

ABSTRACT

HOSTETLER, JEFFREY ALLAN. A dynamic model of Semipalmated Sandpiper migration: Implications for conservation. (Under the direction of Ken Pollock and Jaime Collazo.)

I developed a stochastic dynamic programming model of adult female Semipalmated Sandpiper (*Calidris pusilla*) spring migration for the purpose of adaptive management of wetlands along their migratory route. Semipalmated Sandpipers are small abundant shorebirds that migrate through Merritt Island National Wildlife Refuge, FL, Yawkey Reserve, SC, Pea Island National Wildlife Refuge, NC, and Delaware Bay on their way from the Caribbean and South America to arctic North American breeding grounds. The first three stopover sites mentioned include managed wetlands. To manage these wetlands for Semipalmated Sandpiper and other migratory shorebirds' fitness by changing water levels to alter food availability, it is important to understand how the birds are using these stopover sites.

A stochastic dynamic programming model is a model of organism behavior which assumes that the organism is attempting to optimize its fitness. In this model, the fitness of the birds depends on surviving migration as well as arriving on the breeding grounds close to an optimal date and with sufficient energy reserves. The birds can decide each day whether to stay at the current stopover site and feed, or to fly to the next site. Model parameters include flight constants, ground speed probabilities, energy gain, and predation rates. The values of several parameters were tuned so that average peaks of migration at the stopover sites and average percent fat of the birds on different days and stopover sites correlated well with data taken from published and unpublished studies. The model outcomes include average fitness, seasonal mortality rate, reproductive output,

average length of stay at each stopover site, and percentage skimming (not staying to feed) at each stopover site.

The peaks of migration matched the targets set. The birds stayed longest at the first and last stopover sites; many birds did not stop to feed at the middle two stopover sites. The average mortality of the spring migration season was 0.099, and the average reproductive output (female offspring that reach adulthood) of birds that reach the breeding grounds was 0.332. The model results were most sensitive to changes in the flight parameters and relative predation rates.

I simulated declines in the prey base at Delaware Bay (horseshoe crab eggs). Small declines had no effect on fitness, but large declines did, as the birds depend on Delaware Bay to fatten up for the long flight to the breeding grounds. If the birds are able to adapt to the change, they compensate by feeding longer at the previous stopover site (Pea Island). Increasing the food availability at the first three stopover sites enhances the birds' ability to compensate for declines at Delaware Bay.

I discuss testable predictions and possible further extensions of the model. Combined with a proposed model of the effects of water level changes on prey abundance and availability in an adaptive management framework, this model should help managers to determine the ideal timing and amount of managed wetlands draining, and direct further research in shorebird ecology and preservation.

**A DYNAMIC MODEL OF SEMIPALMATED SANDPIPER MIGRATION:
IMPLICATIONS FOR CONSERVATION**

by

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DEDICATION

This thesis is dedicated to
my mother, Catherine Hostetler,
my father, David Hostetler,
my sister, Janet Hostetler,
and Adelaide Rhodes
for all their support and encouragement.

BIOGRAPHY

Jeffrey Hostetler was born in Cheverly, Maryland in 1974. He developed a love of nature at an early age, despite being raised in the suburbs. He received a B. A. in Biology from Oberlin College in 1996, and worked at Patuxent Wildlife Research Center for several years as a computer programmer and developed web applications and databases for the Breeding Bird Survey and other monitoring programs. He's done field work in Olympic National Forest, Washington, Tongass National Forest, Alaska, the Dolomite Mountains of Italy, and the outer banks of North Carolina. He entered North Carolina State University in fall 2001 to pursue a master's degree in Zoology studying ecological modeling.

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I would also like to thank Jim Lyons and Conor McGowan for letting me get out to do some field work. Last, but certainly not least, I would like to thank Adelaide Rhodes, David Hostetler, Catherine Hostetler, and others who helped review this thesis.

Table of Contents

	Page
LIST OF TABLES	viii
LIST OF FIGURES	ix
INTRODUCTION	1
Migratory Shorebird Conservation and Management	1
Semipalmated Sandpipers	6
Modeling of Migration	9
Semipalmated Sandpiper Migration Model	14
METHODS	15
Model Overview	15
Deterministic Version	15
Stochastic Version	18
Description of Model Elements	20
Stopover Sites, Wintering Area, and Breeding Area	20
Energy Gain at Stopover Sites	21
Flight Models	27
Wind	30
Predation	31
Parameter Tuning	32
Approach	32
Migration and Fat Targets	33
Other Targets	34
Sensitivity Analysis	36
Scenarios	36
RESULTS	37
Tuning Results	37
Base Model Results	39
Sensitivity Analysis	40
Scenarios	41
Reducing Energy Gain Rates at a Single Stopover Site	41
Increasing Energy at a Single Stopover Site	41
Compensating for Declining Energy Gain Rates at Delaware Bay	42
DISCUSSION	43
Implications of Model as Implemented	43
Factors not Included in Model	46
How This Model Could Be Tested with Field Data	48
How This Model Could Be Used in an Adaptive Management Framework	49

REFERENCES

87

APPENDICES

95

List of Tables

		Page
Table 1	Model variables and parameters	51
Table 2	Prey base at the stopover sites	53
Table 3	Energy gain rates at stopover sites	54
Table 4	Weather stations for wind data at sites	55
Table 5	Targets for migration peaks	56
Table 6	Parameter values	57
Table 7	Sample parameter tuning results	58
Table 8	Lengths of stay and percentage skimmed	60
Table 9	Elasticities	61

List of Figures

	Page
Figure 1	62
Figure 2	63
Figure 3	64
Figure 4	65
Figure 5	66
Figure 6	67
Figure 7	68
Figure 8	69
Figure 9	70
Figure 10	71
Figure 11	73
Figure 12	74
Figure 13	75
Figure 14	76
Figure 15	77
Figure 16	78
Figure 17	79
Figure 18	80
Figure 19	

	lengths of stay	81
Figure 20	Effects of scaling down the hourly energy gain rates at Site 3 (Delaware Bay) and scaling up the hourly energy gain rates at Site 2 (Pea Island) on fitness	82
Figure 21	Effects of scaling down the hourly energy gain rates (k) at Site 3 (Delaware Bay) and scaling up k values at Site 2 (Pea Island) on average lengths of stay at the stopover sites	83
Figure 22	Effects of scaling down the hourly energy gain rates at Site 3 (Delaware Bay) and scaling up the hourly energy gain rates at Site 2 (Pea Island) and x_{gainmin} at Sites 0 and 1 on fitness	84
Figure 23	Effects of scaling down the hourly energy gain rates (k) at Site 3 (Delaware Bay) and scaling up k values at Site 2 (Pea Island) and x_{gainmin} at Sites 0 and 1 on average lengths of stay at the stopover sites	85
Figure 24	How the shorebird migration model will fit into the rest of the adaptive management plan for managed wetlands	86

INTRODUCTION

Migratory Shorebird Conservation and Management

Identifying key migratory and wintering sites, and providing suitable habitat for migratory shorebirds are cornerstones of shorebird conservation strategies (Myers et al. 1987). This conservation challenge has become more urgent in light of continued loss of wetlands and declining population trends of several species (e.g., Red Knot *Calidris canutus*, Least Sandpiper *Calidris minutilla*) (Morrison et al. 1994, Dahl 2000). Scant data on nearly all species, particularly those at risk, only underscore the need to formulate a coordinated conservation initiative to address knowledge gaps with respect to their demography and habitat requirements. Accordingly, the US Fish and Wildlife Service, in coordination with Manomet Observatory for Conservation Sciences, have set out to develop a National Shorebird Conservation Plan, establishing regional population and habitat goals and objectives (Brown et al. 2001).

Although these goals and objectives were formulated using available information, it is acknowledged that many are based on broad, untested assumptions (see Hunter et al. 2000). For example, the habitat requirements for migratory shorebirds in the Southeast US were set with the assumptions that the region is important for spring, not fall migrants, that approximately five million birds use the area during the spring (April-June), that shorebirds make two stops within the Southeast before reaching their breeding grounds, that they stay at each stopover site for approximately 15 days, that prey density at these stopover sites during the spring is the same as that of the Mississippi Alluvial Valley during the fall, and that the “average” shorebird needs to store one gram of fat per day (Loesch et al. 1995, Hunter et al. 2000). Untested assumptions stem from scant data

on several fundamental aspects of the life history of migratory shorebirds. First and foremost is that migration cycles are poorly understood, including population regulatory mechanisms (Newton 2004). This is because field research over larger areas (e.g., the hemisphere) is difficult; shorebirds stay put for a short period of time, and spend a good deal of their time in flight. Although conventional wisdom suggests that winter is when mortality is highest, data on other migratory species (e.g., warblers) suggest that mortality during spring migration might be substantial, even higher than during winter (Sillett and Holmes 2002). We also lack good linkages between demographic processes and endogenous cycles (e.g., fat deposition), or how body condition relates to habitat quality. Our ability to understand those relationships is undermined by the fact that most studies are conducted at local scales and for a very short period of time. Interannual variability (e.g., prey base levels), coupled with non-standardized data collection methods, compounds the quest for establishing relationships.

