

Optimal Migration Routes of Dusky Canada Geese: Can They Indicate Estuaries in British Columbia for Conservation?

by

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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 years.

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1 INTRODUCTION

Estuaries in British Columbia (BC) are experiencing habitat loss and degradation at increasing rates, due to expanding industrial, commercial, and recreational development (Kelsey 1995). The long-term persistence of many wildlife species inhabiting the coastal region hinges upon the protection of estuarine habitats. Five million waterbirds use estuarine areas as important resting, foraging, and breeding sites along the Pacific Flyway. The Fraser River Delta, the largest estuarine complex in BC, alone provides a stopover site for 1.4 million birds during peak migration (National Round Table on the Environment and Economy 2002). Since the 1800s, approximately 70 percent of the estuary's original tidal wetlands have been lost to dyking, dredging, draining, and filling (Fraser River Estuary Management Program 2002). Currently, proposed industrial port expansion at Roberts Bank and pollution emanating from the river's mouth pose immediate threats (Western Hemisphere Shorebird Reserve Network 2005). These programs (i.e. Fraser River Estuary Management Program, Western Hemisphere Shorebird Reserve Network) suggest that the loss of habitats in the Fraser River Estuary will have wide scale impacts on waterfowl. The loss of other key BC estuaries may also jeopardize the sustainability of waterfowl.

Coastal wetlands, in particular estuaries, rank among the most productive and ecologically valuable natural ecosystems on earth (Whittaker and Likens 1971, Bildstein and Bancroft 1991). Although estuaries in BC comprise less than 3 percent of the province's coastline, they provide habitat for estuarine-dependent wildlife and ecological services to human settlements (National Round Table on the Environment and Economy 2002). Estuaries are ecologically significant because they export nutrients and organic matter to adjacent coastal waters; provide spawning grounds for fish and invertebrates; provide nesting and staging areas for waterfowl and shorebirds; and assimilate waste and toxic substances to maintain water quality. Salt marshes along the BC coast are unique in that they show little floristic similarity to other Canadian salt marshes (Glooschenko and Martini 1988), and do not freeze due to the mild climate (Nowlan and Jefferies 1996).

The Pacific Estuary Conservation Program (PECP) is a partnership of government and non-government agencies working to protect estuarine habitat along the BC coast, through land acquisition, creation of nature reserves, and stewardship of private lands. Under the auspices of the North American Waterfowl Management Plan, the PECP operates as the land securement arm of the Pacific Coast Joint Venture. The PECP has purchased major portions of coastal marshes in estuaries on Vancouver Island (including the Nanaimo River, Marble River, Salmon River, Englishman River, and Cowichan River Estuaries), and the BC mainland (including the Asseek River and Bella Coola River Estuaries) (Kelsey 1995), totalling approximately 2000 hectares (National Round Table on the Environment and Economy 2002). The PECP has also initiated the conservation designation of over 56,000 hectares of estuarine and intertidal areas under the Crown's jurisdiction. Stewardship programs of the PECP are also in effect for over 20 percent of the 14,000 hectares of farmland in the Fraser River Delta.

Until now, priority areas for conservation have been identified by the PECP with a variety of strategies that have primarily evaluated the conservation significance of each estuary independently of the others. These strategies include using baseline information from inventories (National Round Table on the Environment and Economy 2002); and using biophysical data of estuary size, habitat type and rarity, herring spawn occurrence, waterbird use, and intertidal biodiversity to rank estuaries for biological importance to waterbirds (Ryder and Kenyon 2006). The PECP needs an array of ecologically defensible methods to assess and identify estuaries for acquisition and land stewardship programs. By acquiring alternative methods to prioritize estuaries, the PECP can take part in comprehensive conservation planning. As a result, the costs and benefits of multiple conservation options may be considered systematically and resources directed strategically.

In response to the PECP's need for an ecologically based method to prioritize BC estuaries for conservation, the overall goal of this study is to develop and test a conservation tool that exclusively considers the conservation significance of estuaries within a network for migrating birds, unlike previous ranking methodology. The tool I examine is a dynamic, spatially explicit, animal behaviour model that considers the ecological process of bird migration, and the spatial configuration of estuarine habitat in the landscape with respect to connectivity. The spatial element gives the model an edge over other conservation methods by linking the spatial structure of the landscape with an

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 relate the physiological states of organisms to their environment via a measure of fitness or reproductive success (Clark and Mangel 2000). In contrast to the usual application of DSV models, which is to explain the mechanisms of animal behaviour, the DSV modelling approach in this research problem utilizes our understanding of a bird species' behaviour to predict the importance of stopover sites (i.e. estuaries) during spring migration. The prevailing assumption of DSV modelling that animals behave optimally in order to maximize their fitness, presents a way to link the persistence of an animal population with the design of a reserve network. This conservation tool offers a fitness-based method to assess alternative networks of estuaries for migrating birds on a regional scale.

With the use of a DSV model that predicts the migration event of the Dusky Canada Goose, this study specifically aims to:

1. identify and prioritize key estuaries in BC,
2. postulate the impacts of estuary losses on birds' migratory and reproductive success,
3. determine how the assumption of density dependence at estuary stopovers affects migration pathways, and
4. make conservation recommendations concerning estuary sites that are in need of protection or further study to the PECP.

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 where time, money, and biological inventory data are sparse, this approach can be effective because habitat and life history information are required only for a limited number of species (Lambeck 1997, Lambeck 2002). However, debate centres on the evidence for the direct correlation of the presence of one species or taxon with another

(Andelman and Fagan 2000, Roberge and Angelstam 2004). Also controversial, is how to best choose indicator or surrogate species (Landres and Verner 1988, Simberloff 1998) that indicate the presence and population trends of another group of animals. Regardless, a focal or multi-species approach is useful in its own right for achieving its specific, stated objectives concerning the species of interest. Nikolakaki and Dunnett (2005), and Newbold and Eadie (2004) employed focal species approaches to prioritize sites for protection and management for passerine and waterfowl species; Root and Akcakaya (2003), and Hess and Koch (2006) employed a multi-species approach for various taxa including reptile, cat, and bird species.

As the discipline of conservation ecology develops, the number and complexity of site selection tools added to the conservation toolbox grows. Most methods for site selection are governed by a particular criterion or set of criteria that define how sites should be included in reserve networks. Many criteria exist. Those used previously are: species diversity (richness), species rarity, the vulnerability of species to threat, population viability, complementarity (the need for new areas to be complimentary to existing ones in the natural features they contain (Pressey and Humphries 1993), irreplaceability (the overall importance of an area in achieving conservation targets for the features it contains (Ferrier and Pressey 2000)), representation of ecotypes, area of conservation sites, and cost. Different types of selection methods including, iterative algorithms (e.g. Cabeza and Moilanen 2003), indices (e.g. Turpie 1995), analysis of data layers, and predictive population and distribution models (e.g. Carroll and Noss 2003, Loiselle and Howell 2003, Macdonald and Rushton 2003, Maes and Bauwens 2005) employ these various criteria.

The examples of selection methods given above are all very different in how they view the site selection problem, operate, and ultimately, in the outcomes they produce, i.e. the list of prioritized sites. Iterative algorithms use mathematical techniques to derive solution sets of sites given certain constraints; indices are types of metrics used quantify the conservation value of sites; data layers analysed in a GIS interface explicitly address spatial relationships of features of interest within the landscape; and population/distribution models incorporate detail on biological attributes, such as species survival and reproduction. Researchers have focused much of their efforts on trying to develop methods that are both effective in maintaining biodiversity over the long-term, and efficient in returning the most conservation potential per unit area or cost.

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 indicator of the importance of an area for maintaining population viability (Tyre and Possingham 2001). The quality of the available data is also a concern (Cabeza and Moilanen 2001).

Another pressing problem is the difficulty of integrating critical ecological concepts that presently remain largely conceptual into the selection techniques. For example, within a site selection method it is difficult to define quantitatively the complex interactions among and between species, as well as the processes that maintain the integrity of the ecosystem. Due to such logistical barriers, the majority of previous research has been applied to primarily theoretical landscapes and scenarios (Prendergast and Quinn 1999, Cabeza and Moilanen 2001). Among the foremost criticisms of site selection techniques are that they often focus solely on minimizing the cost of a reserve network while meeting a biodiversity target, with minimal consideration of the spatial configuration of the landscape and/or spatiotemporal dynamics (Cabeza and Moilanen 2003), and that they disregard biological mechanisms and dynamics, which underlie community organization and ecosystem services (Chave and Wiegand 2002).

The Importance of Including Animal Behaviour in Site Selection Methods

Chave and Wiegand (2002) stressed the importance of addressing biological mechanisms and dynamics, which underlie community organization and ecosystem services in site selection methods; Cabeza and Moilanen (2003) stressed the importance of explicitly considering the spatial configuration of the landscape, and its spatial-temporal dynamics in site selection methods. Building on these identified needs, it is pertinent to approach the prioritization problem from a perspective that includes both the behaviour of animals and the dynamic spatial structure of the landscape in which the animals reside.

For the objective of selecting estuaries for conservation, choosing to focus on migratory waterfowl species and their behaviour is an obvious choice. During migration to and from breeding areas, waterfowl use estuaries and other types of wetlands as stopover sites for resting and refuelling (Baldassarre and Bolen 1994). Thus, the presence of migrating waterfowl might also indicate estuaries of ecological importance. Bibby (1999) suggests that ornithologists have an emerging opportunity to contribute extensive data and knowledge of birds for the potential use as environmental indicators, with a role to play in conservation. However, bird distribution and abundance alone do not reflect the quality of estuaries (West and Goss-Custard 2005). The numbers of birds at a site might also point to conditions elsewhere in nonbreeding and breeding areas (West and Goss-Custard 2005). Therefore, by explicitly incorporating the migratory behaviour of waterfowl into a site selection method for estuaries, I can use biological mechanisms and ecosystem dynamics (and not mere abundance records) to predict site importance. Migration is an especially critical element to focus on when along side the goal to protect estuaries, is the goal to protect migratory waterfowl.

Next, I give an overview of the phenomenon of bird migration in the context of its use as an essential component in a site selection method for estuaries. I further assess why bird migration is a valid factor in solving the prioritization problem. To do so, I examine the role of migration in the annual cycle of migratory birds. I also examine the landscape approach that the use of migration as a biological mechanism within a site selection method affords.

Investigating the Use of Bird Migration in Conserving Estuaries

The definition of bird migration encompasses very broad to specific terms, and migratory behaviour can be viewed on multiple scales. In the broadest sense, Baker (1978) defined migration as the act of moving from one spatial unit to another, regardless of the distance travelled or stage within the animal's annual cycle. Likewise, local movements of birds, such as juveniles dispersing or breeders irrupting into new territories due to resource shortages can be considered migratory movements (Berthold 1993). For the purposes of this discussion, I limit the scope of the definition of bird migration to the seasonal movements between breeding grounds and resting (wintering) areas.

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).

The DSV model casts the behavioural decision as an optimization of the fitness reward, where the decision depends on the animal's state and is subject to certain constraints (Clark and Mangel 2000). The assumed fitness function describes how the state variables interact to yield the final fitness payoff in the last time period. The model assigns this final fitness payoff, and then proceeds backwards in time to calculate the fitness value for every possible combination of states, in every time period (i.e. backward iteration). The model chooses the optimal behavioural decision that maximizes expected reproduction, or fitness in each time period. What makes the dynamic state modelling approach distinct from other optimization techniques is that both current fitness and current decisions depend on and affect the state variables. Also, the DSV model implicitly incorporates both past and future considerations into the current decision-making process (Clark and Mangel 2000).

Possibly, the greatest advantage of dynamic state modelling is that multiple factors can be included in a single DSV model, thus representing a high degree of biological realism (Houston and Clark 1988, Clark and Mangel 2000). A positive feature of the backward iteration procedure is that it can sift through many combinations of behavioural decisions and fitness consequences, and isolate those that are optimal. The backward iteration is an efficient way of identifying behavioural strategies and tradeoffs,

not possible otherwise (Clark and Mangel 2000). Another benefit to these models is that they provide a common currency (i.e. fitness) for assessing behavioural choices, and analysing tradeoffs between different actions (Houston and Clark 1988). Because they are mechanistic, they provide insight into the factors that drive the behaviour of the animals and system of interest. DSV models are well suited to solving problems for ecological systems that lack empirical information. For example, a DSV model could suggest the design of new, field experiments by generating predictions of the model system.

Previously, DSV models have been developed to predict optimal strategies for foraging, habitat selection, parental care, and other behavioural decisions of birds (e.g. in Ydenberg 1989, Clark and Mangel 2000). Ecologists exploit DSV modelling as a means to construct and test hypotheses about strategies used by birds in migratory journeys (Alerstam and Lindstrom 1990, Lindstrom and Alerstam 1992, Weber and Houston 1994). These DSV models predict migration patterns assuming birds behave according to a strategy, where a strategy is a rule that specifies how behaviour depends on physiological and environmental states (Pettifor and Caldow 2000). By comparing migration patterns predicted by the model and empirical data collected from the field, ecologists can infer if an observed individual bird or population is behaving according to the likely strategy (Farmer and Wiens 1998). Thus, the strategy may potentially explain the patterns of migratory behaviour observed in the field. Clark and Butler (1999), and Farmer and Wiens (1998, 1999) employed this type of study approach to ask questions regarding the timing and variation, as well as landscape effects, on the migration schedules of shorebirds. DSV model predictions can also reveal information about the migratory use of previously unsurveyed sites by the bird population of interest.

In the context of waterfowl migration, several populations of European geese species and their spring migration routes have been investigated using dynamic modelling. At an international workshop, 'Putting dynamic models of migration to the test' (2001), researchers explored the applicability of dynamic models of migration to well-studied avian migration routes of some geese species (Klaassen and Ens 2001). Spring migration routes were modelled for the Greylag Goose (*Anser anser*) (Nilsson 2001), Pink-footed Goose (*Anser brachyrhynchus*) (Ebbinge and van der Meer 2001), Barnacle Goose (*Branta leucopsis*) (Prop and Rowcliffe 2001), and Dark-bellied Brent Goose (*Branta bernicla*) (Ebbinge and van der Meer 2001) to determine if predictions matched

observed migration routes. Reasonable congruence in the sequence and timing of stopover sites used (between predictions and observations) occurred for the Barnacle Goose and Dark-bellied Brent Goose. Beekman and Nolet (2002) also applied dynamic stochastic modelling to the Bewick's Swan in order to understand the seasonal differences in migration patterns, specifically the skipping of a major stopover site in autumn migration. The hope for the future is that these models can achieve an accuracy, whereby predictions of climate change effects on the routes and survival of migratory birds are possible (Klaassen and Ens 2001).

Klassen and Ens (2001) report the need for a conservation tool that identifies the most vital links in the chain of wetlands for birds and assesses the most likely consequences of human-induced habitat change. By applying a DSV model to a population of Dusky Canada Geese and estuary stopover sites, I aim to identify the most vital links in the chain of estuaries for the BC portion of the Pacific Flyway. With this approach, I explore a practical application of DSV modelling for a regional conservation issue. It also presents a novel approach to conservation planning, and site selection because the model relies on the premise of using a fitness-based currency. Thus, I can compare alternative reserve networks (i.e., chains of estuaries) by examining fitness consequences that relate to the persistence of the population.

2 METHODS

Study System

Dusky Canada Geese (*Branta canadensis occidentalis*) have the shortest migration route of all Canada Geese subspecies migrating along the Pacific coast; their route comprises a distance of 2600 km that spans from northern Oregon to southern Alaska (Bromley and Jarvis 1993, Timm and Rothe 1994). The population migrates from their primary wintering grounds in the central Willamette Valley of Oregon to their main breeding grounds on the Copper River Delta of Alaska's south-central coast (Bromley and Rothe 2003). Other Dusky populations nest on the islands of Prince William Sound, and Middleton Island in the Gulf of Alaska.

The Dusky Canada Goose is one of seven subspecies of Canada geese, and is of medium size compared to the other races (Chapman 1970, Bromley 1981, Sibley 2004). Two main subpopulations of Dusky with minor but unique genetic differences exist: one breeds on the Copper River Delta and another breeds on Green and Middleton Islands (Pearce and Pierson 1988). However, due to the small degree of genetic differences and their tendency to winter sympatrically at common sites, the two subpopulations are recognized and managed as one distinct subspecies (Pacific Flyway Council 1997).

Over the past three decades, population numbers have generally declined, from estimated populations of 20,000 to 25,000 in the 1970s to current estimates approximating 10,000-18,000 (Timm and Rothe 1994, Bromley and Rothe 2003). Two key factors have contributed to population declines: increased nest predation and decreased area for nesting due to successional changes in habitat triggered by a 1964 earthquake in the region (Bromley and Rothe 2003, Hupp and Stehn unknown). Other concerns include threats to and quality of, migratory stopovers and wintering areas across the subspecies' year round range (Pacific Flyway Council 1997). The status given to this subspecies is imperilled (a high risk of extinction) and blue-listed (not immediately threatened but of concern), at global and provincial levels respectively (Conservation Data Centre 2006). To address the low productivity of the Dusky population in the mid

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.

It is essentially unknown where and for how long Dusky Canada Geese stop to replenish their energy reserves during spring migration. However, researchers have observed spring flocks of Dusky at Willapa Bay, Washington, the Queen Charlotte Islands (QCI), British Columbia (BC) and Yakutat Bay, Alaska (Gabrielson and Lincoln 1959, Petersen and Greulich 1980). Other coastal stopover areas with reported use within BC during fall migration include Graham Island (QCI) and the northern tip and

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 orthophotos, 1:15,000 to 1:40,000 scale airphotos, and variable scale Canadian Hydrographic Service marine charts, the locations and boundaries of estuaries were determined. The dataset also provides information on the site-specific attributes, like physical characteristics (e.g. area, ecoregion, and shoreline type), biological conditions (e.g. nearshore vegetation, herring spawn, mussel beds, and waterfowl use), protection status, and stewardship status (i.e. local tenure of estuary and surrounding area) (Ryder and Kenyon 2006).

I used ArcView 3.3 (ESRI 1992) and ArcGIS 9.0 (ESRI 1999) to query the estuary dataset and discern pertinent information for which the migration model required. Specifically, the model required information on the location, total size, and area of backshore and intertidal marsh, and intertidal delta habitat for each estuary. Throughout this report, I refer to the estuaries by their identification numbers assigned by the PECP.

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.

