounds. A dynamic state variable (DSV) model is one way to conceptualize tradeoffs in biology. These models

Background

The Importance of Conservation Planning

To place the use of a bird migration model in the context of prioritizing estuaries, it is important to understand the origin and development of conservation planning over time. The interest in the design of reserve networks and protected areas by conservation ecologists arose from the recognition that the planet is in a biodiversity 'crisis', as described in (Noss and O'Connell 1997). In the 1980s, increasing rates of species' extinction, habitat loss, and degradation reported and projected by scientists (with special attention to the rainforests of neotropical areas) raised global awareness of this crisis. Calculations suggest the rates of species extinction are now on the order of 100 to 1000 times those before humanity's dominance of the earth (Pimm and Russell 1995). The primary force driving this loss of biodiversity is the transformation of land from its natural state to a human-altered one, which encompasses a range of uses from agriculture to urban development (Vitousek et al 1997). Estimates indicate that globally between 39 and 50% of land is transformed or degraded (Vitousek and Ehrlich 1986, Daily 1995). Figures like these spurred the impetus of scientists to investigate ways to maintain viable populations of species and ecosystems worldwide through biological conservation and habitat protection. Brussard and Murphy (1992) state that protection and management of suitable habitat is the most important way to accomplish the goal of no net loss of biodiversity.

The selection of sites for protection has largely occurred in an ad hoc fashion (Pressey 1994) with limited directed planning. One visible result of this lack of conservation planning is an unbalanced proportion of park and wilderness systems represented by alpine ecosystems (and a lot of "rock and ice") in high elevation areas. These areas are seemingly easier to set aside for conservation because less conflict among stakeholders with competing, land-use interests exists. However, as social and economic constraints on land use increase, financial resources become more limited, and widespread threats to biodiversity increase, proactive conservation planning becomes increasingly more important (Rookwood 1995).

Proactive conservation planning is systematic in its approach with respect to locating and designing reserves (Margules and Pressey 2000). It strives to optimize the conservation potential of reserves, as well the use of allocated funds (Pressey 1994,

Prendergast and Quinn 1999). The overriding principals of systematic conservation planning are that along with representing a full variety of biodiversity, reserves should also secure the persistence of species and their populations (Margules and Pressey 2000), and maintain critical ecological processes that sustain biodiversity (Cabeza and Moilanen 2003). Acknowledging that not all lands of ecological significance can be protected, conservation planners seek to answer difficult questions like, 'Which tracts of land do we protect in order to most effectively (and for the long-term) maintain biodiversity?', and 'How do we draw the shape of reserve boundaries on a map?'

Often within the framework that guides conservation planning, site selection based on ecological criteria occurs before the final decision-making process considers socio-economic factors. Therefore, site selection may only constitute one step that provides ecological information within the larger framework of conservation planning. For example, The Nature Conservancy describes conservation planning as a comprehensive process with many interrelated and integrated components, from defining specific conservation targets to implementing strategies (Poiani and Baumgartner 1998). In the real world deciding which sites merit protection is not the 'simple' task of identifying them with acceptable, ecologically based methods; the decision-making process invariably involves many stakeholder groups and contends with social issues. Nevertheless, delineating ecologically significant sites for selection is a worthwhile endeavour because maps contain persuasive powers. A map can represent a transparent and scientifically defensible rationale for prioritizing sites, thereby increasing conservation influence in a sometimes all too political arena.

Methods in Selecting Sites for Conservation

Many studies that address the problem of prioritizing sites for conservation, including this project, take a surrogate species approach (e.g. focal, indicator, multi-species approaches). The surrogate species approach utilizes the needs of one or a few species to identify areas for protection, with the hope that these identified lands will support other non-target species residing in the area (Hess and Koch 2006). In a region

(Andelman and Fagan 2000, Roberge and Angelstam 2004). Also controversial, is how to best choose indicator or surrogate species (Landres and Verner 1988, Simberloff

In attempts to develop effective tools for selection, conservation planners face many challenges. With only sparse empirical information, they struggle to represent entire functioning communities and ecosystems in their reserve designs. Often design plans are forced to use limited datasets that contain records of only species presence in their approach. Thus for portions of the study area, which are not surveyed, the analysis might be based on records incorrectly termed as 'species absence', resulting in a flawed plan. Also, for consideration is that often the presence or absence of individuals is a poor

For the objective of selecting estuaries for conservation, choosing to focus on

Migration is one of the most important and least understood (Hutto 1998, Webster and Marra 2002) stages in the annual cycle of migratory birds. For many species, research has not yet identified specific migration routes and schedules, and the mechanisms for migratory decision-making. The routes migratory birds follow provide a vital link between breeding and wintering ranges (Ogilvie 1978). Ultimately, the importance of these routes (and the act of migration) translates into the survival and reproductive success of a bird species or population.

The fundamental incentive for bird migration appears to be the availability of feeding grounds. Habitats at higher latitudes (e.g. arctic habitats) provide abundant food supplies in the form of insects and vegetation, as well as days of long daylight for increased foraging during the northern summer. Another potential reason to migrate to breeding areas that differ from wintering sites is to avoid competition with conspecifics (Berthold 1993). Additional benefits provided by the arctic to breeding geese, the focal group of this research, are large areas of wetlands with safe nesting sites, and restricted numbers of predators and competing grazers (Ogilvie 1978).

Before most bird species depart for their first migratory flight, they undergo a period of hyperphagia or overeating in order to acquire extensive fat reserves. With the ability to densely store energy, fat reserves serve as fuel essential for migration (Berthold 1993). As the primary energy source, the amount of fat stored prior to migration or deposited en route at stopover sites is one of the factors dictating the flight range a bird can achieve (Klaassen 1996). Birds with insufficient fat reserves may not be able to complete migration or have compromised breeding success (Berthold 1993).

Stopover sites like estuaries provide resources for resting and refuelling birds. Because migratory flights place birds under high physiological demands, these resources can be crucial to their survival (Skagen and Knopf 1993, Hutto 1998). The chain of stopovers provide nutrients critical for migrants to complete the journey and breed afterwards; and the health of populations may rely on the integrity of multiple spring stopover sites (Drent and Fox 2006). Field studies on arctic-breeding geese (e.g. Pink-footed Goose (*Anser brachyrhynchus*) (Madsen and Klaassen 2006), Barnacle Goose (*Branta leucopsis*) (Prop and Black 1998, Prop and Black 2003), Brant Goose (*Branta bernicla*) (Ebbinge and Spaans 1995), Greater Snow Goose (*Chen caerulescens atlantica*) (Reed and Gauthier 2004), Lesser Snow Goose (*Chen caerulescens*

caerulescens) (Davies and Cooke 1983)) demonstrate that carry-over effects from stopover sites visited during spring migration impact breeding success or propensity.

Stopover sites may be even more imperative to larger birds, like geese which carry smaller fat reserves proportional to their body weight (Ogilvie 1978, Berthold 1993) than smaller birds. As body mass increases, the maximum distance a bird can fly decreases. Thus, larger birds need to refuel more frequently during long flights (Klaassen 1996). Energetically-costly, flapping flight (Norberg 1996) common of geese and swans, puts further demand on these birds to stage at multiple stopover sites en route in order to refill their fuel reserves. This energy requirement of larger birds could result in migration pathways that consist of multiple shorter hops between stopover sites.

The strategies bird species employ during migration are diverse. Even within a single species, differences in the timing of migration, stopover length, and habitat use of stopover sites exist among sex and age groups (Klaassen 1996). For example, immature birds and failed breeders of many geese species also take part in a moult migration. These birds migrate to unique areas, usually northward of breeding areas, to moult their flight feathers and gain fat reserves for the autumn migration (Ogilvie 1978, Rees and Matthews 2005).

Research efforts have been invested into understanding how such migratory differences evolved. Current theory in stopover ecology hypothesizes that the selective forces of time, energy, and predation have shaped the behaviour of birds with respect to the use of stopover sites (Alerstam and Lindstrom 1990). Due to the short summer season and harsh winter in the arctic, migratory birds synchronize their reproductive cycles closely, and cram breeding, moulting, and developing fat reserves for autumn migration into a period of three to four months (Rees and Matthews 2005). Earlier arrival and clutch initiation on the breeding grounds generally implies higher levels of reproductive success (Daan and Dijkstra 1990). Thus, the timing of migration involves a trade-off between early arrival on the breeding grounds and the benefits of larger fat reserves achieved by a longer stay at stopover sites (Rees and Matthews 2005). For some species, the trade-off also includes avoiding the migration window of their predators (e.g. Western Sandpiper (*Calidris mauri*) begins southward migration from their breeding grounds before their predators, Peregrine Falcons (*Falco peregrinus*) (Lank and Ydenberg 2003)). Understanding the movements and patterns of habitat use

of birds throughout their annual cycle is important for effective conservation planning (Haig and Oring 2002).

Modelling bird migration within a site selection method implicitly considers the spatial configuration and connectivity of stopover sites (i.e. estuaries) in the landscape. Most often, the approach of waterbird conservation emphasizes protecting areas with seasonally large concentrations of birds over complexes of smaller wetlands (Haig and Mehlman 1998). The majority of studies fail to integrate the concept of landscape connectivity on a regional scale in the evaluation of conservation areas (Haig and Mehlman 1998, Naugle and Johnson 2001). [Landscape connectivity is defined as the functional relationship among habitat patches containing resources and the movement of organisms in response to the landscape structure (Taylor and Fahrig 1993, With and Gardner 1997).] Yet the empirical research on waterbirds and their use of wetlands as migratory stopovers indicates that landscape connectivity matters (Farmer and Parent 1997, Plissner and Haig 2000). For example, Pectoral Sandpipers (*Calidris melanotos*) and American Avocets (*Recurvirostra americana*) exhibited responses in feeding behaviours and movements due to the arrangement of wetland patches of varying connectivity.

Haig and Mehlman (1998) recommend that future studies must consider wetlands as connected mosaics for complete understanding of their use and importance to waterbirds. Recent evidence of biotic connections (e.g. aquatic organisms) between wetlands maintained by bird-mediated dispersal underscores this element of interconnectedness between wetland patches (Amezaga and Santamaria 2002). As a specific type of wetland, estuaries too exist as mosaics and interconnected networks, and must be considered as such in research.

Relating to conservation planning, a landscape approach in prioritizing estuaries is important because it may be able to highlight seemingly small and isolated stopover sites that provide crucial links for migrating birds. Skagen and Melcher (1998) found evidence for small, isolated patches of riparian habitat acting as a 'stepping stones' (MacArthur and Wilson 1967, Pressey 1994) by facilitating the migration of land birds. Smaller wetlands may also influence the suitability of larger wetlands, when viewed as components of the landscape (Naugle and Johnson 2001). This concept is especially significant for mobile species that travel large distances (Naugle and Johnson 2001). Using bird migration in a site selection method broadens the analysis to a regional scale

that disregards transboundaries separating countries, states, provinces etc. It also views the importance of estuaries in the context of the scale on which the ecological process of migration operates.

Applying Dynamic State Variable Models

As techniques for analysing animal behaviour, dynamic state variable (DSV) models use optimization methods to treat behavioural decisions from an evolutionary standpoint. These models embrace the Darwinian concept of evolution that behaviours have evolved in ways to maximize fitness. They attempt to apply the principle of natural selection to fine-scale, behavioural decisions of animals in the context of their life histories (Houston and Clark 1988). Four components comprise a framework for describing dynamic modelling: 1) a set of variables characterizing the state of an animal 2) a set of actions that an animal can perform 3) dynamics that specify the relationship between actions and subsequent states, and 4) a state dependent reward function that specifies future reproductive success or fitness (Houston and Clark 1988).

2 METHODS

1980s, the Oregon Department of Fish and Game implemented management strategies on the wintering grounds, like additional hunting restrictions (Bromley and Rothe 2003). Other significant management efforts undertaken by the Alaska US Fish and Wildlife Service and the US Department of Agriculture Forest Service include population surveys and an artificial nesting program on the breeding grounds (Bromley and Rothe 2003).

As almost exclusive herbivores, Canada Geese shift their diets in response to the seasonal availability of foods and their nutritional requirements during different stages in the annual cycle (Mowbray and Ely 2002). During spring, they consume diets containing more green vegetation compared with their autumn diets, which tend to be dominated by grains and cereals (McWilliams and Raveling 1998). The shift in diet during autumn to foods with larger amounts of carbohydrates is due to the migrant's need to amass energy reserves for the energetically demanding period of migration (Baldassarre and Bolen 1994). During spring and summer, however, protein requirements are higher because females are building up reserves in order to breed. At these times, geese select the newly flushed, green leaves and shoots that contain the highest protein and lowest fibre content (Sedinger 1997). Sedinger and Raveling (1984) also observed a similar diet selection of leafy vegetation in spring for Cackling Canada Geese.

On the Copper River Delta, Hawkings (1982) also noted that leaves are the most important component of the spring diets of Dusky Canada Geese, and as autumn advanced seeds and roots increased in importance. During spring on the delta they forage in freshwater meadows, saltmarshes, and tidal mudflats (Carriere and Bromley 1999), feeding on various plant species including horsetail (*Equisetum* spp.), sedge (*Carex* spp.), grass (*Gramineae* family), plantain (*Plantago* spp.), and rush (*Juncus* spp.) (Hawkings 1982: M.S. thesis). Canada Geese are described as terrestrial grazers because they employ a feeding technique that consists of plucking or cutting shoots and stems of vegetation (Hughes and Green 2005). To a lesser extent, they are also likely to grub or dig in soils and sediments for roots and tubers also rs702 m6971tTj/Ttd pluc9. Thees funkownt

west-central coast of Vancouver Island (Hansen 1960). Bromely and Jarvis (1993) also documented that Dusks meet half of their energy requirements for spring migration by obtaining food en route. Given the results of their experiments, they expect that most geese take advantage of opportunities to supplement their energy reserves; and they infer that the combined factors of high-quality food availability, energy and nutrient demands, and predation risks influence the Dusks' decisions to feed (Bromley and Jarvis 1993). Thus, the staging and stopover sites used by migrating Dusky Canada Geese must be important. It is conceivable and likely that these geese use multiple stopovers that include estuary sites in BC.