The evolution of shorebird migration, like that of other migratory species, was likely influenced by ultimate factors such as patterns of food availability, seasons, habitats, barriers, history, genetics, competition, mortality cost, parasites and immunology, energy cost of transport, size of the bird, and navigation techniques (Lack 1954, Alerstam et al. 2003). The proximate causes of spring or fall migration starting are usually changing photoperiod and endogenous rhythms, although weather may often be a factor (Gwinner 1990, Richardson 1990). For birds that require more energy for migration than they can accumulate on the wintering grounds, the route and timing of migration must be such that they can take advantage of food resources along the way. Many shorebirds are long distant migrants with heavy energy demands for migration.

Shorebirds are champion food consumers, with record rates of energy assimilation shown in laboratory conditions (Kvist and Lindström 2003).

Klassen et al. (2001) and Morrison and Hobson (2004) showed that shorebirds are primarily not capital breeders. That is, the energy used to build eggs and young mostly comes from the breeding grounds rather from stores accumulated on the wintering grounds or during migration. However, this does not imply that arriving at the breeding grounds with fat stored is not important to reproductive success. Reproductive success is usually highly dependent on arriving on the breeding grounds at an appropriate date and with sufficient energy, in shorebirds, passerines, and waterfowl. Farmer and Weins (1999) found that mean egg and chick size increased with increased female body fat in Pectoral Sandpipers (*Calidris melanotos*). Prop et al. (2003) found that the probability of reproductive success in Barnacle Geese (*Branta leucopsis*) increased with increased fat at departure from a spring migratory stopover site and peaked for an intermediate date of departure. Smith and Moore (2003) found a positive relationship between fat on arrival on the breeding grounds and reproductive success in American Redstarts (*Sefophaga ruticilla*) in Michigan, especially for females. Anteau (2002) provided evidence that population declines in Lesser Scaup (*Aythya affinis*) are correlated with decline in stored energy at arrival on the breeding grounds. Both arrival date and condition have been correlated with quality of winter habitat by carbon isotope tracking, suggesting that breeding success is affected by events from the previous fall and winter (Marra et al. 1998).

The prevailing shorebird conservation paradigm rests on the assumption that habitat is limiting, and thus, a determinant of population regulation (Myers et al. 1987).

Shorebirds, unlike other species, such as most passerines, concentrate in a few geographical hot spots as they progress through their migratory routes. Demographically, this feature makes them particularly vulnerable to habitat degradation, or loss. This is especially so if shorebirds are not capable, or slow at responding to changes in habitat quality beyond natural annual variation. Clearly, habitat management presents a tangible mechanism to influence shorebird population health. The fundamental drawbacks, as suggested above, are that the presumed benefits of habitat modification/management on shorebird fitness are poorly understood, and responses to such manipulation are not easy to measure, or require long-term, large scale efforts.

Managed wetlands (also known as impoundments or diked wetlands) are artificially created wetlands in which the water level can be adjusted. Managed wetlands are created for various reasons; one of the most common is waterfowl management. The water levels in these impoundments are adjusted for ideal duck forage and habitat in the fall and winter. Managed and artificial wetlands have been demonstrated to be an important habitat for migratory shorebirds (Barbosa 1996, Weber and Haig 1996, Mihuc et al. 1997). It is possible to slowly drain these wetlands in the spring, which can provide foraging habitat for small shorebirds, such as Semipalmated Sandpipers (O'Harra 2001). The ideal timing and nature of this draining has yet to be fully established.

Adaptive management involves using the results of management actions to better understand the system being managed, and is a useful technique for dealing with uncertainty (Walters 1986). Mathematical models are important parts of adaptive management plans. Adaptive management has been used in the management of hunted

migratory waterfowl. Harvest seasons are set partially on the basis of its results (Johnson and Williams 1999).

As part of the U.S. Shorebird Conservation Plan, a regional plan for the southeastern coastal plain of the U.S. was developed to identify priority species, threats to populations and their habitats, gaps in ecological knowledge, and recommendations for addressing regional conservation challenges (Hunter et al. 2000). A major goal of the southeastern regional plan is to promote protection and management of inland habitats necessary to support successful migration through the planning region. Moreover, the National Shorebird Research Program has identified as a high priority the need to better understand the dynamics of migration, including how and why shorebirds move among stopover sites. A key for a successful shorebird conservation in the southeastern U.S. and elsewhere is the availability of conceptual and analytical tools that can help support an adaptive process of planning, implementation, and evaluation. Modeling approaches can breach the gap between the needs outlined above: gaining insights about migratory behavior and implementing management strategies to promote their conservation. A model should model movements of shorebirds through the Southeast as a function of relevant environmental conditions (e.g., wind conditions, site-specific food availability, water depth), assuming that migratory behavior has evolved to maximize some measure of fitness (e.g., lifetime reproductive success, survival). It should also predict the consequences of changing environmental conditions, ultimately, in terms relevant to the stated objectives of management.

The Southeast provides unique resources and circumstances for the development of such a model and a comprehensive adaptive-management framework for shorebird

conservation. First, shorebirds depend on the region heavily during spring; hence, use of the area matches annual water drawdown cycles and facilitates implementation of management strategies (Hunter et al. 2000). Second, small calidrids (e.g., Semipalmated Sandpipers) dominate species composition in inland/managed wetlands. Finally, ongoing work to assess shorebird responses to management in the northeast (U.S. Fish and Wildlife Service Region 5) provides a natural “bridge” to extend lessons and strategies generated by modeling efforts to the entire Atlantic Flyway (Brown et al. 2001).

Semipalmated Sandpipers

I use Semipalmated Sandpipers (*Calidris pusilla*) as a suitable biological model. Semipalmated Sandpipers have experienced significant declines in the last few decades (Morrison et al. 1994, Hitchcock and Gratto-Trevor 1997), and are of conservation concern. They share migratory habitats and foods with several other species of shorebirds (e.g. Dunlin *Calidris alpina* and Semipalmated Plover *Charadrius semiplamatus*). Therefore, models of their behavior and requirements can possibly be applied to other species. Moreover, data on essential modeling parameters have been collected along a latitudinal gradient from wintering sites (Caribbean) to migratory stopover sites (FL, SC, NC, NJ) (e.g. Tripp and Collazo 1997, Lyons and Haig 1995b, O’Harra 2001, Clark et al. 1993). The species has been researched extensively in the Northeast as well, providing an additional database and insights into their migratory ecology year round (e.g. Dunn et al. 1988). Available estimates and information for the southeastern region include site-specific population numbers, migration chronology, turnover rates, prey base dynamics, determinants of habitat quality, body condition, and fat deposition rates. Local annual survival rates and probability of returning to a specific

site as a function of body condition are available for the Caribbean (Rice et al. unpub.). These data have been collected throughout a network of refuges (state and federal) and private lands across the southeast willing to implement adaptive management strategies.

Semipalmated Sandpipers have been loosely divided up into western, central, and eastern populations, based on their breeding locations (Harrington and Morrison 1979, Haig et al. 1997). The eastern population is defined as those that breed from the western edge of Southampton Island, Nunavut Territory, Canada and eastward (Harrington and Morrison 1979). The Semipalmated Sandpiper winters in northern South America and the Caribbean (Gratto-Trevor 1992). It is uncertain if they segregate by breeding population during the winter season. The eastern population migrates north in the spring through the Atlantic coast of the United States, turning cross country in the northeastern U.S. into southeastern Canada (Harrington and Morrison 1979). In the fall, they migrate east to stage at the Bay of Fundy, in Nova Scotia, Canada, where they feed primarily on the amphipod *Corophium volutator* (Hicklin and Smith 1984). They then migrate south over the Atlantic ocean to the Caribbean and South America (Harrington and Morrison 1979).

Semipalmated Sandpipers breed in the low arctic and subarctic tundra in North America. Most birds do not breed until age two or three, but at the southern site La Pérouse Bay in northern Manitoba, some breed at age one (Gratto et al. 1983, Gratto 1988). The reproductive success of yearlings was lower in some years (Gratto et al. 1983). Although Semipalmated Sandpipers are supposed to have an invariant clutch size of four eggs (Gratto-Trevor 1992), Sandercock et al. (1999) found that birds breeding near Nome, Alaska often laid two or three eggs, especially if breeding late in the season.

Late clutches were also less likely to be successful (Sandercock 1998). Both parents incubate the eggs. The young are precocial and feed themselves, sometimes hours after hatching (Gratto-Trevor 1992). The parents brood the offspring (Gratto-Trevor 1992). Females desert the brood an average of 6 days after hatch (Gratto-Trevor 1991). Males desert around the time of chick fledging, on average 14 days after hatch (Gratto-Trevor 1991).

Lank et al. (2003) suggest that the early departure of the parents in Semipalmated Sandpipers and Western Sandpipers is in part a strategy to be on fall migratory stopover sites and have time to fledge on the wintering grounds before migratory hawks come through. Even so, raptors are the primary predator of Semipalmated Sandpipers during migration (Lank et al. 2003). Semipalmated Sandpipers generally migrate nocturnally, but also diurnally during long, non-stop migrations (Gratto-Trevor 1992). During migration, Semipalmated Sandpipers use saltwater and freshwater wetlands, beaches and intertidal zones, and the edges of lakes as migratory stopover and staging areas (Gratto-Trevor 1992). Potential threats to Semipalmated Sandpipers include degradation of quality of their migratory stopover sites (Shepherd and Boates 1999). Migratory Semipalmated Sandpipers feed primarily on fresh or salt water benthic invertebrates (Gratto-Trevor 1992). This prey includes small crustaceans, adult and larval insects, annelids, and horseshoe crab (*Limulus polyphemus*) eggs (Gratto-Trevor 1992, Tsipoura and Burger 1999). Semipalmated Sandpipers undergo physiological changes during or in preparation for migration, including increased lipid storage, an increase in the size of the pectoral muscle, an increase in the size of the heart (Driedzic et al. 1993), and changes in hormone levels regulating rate of feeding (Tsipoura et al. 1999, Mizrahi et al. 2001).