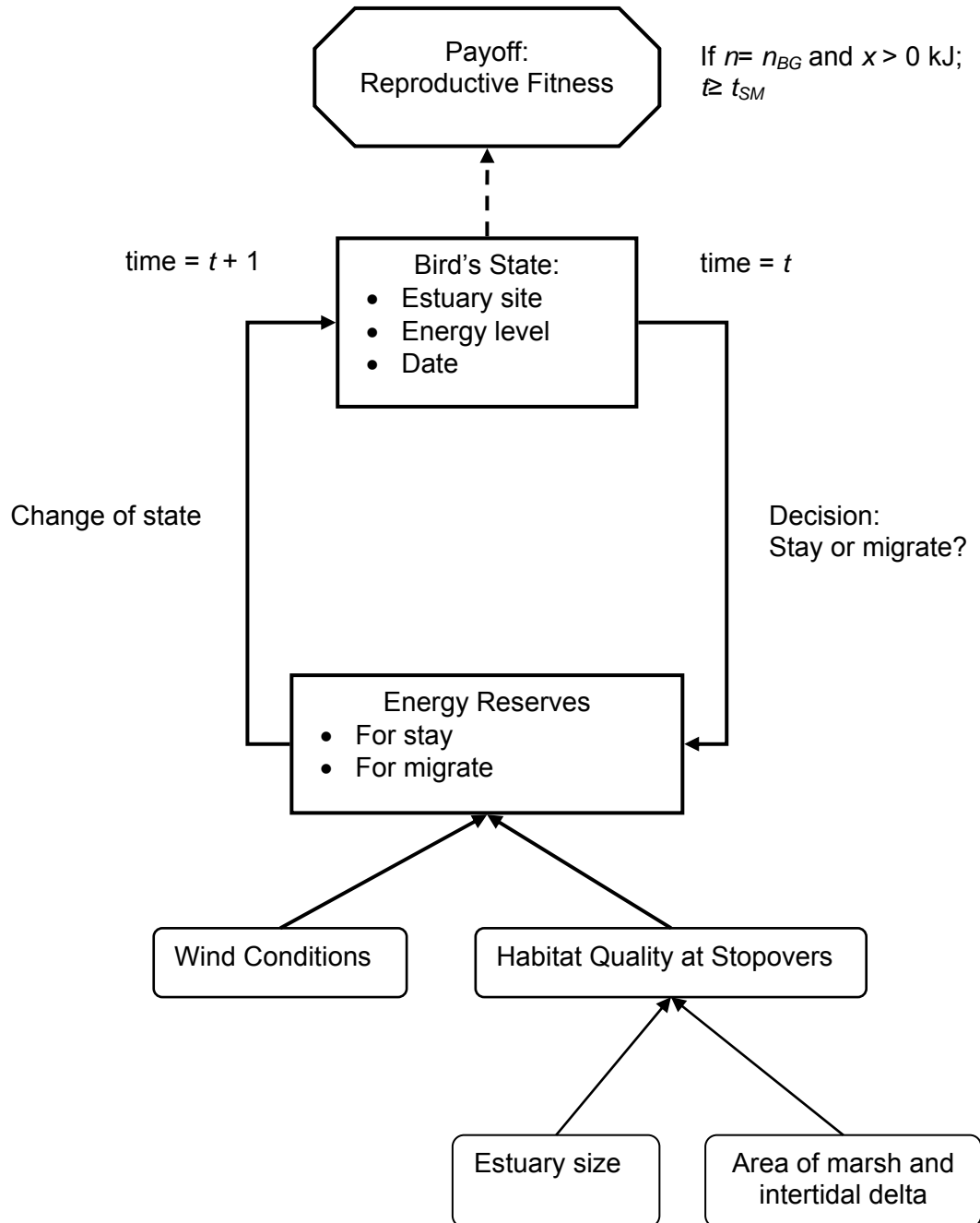
An individual bird experiences daily changes in state depending on the migratory decision it made in the morning. This decision to fly or stay influences its energy reserves and location for the next time step. When an individual stays at a stopover site

to gain fuel, its energy reserves are affected by the quality of habitat at the site. Habitat quality influences the rate of daily energy intake, which in turn affects the total reserves. I explore multiple definitions of habitat quality in the various model versions presented in Table 2.1. I use two surrogates for habitat quality, total size of the estuaries and proportion of marsh and intertidal delta habitat within estuaries. I assume that higher quality sites are more abundant in food with higher nutritional content, and result in greater net intake rates of energy for foraging geese. When an individual migrates in the presence of wind, its energy reserves are indirectly affected by the wind's strength and direction. Deterring winds during flight results in less efficient energy consumption and a bird cannot fly as far as in assisting winds given the same initial energy reserves. Losses in energy due to metabolism during resting, foraging, and flight are considered constant over time. These energetic losses are included in energy intake rates for estuary sites and energy expenditures for flight.

A bird repeats this daily cycle of making a migratory decision until it reaches the hypothetical breeding grounds at the most northerly site; all the while, the model tracks its state (Figure 2.1). Each day, the bird's daily decision is evaluated with respect to the final payoff it receives at the breeding ground, as measured by expected reproduction or number of eggs for the current year. A bird chooses a particular decision option when it maximizes its expected reproduction, which optimizes fitness assumingly. A bird will have higher reproductive success when it arrives earlier and with higher energy reserves. The arrival time of a bird at the breeding grounds is constrained by the date of snowmelt and ground thaw, April 20. Clark and Butler (1999) assumed the Copper River Delta to free of ice at about April 20. Arriving prior to this date would expose a bird to harsh weather and food shortages, threatening its survival.

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 programming language. In explaining how I quantified the DSV model, I focus on the baseline version for simplicity. The baseline version of the model includes the habitat quality of the estuaries with respect to the proportion of intertidal and backshore marsh, as well as the proportion of intertidal delta area for goose foraging (Table 2.1). Effects of wind conditions are not accounted for. Using this baseline model, I also performed the sensitivity analyses and forward iterations.

State Variables

Three variables, site location, energy reserves, and time define the state of an individual goose. Site location and energy reserves are constrained by limits:

$n(t)$: site identification number 1 - 442
 $0 \text{ kJ} \leq x(t) \leq 39,100 \text{ kJ}$

where $n(t)$ is the bird's location at one of the 442 mapped estuary sites in BC and $x(t)$ is the bird's energy reserves.

The bird's state is dynamic, varies with time, and depends on previous decisions. In the baseline model, spring migration begins at a stopover on the BC coast that is the most southerly of all estuary sites: Bilston Creek (Site 147). From this initial starting point, the migratory path chosen by the bird may assume any pattern northward. Breeding can occur only after the bird reaches the hypothetical breeding grounds at Bear River (Site 441). The starting and ending point of the migratory path represent the hypothetical wintering and breeding grounds respectively. For consistency, I included these hypothetical sites versus the true wintering and breeding sites in the baseline model because the complete PECP dataset of estuary sites comprise the BC coast only.

Lipids and proteins comprise a bird's energy reserves, and in flight, a bird metabolizes both. The cap for the highest, possible energy reserves is 39,000 kJ, which I based on the highest mean energy reserves for Dusky Canada Geese recorded at the wintering grounds in the Willamette Valley, Oregon prior to spring migration (Bromley and Jarvis 1993). During this premigration stage, geese exhibited the highest levels in energy reserves, surpassing all other reproductive stages (Bromley and Jarvis 1993).

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:

$$x'(t+1) = x(t) - D_m / Y$$

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

where $x(t)$ are energy reserves at the beginning of day t , $x'(t+1)$ are energy reserves at the beginning of the next day if the bird migrated the previous day; and $x(t+1)$ are energy reserves at the beginning of the next day if the bird stayed at stopover n the previous day. The model calculates the amount of energy metabolized during flight by D_m/Y , where D_m is the flight distance between sites n and n_m , and Y is the flight range parameter, equivalent to the distance a bird can fly per unit of energy. I derived the flight range parameter Y using the flight performance model, Flight 1.16 (Pennycuick 2006) by varying fat levels for a female goose of average mass (3.56 kg), and observing the maximum flight distance achieved for the energy burned.

If a bird decides to stay at a stopover, then the amount of energy that it gains while foraging there for a day is dependent on the quality of the habitat at the site. The term $x(n)$ represents the daily intake of energy at a particular site, and varies according to site quality. Energy intake rates (kJ gained per day) for sites categorized as lowest, low, medium, and high quality habitat are 0 kJ, 269 kJ, 538 kJ, and 807 kJ, respectively. I derived the low energy intake rate (269 kJ) from data on the lowest, average net gain in mass per day for Greater Snow Geese (*Chen caerulescens atlantica*) (Gauthier and Giroux 1992), which I use as a proxy for Dusky Canada Geese. After examining the relationships between the weights and average, daily, mass gains of five geese species (J. Hupp, USGS Alaska Science Center, pers. comm. 2005, Akesson and Raveling 1981, Ebbinge 1989, Gauthier and Giroux 1992, Ebbinge and Spaans 1995, Prop and Deerenberg 1991), I determined the two variables to be uncorrelated by regression

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 Dusky 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:

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

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:

$$w_1(x) = \min(k_1 \cdot x, 1) \quad (2)$$

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

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

based the format of equations (1), (2), (3), and (4) on equations from Farmer and Wiens (1998).

Dynamic Programming Equation

A way to interpret the dynamic programming equation is to regard it as a set of rules that direct a bird in making its migratory decisions where the model assumes that a bird will make the migratory decision (to stay at a current stopover, migrate to a northerly stopover, or breed) that maximizes its expected fitness. The model first calculates expected fitness for the last time step, and then works backwards in time to achieve the optimal solutions. The expected fitness of a bird with energy reserves x at site n on day t is denoted by $F(x, n, t)$.

For a bird of

$$x = x - x_{\max}$$

$$n = 1 - \text{total number of estuaries}$$

$$t = 0 - T; \text{ where } T \text{ is last day of the migration window}$$

$$n_{BG} = \text{the breeding ground}$$

$$F(x, n, t) = \max [\text{payoff if STAY at } n, \text{ payoff if MIGRATE (if not at } n_{BG}), \text{ payoff to BREED (if at } n_{BG})]$$

Where payoff is expected reproduction measured in relative number of eggs

$$= \max_{m \in D_n} \left[\left(1 - \beta_{n,t} \right) F(x + x_n, n, t + 1), \max \left(1 - \beta_{m,t} \right) F(x', n_m, t + 1), \phi(x, n_{BG}, t) \right] \quad (4)$$

Where

D_n are the set of sites that a bird can reach from *site n* given x ; for all sites (1 - total number of estuaries)

Site m is a member of set D_n if they are within achievable flight distance, $A_f = x \cdot Y$

$\beta_{n,t}$ is the predation risk at *site n* at time t

$\beta_{m,t}$ is the predation risk at *site m* at time t

x_n is the energy intake at *site n*

x' is the new level of energy reserves after flight, $x' = x - D_m / Y$

D_m is the distance of flight between n and n_m

Y is the flight range, the distance a bird can fly per unit of energy

I included parameters of predation risk at the estuary sites (β) in the equation for the sake of completeness. Evidence is emerging that Bald Eagles (*Haliaeetus*

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	Inclusion of spring wind conditions	Inclusion of habitat quality for estuaries
3 (baseline model)	No	Yes: birds perceive estuary sites as having varying potential for energy gains during foraging proportional to total area of intertidal and backshore marsh, and intertidal delta within the estuary
4	Yes	No: birds perceive all estuaries as having the same potential for feeding
5	Yes	Yes: birds perceive estuary sites as having varying potential for energy gains during foraging proportional to total size of estuary
6	Yes	Yes: birds perceive estuary sites as having varying potential for energy gains during foraging proportional to total area of intertidal and backshore marsh, and intertidal delta within the estuary

I factored wind conditions into model versions 4 to 6 by adjusting the maximum flight distance achievable (i.e. the flight range parameter) with a wind-scaling factor. Wind scores comprise the wind-scaling factor and are based on a wind surface for the BC coast, interpolated from weather data of 18 weather stations monitored by Environment Canada. The wind surface, created by regular spline interpolation, shows the maximum wind speeds and corresponding directions for April (2005) on the BC coast (Harrold 2005). From this interpolated wind surface, each estuary is assigned a wind score. Those estuaries with strong south-easterly winds, considered to provide the birds with the highest assistance in their spring migration were assigned 'better' wind scores. Ultimately, birds at estuary sites with 'better' wind scores (i.e. tailwinds) have the ability to fly farther for a given energy level compared to birds at estuary sites with 'worse' (i.e. headwinds) wind scores. See Appendix A for details.

Parameter Estimates

Tables 2.2 and 2.3 summarize the parameter estimates for version one and subsequent versions of the model, respectively. I derived parameter estimates from the literature on Dusky Canada Geese where possible. Information about the migration ecology of Dusky is particularly sparse; however, there is abundant literature on the ecology of other geese species. I used this resource to derive parameter estimates

concerning the dynamics of energy/fat reserves. Specifically, I based daily energy intake at estuary sites and flight range on 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
k_2 : penalty for late time of arrival	0.025

Table 2.3 Parameter estimates for model versions of increasing complexity (model versions 2-6) that differ from model version 1.

Parameter Description	Parameter estimate
flight range (km/eu)	Value changes with wind-scaling factor
energy intake at site (eu) (for model versions 2,3,5,6)	0 (0 kJ/day) for site of lowest quality habitat 1 (269 kJ/day) for site of low quality habitat 2 (538 kJ/day) for site of medium quality habitat 3 (807 kJ/day) for site of high quality habitat
wind parameters (for model versions 4-6)	
wind scores for each estuary site	1-50 (assisting-deterring conditions for flight)
wind-scaling factor	(wind score at estuary source + wind score at estuary destination)/2

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 locations. Then I used backward dynamic programming to solve for the optimal migration pathways for each sensitivity analysis.

Next, I describe specifically how I varied each parameter estimate (Table 2.4). I decreased the flight range by approximately 50 and 95% to examine the sensitivity of the model results to flight range estimates that represent a bird with lesser flight capabilities (or efficiencies). I applied two variations on energy intake. One assumes that birds receive less energy foraging at estuary sites than the baseline; thus for sites of lowest, low, medium, and high quality habitat, birds receive negative one, zero, one, and two energy units respectively. The other variation assumes that birds receive more energy foraging at estuary sites; thus for sites of lowest, low, medium, and high quality habitat, birds receive one, two, three, and four energy units respectively. Both parameters k_1 and k_2 , components of the fitness function, were increased and decreased by 10%. In attempt to explore the effects of a spring warming trend due to global climate change I varied the snowmelt date to April 17, three days earlier than the estimate used by the baseline. In the Northern Hemisphere, trends in the annual snow-cover cycle indicate that over the past three decades snow cover disappeared three to five days earlier every decade (Dye 2002). Specifically, for the Alaskan region spring snowmelt has advanced by 1.3 to 3.6 days per decade (Stone and Dutton 2002, Chapin and Sturm 2005). Lastly, I altered the spatial locations of the wintering and breeding sites in the model landscape to the Willamette Valley (Site 443) and Copper River Delta (Site 444), which are the true wintering and breeding sites. (In the model, these sites are analogous to the location where birds start and end migration). The location, size, and amount of wetland marsh and intertidal habitat for these two sites were derived from National Wetlands Inventory data (U.S. Fish and Wildlife Service 2006-05). See Appendix B for the details on how the data were prepared and analyzed in ArcGIS 9.0 (ESRI 1999).

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. The forward iteration simulates the northward migrations of birds with unique states according to the optimal, migration schedule predicted by the DSV output. In each sensitivity analysis, the forward iteration simulated five different types of groups with 1600 birds of varying states. A cohort of 1600 birds was chosen as the group size because it appears to be a reasonable estimate for the relative, current population of female geese completing migration. Sixteen-hundred birds are equivalent to the estimated, population index of breeding pairs of Dusky's on the Copper River Delta for 2002 (Bromley and Rothe 2003). The five different groups of birds vary with respect to their initial energy condition and timing of migration start (See Table 2.5). For example, in each forward iteration 1600 birds were randomly selected from the possible states for a particular bird group. In the case of each sensitivity analysis, the iteration was replicated 100 times for each bird group. Since the compositions of the bird cohorts lead to stochastic predictions that vary for each forward iteration, the replications are important. The replications grant us an overall idea of how each bird group behaves.

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.

Bird groups of different initial ‘states’	Energy state	Timing of migration start (departure)
Null	Simple random sample (SRS) from all energy states 0-145	SRS from all initial start times of day 1-42
High energy/early start	SRS from energy states 74-145	SRS from initial start times of day 1-21
High energy/late start	SRS from energy states 74-145	SRS from initial start times of day 22-42
Low energy/early start	SRS from energy states 0-73	SRS from initial start times of day 1-21
Low energy/late start	SRS from energy states 0-73	SRS from initial start times of day 22-42

Model Validation

No comprehensive data exists describing the staging sites used by Dusky Canada Geese migrating through BC in spring. Instead, I examine the correspondence between model predictions and general Canada Goose records. I use records of Canada Geese observed by volunteers of the BC Coastal Waterbird Study (BCCWS), coordinated by Bird Studies Canada (BSC) in order to validate the DSV model with field data (Bird Studies Canada 2006). Every winter BSC initiates volunteers to survey the BC coast for waterbirds, and the tail end of the survey period in April coincides with the peak spring migration of Dusky. Although the surveys do not identify subspecies, using this information at least gives a general indication of the model’s performance. Possibly, some of the Canada Goose records from the surveys do include Dusky, but how many is indiscernible. I use the baseline model version (model version 3) to compare model predictions with field data in order to maintain consistency with the sensitivity analyses and streamline comparisons.

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 number of birds already present at the stopover. Although the specific probability distributions differ for estuary sites categorized by varying 'qualities', the general shape of the distributions are similar. Generally, as the numbers of birds increase to an optimal flock size the probability of a visiting bird gaining the highest energy unit for that particular site type also increases. I define optimal flock size as the number of birds, which afford the group with the lowest predation risks and the greatest foraging times thus allowing the birds to achieve the greatest energy intake rates. After the number of birds at a site reaches the optimal flock size, the probability of a visiting bird gaining the highest energy unit for that particular site type declines to the point where the food resources are exhausted.

I set the optimal flock size at 250 birds based on a Brent Goose dataset, which shows the decreasing relationship of the proportion of vigilant birds for increasing flock size (Inglis and Lazarus 1981). At a flock size of 250 birds the slope of the relationship changes; the per capita vigilance level is the lowest and the corresponding foraging time would be the greatest, theoretically. At a flock size of 2000 birds I assume that a visiting bird has a zero percent chance of gaining the highest quantity of energy units for a particular estuary site. This assumption is based on observations of Barnacle Geese abandoning feeding areas after 2000 goose days per hectare (Ebbinge and Canters 1975). For estuaries of differing quality (lowest, low, medium, and high quality) the probability distributions of gaining energy units differ, however values for the optimal flock size remain constant. For a graphical display of the probability distributions for estuary sites of high, medium, low, and lowest quality, see Figures 2.2, 2.3, 2.4, and 2.5, respectively.

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

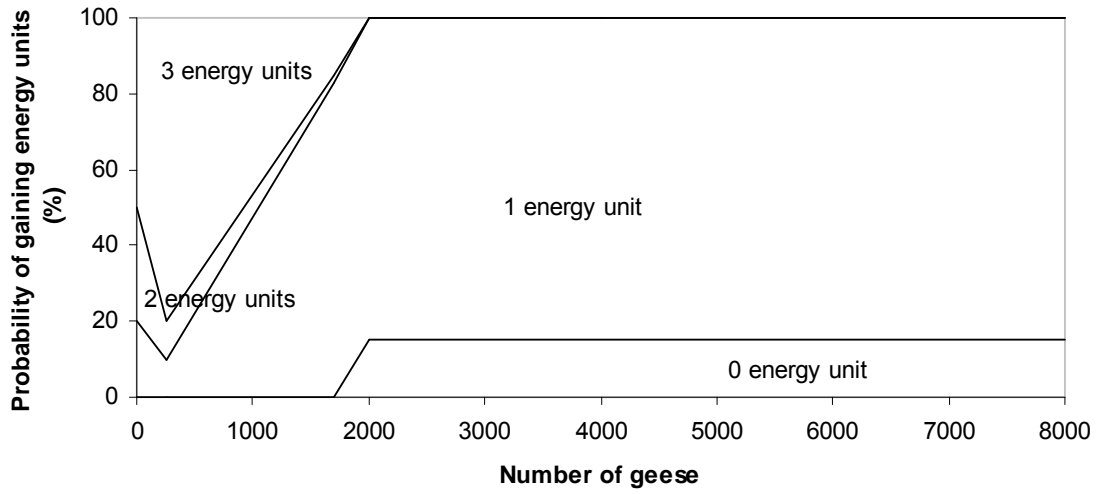


Figure 2.3 Probability distribution for estuaries of 'medium' habitat quality.

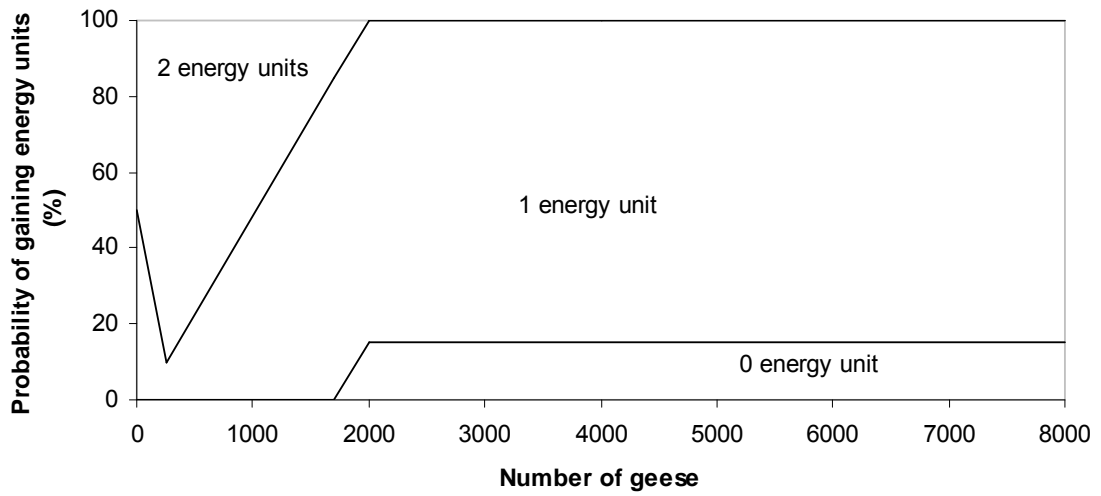


Figure 2.4 Probability distribution for estuaries of 'low' habitat quality.