Spatial Data Inputs

To study migration strategies of Dusky Canada Geese in this system and to determine corresponding estuary sites important for conservation I included mapped estuaries of the BC coast within the model landscape. The mapped estuaries comprise a GIS-based set of 442 discrete sites with spatial and attribute references. The estuary dataset was created (2004) by the Pacific Estuary Conservation Program (PECP) through the technical expertise of Ducks Unlimited Canada and the Canadian Wildlife Service (Ryder and Kenyon 2006). By querying a combination of Terrain Resource Inventory Mapping basemaps at a 1:20,000 scale, National Topographic Series British Columbia Watershed Atlas basemaps at a 1:50,000 scale, 1:20,000 scale digital

Model Development

Conceptual Migration Model

The model predicts migratory pathways of individual female Dusky Canada Geese during their spring migration along the coast of British Columbia (BC), from wintering grounds in the Willamete Valley, Oregon to breeding grounds on the Copper River Delta, Alaska. Migratory pathways are analogous to migratory strategies and are comprised of the sites used as stopover locations en route to the breeding grounds, as well as the corresponding timing of stopovers during the migration period. Females are the focus because of the model's connection with reproductive success.

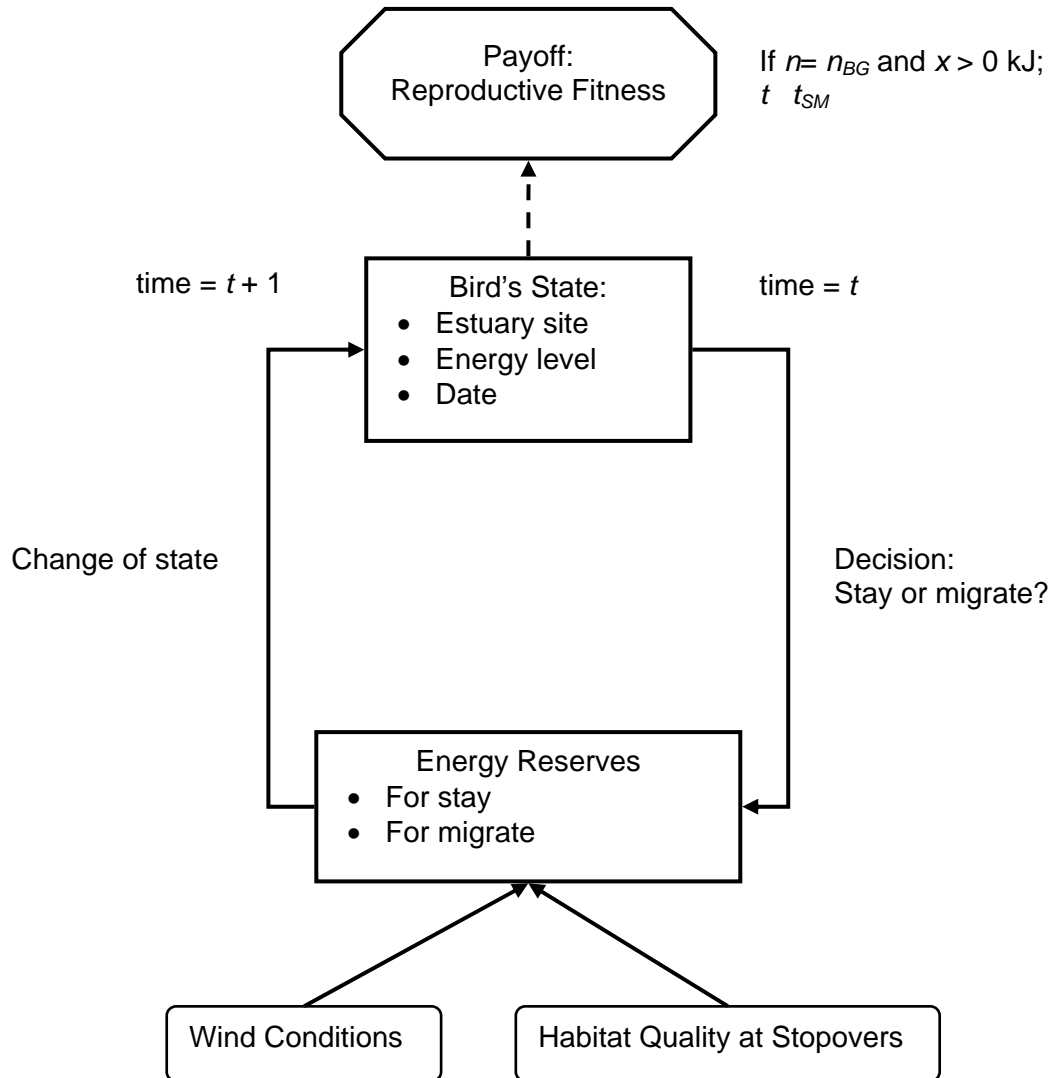
Individual geese begin spring migration at the first stopover located at the most southerly estuary site on the BC coast, which I have designated to represent the hypothetical wintering grounds. A bird starts migration with an initial state defined by its energy reserves and current location, i.e. estuary site, for time t . Each day a bird decides to either remain at the current stopover location or migrate to a more northerly stopover. The bird's decision depends on its current energy reserves, location, and the date. These migratory decisions occur within a feasible period for completing migration or the migration window. The migration window spans the period from the earliest departure date from the wintering grounds to the latest arrival date on the breeding grounds.

At the beginning of each day birds evaluate and make their migratory decisions to initiate a flight or to stay at the stopover location. The estuary sites that are considered as potential stopovers are a function of the current energy reserves of an individual. For example, sites are included as decision options if they can be reached by flying within 24 hours given the bird's energy level. The model assumes a bird can fly the distance of the BC coast within one day if it has sufficient energy reserves. The presence of wind also has an effect on the potential sites included as decision options because wind influences the achievable flight distance. Birds flying with deterring headwinds, which decrease their ground speed, have fewer potential stopover sites available to them than a bird facing tailwinds. I assume that a bird's navigational ability does not vary, thus a bird finds the site that it intended to fly to.

An individual bird experiences daily changes in state depending on the migratory decision it made in the morning. This decision to fly or stay influences its energy reserves and location for the next time step. When an individual stays at a stopover site

Figure 2.1 Conceptual model of Dusky Canada Goose spring migration.

For time t , a bird's decision to stay or migrate north to another estuary site depends on its state, represented by its location, energy level, and date. A bird's energy reserves are influenced by its migratory decision. For example, the energy reserves of a bird that stays at a site is affected by the quality of habitat at the estuary. Also, the energy reserves of a bird that flies north is affected by the presence of wind. When the bird reaches the breeding grounds, it receives a fitness payoff given its energy reserves are greater than zero and the arrival date is no earlier than the snowmelt date.



Quantifying the Dynamic State Variable Migration Model

Kristina Rothley coded the dynamic state variable (DSV) model in the Python

The critical level for energy reserves is set to 0 kJ, and if reserves drop to this level the bird dies and cannot gain any fitness.

Change of State

Changes in the state of a bird depend upon the bird's daily decision to migrate or stay. For a bird migrating to or staying at a stopover, the respective changes in energy reserves are given by the following equations:

$$x'(t+1) = x(t) - c_m$$

$$x(t+1) = x(t) + c_s$$

where $x(t)$ are energy reserves at the beginning of day t ; $x'(t+1)$ are energy

analysis. Thus, I conclude that using Greater Snow Goose data for deriving intake parameters for the Dusky Canada Goose is acceptable.

To derive the energy intake rates for various habitat qualities I used the lowest, average, net mass gain per day for Greater Snow Geese (Gauthier and Giroux 1992) to base all other rates on. Using the energy content of fat (39 kJ/g), I converted the daily, lowest, average, mass gain to energy in kJ. I designated this energy intake for low quality habitats. I assumed the intake rates for medium and high quality habitats to be two and three times greater than low quality habitat, respectively. This assumption is reasonable because the intake value for high quality habitat (807 kJ) is within close range of the highest, average, mass gain for the Greater Snow Goose when converted to energy (kJ). The two values only differ by approximately 25 kJ. I assumed the intake rate for the lowest quality habitat to be equivalent to no net gain in mass (0 kJ). Therefore, the birds visiting the lowest quality sites only meet their metabolic needs of staying and gain nothing more.

The second component of a bird's state is its position along the migratory path, which is updated at the beginning of each day. This position is always the bird's location at an estuary site. Because it is assumed that each leg of the journey takes less than 24 hours, every morning the birds find themselves at an estuary site. All migratory decisions affecting a bird's state are made within the migration window that spans the period from March 20 to May 1. I determined these dates to be the largest window for migration based on records of the earliest and latest arrival of Dusks on the Copper River Delta, April 1 and May 1, respectively (Crouse 1992 in Bromley and Rothe 2003). Since the average completion time for migration is 11 days (Bromley and Jarvis 1993), I deduced that, in theory, birds could begin migration roughly as early as March 20.

Fitness Relationship: Individual Fitness is Constrained by Arrival Date and Energy Reserves

The model measures a female's fitness or expected reproduction by the number of eggs produced during the current year. Low energy reserves and late arrival at the breeding grounds reduce reproductive success linearly. For example, a bird arriving at the breeding grounds early in the season (but still on or after the snowmelt date, t_{sm} =April 20) with higher energy reserves receives a higher fitness payoff, than a bird arriving later with lower energy reserves. Fitness payoff with respect to clutch size also

relates to the survival probability of offspring. Clutches laid earlier in the season tend to be larger because the offspring have greater survival than later laid clutches. I based this fitness relationship on the function described in Clark and Butler's dynamic state model (1999). However, I modified the function to accommodate for the likely possibility that Dusky Canada Geese are income breeders or at least in part.

The view that large-bodied birds breeding in harsh environments, like arctic-nesting geese, are capital breeders and rely extensively on stored nutrient reserves for reproduction has recently been challenged (Meijer and Drent 1999, Gauthier and Bety 2003). Current research suggests that food eaten by arctic geese during incubation, and egg-laying may play a greater role in supplying energy and nutrients than previously thought (Gloutney and Alisauskas 1999). Field studies have indicated that Dusky Canada Geese are able to maintain or increase their lipid reserves during the pre-laying period on the breeding grounds (Bromley and Jarvis 1993), displaying a breeding strategy previously thought to be atypical for geese. Therefore, the modified fitness relationship allows a bird to continue feeding and gaining energy reserves once on the breeding grounds, before initiating egg-laying. The onset of breeding by a bird is not constrained by its arrival date within the migration window, and a bird may initiate reproduction even on the last day of the migration window.

Specifically, the function $\Phi(x, n, t)$ defines the fitness of a bird for a given energy level at time t at the breeding grounds. The equation in its expanded form is:

$$\phi(x) = w_1(x) \cdot w_2(x) \cdot r_{BG} \quad (1)$$

where $w_1(x)$ is equivalent to an energy penalty, $w_2(x)$ is equivalent to a time penalty, and r_{BG} is equivalent to the maximum number of offspring per clutch initiated on the breeding grounds. Functions for $w_1(x)$ and $w_2(x)$ are:

$$w_1(x) = \min\left(\frac{x}{k_1}, 1\right) \quad (2)$$

$$w_2(x) = \begin{cases} 1 - k_2 \cdot (t - t_{sm}) & \text{If } t \geq t_{sm} \\ 0 & \text{If } t < t_{sm} \end{cases} \quad (3)$$

where k_1 is a penalty for low energy reserves, k_2 is a penalty for late arrival, and t_{sm} is the date of snowmelt and thus the date the habitat is accessible for feeding. I

leucocephalus) are a significant predator on eggs, goslings, and nesting, adult Dusky Canada Geese at the breeding grounds (Bromley and Rothe 2003). However, the intensity of depredation varies throughout the breeding season in association with the reproductive stages and vulnerability of the geese. It has been also suggested that the timing of the eulachon (*Thaleichthys pacificus*) run relates to the rates of nest depredation. Lacking information about predation risks at migratory stopovers for Dusky Canada Geese, I assumed no predation risks for adult geese during spring migration. I did not use a surrogate estimate for predation risk at estuaries during migration because predation appears to vary widely with spatial and temporal dynamics. Also, empirical data suggest that non-nesting adult geese are less vulnerable to aerial predators (Bromley and Rothe 2003).

Model Versions

The approach I take in developing the dynamic state variable (DSV) model is to build increasing complexity in stages. The model progresses from a simple representation of a migrating Dusky Canada Goose to one that has more biological realism. Several components make the model system more biologically realistic; these components include an aspect of habitat quality for the estuaries and wind conditions for spring. Each ‘building’ stage represents a different version of the model. Below, Table 2.1 describes each of the six model versions and the sequence of increasing complexity. Note that model version 1 and 4 have no component of habitat quality, and migrating birds in the model landscape perceive estuaries as having the same potential for feeding.

Table 2.1 Descriptions for six versions of the dynamic state variable (DSV) model.

Model version	Inclusion of spring wind conditions	Inclusion of habitat quality for estuaries
1	No	No: birds perceive all estuaries as having the same potential for feeding
2	No	Yes: birds perceive estuary sites as having varying potential for energy gains during foraging proportional to total size of estuary

Model
version

concerning the dynamics of energy/fat reserves. Specifically, I based daily energy intake at estuary sites and flight range or the distance flown per unit of energy on information from other species. See Appendix A for details about the derivation of these parameter estimates.

Table 2.2 Parameter estimates for model version 1.

Parameter Description	Parameter estimate
number of estuary sites	442
Breeding site	site 147
Wintering site	site 441
number of time steps (days)	42 (March 20-May1: Julian date 79-121)
energy cap (energy units: eu)	145 (39,100 kJ)
flight range (km/eu)	32.23
energy intake at site (eu)	1 (269 kJ/day)
t_{sm} : snowmelt date	April 20 (Julian date 110)
fitness function parameters:	
r_{BG} : maximum clutch size (eggs initiated)	8
k_1 : penalty for low energy at arrival	0.085

Model Evaluation

Sensitivity Analyses

For testing the robustness of the DSV migration model to inaccuracies in the parameter estimates, I conducted ten sensitivity analyses using the baseline model (See Table 2.1 for description). In the baseline model, I varied one at a time the estimates for the following parameters: flight range, energy intake at sites, penalty for low energy at arrival (k_1), penalty for late time of arrival (k_2), snowmelt date, and wintering/breeding site

Table 2.4 Description of sensitivity analyses.