Pfister et al. (1998) found a relationship between estimated fat levels at departure of Semipalmated Sandpipers at a fall stopover site before a transoceanic flight and return rate, which may indicate a relationship between fat stores and survival on long migratory flights.

Modeling of Migration

A good deal of progress has been made in recent years studying the theory of bird migration (Alerstam and Hendersstrom 1998). One of the most influential models of bird migration is that of Alerstam and Lindström (1990). They identify three main strategies for migration that the birds could be using (time minimization, energy maximization, and safety maximization). They identify predictions of different optimal departure fat loads, stopover decisions, flight speeds, and flight behavior for birds following primarily a time minimization or an energy maximization strategy. It's likely that timing, energy use, and safety are all important to the birds and they must trade off between these strategies.

Several other models of bird migration have been developed. Weber et al. (1994) extended the model of Alerstam and Lindström to show under what circumstances fat overloads are expected and what controls the amount of overload. Weber et al. (1998a) and Weber and Hedenström (2000) further extended the model to include the effect of winds. Kokko (1999) developed a game-theoretic model of how competition for breeding sites affects timing of arrival on the breeding grounds, Simons et al. (2000) used a window analysis and individual based model to explore how birds use habitat within a migratory stopover, and Erni et al. (2003) developed an individual based model of the evolution of migratory navigation.

Several other studies have calculated the energy budget of migrating birds (e.g. Gudmundsson et al. 1991, Skagen and Knopf 1994, Loesch et al. 1995, Pfister et al. 1998, Clausen et al. 2003). This can prove difficult because of the uncertainties in the values given for cost of feeding, the energy gain rates of the birds, the cost of flight, length of stay at the stopover sites, flight path or destination, and other parameters that go into the calculations.

Stochastic dynamic programming models (Houston and McNamara 1999, Clark and Mangel 2000) are used to determine the optimal strategy for an organism in a stochastic environment, often trying to achieve more than one goal simultaneously. On each discrete time step, the model organism makes a decision based on one or more state variables relating to the organism's condition or environment, which vary over time based on circumstance and the organism's past decisions. Once the optimal strategy (also known as a decision matrix) is developed, test organisms can be run through the model with different environmental and starting conditions to see the results. The multiple goals of an organism are integrated into a single variable, usually lifetime reproductive fitness (R_0 , number of surviving female offspring a newborn female produces over her lifespan). Dynamic programming models have proved a useful tool for exploring the migration of shorebirds (Clark and Butler 1999, Weber et al. 1998b, 1999, Farmer and Wiens 1998, 1999).

Clark and Butler (1999) modeled the spring migration of Western Sandpipers (*Calidris mauri*) from northwestern Mexico along the west coast of North America to their breeding grounds in western Alaska. They do not specify a wintering site, but instead start the birds at a southern migratory stopover site. The model runs from March

31 through May 31 and the time step is one day. The state variables are stopover site location (0 through 4), stored energy (0-600 kJ), and wind (favorable or unfavorable, with different favorable speeds). The decision set for each day consists of: stay at the current site, go to next site, or return to wintering ground. Energy gain is assumed to be constant at all stopover sites, except the last two, which are unavailable until the 20th day. There is a breeding window, with optimal breeding occurring for those birds that arrive on the first day of it. There is a constant predation risk at each site.

Clark and Butler (1999) developed optimal strategy matrices which generated predictions that compared well with observed peaks of migration. They also determined that the inability to detect wind is maladaptive to birds. Different predation risks at the different stopover sites were important in making the migration peaks line up with the data. They looked at the effects on individual bird fitness of decline in food availability at individual stopover sites and all stopover sites, with and without adaptive response.

Farmer and Wiens (1998) developed a model of Pectoral Sandpiper (*Calidris melanotos*) spring migration through the middle of North America. The time step was one day, and the model runs from April 1 through June 30. The state variables are location in degrees latitude (29 degrees N through 70 degrees N), and stored energy (0-1383 kJ). The birds can decide to stay at the current stopover site or fly to any site with greater or equal latitude that they can reach in 24 hours. The daily energy budget of the birds depends on the temperature, which depends on latitude and date. Prey consumption rate was constant at each stopover site, except when temperature is less than or equal to 0 C, then it was half the normal rate. They used Castro and Myer's (1988) flight model to model the energetic cost of flight. Birds can miss (fail to find) targeted sites, in which

case they fly to the next one. Reproductive success can depend on time or energy of arrival on breeding ground. They did not include predation in their model. They tested for plateaus of optimality, which are different strategies with equal fitness. They tested effects of different feeding rates and distance between sites, and did sensitivity analysis on almost all parameters. They showed that declining food resources can lead to a switch from a hop (making small hops between several stopover sites) to a jump (jumping between a few widely separated stopover sites) strategy. A decrease in food availability or number of stopover sites can lead to decrease in the size of the optimality plateau and force a particular strategy.

Farmer and Weins (1999) compared the predictions of this model for energy at arrival selected, date of arrival selected, and unselected birds against data collected at three stopover and one breeding site to determine what strategies the birds are using. The data collected included estimated body fat, length of stay (using radio transmitters), invertebrate prey counts, length of migration window (95% of birds), and measures of fitness on the breeding grounds. They were able to show that male birds were time minimizers, whereas female birds follow a more complex strategy that involves balancing time minimization and energy maximization. Data collected on the breeding grounds suggested the reason for this: female arriving with more energy had larger eggs, which other studies have shown leads to high chick survival. However, arriving early is still the female birds' top priority. The males may be primarily time minimizers in order to capture the best breeding territories.

Weber et al. (1998b) developed a somewhat more theoretical model for migrating shorebirds. The fitness equations penalties were different than those used by Clark and Butler (1999). Weber et al. (1998b) used 5 different predation models:

- 1) None – The only source of mortality is starvation.
- 2) Simple – Each stopover site has a constant predation rate per day. Each bird at a site is equally likely to be eaten.
- 3) Mass dependent predation – Heavier birds are more likely to be predated, as they can not escape predators as quickly.
- 4) Effort dependent predation – Foraging birds are less likely to notice predators, so predation rate depends on percentage of day spent foraging.
- 5) Mass and effort dependent predation – Both the weight of the bird and the time spent foraging affect predation rate, and act multiplicatively, since one affects likelihood of noticing predators, and the other the ability to escape them.

Their flight model was based on Pennycuik (1975). Foraging success, as well as predation, depends on effort, and can be stochastic. The birds can decide to forage or depart. If foraging, they decide intensity of foraging (0-1). If departing, they decide whether to skip stopover sites. The winds are stochastic, and the birds can not determine what they are from the ground. The parameter values were set for the knot (*Calidris canutus*), migrating through a theoretical landscape of a wintering site, two stopover sites, and a breeding site.

Weber et al. (1998b) found that stochasticity in fuel gain rates can affect choice of stopover sites and amount of fuel load with which the birds leave sites. It also allowed for death by starvation, which was a minor source of mortality compared to predation.

They tested their model under a wide variety of conditions, and found how different conditions and selective factors can lead to different migration strategies in waders.

Weber et al. (1999) extended their model to look at the effects of habitat loss at the wintering site and the stopover sites on the birds' behavior and fitness. They modeled habitat loss as a reduction in energy gain rate. They looked at the case of birds acting optimally for the new conditions and the case of birds following the (now suboptimal) strategy for the old conditions. The effects were most severe at the wintering site (which the birds could not skip) in the optimal strategy case. The effects also depended on whether the birds were previously feeding at the maximum intensity and whether the optimal arrival date on the breeding grounds was intermediate or at the beginning of the migration season.

Semipalmated Sandpiper Migration Model

I develop a model of shorebird migration based on the models of Clark and Butler (1999), Weber et al. (1998b, 1999), and Farmer and Wiens (1998, 1999). The model was developed for Semipalmated Sandpiper migrating through eastern North America in the spring and has several novel features. I developed parameter values for the model from a variety of published and unpublished data sources. I attempted to accurately model differences in prey abundances between stopover sites and across time. I developed a new flight model based on the wind tunnel experiments of Kvist et al. (2001).

I looked at whether this model is appropriate for modeling Semipalmated Sandpiper spring migration by testing the results of the model against available field data, for the variables peaks of migration, average percent body fat, and average reproductive output. I examined how the birds are using different stopover sites in the model, and

compared average lengths of stay and percentage of birds staying to feed at each site. I looked at how sensitive the model outputs are to changes in various parameters. Finally, I tested scenarios of declines and increases in food availability at various sites.

METHODS

Model Overview

Here I model the spring migration of Semipalmated Sandpipers up the east coast of North America. It is a stochastic dynamic programming model which keeps track of the energy levels of the birds as they move through the sites. The model is state based. It consists of two parts: the optimization part and the simulation part (Figure 1). The optimization part is where the “birds” decide what they’re going to do in any particular circumstance, and I now describe this in detail. These circumstances are what we call the state. In my model this consists of the date (t), the stopover or breeding site the bird currently occupies (s), and the energy level of the bird (x , in kilojoules (kJ)). First I describe the simpler deterministic version and then move on to a stochastic version.