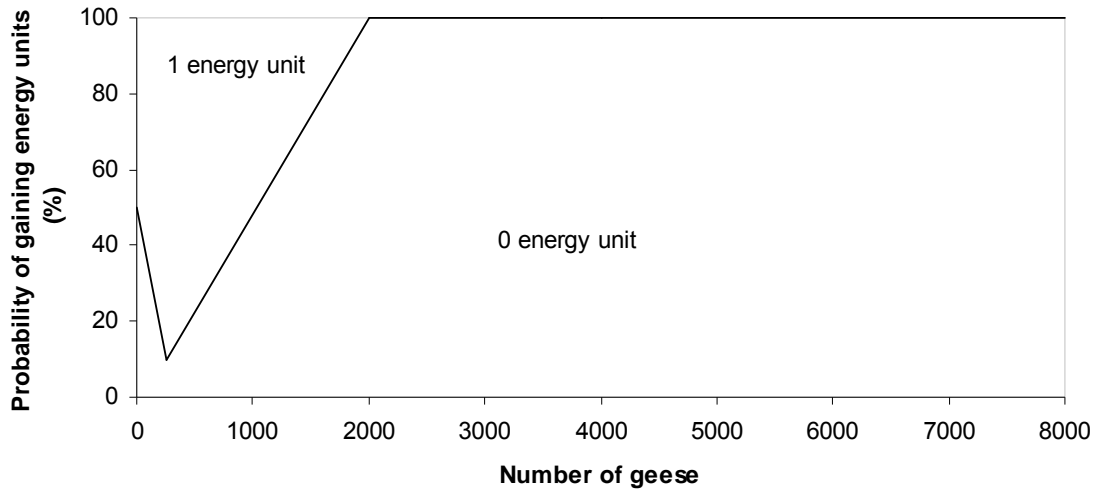
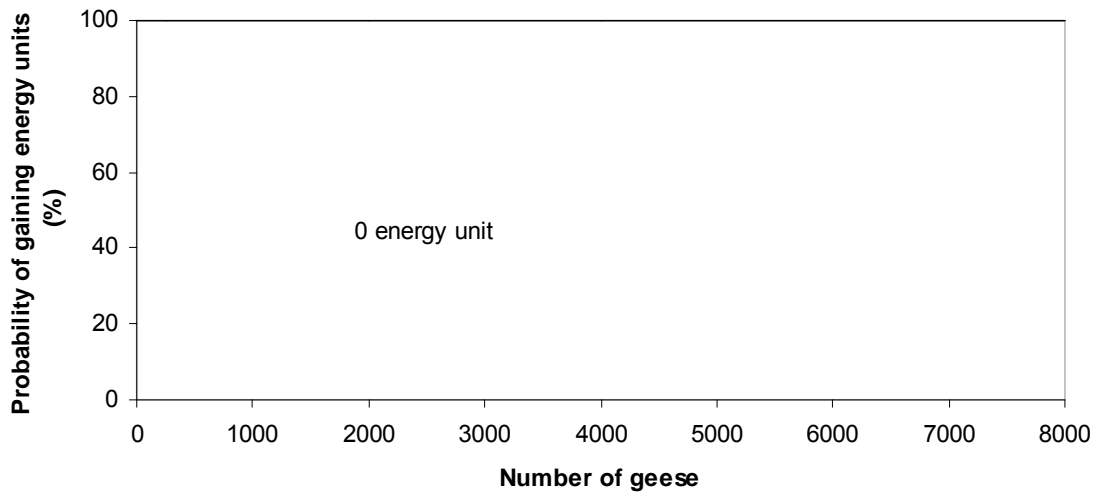


Figure 2.5 Probability distribution for estuaries of 'lowest' habitat quality.



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 consequences. Only in the proactive form of the forward iteration do geese have the option to alter their migratory decisions regarding whether or not to forage at a site predicted as optimal by the DSV output, depending on the number of birds currently using the site and the corresponding probability distribution.

Next, I describe the general workings of the forward iterations and the rules that guide the simulated geese through the landscape. The program for the forward iteration reads the DSV output for the baseline model that includes marsh habitats without any effects of wind (See model version 3 in Table 2.1). I chose this version for consistency, as I also use it in the sensitivity analyses and model validation. The DSV output, representing the migratory decisions and locations of the birds across all 'states' or conditions, is essentially memorized. At time zero of the iteration, migration has not yet begun and the estuaries are vacant. Before the first time step, a group of birds with varying states is selected. With the release of this group into the model landscape, migration starts. Each bird within the group begins migration when its initial start time corresponds with the current time step of the migration window. Therefore, the birds will most likely begin their journey in a staggered procession. The birds begin to follow the optimal pathways as predicted by the DSV output.

For the proactive forward iteration that assumes perfect knowledge of potential fitness consequences, birds fly to the next optimal stopover estuary and evaluate their options before foraging in the following time period. With respect to how many birds are currently using the estuary, the bird assesses the probability distribution and the potential for energy gain. The model calculates the expected energy intake of the bird given the site location and number of birds already present. If the corresponding fitness payoff is greater with the presence of these neighbouring birds, then the bird decides to stay and forage at this site. The actual energy intake rate assumed by the bird is randomly selected with probabilities from the probability distribution for that particular site and number of birds already there. After assimilating the energy, the bird has a new energy state in the next time period and continues to behave according to the optimal

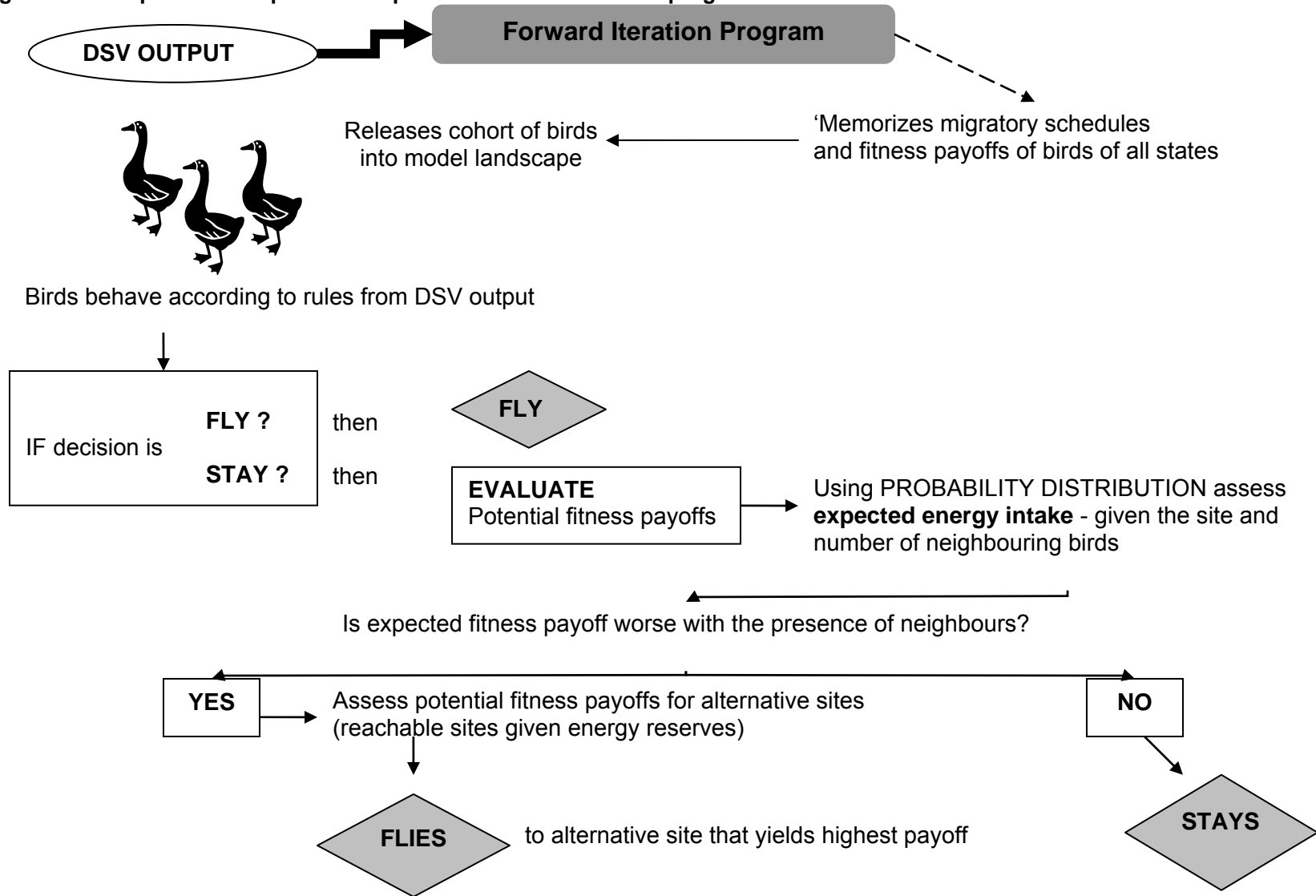
migration strategy. This cycle of how the bird assesses its various options repeats itself in the next time period.

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.

Figure 2.6 Graphical description of the proactive forward iteration program.



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 geese. The population status of the geese altered in the scenarios could reflect the effects of local, national, and international management policies. Management policies both on broad and small scales can affect a bird's survival during its entire annual cycle, including migration, breeding, and wintering stages. The shifts in population status could also reflect effects of natural processes that either depress or raise the numbers of birds.

To examine estuary use of migrating geese under various waterfowl management options that could reflect varying degrees of conservation effort, I use four population status scenarios that I apply to the five groups of birds with different initial 'states' (Table 2.5). The first two population scenarios are as follows: an increase and decrease from the current, relative population of 1600 birds by 25%. See the sensitivity analyses section for the rationalization of setting the relative population to 1600 birds. The 25% increase represents higher conservation efforts and alternatively the 25% decrease represents lower conservation efforts. The last two population scenarios are an increase of 250% and 375% in the number of birds from the relative population of 1600. All iterations for the proposed scenarios are performed using the DSV output of the baseline model (See model version 3 in Table 2.1).

The next category of hypothetical scenarios concerns changes in the landscape. To investigate the effects of estuarine habitat losses on the geese's migratory pathways, use of estuaries, and relative fitness I alter the model landscape by removing estuary sites. This removal represents the degradation or destruction of the estuaries to a point where the habitat no longer provides support to the geese in terms of providing refuge and/or energy. The removal of estuaries is conceptual in that the physical boundaries of the estuaries are not removed; however when the birds arrive they are unable to receive any nutrition and energy from the site. Every day a goose spends at a 'removed' site, its level of energy reserves drops by an amount equal to daily metabolism.

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 model versions. Birds with higher energy reserves fly directly to the breeding grounds in one day.

For ease of interpretation, I separated all model results into four categories defined by birds' initial states. I defined the categories by a bird's initial energy reserves and initial start date of migration. The categories are termed as 'low energy/early start', 'low energy/late start', 'high energy/early start', and 'high energy/late start' (See Table 3.1 for complete definitions). In each category, there are approximately equal numbers of birds (approximately 1530 birds).

Table 3.1 Definitions of state categories for birds of varying initial states.

State category	Range of energy reserves (energy units)	Range of initial start date of migration (days)
low energy/early start	0-73	1-21
low energy/late start	0-73	22-42
high energy/early start	74-145	1-21
high energy/late start	74-145	22-42

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.

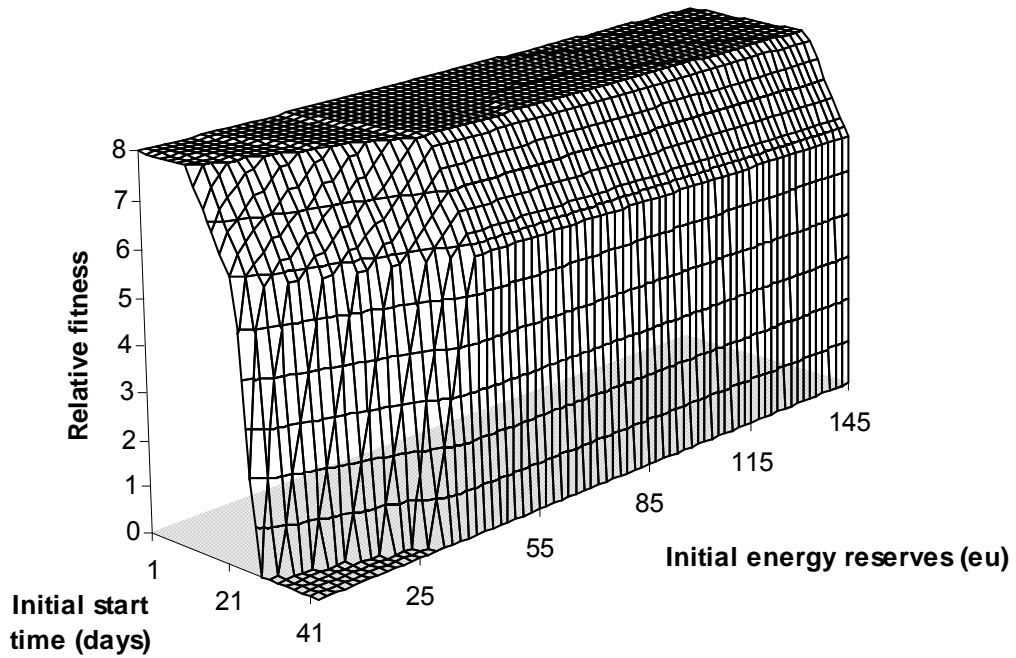
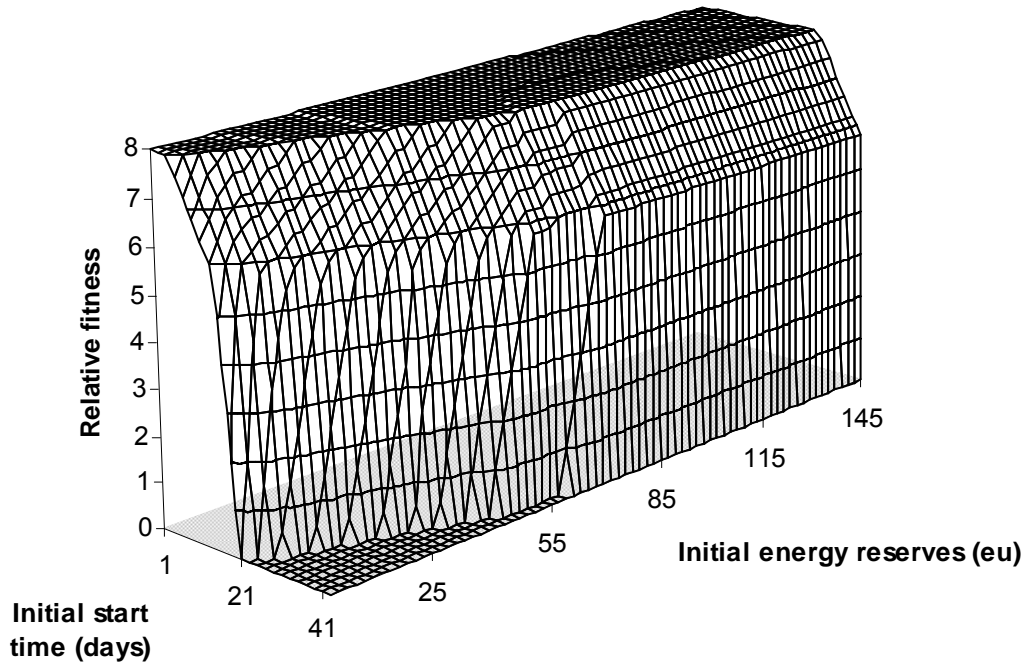


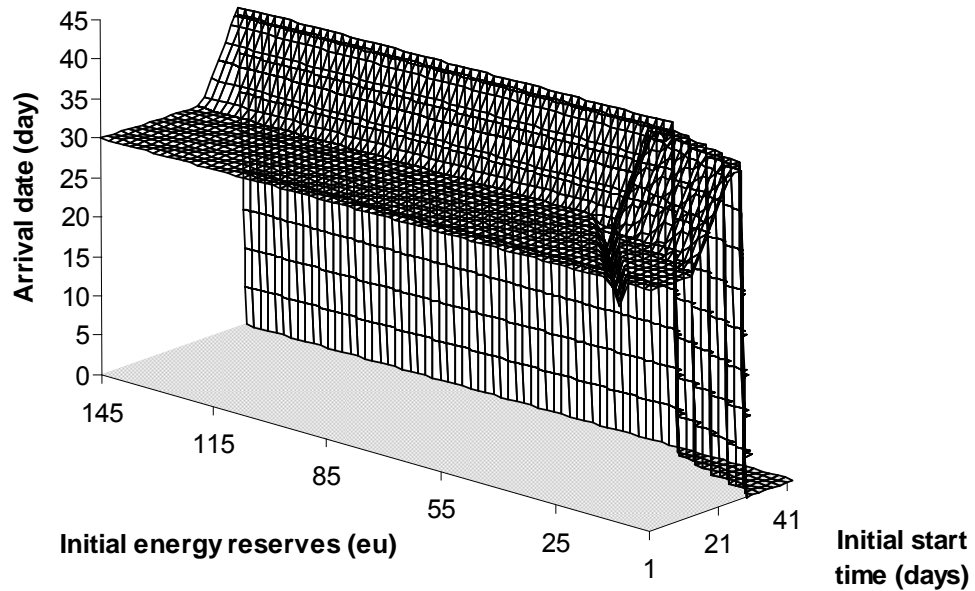
Figure 3.2 demonstrates the effect of winds on relative fitness. Winds make migration more difficult and the numbers of failed migrants increase with this added element. (Note the flat space is larger in Figure 3.2 than 3.1). For model versions 4-6 that include wind conditions the flat space representing failed migrants is consistently larger than for their sister models that do not include the aspect of wind. Overall, birds of low energy categories show higher fitness gains in model versions without the inclusion of winds, whereas birds of high energy categories do not show any changes in fitness across model versions, with and without the inclusion of winds.

Figure 3.2 Relative fitness as a function of bird states for model version 6.



Birds with earlier initial start dates, regardless of their initial levels of energy reserves arrive on the breeding grounds earlier than birds that have later initial start dates, as shown by Figure 3.3. This pattern holds true for the outputs of all model versions. The presence of winds appears to push arrival dates later into the migration window only for birds with initially low-energy reserves (categories 'low energy/early start' and 'low energy/late start'). In contrast, winds do not affect the arrival dates of birds with initially high-energy reserves. Birds of all states initiate breeding one day after arrival and do not breed after day 42, which is the last day of the migration period.