Sensitivity analysis number	Altered parameter estimate	Parameter value	Cohort size (number of birds)
SA1	Flight range	16.77 km/eu	1600
SA2	Flight range	1.34 km/eu	1600
SA3	Energy intake rates	-1, 0, 1, 2 eu respectively for estuaries of lowest, low, medium and high quality	1600
SA4	Energy intake rates	1, 2, 3, 4 eu respectively for estuaries of lowest, low, medium and high quality	1600
SA5	k_1	0.0225	1600
SA6	k_1	0.0275	1600
SA7	k_2	0.0765	1600
SA8	k_2	0.0935	1600
SA9	Snowmelt date	April 17 (Julian date:)	1600
SA10	Breeding site/ Wintering site	Copper River Delta/ Willamette Valley	1600

For each sensitivity analysis, I performed a forward iteration on the DSV output.

Across all replications for each bird group, I tracked the average values for fitness, trip length (defined as the time the birds leave the 'wintering' site until the time they reach the 'breeding' site), number of stops, bird days per visit per site, and number of visits per site. I compared the results of these variables for each sensitivity analysis to those of the baseline model using two-sample t-tests.

Table 2.5 Bird groups that reflect various initial 'states' of energy and timing of migration start or departure from wintering grounds.



The BCCWS survey sites are located on the shoreline and contain coastal habitats including estuaries. The sampling design of the BCCWS consists of a census within a rectangular survey site that is 1-2 km (along the shoreline) by approximately 1 km (out onto the ocean) (Badzinski 2003). Using census results that cover the months of March and April over 6 years (2000-2005), I calculated the average number of Canada Geese at each BCCWS survey site per survey per month of the migration period. Next, I connected these values of average numbers of Canada Geese at BCCWS sites to the PECP estuaries that are located near by. By spatial analysis in ArcGIS 9.0 (ESRI 1999) I found only 19 BCCWS sites to overlap directly PECP estuaries. In order to expand the dataset I included those BCCWS sites that fell within 1000 m of the boundaries of a PECP estuary. A buffer of 1000 m seems to be a reasonable distance because Canada geese can be categorized as generalists that move freely and use multiple habitats. In total 26 PECP estuaries, comprising approximately 6% of the PECP estuaries dataset, are linked to BCCWS data.

Using the baseline model's predictions of estuaries used as stopovers by Dusky Canada geese and the PECP estuaries connected with Canada goose records I aim to compare the amount of correspondence between the identities of the estuary sites and the degree of site use by the geese. I also examine the validity of the DSV model's predictions by spatially comparing the areas, which the BCCWS did not identify Canada geese presence with the estuaries that were not predicted as stopovers by model version 3. An overlap of these locations would also suggest some evidence supporting the validity of the DSV model.

Model Application

Forward Iteration: Simulation of Bird Migration Across the Landscape

Many animal populations experience negative feedback mechanisms that depress their (population) growth rates when many individuals exist in the population. These mechanisms or factors regulating population levels are influenced by the size of the population itself and are described as 'density-dependent'. Animal behaviour as well as population growth may experience density-dependent effects. For example, the number of competing conspecifics may influence how a particular animal uses certain areas within its habitat.

Geese, animals that exhibit flocking behaviour and get benefits from extra anti-predator vigilance, also compete with their flock members for patches of vegetation while grazing. Over time, geese deplete their food resources and as a result, foraging sites degrade and geese abandon depleted sites (Ebbinge and Canters 1975). Thus, varying densities of conspecifics at migratory stopover sites may affect the energy intake rates of individual geese through exploitative and interference competition. Possibly, declining energy intake rates due to increasing numbers of geese at a site could affect the migratory decision of a Dusky Canada Goose to utilize a particular stopover or to move on. In a forward iteration of the DSV model, I introduce a new assumption of density-dependent effects on the site use of estuaries as stopovers by Dusky Canada Geese. I explore how this assumption affects the optimal migratory strategies given by the original output of the DSV model; and predict the estuaries migrating Dusks use, the degree of site use at each estuary and the effects on the birds' relative fitness.

The density-dependent forward iteration incorporates a key concept concerning the grouping behaviour of geese and their tendency to forage in flocks: by foraging within a group, birds experience a trade-off between anti-predator advantages and the costs of increased competition (Carbone and Thompson 2003). Field studies have shown benefits to flocking, such as declines in individual vigilance levels and consequent increases in foraging times for White-fronted Geese, Dark-bellied Brent Geese, and Barnacle Geese (Lazarus 1978, Inglis and Lazarus 1981, Carbone and Thompson 2003, Amano and Ushiyama 2006). Other proposed benefits include reduced predation risks at individual levels because members of the group 'dilute' the risk by acting as alternative targets or facilitating earlier detection of the predator (Carbone and Thompson 2003). Geese might also experience increased opportunities to exploit discoveries of food made by other flock members (Drent and Swierstra 1977).

The primary disadvantage of foraging in a group is increased competition. Research has found evidence for the effects of increased competition in flocks of White-fronted Geese and Barnacle Geese (Carbone and Thompson 2003, Amano and Ushiyama 2006). Seasonal variation observed in the flock size of White-fronted Geese, namely smaller flocks in the spring when resource depletion had progressed, suggests that exploitative competition could control flock size and be a cost of flocking. An experiment that resulted in a significant increase in flock size after food resources were artificially supplemented (by rice additions) gives further support for the hypothesis that

exploitative competition could control flock size (Amano and Ushiyama 2006). Movement patterns of Barnacle Geese flocks perhaps indicate that more intense competition exists in larger than smaller flocks (Carbone and Thompson 2003). Larger flocks expanded more quickly possibly because local depletion of food was more severe (than in smaller flocks), and individuals attempted to avoid competition.

The concept of tradeoffs between the benefits and costs of foraging in a flock is implemented in the forward iteration by a probability distribution for the rate of energy intake at a particular estuary site. For any given site, the probability distribution indicates the likelihood a bird has of gaining various amounts of energy (in energy units of 0, 1, 2, or 3, equivalent to 0, 269, 538, and 807 kJ, respectively) while foraging, given the

Figure 2.2 Probability distribution for estuaries of 'high' habitat quality.

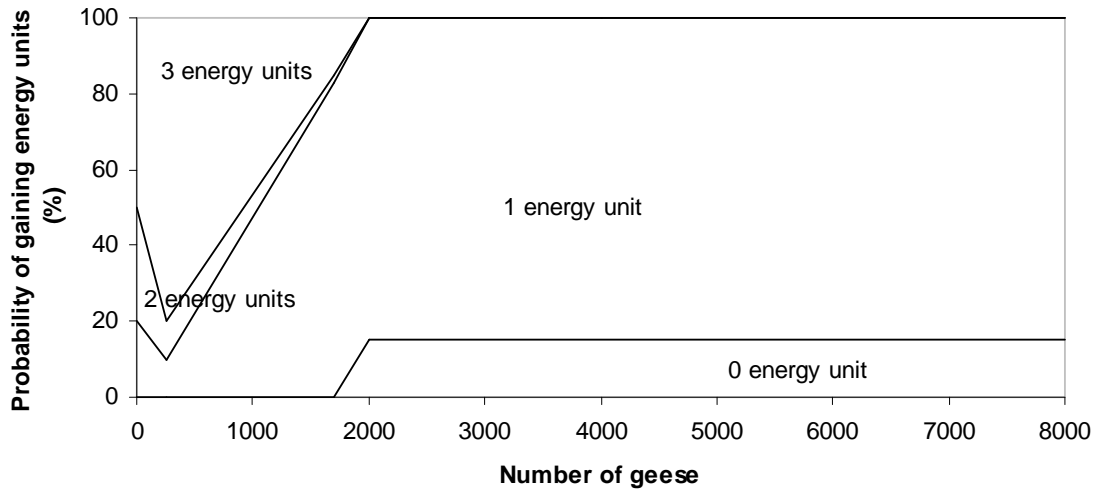


Figure 2.3 Probability distribution for estuaries of 'medium' habitat quality.

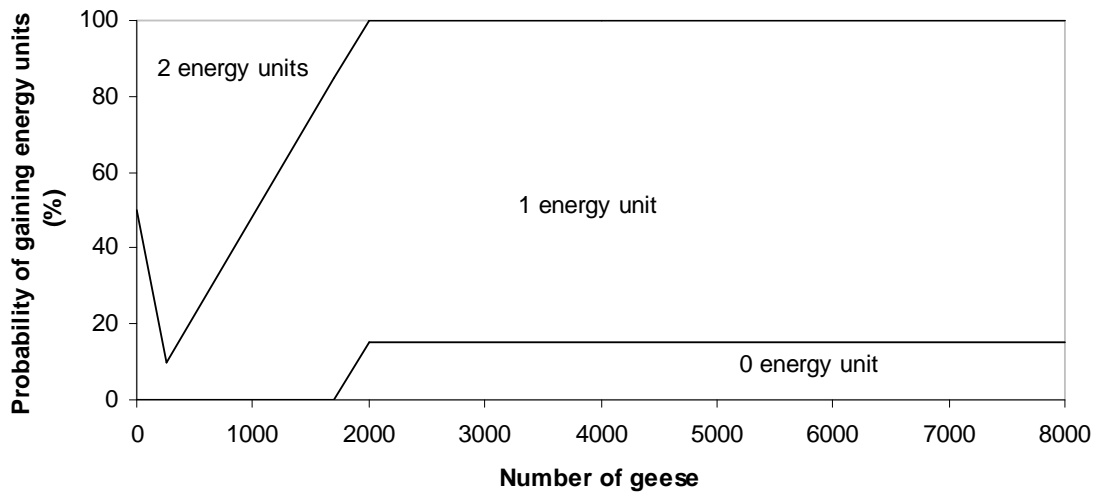


Figure 2.4 Probability distribution for estuaries of 'low' habitat quality.

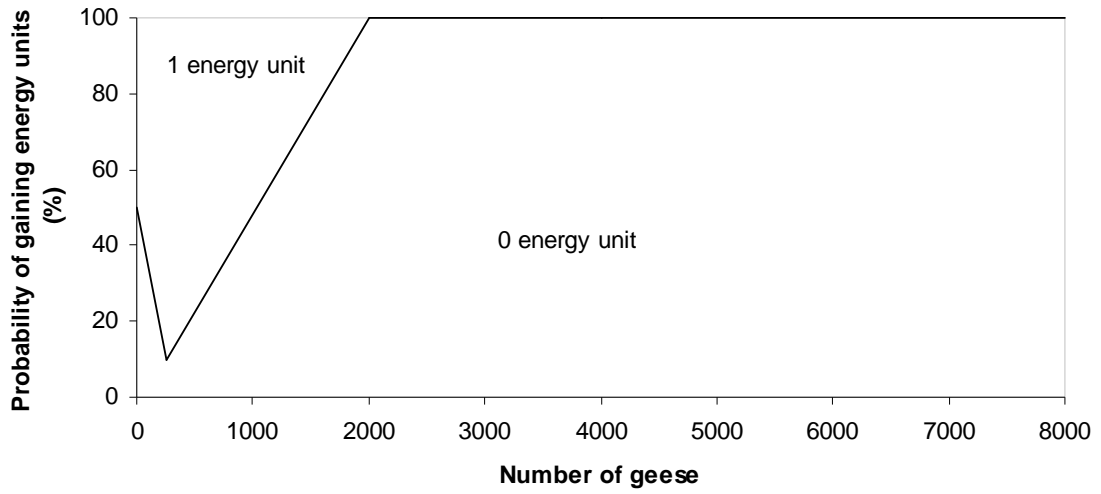
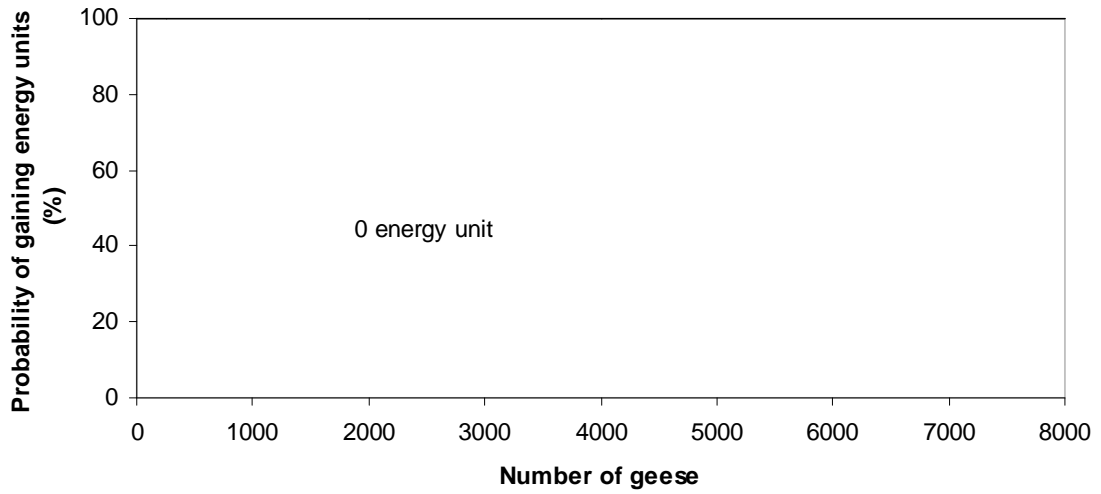


Figure 2.5 Probability distribution for estuaries of 'lowest' habitat quality.



I developed two forms of the density-dependent forward iteration, which I name the 'proactive' and 'reactive' forward iteration. The proactive iteration assumes that migrating geese have perfect knowledge of the potential fitness consequences relating to foraging at optimal sites versus foraging at alternative sites. In contrast, the reactive iteration assumes that migrating geese are ignorant of these potential fitness

migration strategy. This cycle of how the bird assesses its various options repeats itself in the next time period.

On the other hand, if the corresponding fitness payoff is less than what the bird would have received had the site been vacant, the bird then considers other reachable sites (predicted as sub-optimal by original DSV output) given its remaining energy reserves. The bird chooses the stopover site that yields the highest fitness payoff according to the DSV output. After burning energy to fly, the bird has a new energy state and location in the next time period, and continues to behave according to the optimal migration strategy. See Figure 2.6 for a flowchart that describes the proactive forward iteration.

For the second form of the iteration that assumes no perfect knowledge of fitness consequences, birds fly to the next 'optimal' site to receive an energy intake rate that is dependent on the number of birds currently at the site. For example, when a bird stops at its optimal site, the probabilities of energy units are assigned from the distribution relative to how many birds are currently there. Then a random selection of energy units occurs with the assigned probabilities. In the next time period the bird follows the optimal pathway for its new energy state.

To examine the specific effects of the density-dependent assumption I selected a group or cohort size of 1600 birds and ran the proactive and reactive iterations, and the density-independent iteration. I assumed sixteen-hundred birds to be a relative index of the current population size. (See the Sensitivity Analyses section for the rationalization of setting the relative population to 1600 birds). I compared the predictions of these forward iterations to determine the effects of the assumption on the bird's relative fitness and estuary site use.