Deterministic version

The fitness and decision matrices are generated by a process of reverse iteration (Figure 1). I start it at the last time step (t_{\max}), when the birds’ lifetime reproductive fitness (F) is equal to their total expected number of female offspring that survive to adulthood in all future years if they’re not at the breeding site, and the expected number of female offspring that survive to adulthood for this year plus all future years if they are at the breeding site (Equations 1a and 1b). I used lifetime reproductive fitness as the variable the birds are trying to maximize because it allowed me to integrate several goals

of the birds (arrive to breeding grounds on time, arrive with sufficient energy, and survive). The fitness of birds at earlier time steps (Equation 1c) is explained later in the text.

$$F(x, s, t) = \begin{cases} \phi(x, t) + S_{roy} R_0 & \text{if } s = s_{\max} & (1a) \\ S_{roy} R_0 & \text{otherwise if } t = t_{\max} & (1b) \\ \max(V_{stay}(x, s, t), V_{go}(x, s, t)) & \text{otherwise} & (1c) \end{cases}$$

where $\phi(x, t)$ is the expected number of female offspring that reach adulthood for a bird arriving on the breeding grounds with x energy on day t ,

S_{roy} is the probability of survival to the next spring,

R_0 is the lifetime reproductive fitness of a bird at the beginning of the next year's spring migration,

s_{\max} is the breeding site,

t_{\max} is the last possible day of the spring migration (90=June 30),

V_{stay} is the fitness of a bird that decides to stay at the current stopover site for at least one more day,

and V_{go} is the fitness of a bird that decides to fly to the next stopover site.

The current year reproductive output (number of female offspring fledged) of a female bird is a multiplicative function of both date and stored energy at arrival on the breeding grounds, which modify the maximum reproductive rate (r_{\max}) (Equation 2).

$$\phi(x, t) = r_{\max} \phi_e(x) \phi_t(t) \quad (2)$$

where ϕ_e is the reproductive factor from arrival energy (0-1), and

ϕ_t is the reproductive factor from arrival date (0-1).

If the bird arrives on the optimal date (t_{opt}) with at least a threshold level of energy (x_t) stored then the reproductive output is r_{\max} . Otherwise it is the product of r_{\max} and the

$$V_{stay}(x, s, t) = F(x + x_{gain}(x, s, t), s, t + 1) \quad (5)$$

where x_{gain} is the amount of energy a bird can store feeding for a day at site s on date t (potentially limited by current energy stored x).

If a bird decides to fly to the next stopover or breeding site it will lose an amount of energy dependent on how much energy it has stored up, and the distance to the next site. The number of days a flight will take is also dependent on the distance to the next site. The fitness of that decision, therefore, is equal to the fitness at x minus the energetic cost of flight, $s + 1$ (the next site), and $t + t_c$ plus the time cost of flight (Equation 6).

$$V_{go}(x, s, t) = F(x - x_c(x, D(s)), s + 1, t + t_c(D(s))) \quad (6)$$

where x_c is the energetic cost of flying distance D for a bird with x stored energy,

$D(s)$ is the distance from site s to site $s+1$,

and t_c is the number of days (integer) it takes to fly distance D .

Stochastic version

For stochastic versions of the model the birds have probabilities of different states in the next time step (Figure 3). The fitness of a decision is the sum of the probabilities of the different states times the fitness of those states. Sometimes one of the possible outcomes of a decision is death. The fitness of that, of course, is 0.

With starvation and winds incorporated, the fitness levels look like this:

$$F(x, s, t, v_g) = \begin{cases} 0 & \text{if } x \leq 0 & (7a) \\ V_{stay}(x, s, t) & \text{if } v_g \leq v_a & (7b) \\ \max(V_{stay}(x, s, t), V_{go}(x, s, t)) & \text{otherwise} & (7c) \end{cases}$$

where v_g is the ground speed (speed of the bird with wind incorporated), and

v_{air} is the air speed (speed of the bird without wind incorporated).

If x reaches 0 or less, the bird starves (Equation 7a). Practically speaking, this only occurs on arrival at the first stopover site and for long flights where the winds are not predictable the whole way (see below).

Wind is actually a fourth state variable here, although the birds only know whether it is favorable (ground speed is greater than air speed) or not. When the wind is not favorable, the birds automatically choose to stay and wait for a better wind (7b).

Equation 7 can be rephrased to not consider wind explicitly as a state variable:

$$F(x, s, t) = \begin{cases} 0 & \text{if } x \leq 0 & (8a) \\ V_{stay}(x, s, t) & \text{if } V_{stay} \geq V_{go} & (8b) \\ P(v_g \leq v_a)V_{stay}(x, s, t) + P(v_g > v_a)V_{go}(x, s, t) & \text{otherwise} & (8c) \end{cases}$$

where P is the probability of getting a particular ground speed or set of ground speeds at a site. Considering wind also changes the equation for V_{go} :

$$V_{go}(x, s, t) = \sum_i^{G-B} P(v_g(i), s) F(x - x_c(x, D(s), v_g(i)), s+1, t + t_c(D(s), v_g(i))) \quad (9)$$

where G is the number of possible ground speeds, and B is the number of unfavorable ground speeds. Since the actual ground speed is unknown, the sum the probabilities of getting each of the possible favorable ground speeds times the fitness outcome of that ground speed is calculated.

When predation is included, Equation 5 changes to:

$$V_{stay}(x, s, t) = (1 - p_s) F(x + x_{gain}(x, s, t), s, t + 1) \quad (10)$$

where p_s is the daily predation rate at site s .

Equation 9 only applies for the early stopover site flights, whereas, for the flight to the breeding grounds:

$$V_{go}(x, s_{\max} - 1, t) = \sum_i^{G-B} \sum_j^G P(v_g(i), s_{\max} - 1) P(v_g(j), s_{\max}) F(x - x_h - x_c(x_h, \frac{D(s)}{2}), v_g(j), s_{\max}, t + t_c(\frac{D(s)}{2}, v_g(i)) + t_c(\frac{D(s)}{2}, v_g(j))) \quad (11)$$

$$x_h = x_c(x, \frac{D(s)}{2}, v_g(i)) \quad (12)$$

where x_h is the energetic cost of the first half of the flight. Because the flight from the last stopover site to the breeding grounds is so far, I divide it in half, with two different ground speeds chosen. The birds can only determine if the wind for the first half of the flight is favorable (Equation 10). If the birds get an unfavorable wind in the second half, they must continue their flight, and can be blown off course or arrive at the breeding grounds with no energy (in either case they die). The ground speeds associated with the breeding grounds are the speeds coming into the breeding grounds, rather than leaving it.

The second step is the actual simulation of migration. I started out the birds at the first stopover site at a range of energy levels and dates of arrival. The birds then move through their migration based on the choices in the decision matrix.

The program that runs the model outputs: the decision and fitness matrices, the individual histories of the birds, how many birds were at each site each day, the average length of stay at each site, the number of birds that do not stay to feed for each site, the average fitness of the birds, the mortality rate, and the average reproductive output.

Description of Model Elements

Stopover Sites, Wintering Area, and Breeding Area

I chose Merritt Island National Wildlife Refuge, FL, Yawkey Wildlife Center, SC, Pea Island National Wildlife Refuge, NC, and Delaware Bay as my four stopover sites. These were chosen because there is some data for parameterizing and testing the model from them, and they are representative sites heavily used by Semipalmated

Sandpipers. The first three stopover sites are of interest to managers because they contain managed wetlands where water levels can be managed to provide optimal food levels during shorebird migration. Delaware Bay is believed to be a particularly important staging area for many shorebirds, whose occupancy there coincides with massive horseshoe crab spawning and egg production (Clark et al. 1993, Botton et al. 1994).

I did not choose a wintering area, as I am not sure where the birds migrating through this area are leaving from. Wintering Semipalmated Sandpipers do not always stay in the same place all winter (Rodrigues 2000, Rice et al. unpublished). We also don't know if wintering birds segregate by breeding/migrating population or other methods. Instead, I start them out at the first stopover site with a range of arrival dates and energies.

For the breeding site, I chose La Pérouse Bay in northern Manitoba, on the coast of Hudson Bay. It is well studied (e. g. Gratto et al. 1983, Gratto et al. 1985, Gratto and Cooke 1987, Gratto 1988, Gratto-Trevor 1991) and is toward the eastern part of the Semipalmated Sandpiper's breeding range, so it is a breeding site the birds migrating through the east coast of North America would often be using.

Energy Gain at Stopover Sites

The energy stored for the day is the energy stored per hour of foraging times the number of hours spent foraging minus the energy spent during the day (Equation 13). Shorebirds expend $2.5 * \text{BMR}$ (basal metabolic rate) in a day of foraging (Kersten and Piersma 1987), which comes to 73.8 kJ/day for Semipalmated Sandpipers (Castro and Myers 1993).

$$x_{gain}(x, s, t) = \min(\max(h * k(s, t) - 2.5BMR, x_{gain\ min}), x_{\max} - x, x_{gain\ max}) \quad (13)$$

where x_{gain} is the energy stored in a day of feeding,

x_{\max} is the maximum amount of stored energy a bird can carry,

$x_{gain\ max}$ is the maximum amount of energy a bird can store in a day,

$x_{gain\ min}$ is the minimum amount of energy a bird will store in a day (even with low food resources),

h is the number of hours the bird forages per day,

k is the energy gain rate per hour,

and BMR is the basal metabolic rate.