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



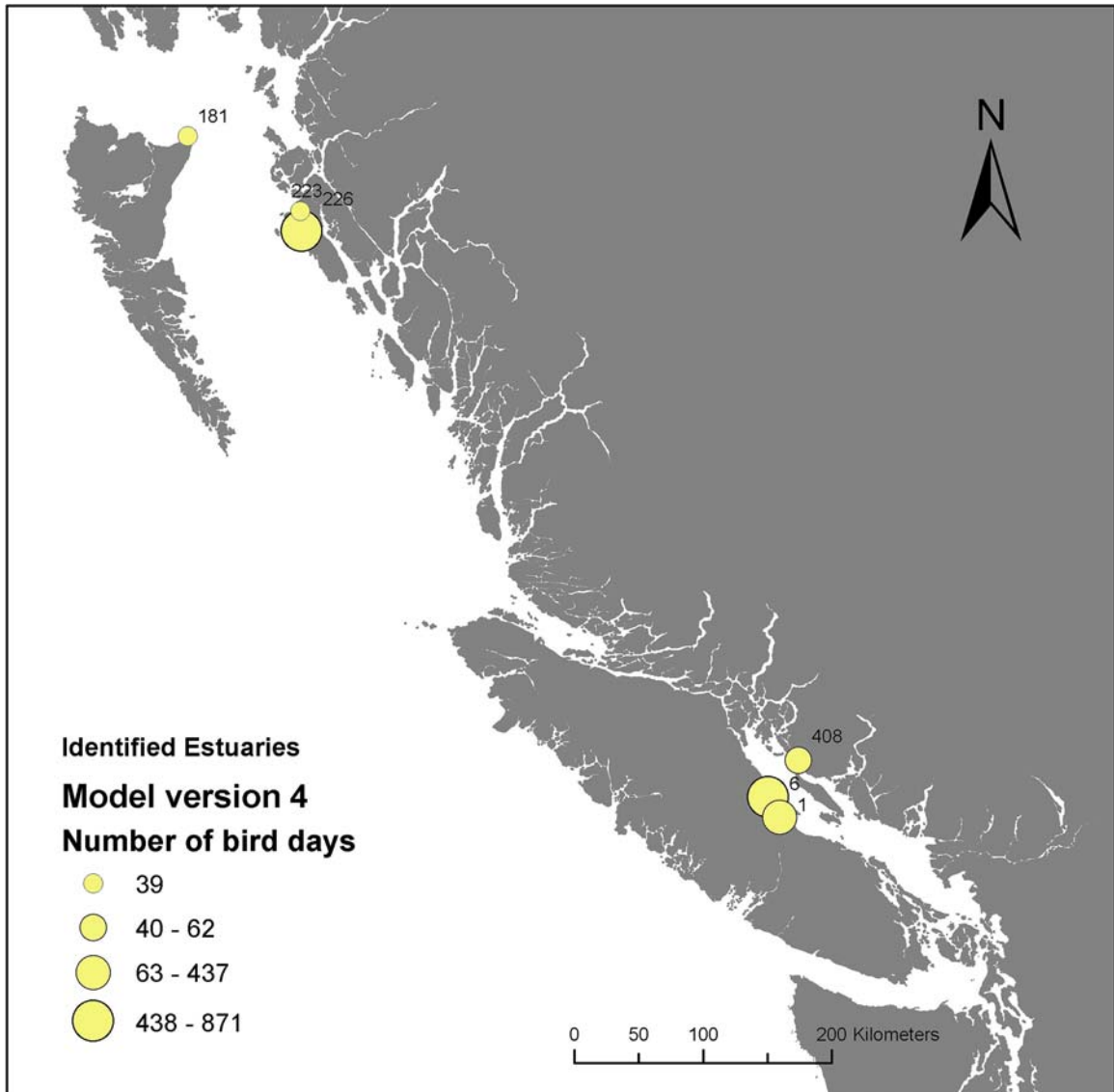
Estuary Site Use

Only birds with initially lower energy reserves use intermediate estuary sites as stopovers during their migratory journeys. As indicated by the outputs of all model versions, the number of intermediate estuary sites used per journey by these birds ranges from one to four sites. Model versions 5 and 6 identified migratory strategies with the most stopover sites per journey, containing four and three sites respectively. Birds utilize increasing numbers of unique sites as stopovers as their initial energy reserves decrease and initial start dates become later. Model version 1 is the only model, which does not identify any intermediate estuary sites for birds of any state category. For the majority of model versions it appears that the bird category, 'low energy/early start' has the highest site use (expressed in average number of stops/journey) of any bird category. It seems that these birds still have a chance to migrate successfully, but to do so need to stop more frequently to refuel. Birds in the category, 'low energy/late start' have a lesser chance for successful migration and it may not be in their interest even to begin the journey.

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.

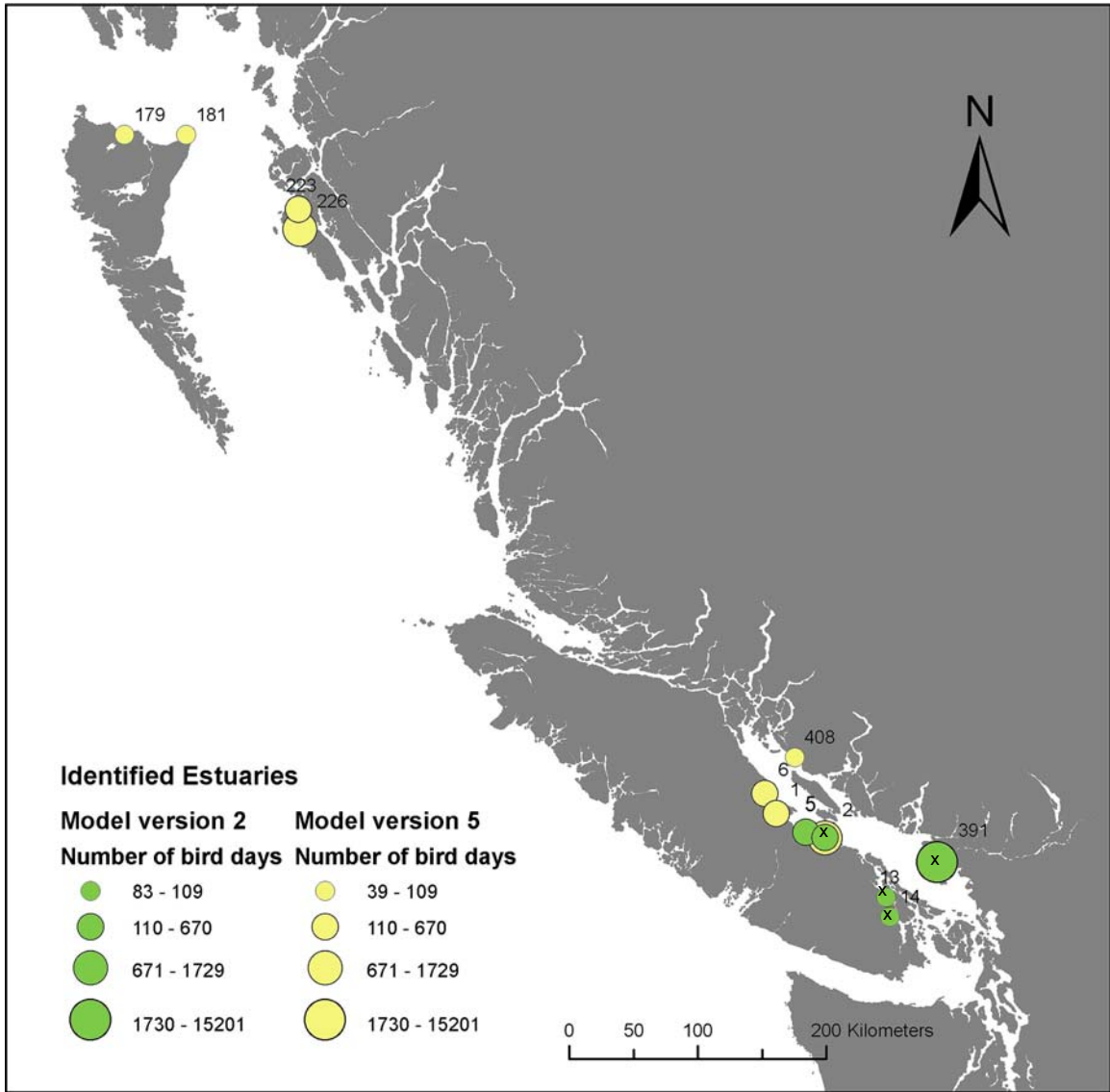
Of all identified sites, the Fraser River Estuary (Site 391) on the BC lower mainland appears most often across all model versions. Model versions 2, 3, 5, and 6 (versions that do and do not include wind trends) identified this site as a stopover. The Fraser River Estuary site also experiences the most 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.



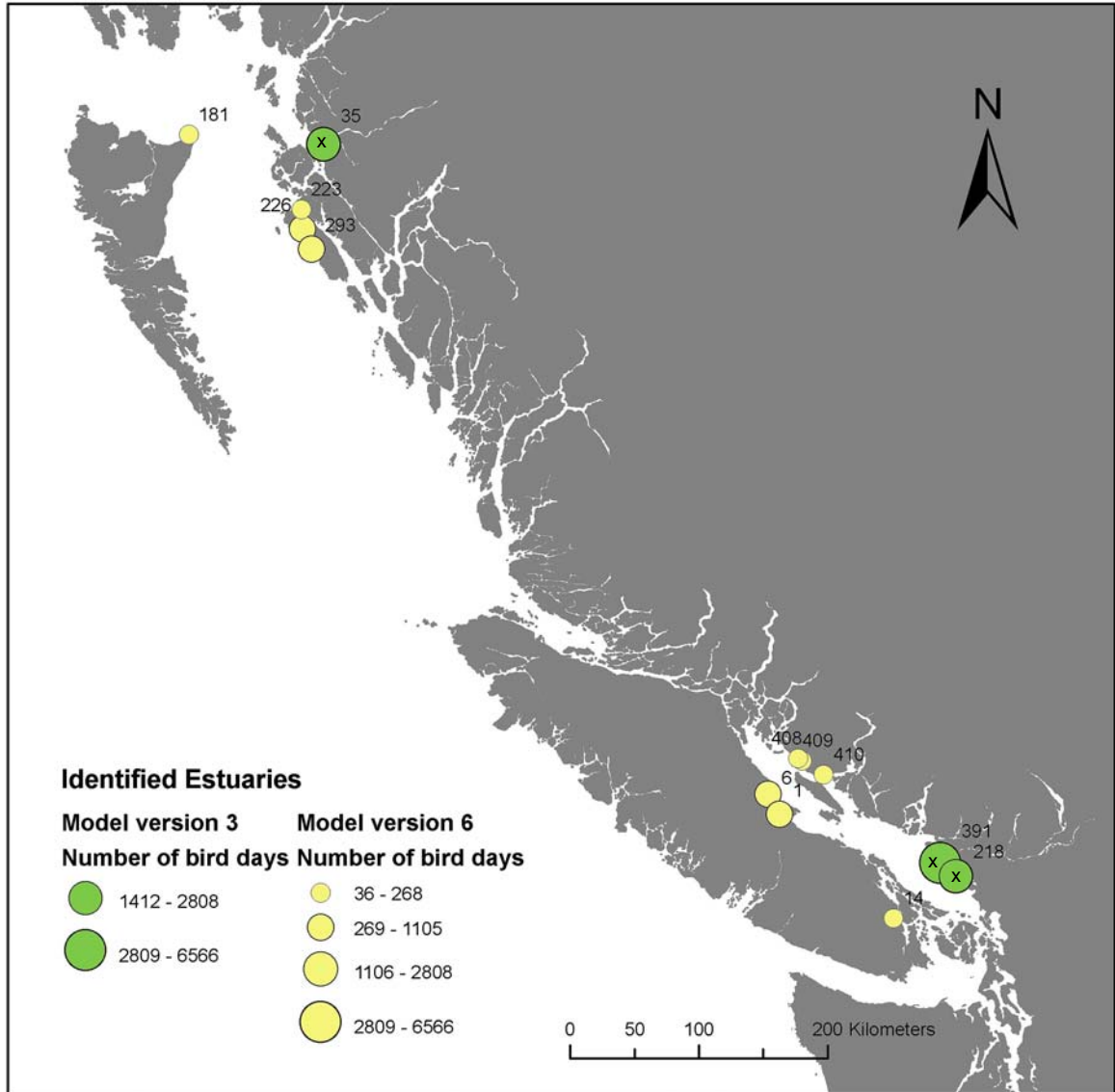
Estuary Site Identification	Estuary Name
1	Fanny Bay/Cowie Creek
6	Trent River
181	Hiellen River
223	Keswar Inlet
226	Kingkown Inlet
408	Siammon Creek

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.



Estuary Site Identification	Estuary Name
1	Fanny Bay/Cowie Creek
2	Englishman River
5	Little Qualicum River
6	Trent River
13	Chemainus River/Bonsall Creek Complex
14	Cowichan River
179	Christie River
181	Hiellen River
223	Keswar Inlet
226	Kingkown Inlet
391	Fraser River
408	Sliammon Creek

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	Kingkown 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.

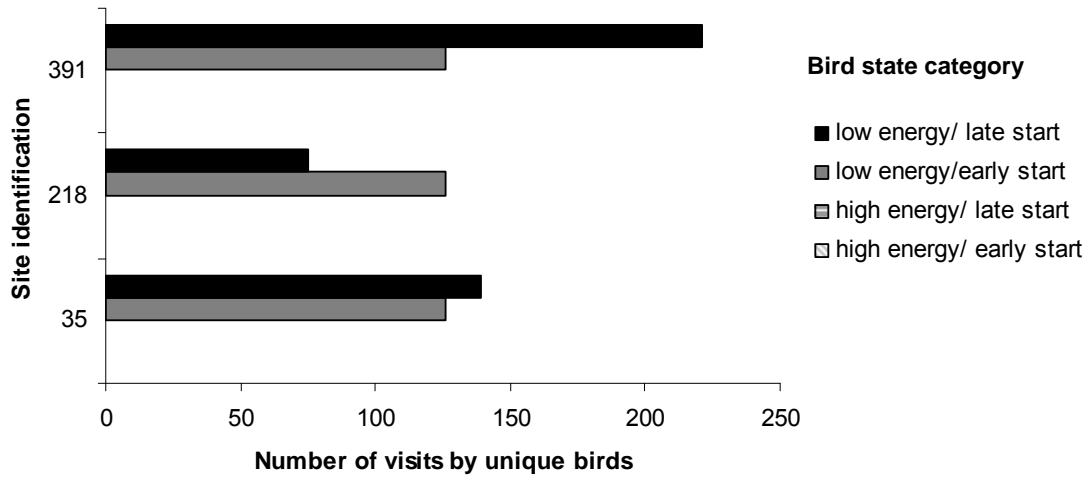
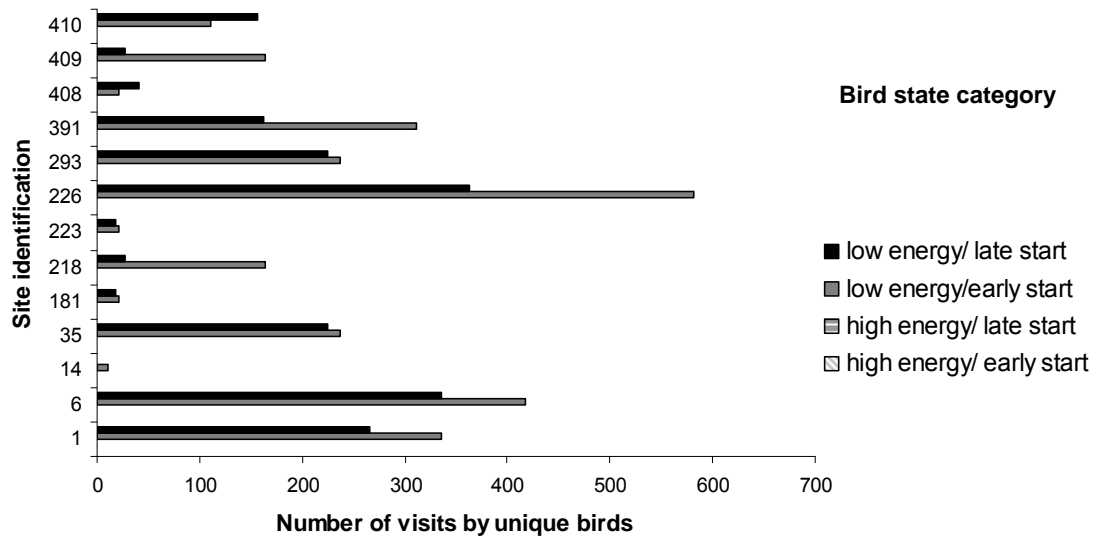


Figure 3.8 Number of visits by unique birds per estuary site for model version 6.

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



Common to those model versions that include the aspect of wind trends (versions 4, 5, 6), are identified estuary Sites 6, 1, 408, 223, 226, and 181 (See Table 3.2 for estuary names). Sites 6 and 1 are located on eastern Vancouver Island; Site 408 is on the southern mainland; Sites 223 and 226 are on the north coast; and Site 181 is on Graham Island of the Queen Charlotte Islands. Generally, most sites experience on

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)
410	Lois 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.

Figure 3.9 Mean relative fitness with associated standard errors across all bird groups for all sensitivity analyses.

Standard errors are barely visible because they are small. SA1 represents the sensitivity analysis in which the flight range parameter was decreased by 50%; SA2 represents the sensitivity analysis in which the flight range parameter was decreased by 97%; SA3 represents the sensitivity analysis in which energy intake parameter was decreased from the baseline; SA4 represents the sensitivity analysis in which the energy intake parameter was increased from the baseline; SA5 represents the sensitivity analysis in which the penalty for low energy at arrival (k_1) was decreased by 10%; SA6 represents the sensitivity analysis in which the penalty for low energy at arrival (k_1) was increased by 10%; SA7 represents the sensitivity analysis in which the penalty for late time of arrival (k_2) was decreased by 10%; SA8 represents the sensitivity analysis in which the penalty for late time of arrival (k_2) was increased by 10%; SA9 represents the sensitivity analysis in which the snowmelt date was advanced by 3 days; SA10 represents the sensitivity analysis in which the departure and destination locations were adjusted to the Willamete Valley and the Copper River Delta.

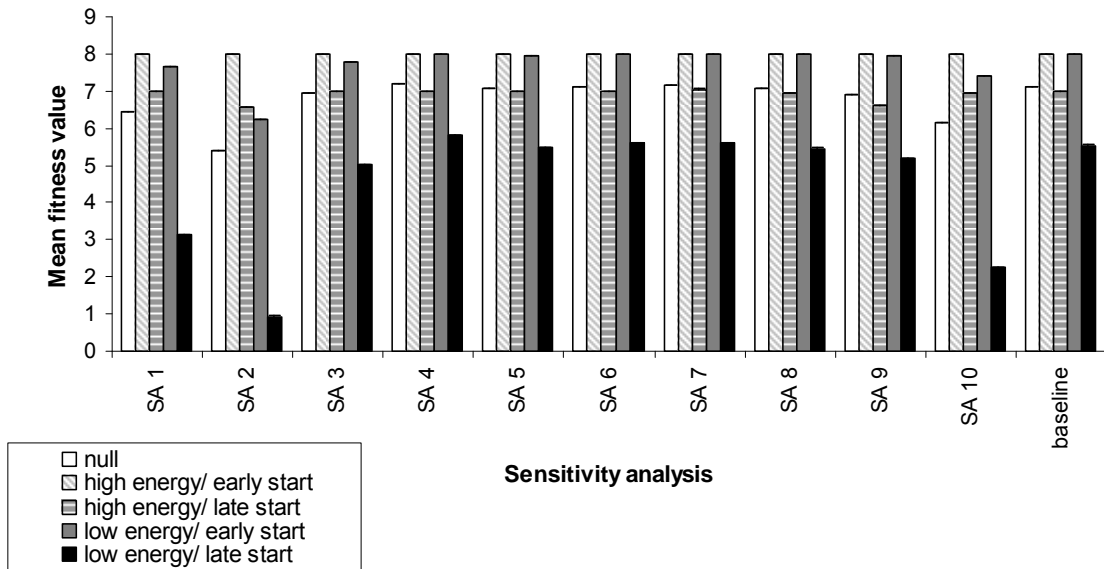


Table 3.3 P-values for two sample t-tests with 95% confidence for all bird groups across all sensitivity analyses.

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 E-151	2.40 E-213	1.51 E-59	2.77 E-24	6.64 E-06	0.15*	2.37 E-05	1.71E-11	4.02 E-70	6.58 E-180
High energy/early start	-	-	-	-	-	-	-	-	-	-
High energy/late start	-	4.60 E-130	0.11*	-	-	-	7.78 E-18	3.50 E-18	5.35 E-129	5.19 E-06
Low energy/early start	1.07 E-196	1.28 E-255	3.81 E-150	-	-	-	-	-	-	5.18 E-223
Low energy/late start	1.39 E-238	2.66 E-302	1.2 E-111	1.33 E-69	4.05 E-07	6.83 E-06	4.12 E-11	2.66 E-12	8.06 E-93	2.20 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 initially low energy reserves and late start dates (bird group ‘low energy/late start’). A reduction in the flight range parameter by 97% results in an approximate 83% decrease in mean relative fitness (from the baseline model) for bird group ‘low energy/late start’. This bird group is also most affected by the locations of the ‘wintering’ or departure site, and the ‘breeding’ or destination site. When I set the ‘wintering’ and ‘breeding’ site to the Willamette Valley and Copper River Delta respectively, the mean relative fitness decreased by approximately 59% for the bird group ‘low energy/late start’. The fitness estimates of these sensitivity analyses when statistically compared to the baseline estimate resulted in significant p-values. Counter-intuitively, the remainder of the sensitivity analyses also resulted in significant p-values (Table 3.3). These results are again a product of very small pooled-variances. I do not believe the size of the differences between the means is ecologically relevant.