Asking Questions About Waterfowl Management

In order to ask questions about potential management strategies for migrating Dusky Canada Geese, I postulate different scenarios with respect to the population status of the subspecies. These scenarios are entirely hypothetical and I use them to illustrate possible effects of different management strategies on goose migration. I use the hypothetical scenarios in the density-dependent and density-independent forward iterations to determine the effects on site use of estuaries, and relative fitness of the

The first set of estuary removals relates to the sites that receive the highest use as indicated by the original DSV outputs. Here, I remove the Fraser River, the site that experiences the highest bird use according to the baseline model (model version 3). I also remove all three sites (Fraser River, Nickomekl/Serpentine Complex, and Skeena/Ecstall/McNeil River Complex Estuaries) predicted by model version 3, and I remove all 13 sites predicted by model version 6 (See Figure 3.6). The next set relates to the elimination of three estuaries (Kitimat River, Chemainus River/Bonsall Creek Complex, Courtenay River) that the Canadian Wildlife Service (CWS) ranked with highest biological importance in an independent study for the PECP that prioritized estuaries based on biophysical data and attributes (Ryder and Kenyon 2006). The last set refers to the elimination of 44 estuaries that the Canadian Wildlife Service defined as unprotected and 50 percent or more threatened (See Appendix C for the derivation and list of these sites). Again, both density-dependent and independent iterations for these proposed scenarios are performed using the DSV output of the baseline model (see model version 3 in Table 2.1). I apply these landscape scenarios to the five groups of birds with varying initial 'states' (Table 2.5). Each bird group contains 1600 birds (equivalent to the current, relative population).

Lastly, I postulate a scenario that acts as a sensitivity analysis to examine the assumed benefits of flocking. By eliminating the portion of each probability distribution that reflects the declining predation risks and increasing foraging times as bird numbers approach the optimal flock size, I can test the sensitivity of the forward iteration's predictions to this assumption. To change the probability distributions I alter the declining slopes to positive ones up to 200 birds to show continual competition between conspecifics as the numbers of geese on an estuary site increase. Both forms of the density-dependent iteration for this scenario are performed using the DSV output of the baseline model (model version 3). I apply this scenario to the five groups of birds with varying initial 'states' (Table 2.5) and containing 1600 birds.

3 RESULTS

Predictions of Optimal Migration Routes

Migration Strategies

The outputs of the DSV model versions indicate optimal decision policies with respect to migration. In general the outputs for all model versions (1-6) show that a bird's initial state, specifically their initial start date of migration and level of energy reserves, greatly determine their respective migration strategies. The length of the migratory journey (in terms of time) and the number of stopovers utilized are both influenced by the bird's initial state. Only birds with lower energy reserves utilize intermediate estuaries as stopovers in order to reach the breeding grounds, as demonstrated by the outputs of all

Across all model versions, birds of the 'low energy/late start' category experience the lowest success in the proportion of birds that complete migration to arrive on the breeding grounds, ranging from 0.48 to 0.83. Model version 4 indicates the lowest success for this category at 0.48. All birds in the category 'high energy/early start' successfully complete migration. Birds in the category, 'high energy/late start' have 0.95 success in completing migration for all model versions. Curiously, this bird category almost consistently experiences slightly lower success by 2-5% than category 'low energy/early start'. Possibly, this discrepancy is an effect of the category sizes because there are slightly fewer birds in the high energy groups. Another explanation is that timing or the initial start date of migration is a factor that outweighs energy reserves in importance for migratory success.

Fitness payoff, expressed in the number of eggs per clutch, appears to decline as a bird's initial energy reserves decrease and initial start dates becomes later in the migration window. A three dimensional plot of relative fitness gained by birds as a function of their initial energy reserves and start dates for the baseline model shows this trend (Figure 3.1). Note the flat, triangular 'space' of the 3-D structure that corresponds to failed migrants. The shape of this flat space and the remainder of the 3-D structure are similar for all model versions.

Figure 3.1 Relative fitness as a function of bird states for model version 3.

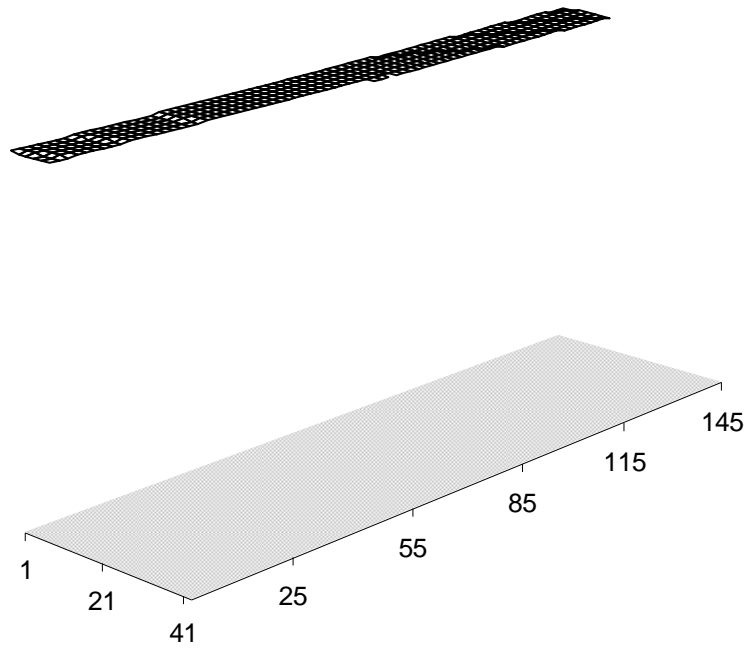
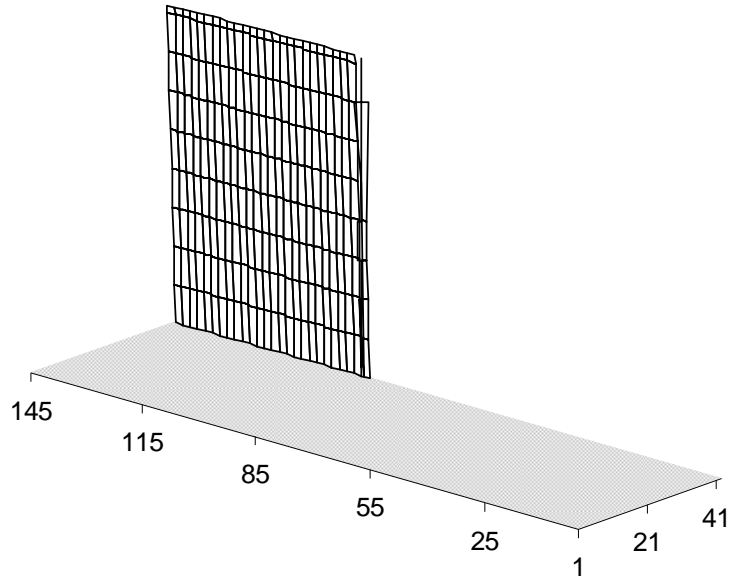


Figure 3.3 Arrival dates on breeding grounds of birds in all states for model version 3.



Figures 3.4 - 3.6 indicate estuary sites identified by running the six model versions. Each map shows the sites identified by the model versions with and without the aspect of winds. It becomes apparent that introducing wind into the model increases the total number of estuary sites identified as stopovers for birds with initially lower energy. Also, the numbers of stopovers per migratory journey increase with the presence of winds.

Of all identified sites, the Fraser River Estuary (Site 391) on the BC lower mainland appears most often across all model versions. Model versions 2, 3, 5, and 6 (versions that do and do not include wind trends) identified this site as a stopover. The Fraser River Estuary site also experiences the most usage (across all versions) with respect to number of bird days, ranging from 3281 to 15,201 bird days, where one bird day equals one bird using the site per day (See Figures 3.4-3.6). Figures 3.7 and 3.8 specifically show the number of visits to sites by unique birds in different initial states for model versions 3 (baseline) and 6. Note, that in model version 6 (which includes wind trends), the Fraser River Estuary does not experience the most number of visits. However, this site continues to experience the highest number of bird days.

Figure 3.4 Identified estuaries by model version 4.

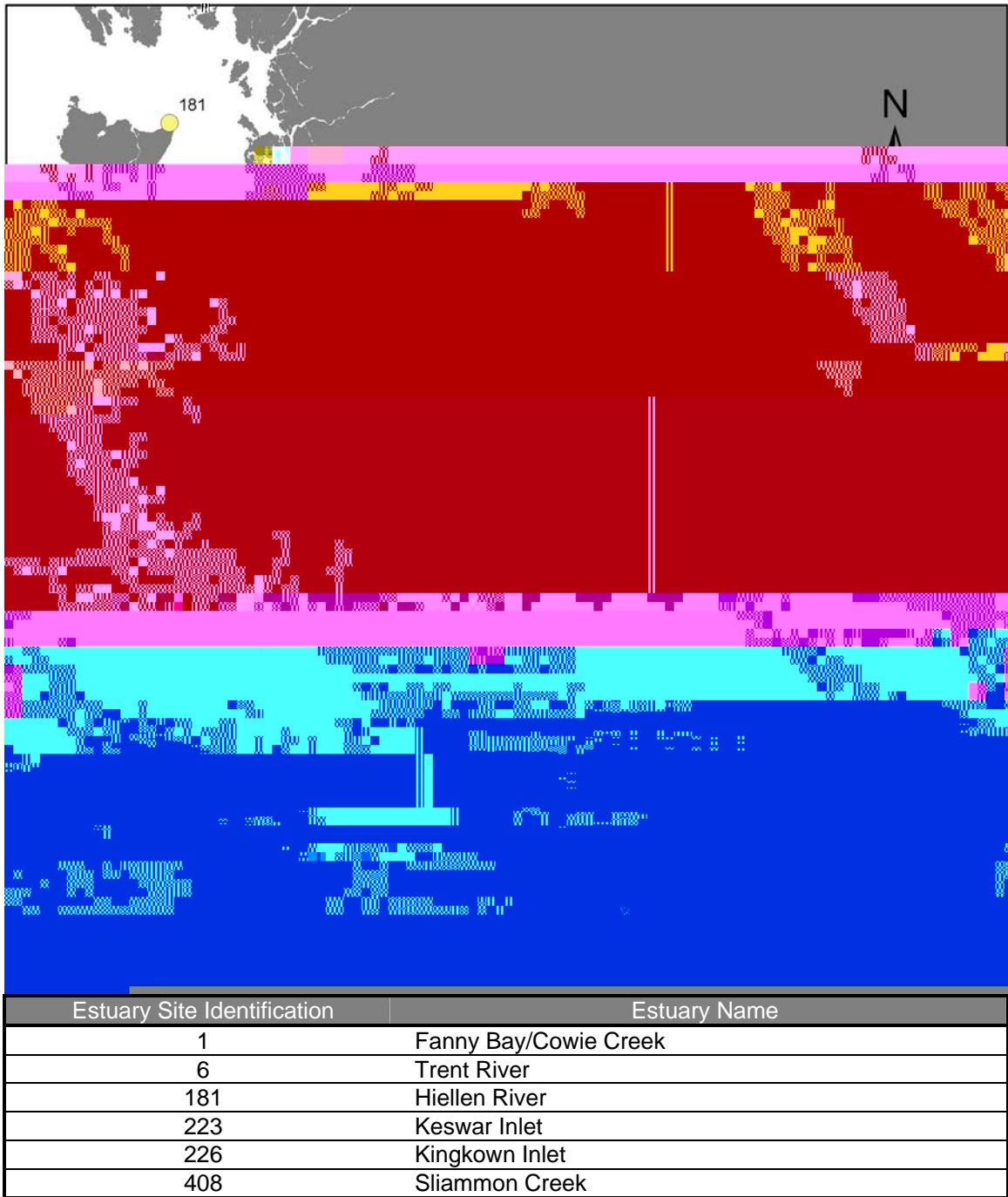
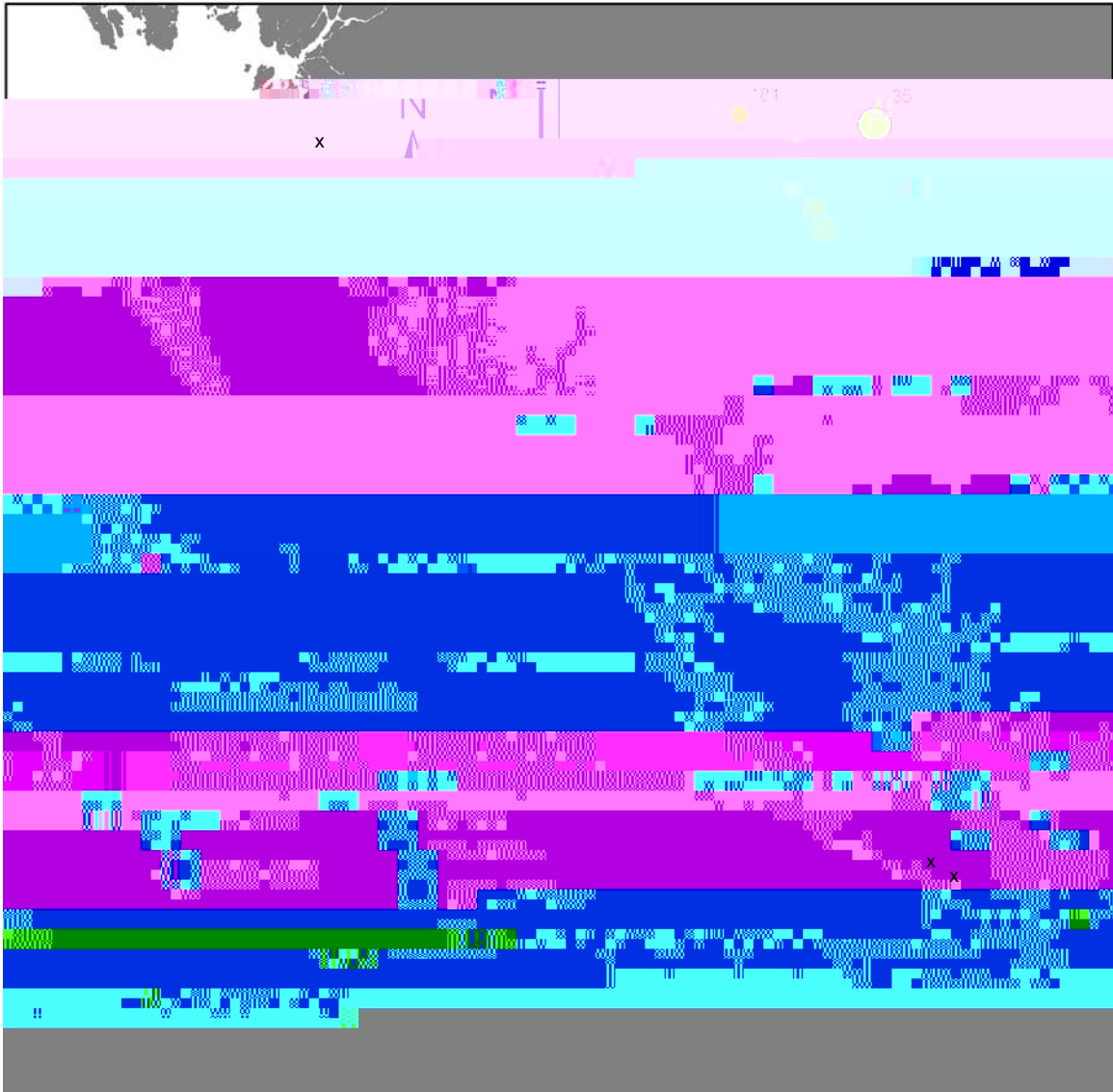


Figure 3.5 Identified estuaries by model versions 2 and 5. Green symbols represent model without winds and yellow symbols represent model with winds. The symbol 'x' identifies sites predicted by both model versions.