To determine how much energy a bird gains per day of feeding, we need to determine how many hours a day it feeds. However, we don't know how many hours a day Semipalmated Sandpipers feed during migration. Observations (Collazo, pers. comm.) suggest about four hours a day, although Curlew Sandpipers (*Calidris ferruginea*) spent between 8.75 and 9.5 hours foraging between dusk and dawn each day in the months leading up to migration in a wintering area (Langebaan Lagoon, South Africa) (Puttick 1979). Also, in the Prairie Pothole Region of northwestern North Dakota, Semipalmated Sandpipers spent most of the day feeding (between 60 and 80%) during both spring and fall migration (De Leon and Smith 1999). Behavior did not differ between diurnal time periods. I made number of hours foraging a day a tuned parameter (see testing section later in methods).

Several factors in the model can interfere with the birds foraging the set number of hours each day (Equation 12). The birds have a maximum amount of energy they can store (1150 kJ), based on the fattest birds found at Delaware Bay (Lyons, unpublished

data). If they reach that maximum while foraging, they will stop. Afterwards, they will only need to forage one hour a day to maintain that weight. The birds also have a maximum they can store per day (100 kJ/day), based on a study of migrating Semipalmated Sandpipers during a period when strong winds prevented emigration or immigration (Lank 1983), as well as the highest weight gain seen in a recaptured individual in another study (Alexander and Gratto-Trevor 1997). If the birds do not gain a minimum threshold value of energy (x_{gainmin}) in the hours allotted, I assume they continue feeding until they reach that threshold.

By multiplying the number of prey consumed per hour, the average weight of the prey, and the average energetic value per gram, I calculated the kJ consumed per hour of foraging (Equation 14). By multiplying this by the assimilation and storage efficiencies, I calculated the kJ stored per hour of foraging (Equation 14). The functional response and the prey density determine the number of prey the birds consume per hour (see below). The average wet weight of a horseshoe crab egg is 0.003722 g, and the average energetic value is 10.25 kJ/g wet weight (Castro et al. 1989). At the other sites, average prey biomass was recorded along with prey number, so I could calculate average prey size by dividing (Table 2). I used an average energetic value of their prey of 16.748 kJ/g dry weight, based on averages across representative taxa (Cummins 1967).

The average assimilation rate for shorebirds is 0.73, which is what I used for the first three stopovers sites (Kersten and Piersma 1987). Castro et al. (1989) found a surprising low assimilation rate for Sanderlings feeding on horseshoe crab eggs (0.386). In this study, however, the eggs were washed, depriving the birds of the sand that can help break down the egg membranes, and large numbers of the eggs passed through the

digestive tracts of the birds unbroken. If unbroken eggs are discarded from the analysis, a much more reasonable assimilation efficiency of 0.69 is arrived at, and that's what I used for Delaware Bay. The fat storage efficiency was 0.88 (Kersten and Piersma 1987).

$$k = 3600Cgn * \alpha * \zeta \quad (14)$$

where k=energy stored (kJ/hour),

C=prey consumption rate (items/second),

g=average mass of prey item (g/item),

n=energetic value of prey (kJ/g) (g and n should both either be in terms of wet weight or dry weight),

α =assimilation efficiency,

and ζ =fat storage efficiency.

The standard assumed relationship between food density and rate of food consumption is the Hollings Type II function response (Holling 1959), in which the consumption rate increases with density, but less so at higher densities:

$$C = \frac{ad}{1 + adH} \quad (15)$$

where C is the feeding rate (prey items/s),

a is the area search rate (m^2s^{-1}),

H is the handling time per prey item (s),

and d is the prey density (prey items m^{-2}).

In the absence of obviously contradictory data, a type II functional response is a reasonable assumption to make. Shorebirds have been shown to feed with a type II functional response (Myers et al. 1980, Piersma et al. 1995, Norris and Johnson 1998, Gill et al. 2001), although some shorebirds studies show interference effects that require a

more complex model (Yates et al. 2000, Skalski and Gilliam 2001). To determine the exact shape of a type II functional response, a and H need to be estimated.

Stillman et al. (2003) tested shorebird feeding rates on a trays filled with a mixture of sand and horseshoe crab eggs set up on beaches at Delaware Bay. They found that the feeding rates closely fit a type II functional response (for Semipalmated Sandpipers, $a=0.00069 \text{ m}^2\text{s}^{-1}$ and $H=0.45 \text{ s}$, $p<0.05$). The limitations of this study are that the results may not apply to sandpipers foraging in different habitats on live prey, and that only the functional response over a small area and time period were measured. They only measured the time the birds were actively foraging on a small area. The per second feeding rate may have little to do with the feeding rate over an hour, which includes flying and walking between foraging sites. To accommodate this, I considered the hours the birds are foraging (h) to be the hours they are intensively foraging, which may be considerably less than the total hours they spend foraging.

Most of the Semipalmated Sandpipers' prey at stopover sites other than Delaware Bay are soft bodied invertebrates, which probably have a similar handling time with horseshoe crab eggs (Mozley, pers. comm.). The area search rate is probably different, due to different substrates, detectability of prey, movement of prey, and prey clustering. Since we don't know how it is different, I used the same area search rate for all stopover sites.

Semipalmated Sandpipers have been known to eat amphipods, tanaisids, oligochaetes, nereid and nonnereid polychaetes, chironomid larvae, coleopteran larvae, hydrophilid larvae, corixids, and cyprinodont larval fish (Gratto-Trevor 1992, O'Harra 2001). I looked at the densities and biomass of prey found in these taxa at the stopover

sites (Table 1). Although Semipalmated Sandpipers have also been known to eat gastropods and mollusks, I excluded those species since they do not appear to be a dominant prey item when softer prey is abundant (Gratto-Trevor 1992). The dominant prey at Delaware Bay is horseshoe crab eggs (Tsipoura and Burger 1999); I assumed it was the only prey for simplicity. Any foraging that takes place before horseshoe crab eggs are abundant should be adequately covered by the minimum energy gain rate.

The Merritt Island data is from samples done by G. Herring (unpublished data). The data set consists of biomass and density of various taxa sampled from January to March, 2001 and 2002. I do not have any data on the prey base at Merritt Island for April through June (the period my model covers) so I averaged the March data and used it for the whole period. This may be an underestimate of the biomass or density of prey in the later months.

The Yawkey data comes from Weber and Haig (1997) and Weber (1994). They did samples of prey biomass and density and exclosure studies, which showed that shorebird predation was responsible for an approximately 50% decline in both biomass and density. I was able to use this data to get an approximation of the density of biomass of different prey types at the refuge over time.

The Yawkey data is interesting because the prey density values are quite high and prey biomass is relatively low. This makes it difficult for the birds in the model to forage successfully there. Since the birds forage using a Holling Type II response, in which the foraging rate increases to an asymptote with increasing levels of prey, there is a limit to how many prey items they can collect. If each prey item is very small, they can't gain much energy. It is not known whether this difference reflects an actual difference in

average prey size between Yawkey and the other stopover sites or a difference in sampling methodology.

The Pea Island data comes from O’Harra (2001), which included weekly surveys of six plots on two impoundments done for 12 weeks from late March to early June in 1998 and 1999. The surveys included both sediment and water column sampling. I averaged all the values for each week and used those values for the weeks falling in my model run. I took the last value and extended it to cover the rest of June.

For Delaware Bay I had several sources of information on horseshoe crab egg density, which was highly variable from beach to beach and year to year. These include Smith et al. (2002, see also Pooler et al. 2003), who collected samples from 16 beaches in May and June of 1999, Botton et al. (1994), who collected samples from 7 beaches in May and June of 1990 and 1991, Weber (2001, 2003), who collected samples from 6 beaches in April, May, June, and July of 2001 and 2002. I only used samples that were limited to 5 cm depth, and then took 2/5 of those densities, since Semipalmated Sandpipers’ bills are only 2 cm long. At other stopover sites the prey is living and congregated at the top layer of sediment; at Delaware Bay it should be mixed fairly evenly through the substrate. To get my average densities, I used the Weber 2002 data, which had the broadest time range, and scaled the averages on each date to the ratio of the average on May 25 in that study and the average on May 25 in all studies with good samples on that date (the ratio was 6.512).

Flight Models

As a starting point, I looked at the flight model from Clark and Butler (1999), which is based on Pennycuick’s theoretical aerodynamics model (1975).

$$P(m_b) \propto m_b^{1.5} (W) \quad (16)$$

$$J(x) = a(1 + bx)^{1.5} \left(\frac{kJ}{km} \right) \quad (17)$$

$$Y(x) = \frac{2}{ab} \left(1 - \frac{1}{\sqrt{1 + bx}} \right) (km) \quad (18)$$

$$x_e = \frac{2}{b} \left[\frac{1 + bx_b}{(abD_{air}\sqrt{1 + bx_b} + 2)^2} \right] (kJ) \quad (19)$$

where P is energy consumption per unit time,

a and b are species specific constants,

m_b is the total mass of the bird,

J is the energy consumption per unit distance,

x is the energy reserves of the bird (in kJ),

Y is the maximum flight range of the bird,

x_b is the energy reserves of a bird before a flight,

x_e is the energy reserves of a bird after a flight,

and D_{air} is the distance flown (relative to the wind).