Overall, these results correspond to my general expectations of the model's behaviour. I expected birds of lower initial energy reserves to have greater difficulties

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.

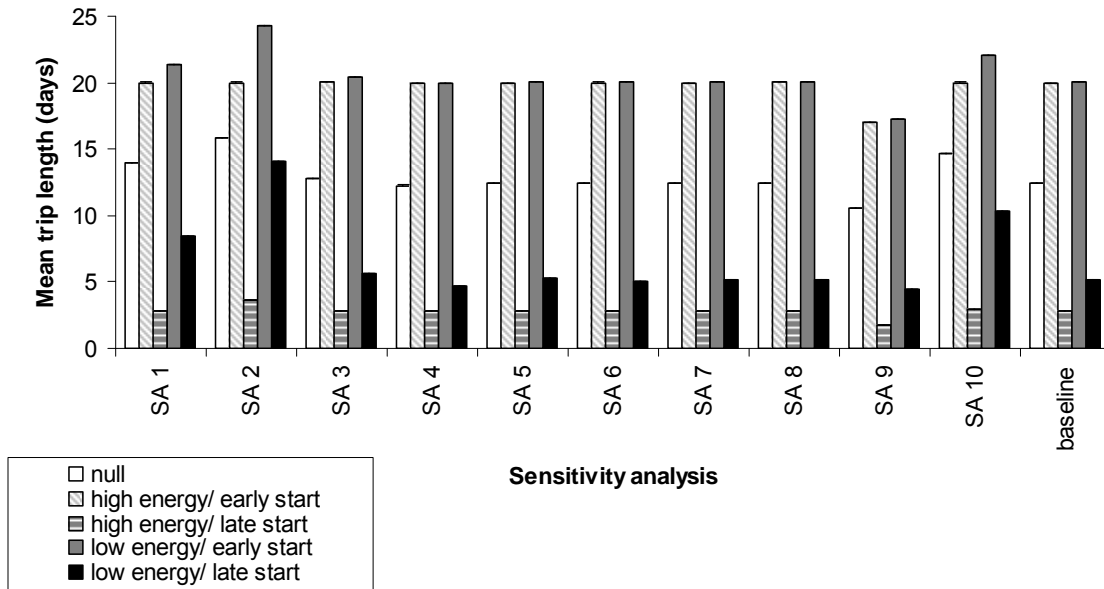
Effects on Trip Length and Number of Intermediate Stopovers

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 errors across all bird groups for all sensitivity analyses.

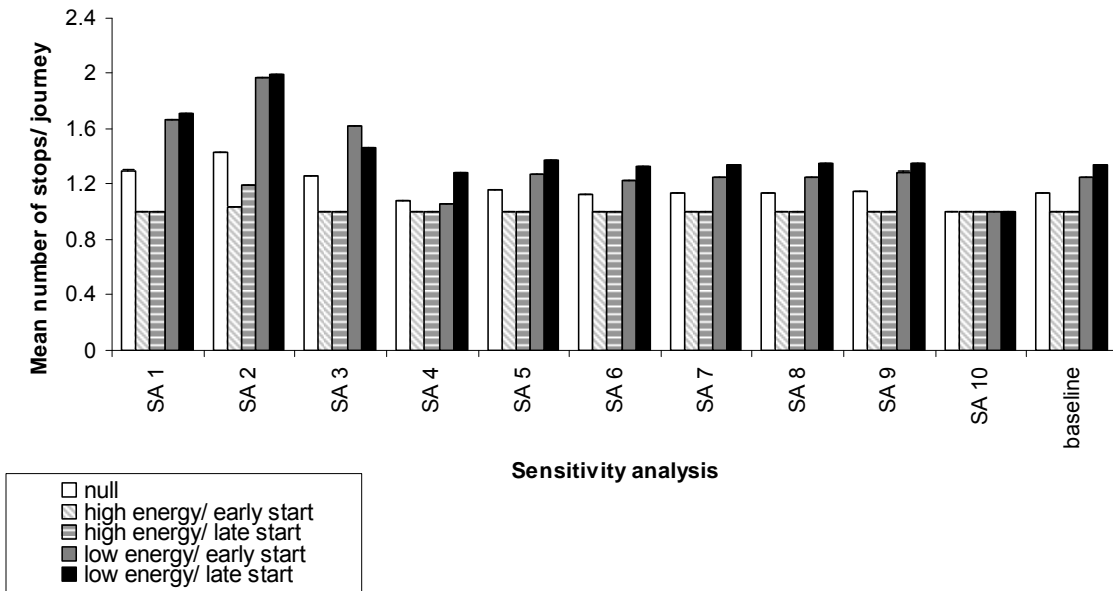
Standard errors are barely visible because they are small.



Across all sensitivity analyses, the numbers of intermediate stopovers used during migration remains unchanged for birds in the higher energy states (See Figure 3.11). Conversely, birds of lower energy reserves show an increased use in the mean number of stopovers for SA1, SA2, and SA3. The comparisons between the baseline and sensitivity analyses 1, 2, and 3 resulted in significant two sample t-tests (p -values < 0.05). This small increase in stopover use is on average less than one quantified stop. This increase in stopover use for birds of lower energies is reasonable because these sensitivity analyses either constrained the amount of energy available at estuary sites or negatively affected the birds' energy efficiencies. Thus, it would be in these birds' interest to use stopovers more frequently in order to gain energy reserves.

It is important to note that statistical comparisons between the baseline and sensitivity analyses 4, 5, 6, 9, and 10 also resulted in significant differences in mean number of stops for bird groups of low energy ('low energy/early start' and 'low energy/late start'). Of these comparisons, the largest difference in means is 0.25 mean stopover, which I think is too small of a difference to be biologically relevant.

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.



Effects on Estuary Sites Identified as Stopovers

The majority of the sensitivity analyses do not result in identified estuary sites that differ from those identified in the baseline model. For sensitivity analyses 4 through 9, the model identified estuary Sites 35 (Skeena/Ecstall/McNeil River Complex), 218 (Nickomekl/Serpentine River Complex), and 391 (Fraser River) with reported bird use, in terms of number of visits and number of bird days/visit, similar to trends of the baseline model (See Figure 3.12).

Those sensitivity analyses with decreased flight range parameters (SA1 and SA2), and energy intake at sites (SA3) identified a greater number of estuary sites as stopovers than the baseline model. These energy constraints place more demand on estuary sites as refuelling stations for birds of initially lower energies. See Figures 3.13 and 3.14 for the identity and use of these sites.

Perhaps, the predictions of SA10 show the greatest deviation from the baseline results; in this scenario, birds of all states did not make any intermediate stopovers. Apparently, intermediate sites were not used because in this model variation because the ‘wintering’ (or departure) site has large amounts of marsh habitat (156 033 022 ha).

All birds forage here until they have enough energy reserves to reach their final destination, the breeding grounds at the Copper River Delta, in one direct non-stop flight.

Figure 3.12 Mean number of unique visits to BC estuary sites across all bird groups as identified by the baseline model.

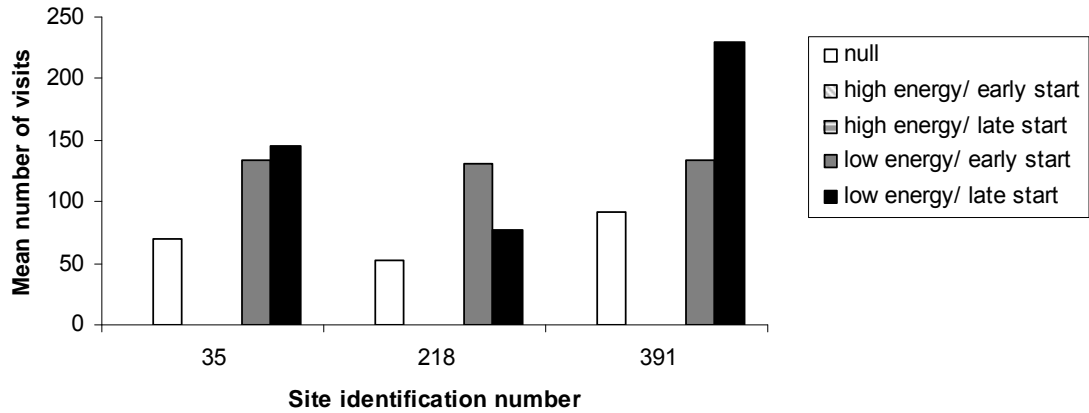


Figure 3.13 Mean number of unique visits to BC estuary sites across all bird groups as identified by sensitivity analysis 1 (SA1).

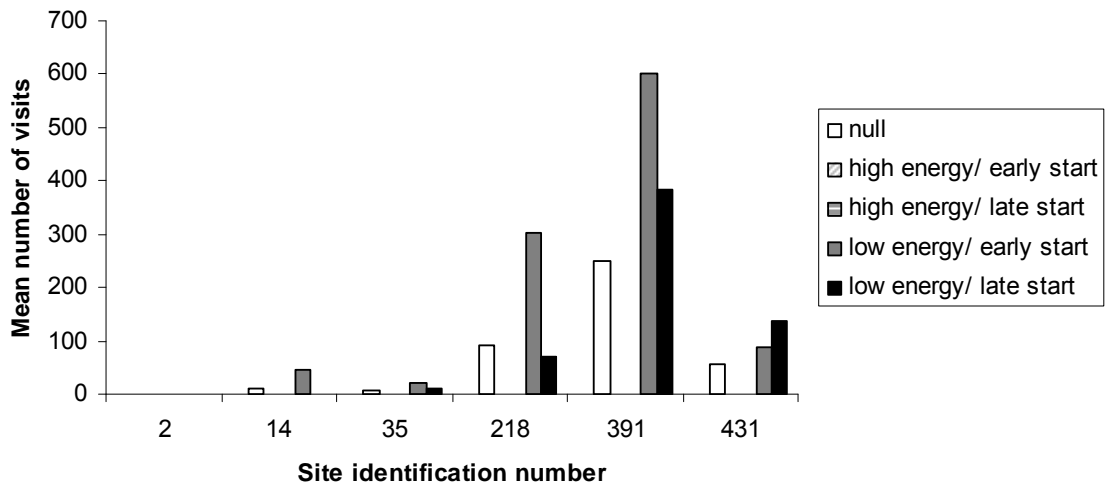
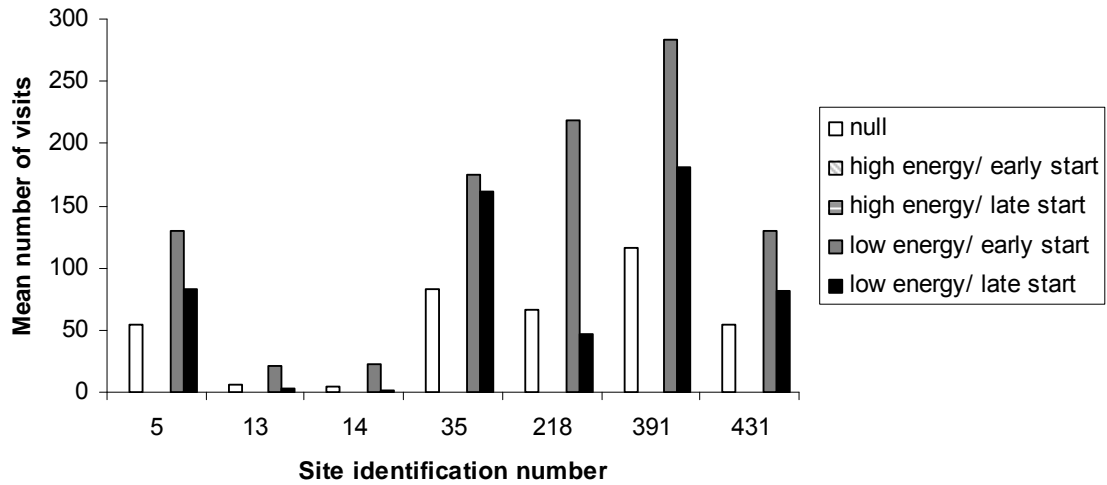


Figure 3.14 Mean number of unique visits to BC estuary sites across all bird groups as identified by sensitivity analysis 3 (SA3).



Model Validation

Comparisons of PECP estuaries connected with Canada Goose records observed by the BC Coastal Waterbird Study (BCCWS) (Bird Studies Canada 2006), and estuary sites predicted as goose stopovers by DSV model version 3 show some degree of correspondence. I could not draw strong conclusions from these data because the majority of the 442 estuaries were not surveyed for waterbirds. However, I present the comparisons as a vague indication of the model's performance. Of the three estuary sites predicted by model version 3 (Sites 391, 228, and 35), two were observed as having large numbers of recorded Canada Geese by the BCCWS. The Fraser River (Site 391) and the Nickomekl/Serpentine River Complex (Site 218) have the highest and third highest Canada Goose (CAGO) counts, respectively (See Table 3.4). Note that for both Sites 391 and 218, I combined the average CAGO counts for multiple BCCWS survey sites. Since these estuaries are considerably larger than the others (by approximately 24 and 8 times for respective Sites 391 and 218), I assumed it was appropriate to combine the counts of all associated BCCWS censuses for those particular estuaries. Thereby, I could achieve a more accurate reflection of the true number of geese at those estuaries. The Skeena/Ecstall/McNeil River Complex (Site 35) identified by the model version 3 does not have any corresponding BCCWS data.

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.

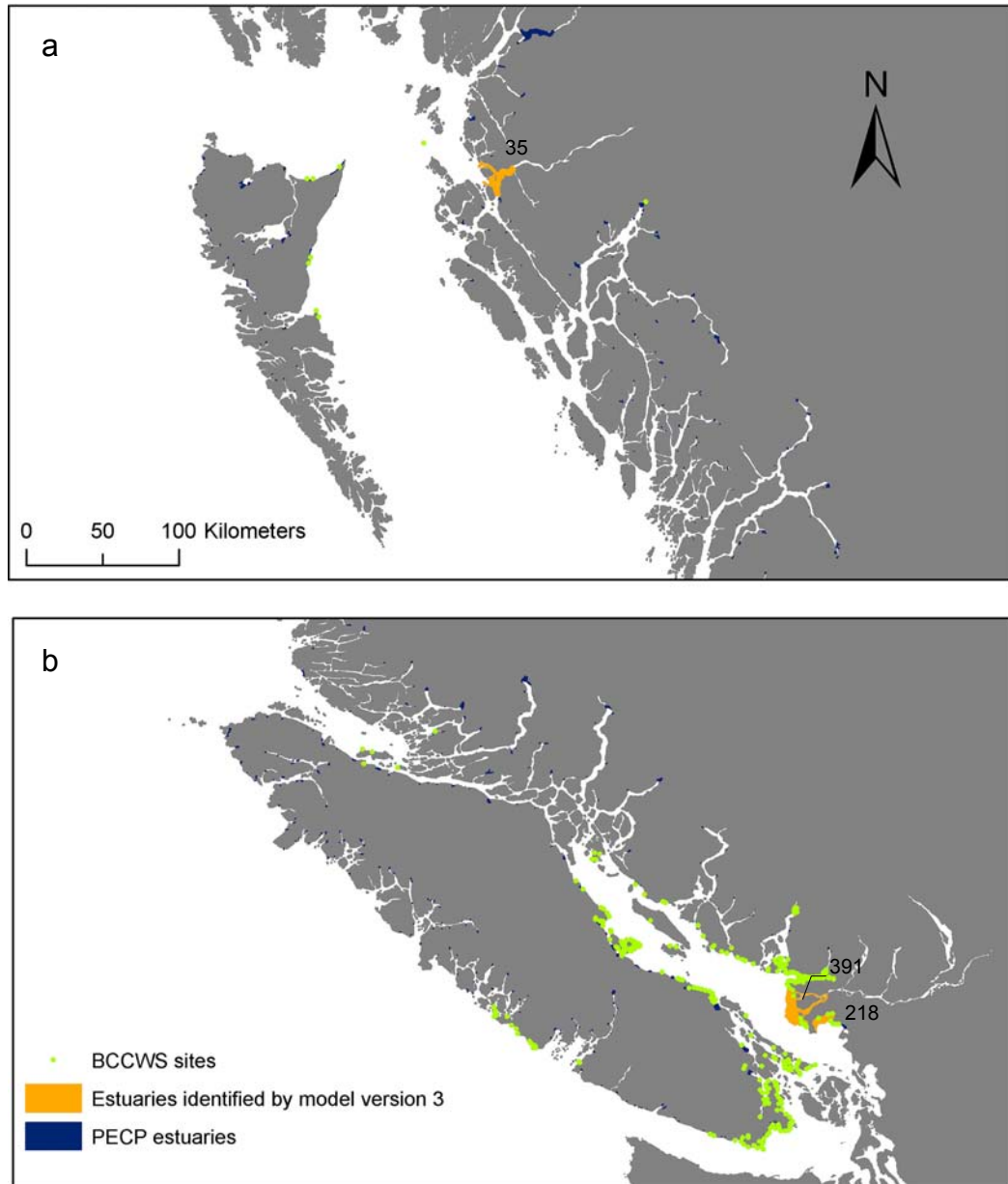
PECP estuary site ID	Estuary name	Average number of CAGO recorded associated at BCCWS census (variance in brackets)	Average number of unique visits /PECP estuary site (predicted by model version 3)
391	Fraser River	114*	91
75	Oyster River	70 (8267.0)	-
218	Nickomekl/Serpentine River Complex	51*	53
35	Skeena/Ecstall/McNeil River Complex	-	70
2	Englishman River	47 (1491.0)	-
274	Mamquam River	47 (1852.0)	-
22	Somas River	34 (67.9)	-
10	Nanoose/Bonell Creek Complex	24 (223.9)	-
24	Squamish River	21 (160)	-
15	Nanaimo River	20 (125.9)	-
12	Gorge Waters/Craigflower Creek	19 (474.3)	-
97	Colquitz River	19 (57.9)	-
5	Little Qualicum River	17 (72.1)	-
26	Capilano River	16 (- one count)	-
9	Campbell River (2)	13 (210.0)	-
25	Kitimat River	10 (4.5)	-
74	Big Qualicum River	9 (94.3)	-
424	Mill Creek	7 (20.3)	-
101	China Creek	6 (9.3)	-
273	Stawamus River	6 (19.1)	-
130	Zeballos River	4 (18)	-
133	Jordan River	4 (- one count)	-
361	Campbell River (1)	4 (12.5)	-
6	Trent River	3 (0.05)	-
16	Courtenay River	2 (0.3)	-
37	Cous Creek	2 (- one count)	-
228	Hart Creek	1 (- one count)	-

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 bird group, mean fitness decreases by approximately 4.5% from the density-independent forward iteration, in the proactive density-dependent iteration. For both bird groups, the declines are larger for the reactive version. This trend likely occurs because birds in the reactive forward iteration have fewer options when faced with larger flocks at estuaries. They must accept lower returns in fitness, whereas birds in the proactive forward iteration can assess and respond to potential fitness payoffs. The average proportion of successful breeders also declines slightly (less than an approximate 1.7%) for low energy bird groups in the density-dependent forward iterations.

The density dependence assumption also influences to a small degree the timing of migration routes, in terms of trip length and number of stopovers per journey. In both reactive and proactive forms of the density-dependent forward iteration, the birds' average trip length increases. For birds of the null group, the average trip length increases by about 0.29 to 0.34 days from the values predicted by the density-independent forward iteration. Birds in the low energy groups experience the most change in average trip length with an increase of 0.32 to 0.87 days from the values predicted by the density-independent forward iteration. The density dependence assumption also seems to increase slightly the average number of stopovers used per journey. In the density-dependent iterations the average number of stops increases by about 0.01- 0.21 stops from the density-independent iteration.