Figure 3.6 Identified estuaries by model versions 3 and 6. Green symbols represent model without winds and yellow symbols represent model with winds. The symbol 'x' identifies sites predicted by both model versions.



Estuary Site Identification	Estuary Name
1	Fanny Bay/Cowie Creek
6	Trent River
14	Cowichan River
35	Skeena/Ecstall/McNeil River Complex
181	Hiellen River
218	Nickomekl/Serpentine Complex
223	Keswar Inlet
226	Kingdown Inlet
293	No name
391	Fraser River
408	Sliammon Creek
409	Powell River
410	Lois River

Figure 3.7 Number of visits by unique birds per estuary site for model version 3.

See Table 3.2 for estuary names corresponding to site identification numbers.

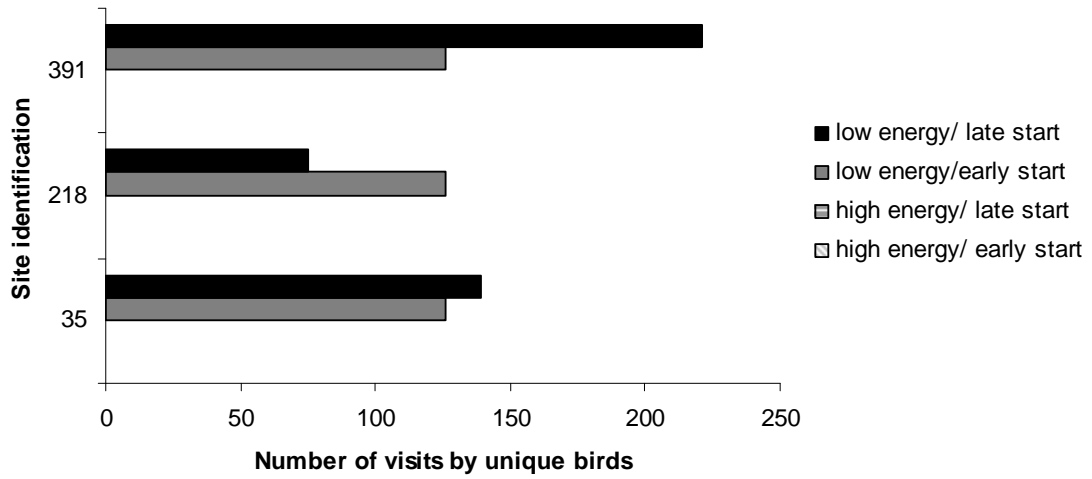
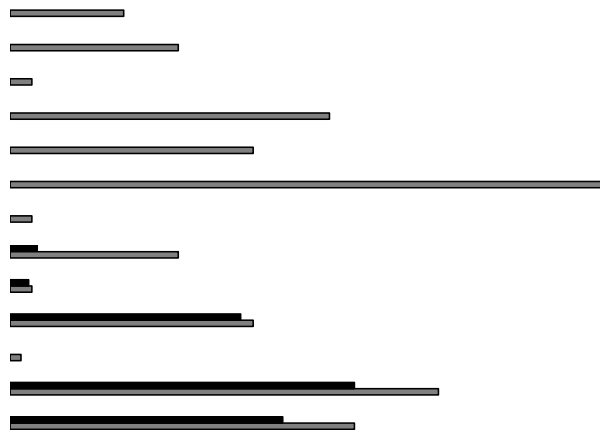


Figure 3.8 Number of visits by unique birds per estuary site for model version 6.

See Table 3.2 for estuary names corresponding to site identification numbers.



average larger numbers of bird days per site per journey, or in other words, birds on average stay for lengthier periods at a site, when wind is introduced into the models. Table 3.2 shows the average number of bird days per unique site per journey from model version 3 (no wind) and version 6 (wind).

Table 3.2 Average numbers of bird days per journey for sites identified by model versions 3 and 6 for bird state categories of lower energies.

Bracketed values correspond to average numbers of bird days per sites for model version 6 which includes wind trends, whereas unbracketed values correspond to average numbers of bird days per sites for model version 3 which does not include winds. Bird state categories for 'high' energy reserves are not included because these categories do not experience any site use.

Site identification	Estuary name	Bird state category	
		Low energy/early start	Low energy/late start
1	Fanny Bay/Cowie Creek	- (1.0)	- (1.0)
6	Trent River	- (1.3)	- (1.7)
14	Cowichan River	- (3.0)	- (3.0)
35	Skeena/Ecstall/McNeil River Complex	5.5 (6.2)	5.2 (5.9)
181	Hiellen River	- (1.0)	- (1.0)
218	Nickomekl/Serpentine Complex	11.1 (14.4)	11.1 (13.0)
223	Keswar Inlet	- (1.0)	- (1.0)
226	Kingkown Inlet	- (1.0)	- (1.0)
293	No name	- (1.0)	- (1.0)
391	Fraser River	9.8 (14.8)	9.3 (12.0)
408	Sliammon Creek	- (1.0)	- (1.0)
409	Powell River	- (1.0)	- (1.0)

Sensitivity Analyses

Effects on Relative Fitness

The sensitivity analyses predict that birds of higher initial energies (bird groups 'high energy/early start' and 'high energy/late start') would experience only minor effects on relative fitness. Figure 3.9 shows the mean values of relative fitness for all sensitivity analyses across all bird groups. These fitness values of birds with higher initial energies differ only slightly from values of the baseline model. For the majority of the higher energy bird groups I was unable to perform two sample t-tests, because there were no differences between observed means and/or the pooled-variances were zero. For those comparisons that were statistically possible, the majority of the t-tests unexpectedly resulted in statistically significant results. However, I believe that this statistical significance does not translate to a biological significance because the degree of difference between the two means of relative fitness is small. The statistical significance is due likely to the small, pooled-variances. Table 3.3 shows the p-values at alpha 0.95 for t-tests across all sensitivity analyses.

Table 3.3 P-values for two sample t-tests with 95% confidence for all bird groups across all sensitivity analyses.

All p-value are statistically significant except for values with an asterix.

Bird Group	P-values for two sample t-tests across all sensitivity analyses									
	SA1	SA 2	SA 3	SA 4	SA 5	SA 6	SA 7	SA 8	SA 9	SA 10
Null	1.25	2.40	1.51	2.77	6.64	0.15*	2.37	1.71E-11	4.02	6.58
	E-151	E-213	E-59	E-24	E-06		E-05		E-70	E-180
High energy/early start	-	-	-	-	-	-	-	-	-	-
High energy/late start	-	4.60	0.11*	-	-	-	7.78	3.50	5.35	5.19
		E-130					E-18	E-18	E-129	E-06
Low energy/early start	1.07	1.28	3.81	-	-	-	-	-	-	5.18
	E-196	E-255	E-150							E-223
Low energy/late start	1.39	2.66	1.2	1.33	4.05	6.83	4.12	2.66	8.06	2.20
	E-238	E-302	E-111	E-69	E-07	E-06	E-11	E-12	E-93	E-264

In contrast, mean relative fitness values for birds of lower initial energy (bird groups 'low energy/early start and 'low energy/late start' indicated in Figure 3.9) show that model results are most sensitive to the flight range parameter and the locations of wintering/breeding sites. The flight range parameter most dramatically affects birds with

successfully completing migration. This trend became apparent in the sensitivity analyses that varied parameters concerning energy reserves such that flight efficiency was diminished. Model birds in initially poorer conditions are more sensitive to inaccuracies in the flight range parameter, as well as the departure/destination locations in the model landscape. Altering the departure/destination locations relates to the birds' energy reserves because by increasing the total distance of the migration journey also increases the energy reserves required.

Effects on Trip Length and Number of Intermediate Stopovers

Only four sensitivity analyses demonstrate effects on the birds' trip length in terms of time (i.e. average number of days) when compared to results from the baseline model (See Figure 3.10). Advancing the snowmelt date by three days appears to affect birds of all bird groups by shortening their mean trip lengths. For all bird groups the differences in mean trip length between the average estimates for SA9 (altering snowmelt date) and the baseline were significant (p -values < 0.05 at alpha 0.95). Advancing the snowmelt date opens the breeding grounds earlier for goose arrival and the model birds take advantage of this opportunity. A smaller flight range parameter (in SA1 and SA2) increases the mean trip length for birds of lower initial energies because the birds achieve less daily mileage. For bird groups of lower initial energies the differences in mean trip length between the average estimates for SA1 or SA2, and the baseline were significant (p -values < 0.05 at alpha 0.95). The mean trip length also increases for all bird groups except bird group 'high energy reserves/early start' in SA10, when the locations of breeding and wintering sites are set to the Willamette Valley and the Copper River Delta. Comparisons between the mean trip length for SA10 and the baseline across all bird groups resulted in significant tests except for the bird group 'high energy reserves/early start'. The longer migration distance results in birds of lower initial energies remaining longer at the wintering site in order to gain fuel reserves.

Statistical comparisons between the baseline and sensitivity analyses 3, 4, 5, 6, and 8 also resulted in significant differences in mean trip length for some bird groups. However, when I examined the treatment effects or the sizes of these differences it is apparent that they are small and of minor ecological importance.

Figure 3.10 Mean trip length (in days) of migratory journey with associated standard

Figure 3.11 Mean number of stops at unique estuary sites per migratory journey with associated standard errors across all bird groups, for all sensitivity analyses.

Standard errors are barely visible because they are small.

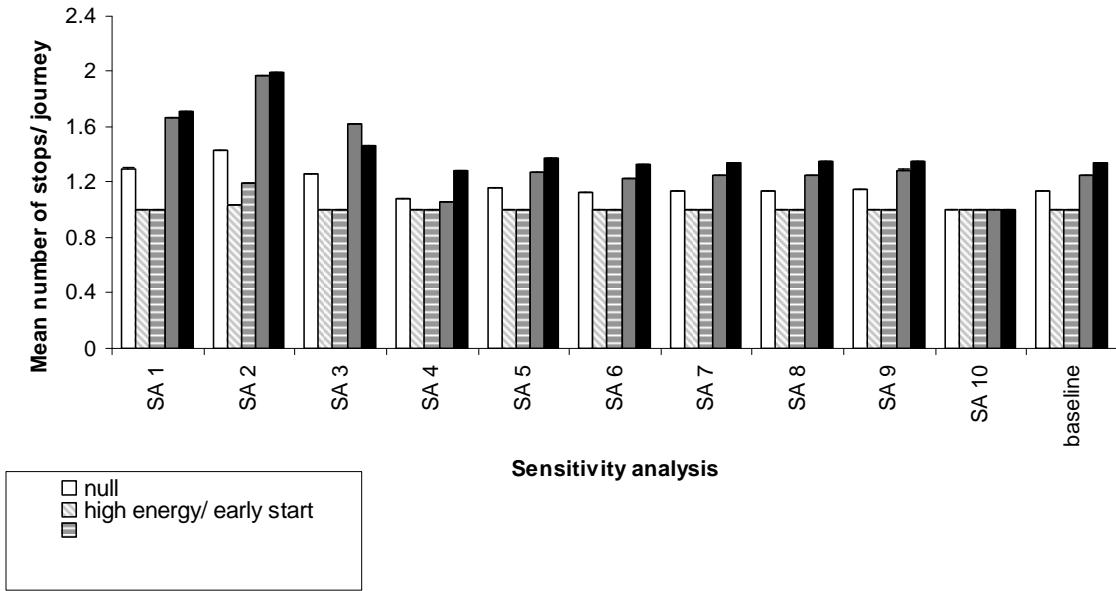
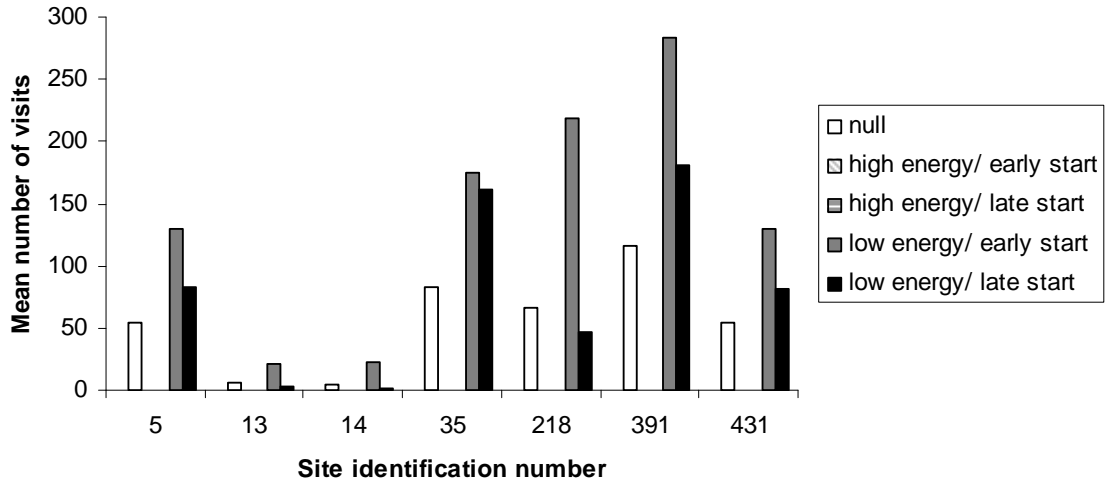


Figure 3.14 Mean number of unique visits to BC estuary sites across all bird groups as identified by sensitivity analysis 3 (SA3).