This model assumes that efficiency of converting power input to output is constant. Power consumption per unit time scales with weight taken to power 1.5. This is a commonly used flight model, used in both the Clark and Butler (1999) and Weber et al. (1998b) migration models.

There is new data that suggests the Pennycuik model may not be the best way to model the energetic cost of flight. Kvist et al. (2001) did wind tunnel experiments with Red Knots (*Calidris canutus*) making long flights in a wind tunnel using doubly labeled water to measure total metabolic power input with different starting fuel loads. This was the first study that directly measured power input of individual birds flying under

different fuel loads. They showed that for Red Knots, although power input scales with weight, it does it to the exponent 0.35 rather than 1.5, as power output should. This implies that flight muscle efficiency increases at higher fuel loads. They conjectured that this may be due to measured increases in flight muscle size and represents a tradeoff with increased maneuverability at lower fuel loads. I developed a model of the energetic cost of flight based on Kvist et al.'s findings.

$$P(m_b) = um_b^{0.35} \quad (W) \quad (20)$$

$$J(x) = \frac{3.6u}{v_g} \left(m_l + \frac{x}{f}\right)^{0.35} \left(\frac{kJ}{km}\right) \quad (21)$$

$$Y(x) = \frac{v_g f}{2.34u} \left[\left(m_l + \frac{x}{f}\right)^{0.65} - m_l^{0.65} \right] \quad (km) \quad (22)$$

$$x_e = f \left\{ \left[\left(m_l + \frac{x_b}{f}\right)^{0.65} - \frac{2.34uD_{air}}{v_g f} \right]^{1/0.65} - m_l \right\} \quad (kJ) \quad (23)$$

where u is a species specific constant,

v_g is the flight speed of the bird (relative to the ground),

m_l is the lean mass of the bird,

and f is the energy capacity of the bird's fat and protein reserves (in kJ/g).

The graph of energy versus flight range comes out looking close to linear (Figure 4). At higher fuel levels, a bird can fly further than with the Pennycuick model.

To estimate the flight parameters, I used a sample of adult birds taken by Lyons and Haig (1995b) at Yawkey Reserve, SC. The average total body mass was 25 g and the average estimated lean mass was 21 g. This lean mass includes energetic stores of protein; when that was removed, the average lean mass was 20 g. To estimate f , I used Jenni and Jenni-Eiermann's (1998) conclusion that a bird optimizing its energy storage

will store 95% of its energy as fat and 5% as protein. As fat is 39 kJ/g and protein is 18 kJ/g, I got $f=36.85$ kJ/g. To estimate u , I used Norberg's (1996) multiple regression for metabolic power as a function of body mass and wing span.

$$P = 51.5 \left(\frac{m_b}{1000} \right)^{1.37} z^{-1.6} \quad (24)$$

where z is the wing span of the bird in meters. I set $z=0.3$ m (Burns pers. comm., Chandler 1989), and set Equations 19 and 23 equal to each other. From that, I estimated u to be 0.7409.

Wind

The ground speed of the birds is calculated by adding the vectors of the air velocity and the wind velocity (Figure 5, Equation 25):

$$v_g = \sqrt{v_a^2 - w^2 \sin^2 \theta} + w \cos \theta \quad (25)$$

where w is the wind speed,

and θ is the angle between the wind vector and the intended direction of flight. For information on how this equation is derived, see Clark and Mangel (2000, pages 142-143). In reality, birds can adjust both the speed and direction of its air velocity vector to control the resulting ground speed. To simplify my model, I assumed that the air speed was fixed and that the birds could only control the direction of their flight (they choose the direction of their air velocity vector so that the resulting ground velocity vector will be in the direction of the destination).

Birds trying to minimize the energy they expend during migration are predicted to fly at the maximum range air speed (v_{mr}), and birds trying to minimize the time they spend on migration will fly at a higher speed, dependent on the rate of energy gain at the

stopover sites (Alerstam and Lindström 1990). However, both speeds are reduced with wind assistance, which is generally the condition under which birds are flying in this model. With wind assistance, migrating birds often fly close to the minimum power speed (v_{mp}) (Bruderer and Boldt 2001). I tuned the model results to best fit the data using the air speed, as described in the next section.

I downloaded wind data from the NOAA Forecast System Laboratory (FSL) at raob.fsl.noaa.gov. I used the wind data from the years that were available for free on the internet (1998-2003). For each flight, I used the wind recordings taken at the recording station closest to the takeoff stopover site with a good set of wind data (Table 3).

I took the wind measurements from one time (as close to midnight as possible) for each day of my model period (April 1 to June 30). The RAOB data provides wind speeds and directions at a variety of elevations. I assumed that the birds would choose the elevation with the most favorable wind (Bruderer et al. 1995). The most favorable wind is the one that results in the highest ground speed in the direction of the destination. For each night I picked the best ground speed for each stopover site. From the six years of data, I calculated the empirical probability of getting different representative ground speeds leaving each stopover site and arriving at the breeding site (Figure 6). I chose nine representative ground speeds, each 18 km/hr apart. During the model run, the ground speed is chosen randomly for each site and day and fed into the flight equation of any birds leaving that stopover site on that day.

Predation

There is very little data on the rate of predation on shorebirds at stopover sites. However, it is important to consider predation in this model, as predation risks may have

a large effect on the decisions the birds make. I set the predation rates by stopover site, and assumed it was constant by date and that all birds were equally likely to be predated. I made the predation rates at the stopover sites tuned parameters (see below).

Parameter Tuning

Approach

Most parameter values were set from various data sources (Table 6). For the unknown parameters (Table 7), I ran tests to select between different parameter values (subsequently referred to as different versions of the model). I ran each version of the model 5000 times, with 100 birds in each run, and averaged the results.

First, I ran different versions of the model to see whether the peaks of migration at the stopover sites (when the most birds were there) from the model results match those from the data. From the data, I developed a window for when the migration peaks should hit for three of the stopover sites (see below). The peak date for a stopover site was the day on which the most birds were there. When there was a tie, it was considered a fit if at least half of the migration peaks for a stopover site landed within the window. A particular version of the model passed this test if all three stopover sites' migration peaks lined up.

Next, I ran versions of the model to see if the average morality rate over the migration season fit within a window of plausible spring mortality rates (see below).

I then compared models that fit the window tests to see which had the best fit for average percent fat. I collected average estimated percent fat from raw data sets at all four stopover sites (see below). For each site and day where data was available I compared the average estimated percent fat from the data with the average percent fat

from the model results. I picked the version of the model that yielded lowest sum of relative squared deviation:

$$RSSD_{i,s} = \sum_t \frac{(O(s,t) - E_i(s,t))^2}{E_i(s,t)} \quad (26)$$

$$RSSD_i = \sum_s RSSD_{i,s} \quad (27)$$

where $RSSD_{i,s}$ is the relative sum of squares deviation for model version i and site s , $O(s,t)$ is the average estimated percent fat from the data at site s on day t , $E_i(s,t)$ is the average percent fat from the model for site s on day t , and $RSSD_i$ is the sum of relative sum of square deviations across stopover sites.

The model version that had the lowest $RSSD_i$ was chosen as the best fit to the fat data. The model version with certain parameter values was chosen if it passed the migration peak and mortality tests and had the best fit for the fat data.

The rest of year survival was scaled to average spring survival so that the product equals the estimated annual survival. The optimal reproductive output was scaled so that the average reproductive output fit within a range set by the data (see below) and that the average fitness was one.

Migration and fat targets

I have no reliable data on dates of migration peaks for Merritt Island. Weber and Haig (1996) and Lyons and Haig (1995b) put migration peaks in 1991-1993 at Yawkey between May 16 and May 25. O’Harra (2001) puts migration peaks at Pea Island in 1998 and 1999 between May 21 and May 28. Clark et al. (1993) puts average peaks at Delaware Bay between 1986 and 1992 on June 2-5, with values almost as high on May 27-30.

One caveat on the use of these numbers is that these are the peaks of all migrating Semipalmated Sandpipers, but I modeled only after second year female birds. Second year birds migrate later in the spring than after second year birds (Lyons and Haig 1995b) while male birds probably migrate early, as they arrive on the breeding grounds a few days before the females (Gratto-Trevor 1992). Second year birds made up approximately 12.5% of the birds captured by Lyons and Haig (1995b) at Yawkey Reserve, and males are presumably about half of the migrating population. The peaks for mature females are probably similar to those for the whole population.

For each stopover, I calculated an average adult estimated percent fat (EPF) based on all available data. Estimated percent fat estimates for Yawkey Wildlife Center were based on data collected in 1992 and 1993 (n = 805 after second year birds; Lyons and Haig 1995b), and in 2002 (n = 58; Lyons, unpublished data). I also used data collected in 2002 at Merritt Island, Pea Island, and Delaware Bay (n = 20 at Merritt Island, n=81 at Pea Island, and n=50 at Delaware Bay; Lyons, unpublished data). All EPF estimates were calculated using the equation developed by Lyons and Haig (1995a):

$$EPF = \frac{m_b - 30.35 + 0.14l_w - 0.58l_c - 0.83l_t}{m_b} \quad (28)$$

where EPF is the estimated percent fat,

l_w is the wing length,

l_c is the culmen length,

and l_t is the tarsus length.

Other targets

Local annual survival for adult females estimated from the breeding grounds is 0.56 (Sandercock and Gratto-Trevor 1997). This includes emigration and therefore is

smaller than the actual annual survival rate, which was estimated at 0.7 (Gratto et al. 1985). The product of the average spring migration survival rate and the estimated survival for the rest of the year (a parameter) should be approximately 0.7.