The reactive density-dependent forward iteration and the density-independent forward iteration predict the use of similar estuary sites by migrating geese (See Figures 3.16 and 3.17). For both of these forward iterations, birds of the low energy groups use Sites 35 (Skeena/Ecstall/McNeil River Complex), 218 (Nickomekl/Serpentine River Complex), and 391 (Fraser River). However, one difference between iterations is that a

larger number of birds in the low energy groups use the sites as stopovers in the density-dependent forward iteration.

Figure 3.16 Average number of unique visits to BC estuary sites across all bird groups as identified by the density-independent forward iteration using a cohort of 1600 birds.

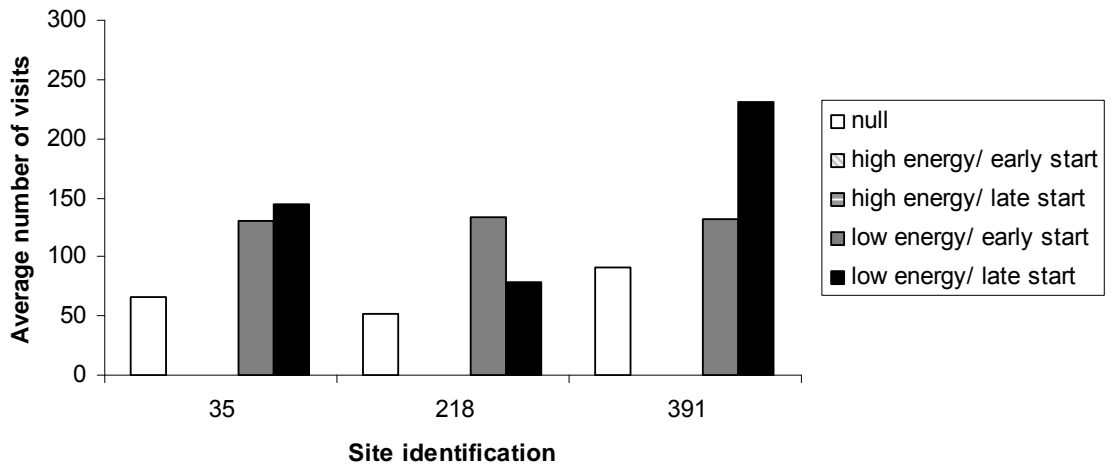
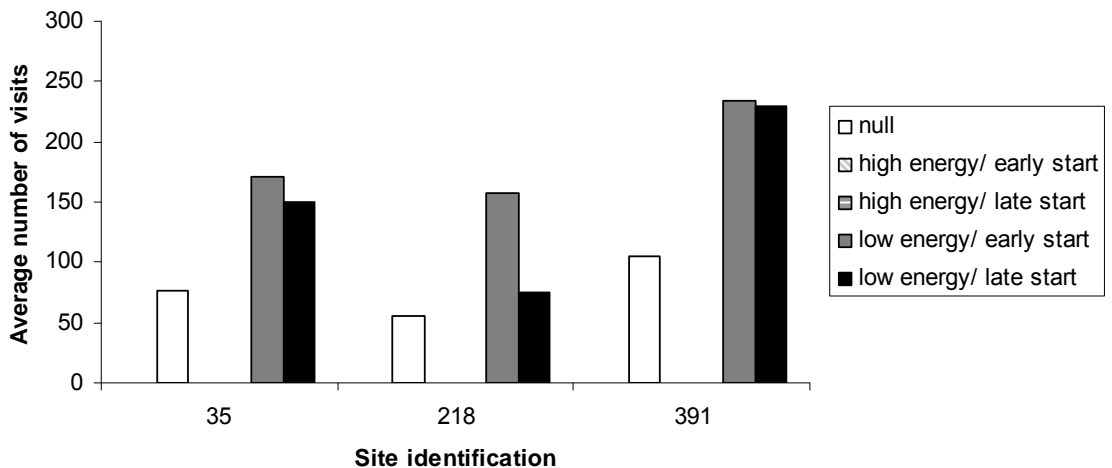


Figure 3.17 Average number of unique visits to BC estuary sites across all bird groups as identified by the reactive density-dependent forward iteration using a cohort of 1600 birds.

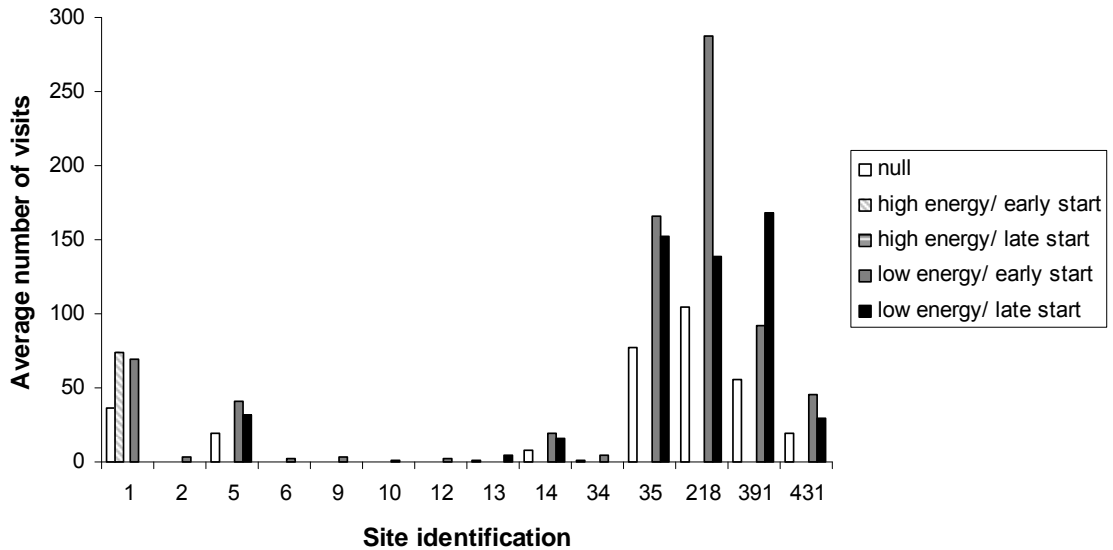


In the proactive density-dependent forward iteration, predictions of estuary use largely deviate from predictions of the other iterations. Overall, BC estuaries experience greater use by geese (Figure 3.18). Apparently, the constraint of density dependence causes migrating birds to spread out across the landscape and use various estuaries as

stopovers that now provide a fitness advantage. During the simulated migration, birds visited fourteen unique sites, including Sites 35, 218, and 391 (See Figure 3.18 for site identities). Sites 35, 218, and 391 still experience the highest number of visits out of all estuary sites predicted as stopovers. Only birds of group, 'low energy/early start', use Sites 2, 6, 9, 10, and 12 (See Figure 3.18 for estuary names). Interestingly, birds of group, 'high energy/early start' use Site 1, whereas in the other forward iterations birds of high energy groups do not use any intermediate sites in their migrations.

Figure 3.18 Average number of unique visits to BC estuary sites across all bird groups as identified by the proactive density-dependent forward iteration using a cohort of 1600 birds.

See the following table for estuary names of the sites.



Site identification	Estuary name
1	Fanny Bay/Cowie Creek
2	Englishman River
5	Little Qualicum River
6	Trent River
9	Campbell River (2)
10	Nanoose/Bonell Creek Complex
12	Gorge Waters/Craigflower Creek
13	Chemainus River/Bonsall Creek Complex
14	Cowichan River
34	Black Creek
35	Skeena/Ecstall/McNeil River Complex
218	Nickomekl/Serpentine River Complex
391	Fraser River
431	Nass/Ksi'Ilginx/Burton/Iknouck/Chambers/Kincolith River Complex

Effects of Waterfowl Management and Estuarine Losses on Migration and Survival

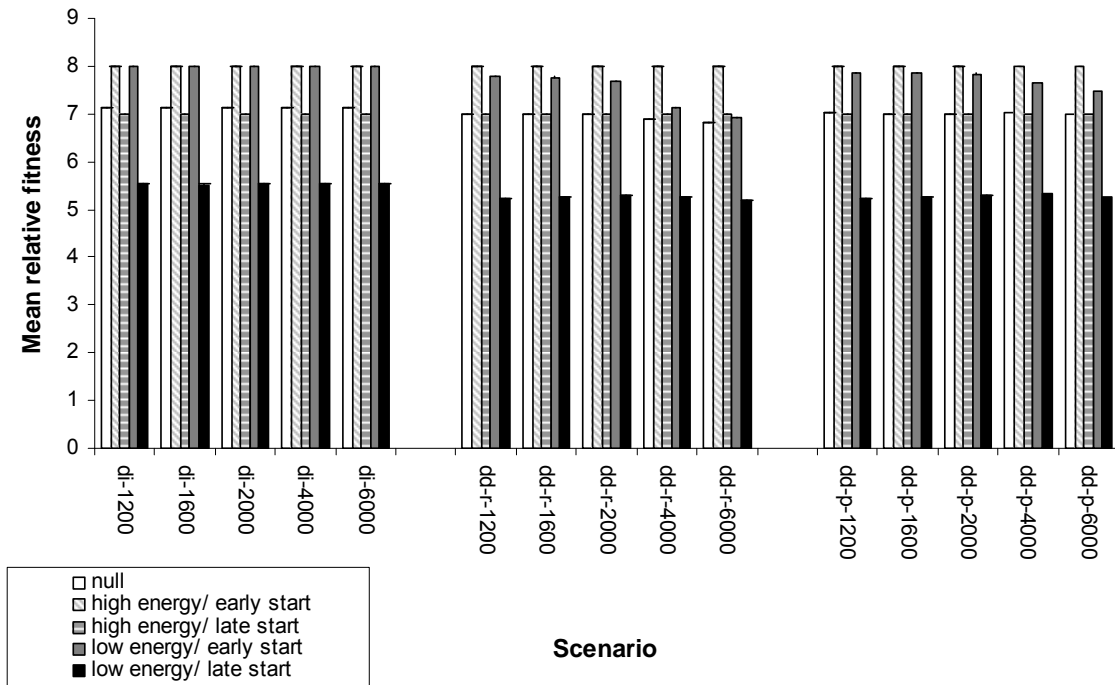
Applying Population Scenarios to Goose Migration

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.



Predictions of the Reactive Density-Dependent Forward Iteration

Increasing numbers of geese in the initial cohort, as reflected by scenarios of a population increase from 1200-6000 birds, indicate that birds of initially lower energies experience the greatest effects. Specifically, geese of bird group, 'low energy/late start', experience the most changes in their optimal migration routes and in fitness consequences. Small changes occur in the average trip length and average number of stopovers per journey for these birds. As the population increases, the average trip length responds by slowly increasing; the largest increase of an average 0.97 day occurs when the population shifts from 2000-4000 birds. The average number of stopovers also begins to slowly rise as the goose population increases, demonstrating the interrelation between trip length and number of stopovers. The rise is subtle and increases in average stopovers range between 0.01-0.04. The identity of these estuary stopovers remains constant and is similar to the sites predicted by the density-

independent iteration (i.e. Sites 391 (Fraser River), 218 (Nickomekl/Serpentine River Complex), and 35 (Skeena/Ecstall/McNeil River Complex)). Across the increasing population scenarios, bird use with respect to numbers of visits at sites displays similar patterns. The average intensity of use (expressed as average bird days per unique visit at site) also remains unchanged. As anticipated, expected relative fitness declines as the population increases (See Figure 3.19). The declines in fitness are small and do not occur until the population passes the threshold of 2000 birds. Mean fitness decreases 7% as the initial cohort increases from 2000-4000 birds. As the initial cohort increases between 4000-6000 birds, mean fitness decreases by 2.25%.

Predictions of the Proactive Density-Dependent Forward Iteration

Predictions of the proactive density-dependent forward iteration show subtle changes in the optimal migration routes of geese in groups, 'low energy/early start' and 'high energy/late start', as the initial cohort size increases. For 'low energy/early start' birds, the average time for completing the migratory journey slowly increases once the cohort size reaches 2000 birds. Trip length increases by an average 1.02 day as the population increases from 2000-6000 birds. The number of stopovers also increases slightly with increasing trip length; the increase ranges from 0.01-0.03 average stopovers per journey. In contrast, the number of stopovers declines by an average 0.05 stopover once the population reaches 2000 for geese in bird group, 'high energy/early start'. These geese use one intermediate estuary site as predicted for scenarios with cohorts of 1200-2000 birds.

Once the cohort size passes 4000 birds, a shift takes place; geese of the 'high energy/early start' group stop using Site 1 (Fanny Bay/Cowie Creek) and geese of 'low energy/early start' use less sites in their journeys. For example, in the scenario of 2000 birds or less, 'low energy/early start' birds use a total of 14 intermediate estuary sites, whereas in the scenario of 4000 birds or more, these birds only use a total of seven intermediate estuary sites. Figures 3.20 and 3.21 show this change in use of total numbers of estuaries by 'low energy/early start' and 'high energy/late start' birds, when the population increases from 2000 to 4000 birds. In the scenario, which increases the population to 4000 birds, the frequency of site use (i.e. average number of visits) at the seven common sites increases. However, there is no reallocation of effort and the intensity of site visits (i.e. average bird days per visit) tends to remain the same.

Figure 3.20 Average number of unique visits to BC estuary sites across all bird groups as identified by the proactive density-dependent forward iteration using a cohort of 2000 birds.

See Figure 3.18 for estuary names of the sites.

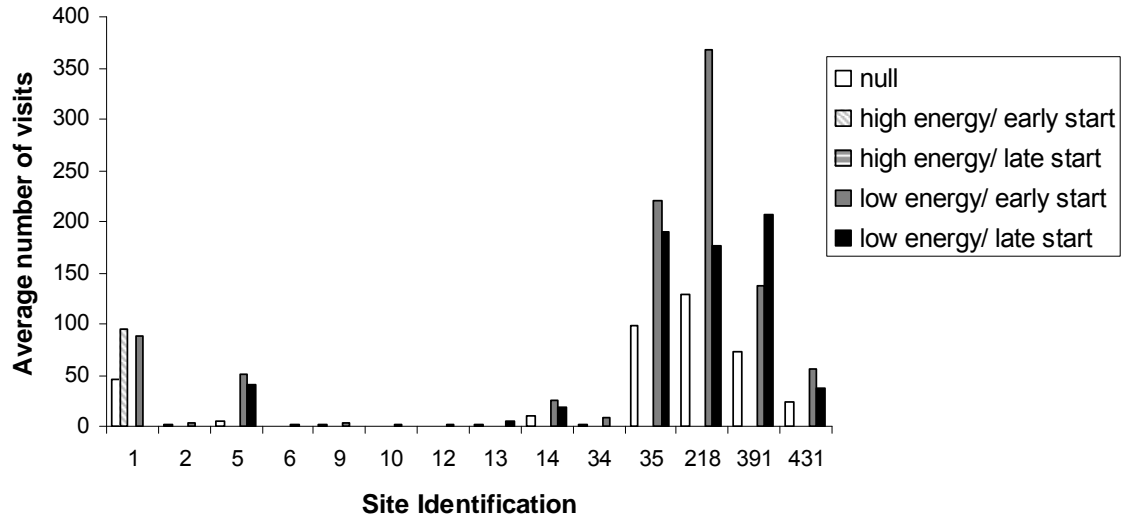
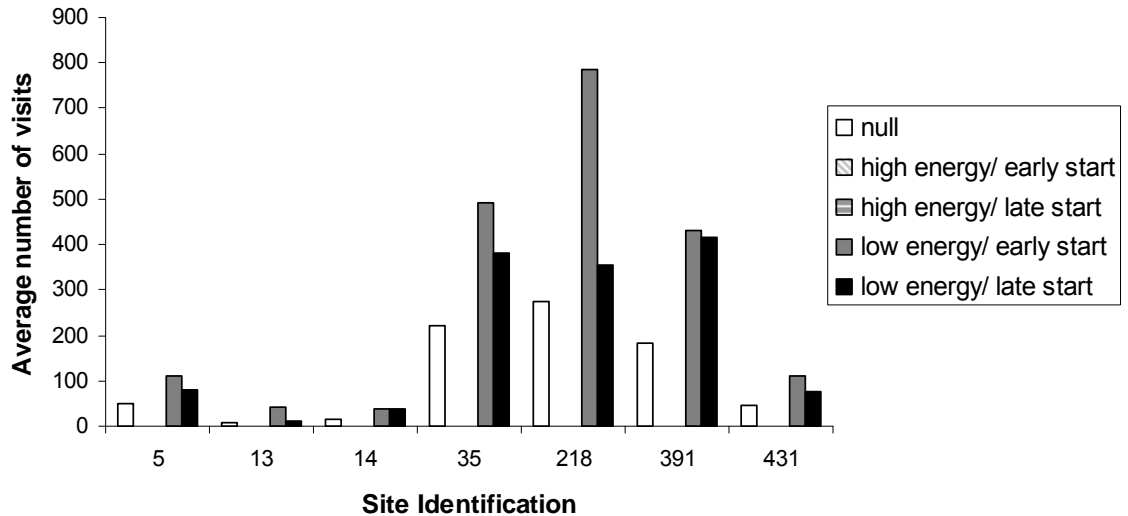


Figure 3.21 Average number of unique visits to BC estuary sites across all bird groups as identified by the proactive density-dependent forward iteration using a cohort of 4000 birds.

See Figure 3.18 for estuary names of the sites.



Consequences for relative fitness payoffs appear to be most prevalent for geese in bird group, 'low energy/early start'. As cohort size increases from 4000-6000 birds,

fitness decreases by 2% (See Figure 3.19). The relative fitness of all other bird groups seems unaffected.

Applying Scenarios of Estuarine Losses to Goose Migration

Predictions of the Density-Independent Forward Iteration

The density-independent forward iteration predicts habitat degradation of estuaries identified as stopovers (by the original DSV outputs) to affect the timing of optimal migration and expected fitness of geese of lower initial energies. Geese in 'high energy/early start' and 'high energy/late start' groups remain unaffected by habitat loss at stopover sites because they do not rely on using estuaries en route to breeding grounds.

Scenarios that remove greater numbers of estuaries predicted as stopovers by the DSV model have greater consequences for the migration and fitness of low energy bird groups. For example, in scenarios that remove stopovers predicted by DSV model versions 3 and 6, the average number of stopovers per journey slightly increases for birds with initially lower energies. Bird group 'low energy/late start' experiences the biggest increase of 0.18 average stopover, in both of the above scenarios. These same scenarios also have a small effect on the average time for completing the migratory journey. For bird group, 'low energy/early start' the average trip length increases slightly, whereas for bird group, 'low energy/late start' average trip length decreases slightly. The identity of the intermediate estuaries used by geese of low initial energies is identical to the forward-iteration run with all estuary sites intact. Sites 391 (Fraser River), 218 (Nickomek/Serpentine River Complex), and 35 (Skeena/Ecstall/McNeil River Complex) experience similar frequencies of bird use (i.e. average number of unique visits) across all habitat degradation scenarios. However, the intensity of use (i.e. average bird days/unique visit at estuary) shifts from the stopover sites to Site 441 (Bear River: destination site) when estuaries predicted as stopovers by the DSV model are degraded. The scenarios that degrade or remove the highest numbers of DSV-predicted stopovers show the greatest increase in average number of bird days at Site 441. Figures 3.22 and 3.23 show the pattern of the length of stay shifting from Sites 391, 218, and 35 to Site 441 as stopover sites are removed.

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.