Model Validation

Comparisons of PECP estuaries connected with Canada Goose records observed by the BC Coastal Waterbird Study (BCCWS) (Bird Studies Canada 2006),

Table 3.4 A list of all PECP estuaries with associated BCCWS data of Canada Goose records and PECP estuaries identified as migratory stopovers by DSV model version 3.

Observed Canada goose records are expressed in average number of geese/census and model predictions are expressed in average number of visits/unique bird/migratory period. Average number of recorded CAGO with an asterix corresponds to summed, average CAGO counts.

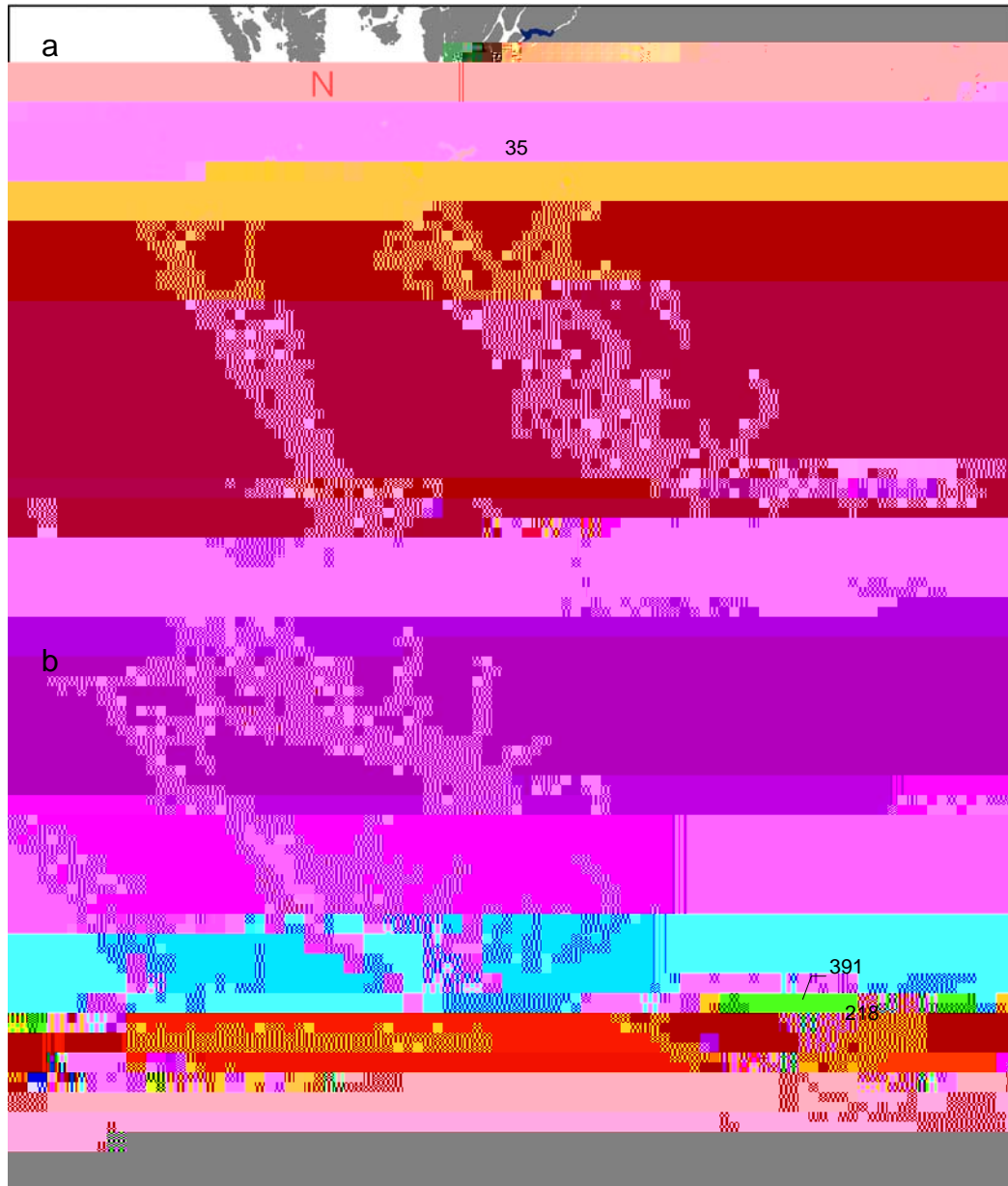
PECP estuary site ID	Estuary name	Average number of CAGO recorded associated at BCCWS census (variance in brackets)	Average number of unique visits /PECP estuary site (predicted by model version 3)
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Perhaps encouraging, is the similarity in the values for the average numbers of unique bird visits at estuary sites predicted as stopovers by the DSV model and the average numbers of Canada Geese recorded at the associated estuaries (See Table 3.4). Granted a direct comparison is not possible because the measures are of a different nature. The BCCWS census gives a snapshot of the number of CAGO present at an estuary on one day of the migratory period, whereas the model prediction gives an idea of how many bird visits the site receives over the course the migratory period. (A forward iteration of a cohort of 1600 birds of random states, replicated 100 times using the DSV output of model version 3 generated estimates of the average numbers of visits by unique birds to the estuaries). Another important caveat is that the BCCWS observations of CAGO at survey sites on the southern BC coast may be confounded by observations of introduced, resident CAGO (R. Butler, Canadian Wildlife Service, pers. comm. 2007). The presence of introduced CAGO would inflate estimates of average numbers of migratory CAGO associated with PECP estuaries.

Another way to approach the validation of the DSV model with field data is to examine the locations of BCCWS sites without Canada Goose observations and compare them with areas that the model predicted as unused by the geese. Figure 3.15 shows the locations of BCCWS sites that did not observe any CAGO from 2000-2006, in relation to the locations of the PECP estuaries identified as stopovers by model version 3. BCCWS sites on the west coast of Vancouver Island without CAGO records correspond to an area, which the model predicted as unused by migrating geese. Many BCCWS sites exist on the southern tip of Vancouver Island. Of the 53 BCCWS sites that dot the coast from Finlayson Arm south to Sooke, only one site has records of CAGO. Again, model version 3 did not predict geese to use stopover estuaries in this region. Another area of congruence is the Queen Charlotte Islands. Here, BCCWS censuses did not reveal CAGO presence, nor did the model predict stopover use.

Overall, I believe these comparisons lend some validation to the DSV model and perhaps suggest that its predictions are on track. How much on track however is difficult to discern without a more detailed and standardized survey of Dusky Canada Geese on the BC coast.

Figure 3.15 Locations of BCCWS sites without CAGO counts in relation to estuary Sites 35, 218, and 391 identified by predictions of version 3. Part a of the map identifies the northern coastline and part b identifies the southern coastline.



Density-Dependent Effects in the Forward Iterations

Introducing the assumption of density dependence at estuary sites into the forward iteration is predicted to minimally affect the expected relative fitness of Dusky Canada Geese. By comparing the results of both forms of the density-dependent forward iteration and the density-independent forward iteration using a cohort of 1600

birds, shows that geese of the low energy groups experience small declines in mean relative fitness under this assumption. In the reactive density-dependent forward iteration, mean fitness decreases by approximately 2.7% from the density-independent iteration for the bird group 'low energy/early start'. In the proactive density-dependent forward iteration, mean fitness decreases by approximately 1.7% from the density-independent iteration for the bird group 'low energy/early start'. For the bird group, 'low energy/late start', mean fitness decreases by approximately 4.8% from the density-independent forward iteration, in the reactive density-dependent iteration. For the same

stopovers that now provide a fitness advantage. During the simulated migration, birds

Effects of Waterfowl Management and Estuarine Losses on Migration and Survival

Applying Population Scenarios to Goose Migration

Predictions of the Density-Independent Forward Iteration

The application of scenarios that represent an increase or decrease in the Dusky Canada Goose population (from the current population status) using the density-independent forward iteration do not result in any effects on optimal migration routes and expected relative fitness. Varying the size of the initial cohort between 1200 and 6000 birds does not change the migratory pathways or the estuary sites used by birds of varying states. The average time for completing the migration journey and the average number of stopovers per journey remains the same. Increasing numbers of geese in the cohort also do not affect the expected fitness of individuals (See Figure 3.19). This lack of change across all variables is not surprising, because according to the rules of the iteration birds follow optimal routes oblivious to flock sizes.

Figure 3.19 Mean relative fitness for population scenarios using density-independent forward iterations (first group, from left to right), reactive-density-dependent forward iterations (second group, from left to right), and proactive-density dependent forward iterations (third group, from left to right).

For each scenario type, di refers to density-independent iteration, dd-r refers to reactive density-dependent iteration, and dd-p refers to proactive density-dependent iteration. The number following the iteration prefix refers to the size of the initial cohort. Mean fitness values are also associated with one standard error. However, standard errors are barely visible because they are small.

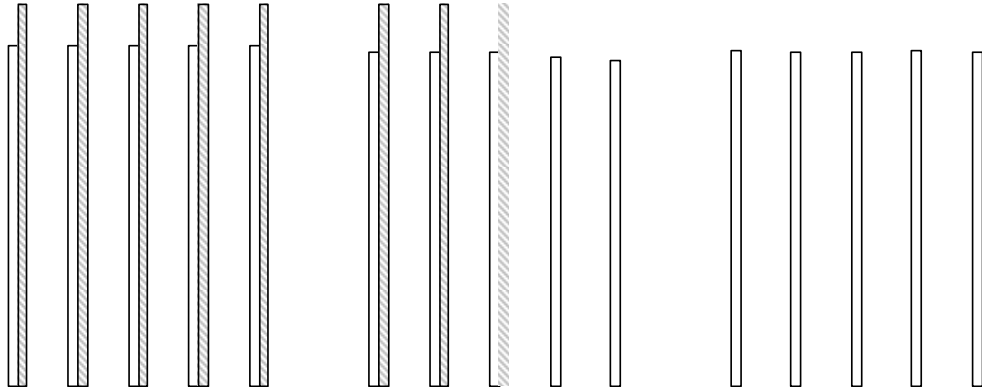
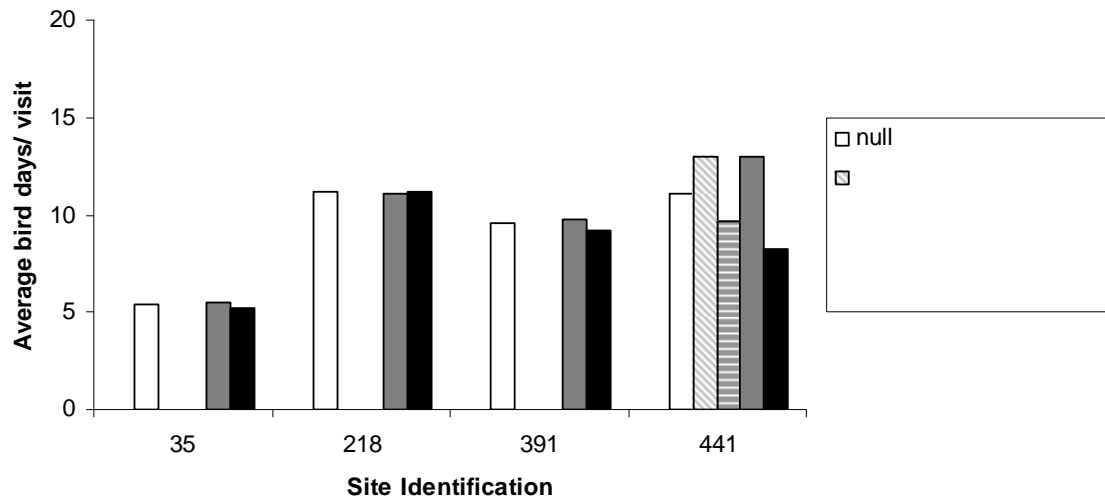


Figure 3.22 Intensity of bird use expressed in average bird days/visit, as predicted by the density-independent forward iteration with all estuarine habitat intact.

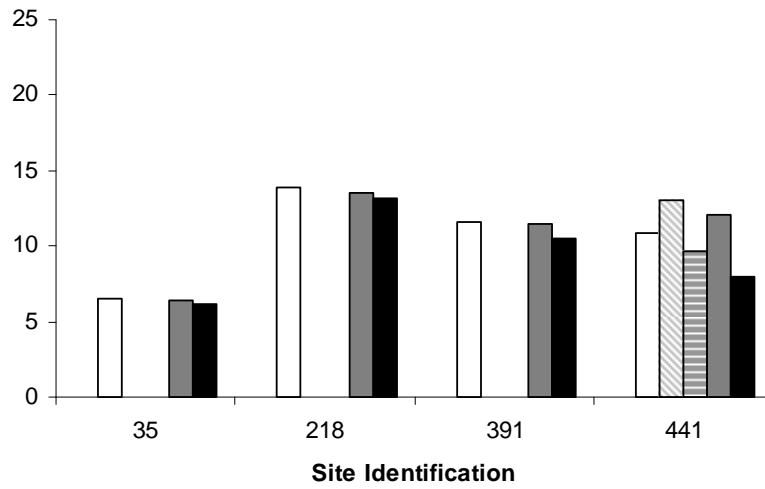


Predictions of the Reactive Density-Dependent Forward Iteration

The application of estuarine habitat degradation scenarios to the density-dependent forms of the iteration show generally, how habitat loss at stopover sites has a greater effect on the resulting timing of optimal migration and relative fitness than the assumption of density dependence. There is greater variation in the results (for mean relative fitness, average trip length, and number of stops) between the scenarios than between iteration types (See Figure 3.24). The results of the reactive density-dependent forward iteration indicate that habitat degradation specifically at estuaries predicted as stopovers by the DSV model, have the greatest effects on the migration and fitness of birds with initially lower energies. According to predictions, birds of higher initial energies are not affected by habitat losses at stopovers.