There are no estimates of seasonal survival rates for Semipalmated Sandpipers. Sillett and Holmes (2002) found that approximately 85% of apparent annual mortality of the Black-throated Blue Warbler *Dendroica caerulescens* took place during the migratory seasons. If at least half of the mortality of Semipalmated Sandpipers takes place during migration, and the spring and fall mortality rates are similar, then between 25 and 50% of annual mortality takes place during spring migration. I assumed that was the case, and that the true annual survival was around 0.7. Spring mortality should therefore be between 0.085 and 0.163.

I wanted to estimate the average number of female chicks that reach adulthood per female that reaches the breeding grounds, to see if the output produced by the model is realistic. Hitchcock and Gratto-Trevor (1997) and Sandercock and Gratto-Trevor (1997) estimate the probability of breeding at La Pérouse Bay at 0.95 for mature females that arrive at the breeding site. The average number of eggs hatched per nest varied from year to year between 1 and 3. I averaged the values for the years 1983-1987 to get 1.85 eggs hatched/nest. Survival from hatching to fledging was only measured in one year of low predation and was 50%. They used 50% as the high estimate and 9.4% as a low. Since there are no good estimates of juvenile survival after fledging, I assumed that it was the same as adult survival, and that survival from fledging for the year and a half until they are ready to start spring migration for breeding at age 2 equals $0.7^{1.5}=0.5856$. From

these numbers I calculated that the average number of female offspring per female that reaches the breeding ground should be between 0.059 and 0.307.

Sensitivity Analysis

I tested the sensitivity of model outputs to changes in model parameters. I looked at the changes in length of stay at the four stopover sites and in fitness when parameters were increased and decreased slightly (usually 10%). I recorded the elasticities (percent change in the output divided by percent change in the parameter) for both positive and negative changes, when possible. I did not record the elasticities for parameters which were dates or which had a base value of 0.

Scenarios

I looked at the changes in fitness and behavior for various scenarios involving changes in the energy gain rates at the stopover sites. I looked at what would happen if the birds followed the (now suboptimal) strategy for the original conditions, and what would happen if they developed a new strategy based on the new conditions, and followed it. In each of these cases, I looked at the effect of one season of the change on the lifetime reproductive fitness, and the effect of carrying the change out indefinitely on the lifetime reproductive fitness. To do this, I calculated the average fitness as

$$F_{avg} = S_{spr} (\phi_{avg} + S_{roy} (S_{spr} (\phi_{avg} + S_{roy} (\dots)))) \quad (29)$$

where F_{avg} is the average fitness of the population,

S_{spr} is the survival rate through the spring migration,

S_{roy} is the survival rate through the rest of the year,

and ϕ_{avg} is the average reproductive output of the birds that survived spring migration.

I looked at changes in behavior by looking at changes in average length of stay at the four stopover sites. The scenarios I looked at were a) decreasing the energy gain rate at each of the four stopover sites, b) increasing the energy gain rate at each of the stopover sites, c) decreasing the energy gain rate at Delaware Bay (Site 3) and increasing it at Pea Island (Site 2), and d) decreasing the energy gain rate at Delaware Bay and increasing it at the other three stopover sites. I looked at scenarios c and d to see if managing the food supply at the early stopover sites would help compensate for the decline in horseshoe crab egg production. At Delaware Bay and Pea Island, I adjusted the energy gain rate by adjusting the energy stored per hour foraging (k , Table 3). At the first two stopover sites, the k values were low enough that the minimum energy stored per day (x_{gainmin}) was the factor that controlled the energy gain rate, so I adjusted it individually for those sites.

RESULTS

Tuning Results

The best value for the last possible date of arrival at the first stopover site ($t_{0\text{max}}$) was day 45 (May 16) (Table 7). A range of values fit the migration peaks and mortality, but May 16 provided the best fit to the proportion body fat levels. It was also the latest date tested, as we felt later start dates at Merritt Island would not be reasonable biologically.

The best value for the highest possible energy level at arrival at the first stopover site ($x_{0\text{max}}$) was 300 kJ (Table 7). A range of values fit the migration peaks and mortality, but 300 provided the best overall fit to the fat levels. It provided the best fit at Yawkey

and Pea Island (Sites 1 and 2), while lower values provided a better fit at Merritt Island (Site 0) and higher values a better fit at Delaware Bay (Site 3).

For the minimum daily rate of energy gain at the stopover sites (x_{gainmin}), the best value was 10 kJ (Table 7). I tested x_{gainmin} and $x_{0\text{max}}$ against each other to see if there was an interaction between the parameters that most affect fat levels at the first two stopover sites. Low values of both parameters caused the migration peak at Site 2 to fall too early. The values chosen gave the best fits to the fat levels.

The best value for number of hours intensively foraging per day (h) was 2 hours (Table 7). Foraging one hour caused the migration peaks to fall too early; higher values of hours foraging fit the migration peaks but did not fit the fat levels as well.

If the predation levels at the four stopover sites (p_s) are the same, the migration peaks fall too early, as the birds rush to the last stopover site. The migrating birds spend a majority of their time at whatever stopover site has the lowest predation; if there is a tie for lowest predation, they spend the majority of their time at the last one. Many different combinations of predation levels fit the peak and mortality targets. Those combinations where the predation was lowest at Site 0 (Merritt Island) fit the fat levels best. From these, I chose $p_0=0.002 \text{ day}^{-1}$, $p_1=0.003 \text{ day}^{-1}$, $p_2=0.003 \text{ day}^{-1}$, and $p_3=0.003 \text{ day}^{-1}$.

The air speed (v_a) that fit the fat levels best was 32 km/hr. The threshold level of energy for optimal reproduction (x_t) that fit the fat levels best was 500 kJ. Optimal arrival dates at the breeding site (t_{opt}) values between 64 to 68 (June 4-June 8) resulted in migration peaks that did meet the criteria. Of those that did fit the migration peaks, 66 (June 6) fit the fat levels best.

To make the fitness equation calibrate, I calculated rest of year survival (S_{roy}) to be 0.7776 and optimal reproductive output (r_{max}) to be 0.3549.

Base Model Results

The birds peaked at Site 0 on day 45 (May 16), at Site 1 on day 50 (May 21), at Site 2 on day 51 (May 22), and at Site 3 on day 63 (June 3) (Figures 7 and 8). The average length of stay at Site 0 was 25.83 days ($s=0.83$), 2.62 days ($s=1.44$) at Site 1, 1.94 days ($s=1.00$) at Site 2, and 10.69 days ($s=1.94$) at Site 3 (Table 8). Less than 1% of the birds, on average, skimmed Sites 0 and 3 (that is, they stayed only one day and did not stop to feed), while 37.98% skimmed Site 1 and 49.95% skimmed Site 2 (Table 8). Removing those that skimmed the stopover sites, the average lengths of stay were 26.01, 3.61, 2.89, and 10.75 days.

The model predicts higher average fat levels than the average estimated fat levels of birds captures at Sites 0 and 3 (Figure 9 a and d). The percent fats are quite close at Sites 1 and 2 (Figure 9 b and c).

The average mortality was 0.09923. Mortality ranged between 0.07 and 1.00 between years. Average reproduction of the population was 0.2999. Reproduction ranged between 0 and 0.33. Average reproduction of the birds that reached the breeding grounds was 0.3319. The average date of arrival on the breeding grounds was 66.72 ($s=1.8256$). The average energy at arrival was 837.45 kJ ($s=173.96$).

The decision matrix shows the birds' decisions based on stopover site, date, and energy level (Figure 10). At all four stopover sites, the decision to take off depends on the interaction of energy and date. For Site 0, however, the time is clearly the most important element, as most energy levels provide enough energy to fly to the next site.

The birds will decide to leave Site 1 at all dates and for all but very low energy levels. Site 2 is similar but has some anomalies. The birds will stay for some early days for which the energy gain rates at Site 3 are still low. Leaving the final stopover site only takes place for a small subset of times and energy levels. There is a tradeoff: at high energy levels the birds are ready to leave between $t=60$ and $t=65$, but at intermediate energy levels, they will wait around longer.

Sensitivity Analysis

Lengths of stay at the four stopover sites were most sensitive to changes in flight parameters scaling constant (u), air speed (v_a), and flight exponent (c), relative predation levels, and maximum energy storage per day (x_{gainmax}) (Table 9). The lengths of stay were least sensitive to increases in the number of hours foraging (h), and changes in the energy gain rates at the last two stopover sites (k_2 and k_3).

The average fitness of the birds was most sensitive to the “black box” parameters that feed directly into it (maximum reproduction r_{max} and rest of year survival S_{roy}) and was also sensitive to changes in air speed (v_a) and the predation rate at Site 0 (p_0), and decreases in hours intensively foraging (h) (Table 9). The average fitness was least sensitive to changes in k_2 and k_3 , increases in h , and changes in the predation rate at Site 2 (p_2).

Positive and negative changes of parameters from the base values had different effects in some cases (Table 9). Some examples are the effects of h on length of stay at Merritt Island (Site 0), the effects of maximum starting energy ($x_{0\text{max}}$) on length of stay at Yawkey (Site 1), and predation rates at Pea Island (Site 2) and Delaware Bay (Site 3) (p_2 and p_3) on lengths of stay at Sites 2 and 3.