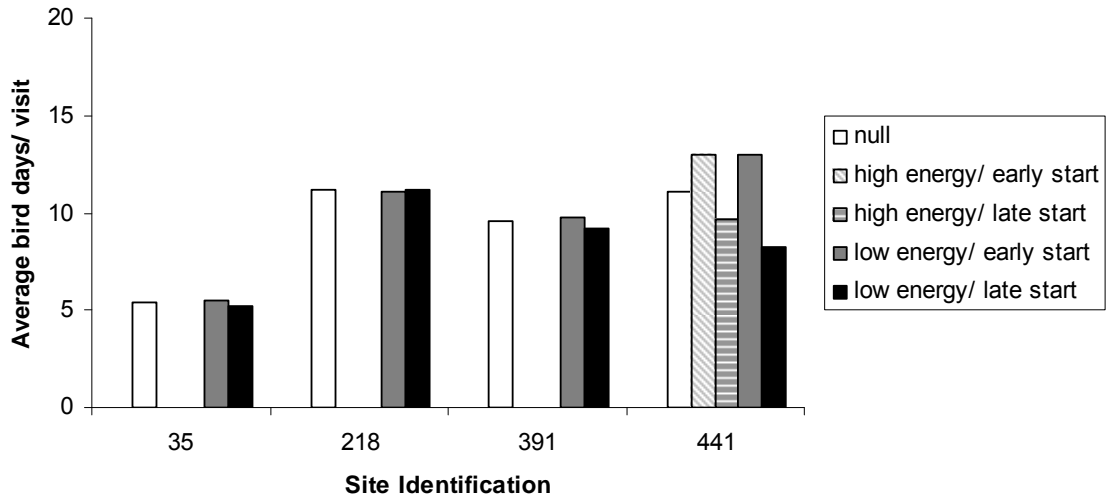
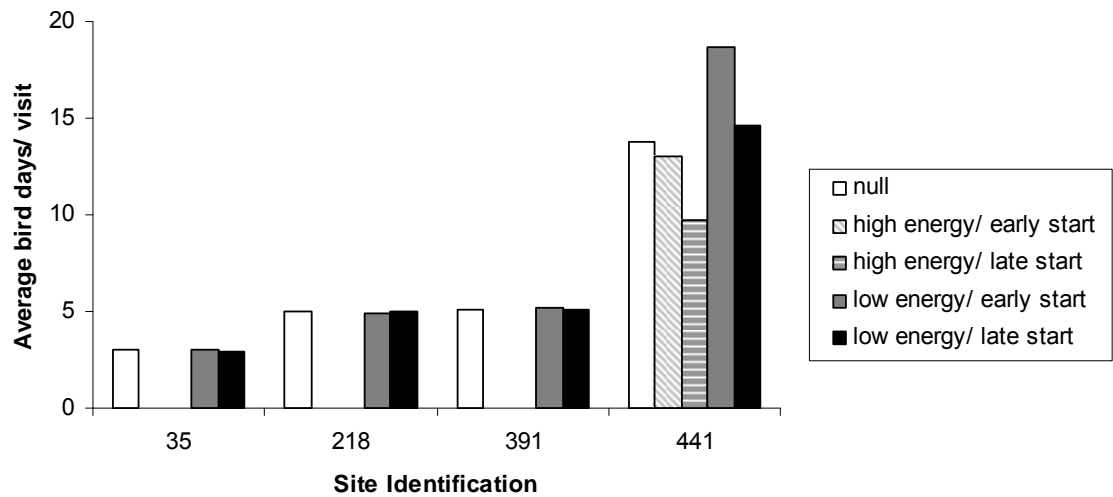


Figure 3.23 Intensity of bird use expressed in average bird days/visit, as predicted by the density-independent forward iteration with estuary sites predicted by model version 6 removed, including Sites 35, 218, and 391.

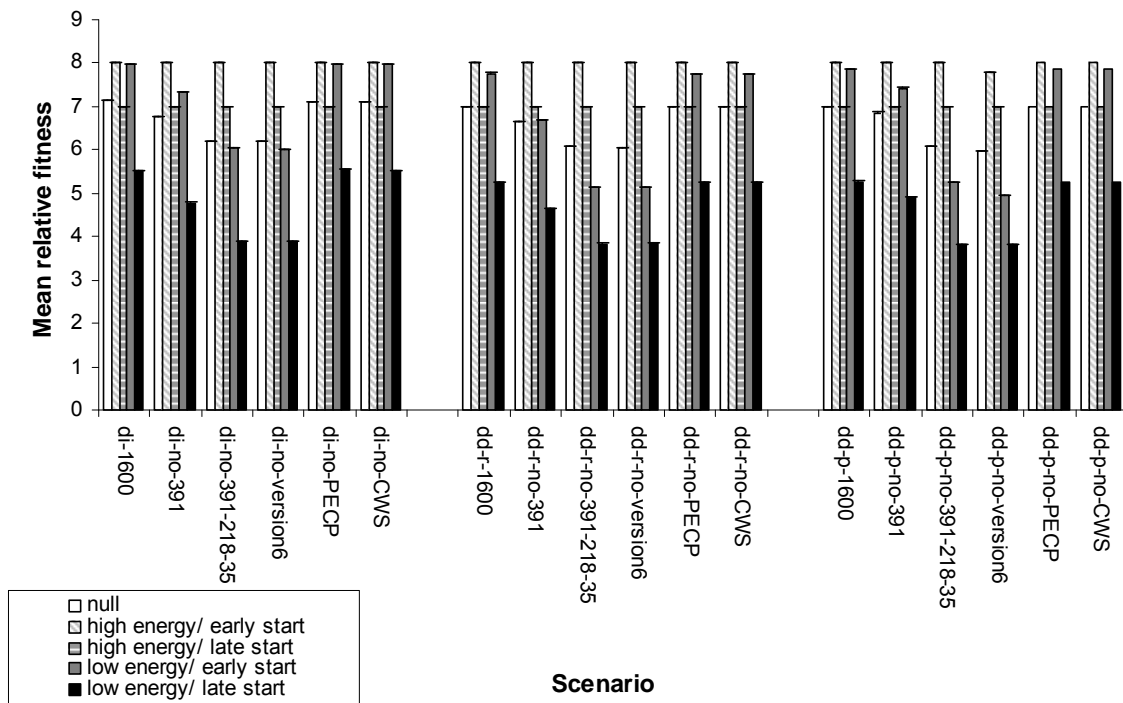


Declines in mean relative fitness occur for birds of low energy groups as greater numbers of stopover sites predicted by the DSV model are degraded within the model landscape. The application of scenarios that remove sites predicted by model version 3 and 6 cause the greatest declines in fitness (Figure 3.24). Average relative fitness declines by approximately 25% and 20% for bird groups, 'low energy/early start' and 'low energy/late start', respectively. Interestingly, the scenario which eliminated estuaries ranked as unprotected and threatened by the Canadian Wildlife Service (CWS) does not

affect the relative fitness or timing of migration for any geese. Eliminating the three most important estuaries ranked for the Pacific Estuary Conservation Program (PECP) (i.e. Sites 25 (Kitimat River), 16 (Courtenay River), and 13 (Chemainus River/Bonsall Creek Complex)) also does not result in fitness effects or changes in migration routes.

Figure 3.24 Mean relative fitness for habitat loss 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 habitat loss scenario. The first scenario 1600 refers to no habitat loss; scenario no-391 eliminates Site 391; scenario no-391-218-35 eliminates Sites 391, 218, 35 (sites predicted by model version 3); scenario no-version 6 eliminates all 13 sites predicted by model version 6; scenario no-PECP eliminates Sites 25, 16, 13 (sites ranked by the PECP); scenario no-CWS eliminates 44 sites ranked by CWS. Mean fitness values are also associated with one standard error. However, standard errors are barely visible because they are small.



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 average trip length. The identity of stopovers visited on migration routes of the low-energy birds does not change. The pattern of bird use, expressed in average numbers of visits at Sites 391 (Fraser River), 218 (Nickomekl/Serpentine River Complex), and 35 (Skeena/Ecstall/McNeil River Complex) is similar across all habitat degradation scenarios. Degrading habitat quality at these stopovers does appear to affect how the sites are used. For example, the low energy birds spend less time per visit at Sites 391, 218, and 35, and spend increasing amounts of time at Site 441 (Bear River: destination site). The scenarios, that eliminate sites predicted in model version 3 and 6, result in the greatest shift in use to Site 441 at averages of 22.1 and 14.6 bird days per visit for respective 'low energy/early start' and 'low energy/late start' bird groups (See Figures 3.25 and 3.26).

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.

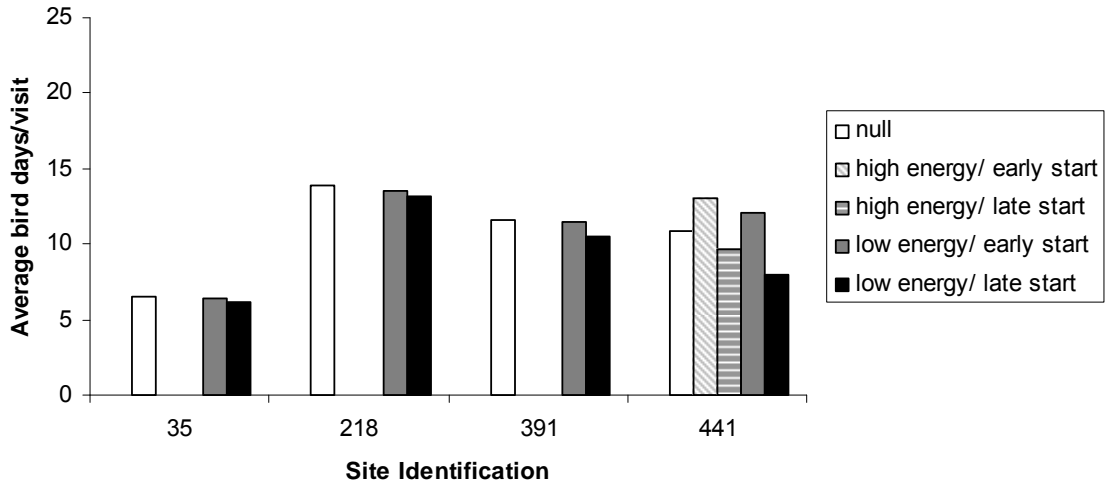
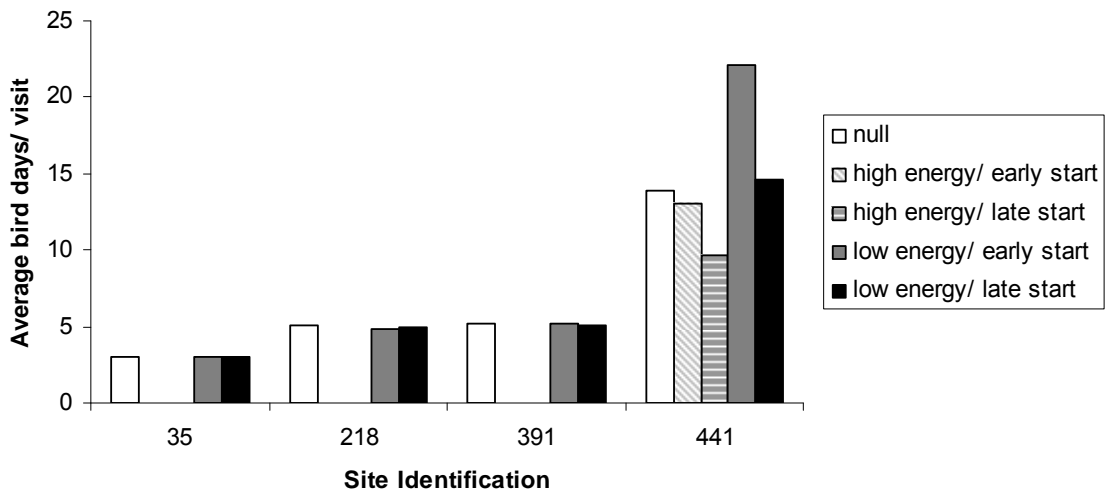


Figure 3.26 Intensity of bird use expressed in average bird days/visit, as predicted by the reactive density-dependent forward iteration with estuary sites predicted by model version 6 removed, including Sites 35, 218, and 391.



As greater numbers of estuaries, predicted as stopovers are removed in the scenarios, the declines in fitness payoffs increase for birds of initially low energies. The application of scenarios that remove sites predicted by model version 3 and 6 cause the greatest declines in fitness (Figure 3.24). Mean relative fitness declines by approximately 33% and 18% for bird groups, 'low energy/early start' and 'low energy/late

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 optimal migration routes of birds of initially lower energies. In most scenarios, the same 14 estuaries experience bird use (see Figure 3.18 for the site identities) by birds of lower energies. While there is little variation in the number of unique visits at these sites, the average length of stay per visit shifts among sites as the habitat quality of predicted stopovers degrades. As demonstrated by the results of the reactive density-dependent iteration, as Sites 391 (Fraser River), 218 (Nickomekl/Serpentine River Complex), and 35 (Skeena/Ecstall/McNeil River Complex) are removed bird use with respect to the length of stay at a site (i.e. average bird days per site), shifts from Sites 391, 218, and 35 to Site 441 (Bear River). How the results differ in the case of the proactive density-dependent iteration is that other sites, such as Sites 2 (Englishman River), 5 (Little Qualicum River), 6 (Trent River), and 12 (Gorge Waters/Craigflower Creek), also experience increased use across various habitat loss scenarios. In the proactive version, birds have the ability to assess fitness consequences and make appropriate decisions regarding where to stop and refuel.

Perhaps, the scenario that removes sites predicted as stopovers by model version 6 shows the most divergent results. First, Site 6 is not identified as a stopover at all, limiting the total number of stopovers to 13. Second, this is the only instance in which birds of the 'high energy/early start' bird group use intermediate stopovers apart from Site 1 (Fanny Bay/Cowie Creek). In descending order of bird use, Sites 35, 9 (Campbell River (2)), and 431 (Nass /Ksi'Hlginx/Burton/Iknouck/Chambers/Kincolith River Complex) are also visited by birds of initially higher energies. As bird use shifts, the average number of bird days per visit decreases for Sites 35, 218, and 391, as well as Site 1 and

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.

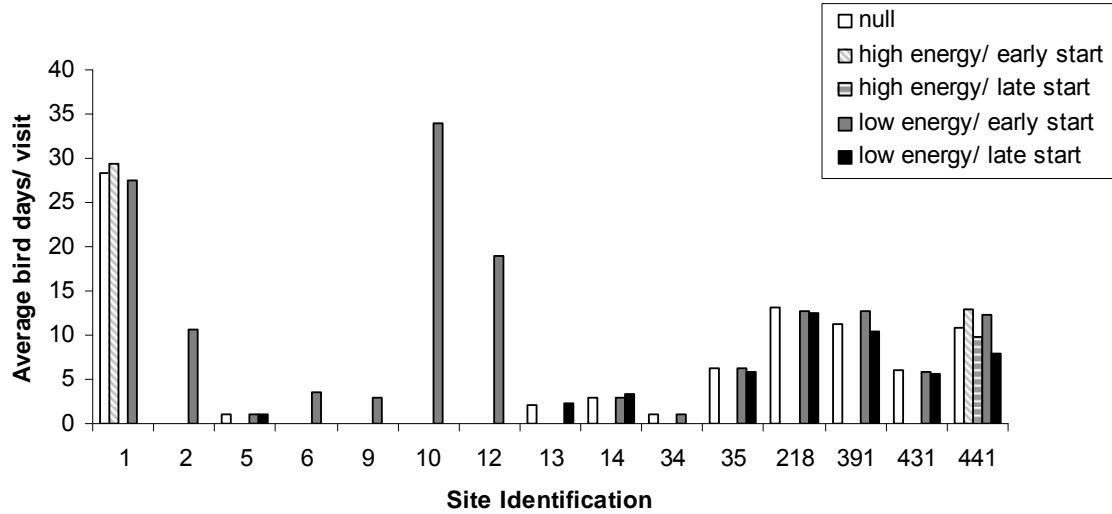
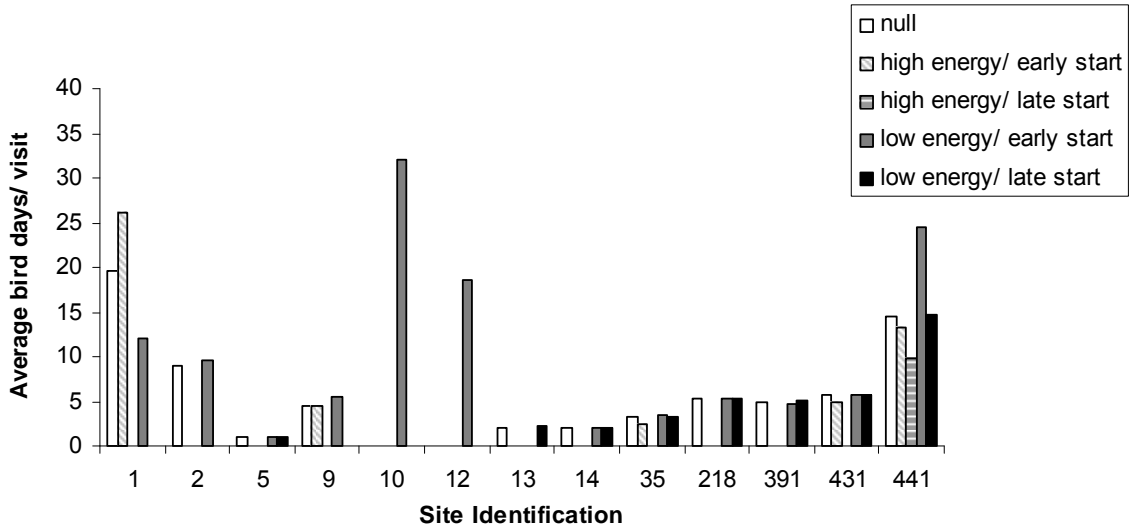


Figure 3.28 Intensity of bird use expressed in average bird days/visit, as predicted by the proactive density-dependent forward iteration with estuary sites predicted by model version 6 removed, including Sites 35, 218, and 391.



With respect to the average numbers of stopovers and trip length predicted for geese of lower initial energies, the results are similar to the other two forms of forward

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.

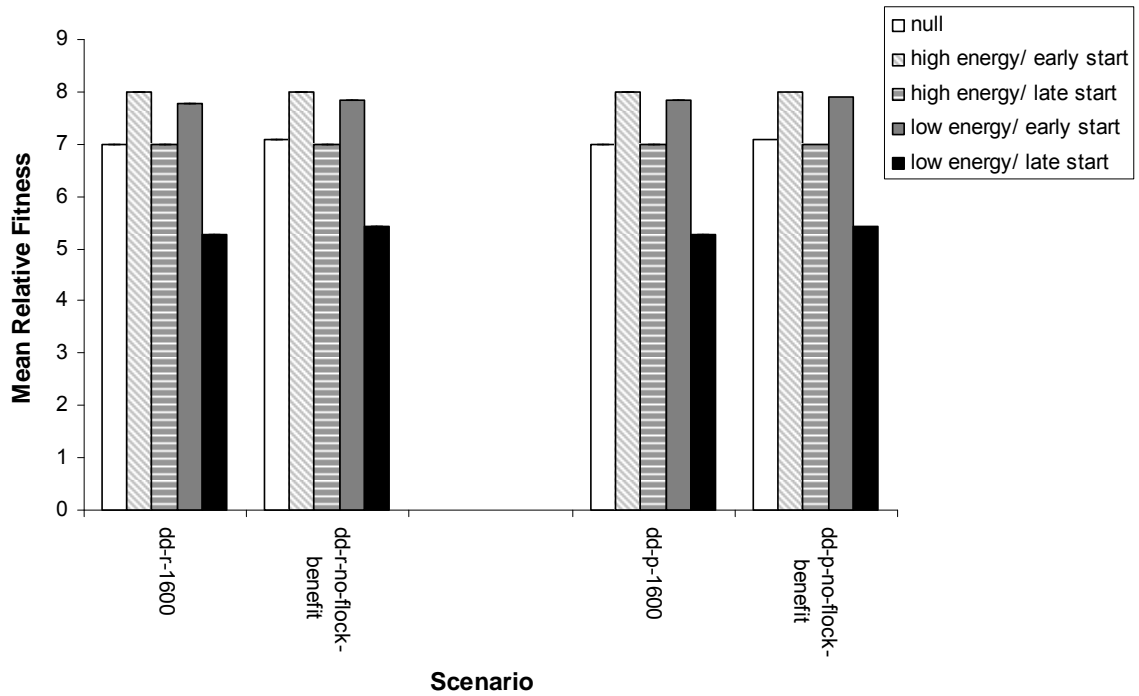
Fitness effects are only prevalent for birds of lower initial energies, across the habitat degradation scenarios. As predicted stopovers (i.e. those predicted by model version 3 and 6) are removed relative fitness declines. Birds of 'low energy/early start' group have the largest decrease in mean fitness 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 the six model versions also identify this site as a stopover. Currently, the Fraser River has PECP designation and holds the status of an Important Bird Area (IBA) (BirdLife International 2004). IBAs are sites of international status selected for their ability to provide essential habitat for one or more species of breeding or non-breeding birds, but do not provide legal protection (BirdLife International 2004). The Nickomekl/Serpentine River Complex was predicted by model version 3 to experience the second highest bird use (in average bird days). According to the Canadian Wildlife Service (CWS), approximately 98% of its area is already under protection (Ducks Unlimited Canada 2006). The Skeena/Ecstall/McNeil River Complex has 0% protection (Ducks Unlimited Canada 2006).