Effects on optimal migration routes and timing are similar to results of the density-independent forward iteration. As the habitat quality of estuaries (predicted as stopovers) degrades, the numbers of stopovers used by low-energy geese en route to breeding grounds increase. Geese in 'low energy/early start' groups show the largest increase of an average 0.2 stopover. Average trip length follows a pattern similar to before; bird group, 'low energy/early start' experiences a very slight increase in average trip length, and; bird group, 'low energy/late start' experiences a slight decrease in

Figure 3.25 Intensity of bird use expressed in average bird days/visit, as predicted by the reactive density-dependent forward iteration with all estuarine habitat intact.



start', respectively. Note that the fitness decline for the 'low energy/early start' bird group is 8% larger than the density-independent forward iteration. This result is likely due to the density-dependent assumption in which flock members affect fitness payoffs.

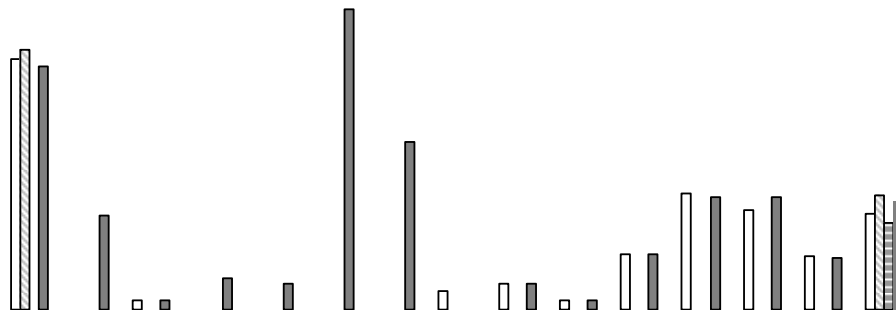
Scenarios, which remove sites, not predicted as stopovers, do not incur fitness effects on any birds. For example, the scenarios that remove estuaries ranked by the CWS and PECP do not affect the relative fitness or optimal migration strategies for any geese.

Predictions of the Proactive Density-Dependent Forward Iteration

Across the majority of the habitat degradation scenarios, the predictions of the proactive density-dependent forward iteration show that small changes occur in the

10 (Nanoose/Bonell Creek Complex) for birds of low energy groups (Figure 3.27 and 3.28).

Figure 3.27 Intensity of bird use expressed in average bird days/visit, as predicted by the proactive density-dependent forward iteration with all estuarine habitat intact.



iterations. As the habitat quality of estuaries (predicted as stopovers) degrades, the numbers of stopovers used by low energy birds en route to breeding grounds increase. Birds in 'low energy/early start' groups show the largest increase of an average 0.26 stopover. Average trip length follows a pattern similar to before; bird group, 'low energy/early start' experiences a very slight increase in average trip length, and; bird group, 'low energy/late start' experiences a slight decrease in average trip length.

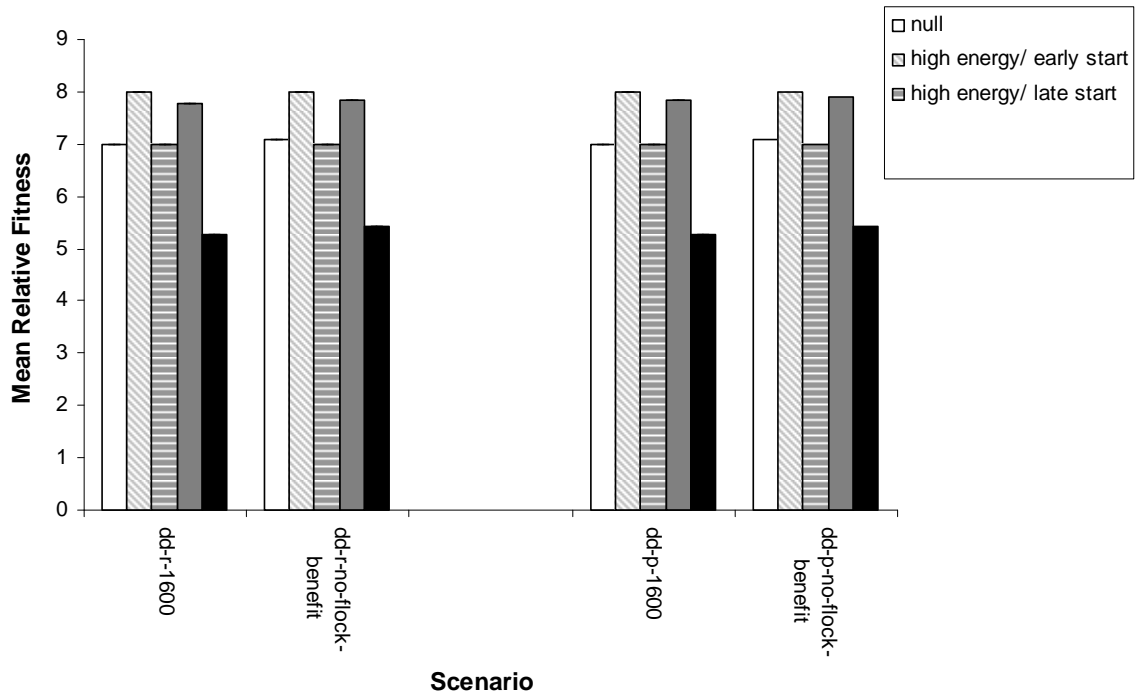
Fitness effects are only prevalent for birds of lower initial energies, across the habitat degradation scenarios. As predicted stopovers (i.e. those predicted by model version 3 and 6) are removed relative fitness declines. Birds of 'low energy/early start' group have the largest decrease in mean fitness at 36% under the scenario that removes predicted sites of model version 6. Scenarios, which removed sites, not predicted as stopovers, do not affect relative fitness, average trip length, or average number of stopovers per journey for birds of any state. Scenarios that remove estuary sites ranked by CWS and the PECP demonstrate this result.

Altering the Density-Dependent Assumption

Applying a scenario, that alters the density-dependent assumption by reducing the benefits of flocking, shows the predictions of the forward iteration to be insensitive to this component. Overall, little variation exists between results for the density-dependent iterations that do and do not assume benefits of flocking. Therefore, inaccuracies in how the probability distributions are drawn are not likely to drastically affect the predictions of the density-dependent forward iterations. For both reactive and proactive density-dependent iterations, I compared mean relative fitness, average trip length and average number of stopovers across scenarios with and without the altered assumption, and found little differences. Figure 3.29 shows the predicted fitness values of scenarios with and without assumed benefits of flocking, for both forms of the density-dependent iterations. However, some small changes do occur with respect to estuary use for the proactive density-dependent iteration when the scenario with the altered assumption is applied. The predictions show geese never to use Site 6 (Trent River) (which is predicted when the benefits of flocking are assumed), and the intensity of their use (average bird days/unique visit) shifts to Sites 2 (Englishman River) and 10 (Nanoose/Bonell Creek Complex).

Figure 3.29 Mean relative fitness for the scenario that alters the assumed benefits of flocking in the probability distributions using reactive-density-dependent forward iterations (first group, from left to right), and proactive-density dependent forward iterations second group, from left to right).

For each scenario type, dd-r refers to reactive density-dependent iteration, and dd-p refers to proactive density-dependent iteration. The first scenario 1600 assumes benefits of flocking; the second scenario-no-flock-benefit assumes no benefits of flocking. Mean fitness values are also associated with one standard error. However, standard errors are barely visible because they are small.



4 DISCUSSION

What Does the DSV Migration Model Predict for BC Estuaries?

The DSV migration model for Dusky Canada Geese predicts that only birds beginning migration in poorer condition with respect to fat deposition need to use estuaries on the BC coast as refuelling stopovers to successfully complete migration. Interplay exists between the birds' levels of energy reserves, timing of departure for migration, the quality of estuarine habitat, and the corresponding numbers of stopover estuaries used. Generally, migrating birds use greater numbers of stopovers as their condition worsens and as the initiation date of departure advances. The predictions from DSV model versions that incorporate wind also show that climatic conditions, which present a challenge to flight, affect optimal migration strategies. The presence of wind causes birds that begin migration with lower energy reserves to stop at estuaries more frequently than birds of initially higher energy reserves. Wind also increases the numbers of failed migrants and consequently decreases the breeding success for birds of lower initial energy reserves.

The question then presents itself; what do these results mean from a conservation standpoint? When only a segment of the goose population is predicted to use BC estuaries during spring migration, do these sites still merit protection? In the face of environmental stochasticity, especially as trends of global climate warming become obvious, assuming a precautionary approach in the planning of protected habitats for migratory waterfowl is key.

A warming climate may well have implications for mortality and survival rates of Dusky Canada Geese during migration, breeding, and wintering stages. Potential consequences with effects on geese are: an increase in the propensity of extreme storm events (Meehl and Zwiers 2000), a change in the successional stages of habitat on breeding grounds (Sturm and Racine 2001) (which could affect predation risks), a change in food abundance and availability on wintering grounds, and losses in estuarine areas (Nicholls and Hoozemans 1999, Scavia and Field 2002). Possibly, in future a larger proportion of the Dusky population could have poorer body conditions during

migration due to changes in the environment, from a climate shift. A projected rise in sea level due to climate warming (Nicholls and Hoozemans 1999, Scavia and Field 2002) could also affect the energy potential of estuaries for feeding geese, as the area of marsh habitats within estuaries decreases. Variability in the effects of climate warming might suggest that the reserve network requires a greater number of estuary sites for protection to ensure the Dusky population's survival. Since the predictions of the DSV model reinforce that weather and climate conditions affect the use of estuaries, especially for geese in poorer conditions, it is critical to consider the protection of these sites. As environmental conditions change, the importance of specific BC estuary sites to migrating geese might also change.

Given considerable uncertainty in the accuracy of the DSV model's predictions (due to a lack of empirical data with which to test predictions), it is reasonable to focus on identified estuaries, rather than the prioritization of these sites. Of a possible set of 442 estuaries, the baseline model (version 3) identifies the Fraser River Estuary, Nickomekl/Serpentine River Complex, and the Skeena/Ecstall/McNeil River Complex as migratory stopovers. The Fraser River Estuary experiences the highest bird use (in average bird days) according to model version 3. To give further support to the importance of the Fraser River is that four of

close to three sites maintained by the PECP, Nanaimo River, Englishman River and Courtenay River. Fanny Bay/Cowie Creek is also situated in Baynes Sound, which has IBA status. Little Qualicum Estuary also has IBA status and is 57% protected (Ducks Unlimited Canada 2006). Hiellen River is near the PECP site of Kumdis Bay, however has no protection status itself. Kingkown Inlet and Keswar Inlet Estuaries have 0% protection (Ducks Unlimited Canada 2006).

Running forward iterations on the DSV model enables me to explore the assumption of density-dependence effects at estuaries, where Dusky Canada Geese compete with flock members for resources. With respect to the relative fitness of geese of all states, density-dependence has little effect at a population index of 1600 birds. The most interesting density-dependent effect occurs with the proactive forward iteration; the number of intermediate estuaries required by geese of initially low energy reserves increases. Compared to the density-independent version, these birds use an additional eleven estuaries in total to reach the breeding grounds. These additional estuary sites are Fanny Bay/Cowie Creek, Englishman River, Little Qualicum River, Trent River, Campbell River (2), Nanoose/Bonell Creek Complex, Gorge Waters/Craigflower Creek, Chemainus River/Bonsall Creek Complex, Cowichan River, Black Creek, and Nass/Ksi'Hlginx/Burton/Iknouck/Chambers/Kincolith River Complex Estuaries. Birds of higher initial energy reserves also use Fanny Bay/Cowie Creek as a stopover, an event that never arises in the density-independent iteration.

I also postulate the potential impacts of population changes of Dusky Canada Geese and estuarine habitat losses on the birds' migration routes and reproductive

effect. The spatial configuration of habitat losses within the landscape matters and has ramifications for population viability. This result also emphasizes that the DSV migration model's predictions of important estuaries differ and is unique from other rankings.

If the density-dependent assumption is consistent with the Dusky population's true dynamics, then both population increases and estuarine habitat losses could cause a shift in bird use of the predicted stopover sites. The proactive form of the density-dependent forward iteration appears to show the most response by birds of initially low energy reserves to the two types of scenarios. At higher populations of geese (i.e. above the population index of 4000), birds decrease their frequency of estuary use. Both bird groups of high and low energies visit lower numbers of sites, in total. Therefore, bird use of estuaries as stopovers is dynamic and changes with population dynamics.

Removing estuaries by eliminating their energetic value also results in a shift in the intensity of predicted site use by geese. For example, the removal generally causes birds to spend less time per visit at the removed estuaries (especially those predicted as stopovers), and on average to spend more time per visit at other sites. Generally, the average number of visits remains constant. Englishman River, Little Qualicum River, Trent River, Gorge Waters/Craigflower Creek, and Bear River Sites experience higher use by birds of low initial energies under scenarios of habitat loss. There is even one scenario of habitat loss in which birds of higher initial energies require various intermediate stopovers, and use Fanny Bay/Cowie Creek, Campbell River (2), Skeena/Ecstall/McNeil River Complex, and Nass/Ksi'Hlginx/Burton/Iknouck/Chambers/Kincolith River Complex Sites. Again, this result emphasizes that stopover use of estuaries by Dusky Canada Geese is dynamic and responds to changes in the configuration of the landscape. Empirical data on Brant Geese point to a similar trend, where birds displaced by the loss of a spring staging site appear to move more often to less preferred sites that were not filled to capacity (Ganter and Prokosch 1997). However, Ganter and Prokosch (1997) found no significant differences in the survival and fecundity of Brant Geese experiencing habitat loss.

The estuarine habitat loss scenarios reveal the significance of protecting the key estuaries comprising stopovers along optimal migration routes (as predicted by the DSV model). The fitness of Dusky Canada Geese in initially poorer conditions declines without these sites. Another finding with far-reaching implications is that estuary use by geese is dynamic and responds to an increasing population and habitat alterations in the

landscape. Predictions show that Dusky most often shift the intensity of their site use (length of stay at an estuary site) under scenarios of estuarine habitat losses. These shifts likely alter migration strategies to maintain or increase survivorship. This shifting in use sends us an important message that estuary importance from the perspective of migrating waterfowl also shifts as conditions change. Because estuary importance is dynamic and likely changes with environmental conditions and population dynamics, we need flexibility as a component in conservation planning techniques. The ability in the future to add estuary sites with increased and changing importance to the reserve network will enhance its effectiveness.

Further Developments for the DSV Migration Model

To develop a DSV model as a conservation tool that best predicts important estuaries used by Dusky Canada Geese during migration, it is essential to include all, important variables. I consider a variable important when it influences migratory behaviour and fitness. Since the quality and reliability of this tool hinges on the model's structure, there is value in exploring further developments and variables that may be essential.