Other estuaries that I qualify as important are those, which are repeatedly identified by numerous DSV model versions. Three model versions, all which incorporate wind conditions, identify Fanny Bay/Cowie Creek and Little Qualicum Estuaries on eastern Vancouver Island, Hiellien River Estuary on the Queen Charlotte Islands, Sliammon Creek Estuary on the southern mainland coast, and Kingkown Inlet and Keswar Inlet Estuaries on the north coast. Fanny Bay and Little Qualicum are located

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 success, with the use of the forward iterations. Overall, scenarios implying losses or degradation in estuarine habitat have more dramatic effects on the reproductive success of birds with lower initial energy reserves than scenarios implying a population increase. Migrating birds of initially lower energy reserves that face stopover-habitat losses experience mean fitness declines in the range of 18-36%, whereas those migrating birds in increasing populations experience fitness declines in the range of 2.5-7%. In either case, the relative fitness of birds with higher initial energy reserves are not affected.

The habitat loss scenarios effectively demonstrate that where estuarine degradation occurs in the landscape is significant. Removing sites identified as important by the PECP and CWS does not affect the birds' fitness according to the forward iteration's predictions; yet removing DSV-predicted stopovers has a definite fitness

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). Ebinger (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) relates to each estuary site. Using these static states of wind at estuary sites, I solved for the optimal migration strategies with backward iterations. By incorporating wind into the solutions for the original DSV outputs, I assume that these static, extreme, wind conditions have prevailed over time

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 effects of wind on the bird's ground speed and direction.

Another ambitious extension of the current model is to include the entire annual cycle of the Dusky Canada Goose. In theory, all stages experienced by geese throughout the year affect fitness, not solely the spring migratory stage. Incorporating autumn migration and wintering as additional stages would complete the representation of the annual cycle. Pettifor and Caldow (2000) stressed the importance of considering the year-round dynamics in understanding population responses of long-distance migrants, like Barnacle and Brant Geese, to environmental change. In future, this approach could also be applied to DSV modelling, although extensive data requirements for parameterization and large computational times may present obstacles. Nevertheless, it is a deserving goal to strive for as more data become available.

Canada Geese display generalist tendencies in their foraging and habitat selection, and possibly, during migration visit stopover sites other than estuaries. For this reason, I would consider the inclusion of other habitat types, like patches of farmland, as discrete stopovers in future versions of the model. In this way, I could indirectly address threats occurring upland of the estuaries and test the effects of environmental changes taking place in the landscape on goose fitness.

Certainly, including all of these additional variables into the DSV model does not necessarily produce a more realistic model. Complexity within a model does not always imply realism of the modelled system. Ideally, building alternate versions of the model with varying combinations of the suggested additions and then testing the predictions of each model against field observations would reveal the most robust form. This testing would also show which variables have the greatest influence on the birds' migratory strategies. A dataset of satellite transmitter tagged Dusky Canada Geese indicating their stopover locations en route to the breeding grounds, as well as data on their body

conditions at departure (on the wintering grounds), and their subsequent breeding success would be ideal for the comparisons.

Practicality of DSV Migration Model as a Conservation Tool

The more practical a conservation tool, the more application it will receive to real problems by natural resource managers and conservation planners. If using the tool is a cumbersome process, it will not be effective regardless of the accuracy of its predictions. Or if the tool has an extremely limited set of conditions under which it can be applied, use will also be restricted. Based on my experience of developing and using the (Dusky Canada Goose) DSV migration model, I assess the practicality of this conservation tool, with respect to applicability and ease of use.

In order to generate meaningful predictions from my current DSV model for other reserve network problems, it is critical to select the focal species carefully. I believe that the model can be applied to other systems for different migratory bird species; however, this needs to be done with care. A thorough understanding of the species' natural history is required, so that assumptions made in the model have an ecological and empirical basis. For example, interpreting how the state variables interact to define the fitness relationship has serious implications for the model's outputs. Also important to consider in the selection of a focal species is if the available empirical data are sufficient to derive parameters.

Another possible application of the DSV model to site-selection problems is to explore its use on various landscape-level scales. Instead of using a scale that spans the Pacific Flyway, it would be interesting to consider smaller scales and focus on local movements of migratory birds. For instance, the DSV model could predict the local movements of a migratory species on its wintering grounds. Subsequently, the model could provide information for the design of a reserve network within the wintering area. I also think the opportunity exists to apply this type of model to non-migratory animals that use multiple habitat patches within their home range. Perhaps, amphibian species like the nationally endangered Oregon Spotted Frog (*Rana pretios*), that live in floodplain wetlands associated with permanent waterbodies (Conservation Data Centre 2006), could be prime candidates.

To assess the overall ease of use of the DSV migration model as a tool, I examine its informational requirements, length of computation, and user-friendliness in

terms of running the model and interpreting results. In general, informational requirements for data inputs are substantial. In addition to species-specific information on the energetics of foraging and travelling needed for estimating parameters, spatial data of the habitats where the animal occurs (and habitat preferences) are also required. Another factor to consider is that computational time increases as the number of state variables increase. Once the parameters and program are available, setting up and running the model is relatively easy. On the other hand, interpreting the large reams of outputs that the model creates can be organizationally difficult. There are three types of output tables; the tables describe a bird's decision with respect to location, fitness payoffs, and energy state for every time step. A feasible option to increase user-friendliness is to set up the program with visual menus for parameter inputs and desired forms of outputs, similar to the concept of the DYNAMIG simulation toolbox (Klaassen and Ens 2001). The construction of this simulation toolbox was developed so that the migration journey of any species with discrete stopover sites can be modelled (Klaassen and Ens 2001).

Recommendations for the Pacific Estuary Conservation Program

It is unrealistic to expect a single site selection method to be able to fulfill a myriad of conservation objectives. Asking a conservation tool to produce a reserve network that indicates a set of sites that maximizes biodiversity, the representation of ecosystems, rare features, and the persistence of all species simultaneously is far-fetched. Focusing on conservation objectives and societal values specific to a region is probably the most realistic and effective way to approach the problem. The regional diversity of ecosystems and associated land-use issues creates the need for conservation solutions that are custom-built.

The DSV migration model demonstrates the successful application of a custom-built conservation tool to solve a regional problem. The DSV migration model works to solve the broader issue of protecting BC estuaries by viewing the problem through a narrow lens that values waterfowl. The model achieves its specific objectives of predicting a chain of estuarine stopovers that grant optimal fitness payoffs to Dusky Canada Geese. The predicted estuaries are implicitly connected within the landscape, because the model incorporates the estuaries' locations and spatial relationships as factors for geese to consider in their optimal decisions. Thus, the model expresses

landscape connectivity from the perspective of a migrating Dusky Canada Goose in its predictions.

I recommend that the Pacific Estuary Conservation Program (PECP) use the predictions of the DSV migration model as one part of the larger picture in order to identify important BC estuaries. The predicted estuaries indicate the sites that are potentially important for the Dusky population and other goose species with similar energetic needs. I recommend the model's results be used in combination with results from other site selection methods that encompass different values, such as shorebird species, rare species, aquatic plant diversity etc. Employing multiple strategies in the overall, decision-making process that guides the allocation of conservation resources will lead to greater balance in the reserve design.

To paint the part of the picture that relates to waterfowl (specifically goose) values, I suggest that the PECP protect, restore, and monitor estuary sites identified by the baseline DSV model, by numerous DSV model versions, and by the density-dependent forward iterations. These BC estuaries are the:

- Black Creek Estuary
- Campbell River (2) Estuary
- Chemainus River/Bonsall Creek Complex Estuary
- Cowichan River Estuary
- Englishman River Estuary
- Fanny Bay/Cowie Creek Estuary
- Fraser River Estuary
- Gorge Waters/Craigflower Creek Estuary
- Hiellien River Estuary
- Keswar Inlet Estuary
- Kingkown Inlet Estuary
- Little Qualicum Estuary
- Nanoose/Bonell Creek Complex Estuary
- Nass/Ksi'Hlginx/Burton/Iknouck/Chambers/Kincolith River Complex Estuary
- Nickomekl/Serpentine River Complex Estuary
- Skeena/Ecstall/McNeil River Complex Estuary
- Sliammon Creek Estuary
- Trent River Estuary

Four sites of these listed estuaries stand out with potentially higher conservation value. The Fraser River and Nickomekl/Serpentine River Complex Estuaries appear to have higher conservation significance because empirical data of Canada Geese validate the predicted site use with greater certainty. Fanny Bay and Little Qualicum Estuaries are repeatedly identified as important; these sites are predicted by numerous model versions that include winds and the simulation that assumes density dependence at estuaries. Additionally, these sites experience increased use by birds of initially low and/or high energy reserves under estuarine habitat loss scenarios.

Implementation of these recommendations will be challenging, because most likely the PECP will not be able to take them at face value. The PECP will need to evaluate the importance of these listed sites according to the program's specific goals, which are broader than protecting estuarine habitat solely for migrating waterfowl. The PECP may want to consider how the above listed sites compare with the results of other site selection methods. Overlap between methods may constitute more justification for conservation. For those listed sites, such as the Fraser River and Englishman River Estuaries that already have PECP status, the program may want to consider acquiring more habitat within these sites or improving habitat conditions through restoration.

I also encourage the Pacific Coast Joint Venture (PCJV) to initiate empirical research on the timing and use of migratory stopovers along the Pacific coast by Dusky Canada Geese. Research in the field would contribute to the data needed for comprehensive validation of this conservation tool. Specifically, field observations of Dusky Canada Geese at BC estuaries could be used to test the predictions of the DSV model. At the outset, the predicted stopover estuaries of the DSV model could be the preliminary focal areas for Dusky survey. Additionally, the PCJV could initiate a study that follows the spring migration routes of Dusky Canada Goose individuals marked with satellite transmitters. The data from this study would also indicate the Dusky's stopover locations, as well their fat reserves at departure, and their subsequent breeding success on the Copper River Delta. These measured parameters then could be compared with the DSV model's predictions of estuary use along the BC coast and fitness consequences for geese of varying body conditions.

Finally, I recommend that the PECP's evaluation process to allocate resources for estuary conservation is flexible. Estuary importance, as described from the perspective of migrating Dusky Canada Geese is likely dynamic and changes with

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: $\text{SIN}((\text{direction of maximum wind speed at station}^\circ + 315^\circ) * 0.01745 * (\text{maximum wind speed at station}))$ 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) recorded during premigration at the Dusky Canada Goose's wintering grounds in the Willamete Valley, Oregon (Bromley and Jarvis 1993). I decided to use energy levels at the premigration stage as an estimate for the energy cap, because during this time the female geese had the highest energy reserves out of all reproductive stages including arrival, prelaying, post-laying, and hatching stages.

Flight range

To determine the flight range parameter or the distance a Dusky Canada Goose could fly given its available energy reserves, I used flight model, Flight 1.16 (Pennycuick 2006). In order to examine the relationship between energy reserves (i.e. fat levels), and achievable flight distances I ran the flight model numerous times, with each run set at an incremental fat level. For a female goose with an empty body mass of 3.56 kg, I commenced the incremental fat level at 1.04 kg and decreased it steadily in 0.8 kg intervals. Each model run predicted a maximum flight distance and a corresponding amount of total energy burned. From this data, I plotted the flight distance versus initial energy reserves.

Model Flight 1.16 called for species-specific parameters. I based the estimate for empty body mass on field data for the mean body mass of Dusky females during the premigration stage on the wintering grounds in the Willamette Valley, Oregon (Bromley and Jarvis 1993). I chose to set the initial empty body mass at 3.56 kg, the heaviest of

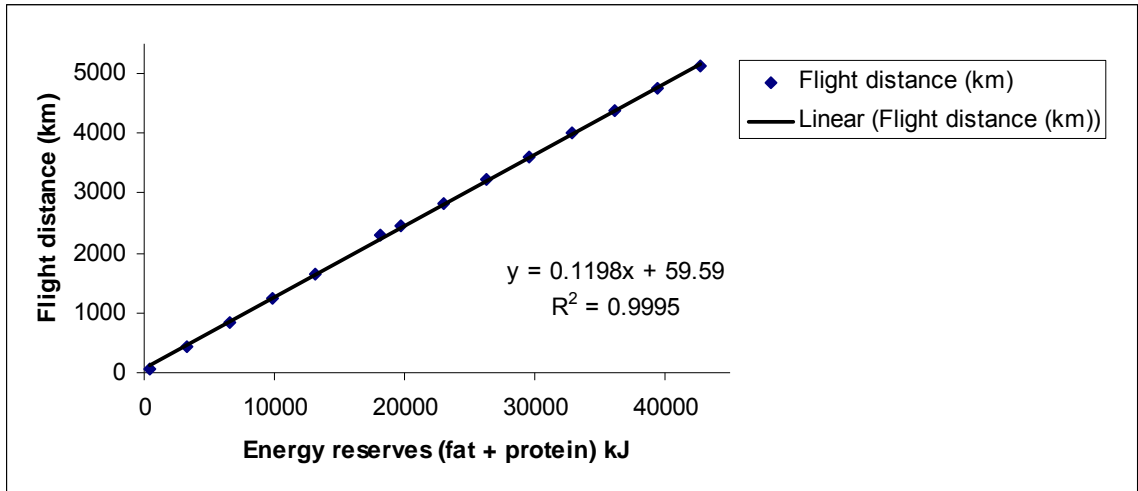
the recorded mean masses ((Bromley and Jarvis 1993): in Appendix 1). I commenced the incremental fat level at 1.04 kg because this value is the highest fat level recorded at premigration (Bromley and Jarvis 1993), and represents the largest amount of fat possible for burning.

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 energy reserves as predicted by Pennycuick's model, Flight 1.16.



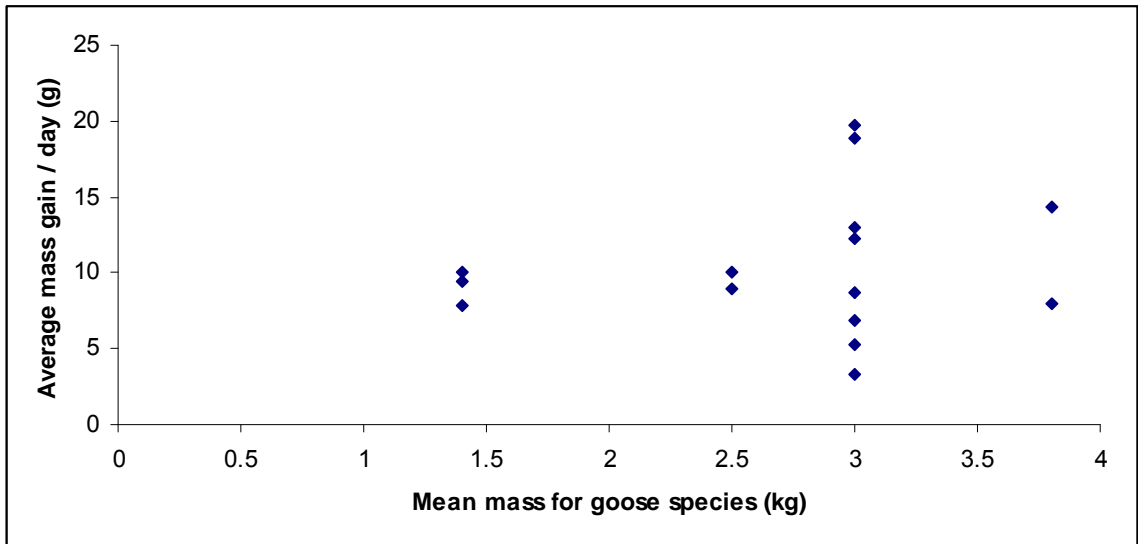
Because this relationship (Figure 5.1) is linear, the flight range (km/kJ) is simply the slope of the relationship. Therefore, the estimate for the flight range parameter is **0.1198 km/kJ** or **32.23 km/energy unit**, where one energy unit equals 269 kJ. The satisfactoriness of this parameter estimate is reinforced by the flight model's predictions of average airspeed, which range from 66.9 to 74.9 km/hour for respective energy reserves of 415 to 42700 kJ. This range includes the average ground speed recorded for Canada geese at 65 ± 4 km/hour (Wege and Raveling 1984).

Energy intake rates at estuary sites

Due to limited information on the energy and nutrient requirements of Dusky, I explored the energetics research on other geese species. To calculate an estimate for energy intake at an estuary site, I first investigated the relationship between goose weight and average net gain in mass per day. I utilized the daily, average, net, mass gain for five different geese species observed in wetland and agricultural areas. The geese species included the 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*) (in corresponding studies: J. Hupp, USGS Alaska Science Center, pers. comm. 2005, Akesson and Raveling 1981, Ebbs and Spaans 1995, Ebbs 1989, Gauthier and Giroux 1992, Prop and Deerenberg 1991). I did not find a statistically

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 Greater Snow Geese to be 6.9 g per day. Because Greater Snow Geese are similar in weight to Dusky Canada Geese, I interpreted 6.9 g to be the minimal (net) mass gain per day for Dusky. Using the energy content of fat (39 kJ/g-fat), I converted this net mass gain of 6.9 g to an energy intake of **269 kJ/day** for

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

Appendix C: Generation of Vulnerable Estuaries Dataset

Vulnerable BC Estuary Sites According to Protection and Threat Status

I acquired data pertaining to the protection and threat status of BC estuaries (Ducks Unlimited Canada 2006) in an excel spreadsheet from Ducks Unlimited Canada. The creation of this excel spreadsheet was based on shapefiles obtained from the Canadian Wildlife Service (CWS) that describe the boundaries of protected and threatened areas within the intertidal zones and backshore marshes of the master estuaries. The term 'protected' refers to provincial and/or federal conservation (including PECP) tenure and the term 'threatened' refers to non-conservation tenure. From the CWS shapefiles, Ducks Unlimited Canada created new shapefiles in a GIS (November 2006), with map projection: NAD 83, Albers Conical Equal Area.

In ArcGIS 9.0 (ESRI 1999) I appended data from the excel spreadsheet that describes the proportion of protected and threatened area within the estuaries, to the spatial locations of the estuaries. I queried the dataset for estuaries with a protection status of 0% and a threat status of 50% or greater in order to generate a set of vulnerable sites. Table 5.2 lists the results of the query, which form the set of estuary sites for elimination in one hypothetical scenario of habitat loss.

Table 5.2 PECP estuary sites that have a protection status of 0% and a threat status of 50% or greater.

PECP estuary number	Estuary name
10	Nanoose/Bonell Creek Complex
23	Sarita River
25	Kitimat River
30	Nahmint River
37	Cous Creek
38	Macktush Creek
40	Unnamed12
41	Coeur d'Alene Creek
42	Snug Basin
48	Stranby River
61	Grant Bay
80	Keogh River
101	China Creek
102	Coleman Creek

PECP estuary number	Estuary name
119	Irony Creek
165	Seal Inlet
175	Security Cove
183	Braverman Creek
186	Flat Creek
187	Tasu Creek
193	Kumdis Creek
220	Billy Creek
222	Hankin Point
232	Foch Lagoon
235	Kiskosh Creek
263	Canooka River
273	Stawamus River
274	Mamquam River
285	Kdelmashan Creek
292	Betteridge Inlet Area
327	Clayton Falls Creek
328	Bella Coola/Necleetsconnay River Complex
333	Dunn Point Area
347	Doc Creek
350	Koeye River
360	Draney Creek
385	Blind Creek
399	Bear River [1]
400	Southgate River
409	Powell River
425	Furry Creek
429	Lime Creek
434	Oona River
437	Gilttoyees River

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