Given greater resources, I would consider three major extensions of the current model: 1) to include wind trends as a stochastic event, 2) to include the entire annual cycle of the sub-species, and 3) to include other discrete habitats distinct from estuaries that Dusky might use as migratory stopovers. Increasing evidence suggests that favourable wind conditions are an important factor in the successful migration of many bird species (e.g. Butler and Williams 1997, Clark and Butler 1999). Ebbinge (1999) demonstrated that the reproductive success of Brant Geese correlates with favourable tailwinds during spring migration, in years when predation pressure by foxes is low. Thus, wind seems to be an important variable that should be included in a migration model.

In the model versions 4, 5, 6, I included wind conditions; however, they represent a static picture. A snapshot of extreme wind conditions as the maximum wind speed and direction for the month of April (2005) s when pw[oese

and birds in response have adapted their migratory decisions. Another way to approach the problem is to incorporate wind conditions as a stochastic event in the forward iteration of the DSV model. Daily wind conditions at estuary sites could be a probabilistic determination based on time-series, wind data for the BC coast. The hope is that the stochastic representation of wind is more realistic and as a result, the predicted migratory strategies would be truer to patterns occurring in nature. The forward iteration would also require species-specific information relating to flight performance, like the

terms of running the model and interpreting results. In general, informational requirements for data inputs are substantial. In addition to species-specific information

landscape alterations and population dynamics. This concept of dynamic use of estuaries by waterfowl may become increasingly important as the environment experiences effects of climate warming. Potential impacts on weather conditions and diminishing areas of estuaries could change how geese use estuaries over time. Hence, the ranking of BC estuaries for ecological importance could also change. Due to variability in the effects from climate warming and the dynamic nature of estuary use predicted for Dusky Canada Geese, the PECP needs flexibility in how it evaluates estuaries for conservation. The evaluation process should continually reassess the conservation priority of BC estuaries as environmental conditions change and new ecological information is available.

5 APPENDICES

Appendix A: Derivation of Parameters

Wind scores

Wind scores for estuary sites range from 0-50, signifying assisting to deterring conditions, or tailwinds to headwinds. The wind scores were derived from the interpolation of a wind surface for the BC coast, using regular spline as the interpolation method. Rebecca Harrold (2006) interpolated this wind surface using ArcView 3.3 (ESRI 1992). The interpolation required wind data (i.e. the maximum wind speeds and corresponding directions for April 2005) of Environment Canada's eighteen weather stations along the BC coast (Meteorological Service of Canada, PYR Environment Canada 2005). Harrold chose regular spline as the interpolation method because it produced the smallest difference between the predicted and real wind speed values for each cell of the rasterized coastline (R. Harrold, Simon Fraser University, pers. comm. 2006).

The interpolation steps were as follows: First, the maximum wind speeds and directions recorded at the weather stations were transformed to travel cost values relative to the southeast wind direction that provide the ideal tailwind for spring migration. For example, low travel cost values correspond to strong assisting tailwinds for spring migrants (i.e. strong southeast winds). High travel cost values correspond to strong deterring headwinds (i.e. strong northwest winds). The equation: $\text{SIN}((\text{direction of maximum wind speed at station} + 315) * 0.01745 * (\text{maximum wind speed at station}))$ gave the transformation (Rothley 2006). Then, Harrold interpolated the surface using the travel cost values of the weather stations. The resulting surface of interpolated travel cost values for the estuary sites was rescaled to a scale of 0-50 to produce the wind scores.

Wind-scaling factor

The wind-scaling factor adjusts the maximum flight distance achievable by adjusting the flight range parameter. The wind-scaling factor calculates the average wind

score of departure and destination estuary sites, using the equation: (wind score at estuary source + wind score at estuary destination)/2 (Rothley 2006). The inverse of the wind-scaling factor multiplied by the flight range parameter gives the new flight range parameter or flight efficiency, with wind conditions present. For example, if strong headwinds are present at both departure and destination estuaries, the flight range parameter will decrease due to the wind-scaling factor and the bird's maximum flight distance will be reduced. Thus, for a bird with a given energy reserves the number of reachable estuaries from the departure site will decrease with strong headwinds present.

Energy cap

The energy cap represents 'topped-off' energy reserves or the largest, possible reserves level. I based this parameter's estimate of **39 100 kJ** on the highest mean for energy reserves (from three seasonal means) for the Dusky. (4.9 for)Tj-27.33l

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the recorded mean masses ((Bromley and Jarvis 1993): in Appendix 1). I commenced the incremental fat level at 1.04 kg because this value is the highest fat level recorded at premigration (Bromley and Jarvis 1993), and represents the largest amount of fat possible for burning.

Measurements of wingspan (defined as the length from one wing tip to another) for Dusky have not been reported in the literature and do not exist in government databases (T. Rothe, Alaska Department of Fish and Game, pers. comm. 2006). As a solution to this data inadequacy, I used estimates for wingspan and aspect ratio based on Greylag Geese (*Anser Anser*) found within the species database of Flight Version 1.16. The Greylag Goose estimates for wingspan and aspect ratio are 1.6 m and 7.73 respectively. The Greylag Goose appears to be an acceptable surrogate for the Dusky Canada goose because of their similar wing lengths and life-history traits. Wild populations of Greylag Geese are migratory in Europe, breeding in the sub-arctic of Eurasia (Robinson 2005). They utilize similar habitats to Dusky's, such as estuaries, marshes and lakes, and have a diet of plant material including leaves and roots (Robinson 2005). An adult female Greylag Goose has a wing length within the range of 436.3 ± 13.4 mm (Robinson 2005), comparable to the an average wing length of 450 mm (Standard deviation, 15.1) for an adult female Dusky Canada Goose (Chapman 1970). I held the option for burning muscle mass constant because Dusky are not extreme long-distance migrants. Thus, I assume that the birds will not burn muscle during flight. All other parameters required by the Flight Version 1.16 remained at the default selections.

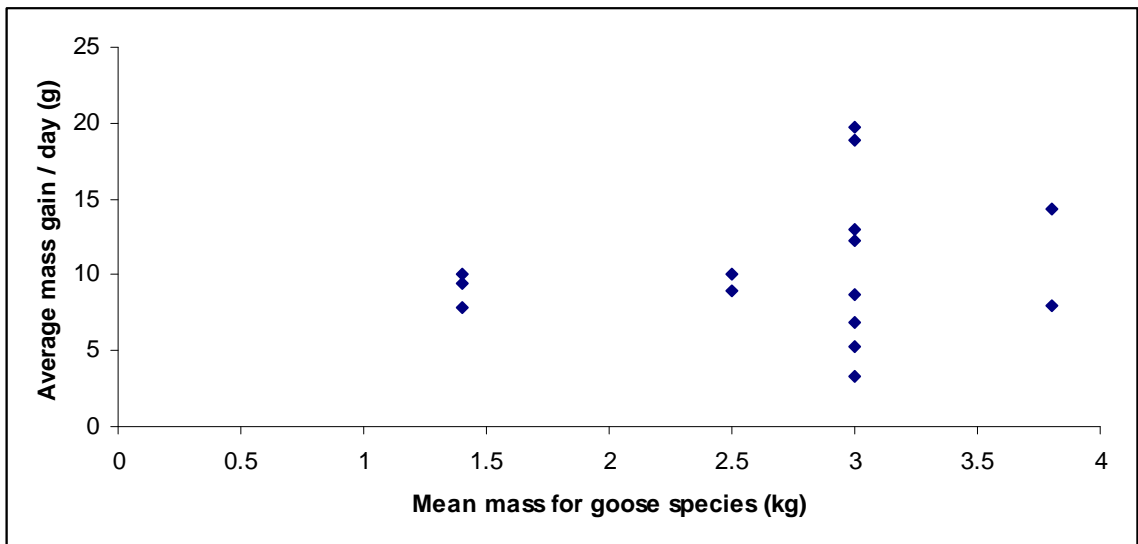
To assess the potential error that could arise from inaccuracies of a wingspan estimate based on the Greylag Goose, I performed a sensitivity analysis on the wingspan parameter. I varied the wingspan estimate in intervals of 10 cm in both the positive and negative directions. I discovered that each 10 cm change in wingspan resulted in an approximate 300 km change in flight distance. A 300 km change in wingspan signifies an approximate 6% divergence from the original flight distance predicted with maximum fat reserves (with the original settings of Flight 1.16). I decided for the purposes of the DSV model that this amount of inaccuracy in the resulting flight range is acceptable.

The flight model, Flight 1.16, demonstrated that the relationship between energy reserves and achievable flight distances is linear. Figure 5.1 shows the flight distance given a bird's initial energy level as predicted by Flight 1.16.

Figure 5.1 Flight distance achieved by a female Dusky Canada Goose given its initial

significant relationship between average mass gain per day and average goose weight (p-value 0.537 at 95% confidence) across geese species whose average weights ranged from 1.4–3.8 kg (Figure 5.2).

Figure 5.2 Daily, average, net, mass gain (g) for 14 datasets of five different goose species, including Greater Snow Goose (*Chen caerulescens atlantica*), Moffitt's Canada Goose (*Branta canadensis moffitti*), Taverner's Cackling Goose (*Branta hutchinsii taverneri*), Brant (*Branta bernicla*), and Dark-bellied Brent Goose (*Branta bernicla bernicla*).



Having determined that goose weight does not significantly influence the daily, average mass gain, I concluded that using data of a surrogate species to calculate energy intake rates for the Dusky Canada Goose was acceptable. For model versions that incorporated the concept of habitat quality, I aimed to categorize the PECP estuaries by habitat quality according to four groups: lowest, low, medium, and high quality. Specifically, these grades of habitat quality are a reflection of the available energy intake for a goose. For example, if a goose uses an estuary in the habitat group of low quality, it would receive a lesser energy intake than if the site occurred in a medium or high, habitat quality group. For an estuary site of low quality habitat, I assumed a bird to gain an average 6.9 g per day. Gauthier and Giroux (1992) recorded the lowest average mass gain for Grea8srs7.3 Gehese tobge 6.9 g per 9 T5.(og6 456aintake than if0se

low quality sites. I assumed the intake rate for the lowest quality habitat to be **0 kJ/day** or equivalent to no net gain in mass. I assumed medium habitat quality to be two times better than low quality and high habitat quality to be three times better than low quality. I designated sites of medium and high quality with energy intake estimates of **538 kJ/day** and **807 kJ/day** respectively. Since the average, daily mass gain indicates a net gain, the parameter estimates of energy intake account for a goose's energy expenditure due to metabolism during resting and foraging.

For those model versions that assume estuary sites have equivalent potential for feeding and nutrient potential, I assigned **269 kJ/day** to be the consistent value of energy intake across all sites. Above, I explain the derivation for this parameter estimate.

r: maximum clutch size

One of the fitness function parameters, r represents the maximum clutch size initiated by Dusky Canada Geese. The r parameter translates the fitness function into a value of reproductive success. Bromley and Rothe (2003) state that individual clutches of Dusky range from 2 to 8 eggs (Bromley and Rothe 2003).

k_1 : penalty for low energy at arrival

The estimate for k_1 , a fitness function parameter, represents the threshold for a low energy reserves penalty and is based on the dynamic state migration model of Western Sandpiper (*Calidris mauri*) (Clark and Butler 1999). In the absence of specific information, I set the parameter's estimate low at 0.085.

k_2 : penalty for late time of arrival

One of the fitness function parameters, k_2 represents a penalty for late time of arrival at the breeding grounds on the Copper River Delta, AK. I based the estimate for k_1 on the same parameter used in the dynamic state model of the migration of Western Sandpiper (*Calidris mauri*) (Clark and Butler 1999), and set to the value of 0.025.

Appendix B: Spatial Data Preparation for Oregon and Alaska Sites

In order to include the Willamette Valley, Oregon and the Copper River Delta, Alaska into the model landscape as the departure and destination sites for migrating Dusky Canada Geese, I required information on the location, size, and amount of wetland marsh and intertidal habitat for these two sites. I derived these parameters from the database of the National Wetlands Inventory. I used digital, polygon data (map projection: NAD 83, Albers Conical Equal Area) of the National Wetlands Inventory (NWI), which was originally compiled by the US Fish and Wildlife Service at a scale of 1:24 000 and 1:25 000 (U.S. Fish and Wildlife Service 2006-05). These data indicate the extent, approximate location and type of wetlands and deepwater habitats. These data delineate the areal extent of wetlands and surface waters as defined by Cowardin and Carter (1979).

I performed the preparation of all data in ArcGIS 9.0 (ESRI 1999). For each site, I merged the appropriate map tiles containing the wetlands information for the Willamette Valley and Copper River areas. I delineated the boundaries of the Willamette Valley site using the approximate boundaries of important wintering distributions of Dusky (Naughton 1985-1991) created by Naughton (1992) in (Bromley and Rothe 2003). I extended the site's boundaries based on Naughton's (1992) map to include adjacent NWI map tiles with suitable wetland types. I delineated the boundaries of the Copper River Delta site by overlaying the boundaries of the Copper River Delta Planning Units (Ecotrust 2004) (map projection: Clarke 1866, Albers Conical Equal Area) which were created by Ecotrust on behalf of the Copper River Collaborative to reflect distinct ecological regions of interest, using map projection, Albers Conical Equal Area.

After I created distinct boundaries for both sites, I queried the digital maps for two wetland types, 'palustrine emergent wetland' and 'estuarine and marine systems'. Palustrine emergent wetland represents vegetated wetlands, marsh, swamp, bog, fen, and prairie. I considered this wetland type to similar and essentially analogous to the backshore marsh category of the PECP estuaries dataset. Estuarine and marine systems represent vegetated and non-vegetated brackish and saltwater marsh, shrubs, beach, and mud flat. This wetland type, I considered analogous to the intertidal marsh, and intertidal delta category of the PECP estuaries dataset.

A spatial query resulted in the estimates for parameters of site location, total site area, area of backshore marsh, and area of intertidal marsh and intertidal delta. See Table 5.1 for the results.

Table 5.1 Parameters for Willamette Valley, OR and Copper River Delta, AK sites derived from a spatial query in ArcGIS 9.0.

Site	Location (coordinates projected in Albers Conical Equal Area)	Total size (ha)	Area of backshore marsh (ha)	Area of intertidal marsh and intertidal delta (ha)
Willamette Valley, OR	1249647,18526	726 387 621	156 033 022	0
Copper River Delta, AK	-46304,1855894	1 959 840 354	371 549 046	606 733 284

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