Scenarios

Reducing Energy Gain Rates at a Single Stopover Site

Reducing x_{gainmin} at Site 0 reduced the single season and cumulative fitness of both optimized (following new strategy) and unoptimized (following old strategy) birds (Figure 11). There was little change in fitness for small and moderate reductions.

Intermediate reduction of x_{gainmin} at Site 0 decreased length of stay there slightly, while dramatic reduction increased length of stay for both optimized and unoptimized birds (Figure 12). Reduction in x_{gainmin} at Site 0 slightly increased the length of stay at site 3.

Reducing x_{gainmin} at Site 1 had little effect on fitness, but fitness was slightly reduced for extreme reduction in the unoptimized case (Figure 13). In the unoptimized case, reducing x_{gainmin} at Site 1 slightly increased how long the birds spent there (Figure 14).

Reducing the food levels at Site 2 had little effect on fitness (Figure 15). It also had little effect on behavior, although the birds spent a bit longer at Site 3 and slightly less time at Site 0 in the optimized case (Figure 16).

Reducing the food levels at Site 3 to 0 brought the fitness to 0.738 for unoptimized birds and 0.995 for optimized, and the cumulative fitness to 0.236 for unoptimized birds and 0.977 for optimized (Figure 17). There was little change in fitness for a scaling factor of 0.5 or above. The optimized birds spent more time at Site 2, less time at Site 3, and a bit less time at Site 0 (Figure 18). The unoptimized birds spent longer at Site 3.

Increasing Energy at a Single Stopover Site

In all cases, increasing the x_{gainmin} or food levels at a single site had little effect on fitness. Increases in x_{gainmin} at Site 0 caused the birds to spend a bit more time there and a bit less at Site 3 (Figure 19).

Compensating for Declining Energy Gain Rates at Delaware Bay

In the unoptimized case, increasing the food levels at Site 2 barely changes the effect of reducing the food levels at Site 3 (Figure 20 a and b). Length of stay at Site 3 was increased, with little interaction effect from increasing the food levels at Site 2 (Figure 21d). Increasing the food at Site 2 slightly increased fitness for reduced food at Site 3 in the optimized case (Figure 20 c and d). As with a simple reduction in energy gain at site 3, length of stay was decreased at Sites 3 and 0 and increased at Site 2. However, increased energy gain at Site 2 reduced all of those effects slightly (Figure 21 e, g, and h).

Increasing the x_{gainmin} at Sites 0 and 1 at the same time had similar, though more dramatic effects on fitness (Figure 22). When the energy at Site 3 is reduced, increasing it at the other sites did increase fitness in the unoptimized case. In the unoptimized case, increased energy gain increased length of stay slightly at Site 0, with no interaction from energy reduction at Site 3 (Figure 23 a). There was an increased length of stay at Site 3 with energy reduction there; this was reduced by increasing the energy gain at the other stopover sites (Figure 23 d). In the optimized case, again there was a reduction in the time spent at sites 3 and 0 and an increase in the time spent at Site 2 with a decrease in the energy gain rates at Site 3, all of which were reduced by increasing energy gain rates at the other stopover sites (Figure 23 e, g, and h).

DISCUSSION

Implications of Model as Implemented

This model expands upon the shorebird migration model of Clark and Butler (1999) by using a different flight model and modeling the effects of different food levels at the stopover sites. The model provides a useful framework for exploring questions about migration and testing scenarios of habitat change. Some of the data that parameterize the model were incomplete and the insights gained from this work should be viewed as preliminary. This is because although I was able to model Semipalmated Sandpiper migration in such a way that the birds migrated through the stopover sites at the right times, with reasonable mortality and fat levels, this is not proof that the model is an accurate model of the spring migration; the results could be fitting correctly for the wrong reasons. This is especially true of models, like this one, where parameters were tuned to get a desired result (Hutchinson and McNamara 2000). The model, however, is an invaluable tool to single out directions for future research. Moreover, greater confidence in its usefulness as a guiding tool for shorebird conservation is assured because it was designed so that it can be updated as more data become available.

The reproductive rate of the birds that make it to the breeding grounds in the model (0.33) is higher than the data suggests (between 0.0489 and 0.257). This is probably due to the fact that the real population at La Pérouse Bay is declining (Hitchcock and Gratto-Trevor 1997), not stable, as my model assumes. Also, I did not count yearling reproduction in my model, which may be a significant factor. The method I used for calculating the survival from fledging to age 2 (which feeds into what the data suggests the reproductive rate should be) was speculative and may have included errors.

The model suggests that most of the birds are stopping to feed at the first and last stopover site, but that a significant portion of the birds skimmed through the middle two stopover sites. Intuition suggests and the model makes clear that a bird does not have to stop and feed at all four stopover sites. Whether their choice of site is accurate or an artifact of the model merits further investigation.

We do not know how long the birds are staying at Merritt Island (Site 0). The model predictions (25.83-26.01 days) seem a bit high, and it may be the birds are arriving there from their wintering grounds or previous sites later, and not staying as long. Recent analysis of mark-resight data of Semipalmated Sandpipers collected at Yawkey (Site 1) suggests that the average length of stay there was 2.3 days (Lyons and Collazo 2004). This corresponds well with model predictions of 2.62-3.61 days. However, the estimated length of stay at Pea Island (Site 2) is 12 days (O’Harra 2001), which differs considerably from the model predictions of 1.94-2.89 days. Introducing stochasticity in the energy gain rates at the stopover sites might put this model prediction closer to the data, as birds at Pea Island would have an incentive to feed longer as insurance against low food availability at Delaware Bay (Site 3). Allowing the birds to skip stopover sites might have caused some birds to stay longer at Pea Island and skip Delaware Bay. I am not aware of any studies showing the length of stay at Delaware Bay.

If the model assumptions are correct, the decline in horseshoe crab egg density is not yet a factor in the decline of Semipalmated Sandpipers. The average densities are still high enough for the birds to be able to consume more eggs in a day than they can assimilate. This may not be the case for larger shorebirds, which have to consume more per day, and which have similar feeding rates (Stillman et al. 2003). Since there is little

impact on Semipalmated Sandpiper fitness for reductions in hourly energy gain rate of less than 50%, one might assume that further declines in horseshoe crab egg density would be unlikely to affect them. However, there are biological reasons that a decline in horseshoe crab egg production of less than 50% could affect Semipalmated Sandpiper energy gain rates enough to have an impact on fitness.

1) Consumption: If a similar number of birds are competing for a declining resource, the resource is likely to be consumed faster, making the density decline faster than it would if a constant proportion of the eggs were consumed. This would especially affect birds arriving late in the season.

2) Competitive exclusion: Semipalmated Sandpipers have to compete with other, larger species for the same resource. These other species may be able to force Semipalmated Sandpipers out of the remaining dense patches.

3) Variability: There is a high degree of variability in horseshoe crab egg density between years and beaches. An overall decline could lead to some very bad years in which few Semipalmated Sandpipers get enough food to breed optimally.

The model suggests that if the energy gain rates at Delaware Bay (Site 3) decline sufficiently and the birds are aware of this, they will compensate by feeding longer at Pea Island (Site 2), and that increasing the food available there increases the compensatory advantage. It may be that the Delaware Bay stopover site is hardwired into the birds' migration plan, or heterogeneity in the lengths of stay and amount of fattening birds do at different stopovers may allow a changing in staging area to evolve. It also may be that the food resources or space at Pea Island are insufficient to support a large influx of birds feeding there extensively, as this model does not incorporate the effects of competition.

The model does suggest that enhancing the food resources at the first three stopover sites may enhance the reproductive success of the birds faced with a decline in food available at Delaware Bay.

It is unclear whether and how quickly shorebirds will adjust their migration strategies to fit changes in the environment. Like any behavior, migration consists of both genetic and learned components (Perdeck 1967). Genetic change is likely to be slow, but other aspects of migration may change more quickly. Many species of birds have adapted their migratory behavior in recent years, apparently in response to human induced change (Fiedler 2003). The best we can do is to model the extreme cases (no change in strategy and full change of strategy) and expect the true response will be somewhere in between.

Factors Not Included in Model

I did not include competition for food on the stopover sites or flocking behavior in my model; in my model, the birds are not affected by each other and do not make decisions based on what other birds are doing. There are several reasons for this. Although some exclosure studies have been done, most of the data I have on prey availability is based on what is available in the natural environment, which is affected by current and previous predation by these birds and other species. To accurately measure the effect of competition, I would need population models of the various prey species, and how each prey species' numbers and biomass is affected by predation, which is outside the scope of my study. For the current model, therefore, I treated food availability at a location and time as a parameter of the model, not a result.

It may be that the birds are not making decisions based entirely on their energy levels and timing, but also on when other birds are flying to the next stopover site. Flying in flocks is believed to provide aerodynamic benefits as well as increased safety, and sandpipers do tend to fly in flocks. However, the aerodynamic benefits of flying in non v-shaped flocks (such as those sandpipers fly in) have not yet been calculated, and other benefits are also very hard to quantify. Even without these problems, any model in which the birds base their decisions on what other birds are doing would be much more complex.

Incorporating stochasticity in energy gain rates at the stopover sites might be a useful addition to this model. Three levels of energy gain stochasticity could be implemented: 1) variation between years, 2) variation between days within a year, and 3) variation between individuals feeding on the same day. These sources of variation certainly all exist. There is a high degree of variability in horseshoe crab egg density between samples taken in segment of beach, between segments of beach, and between beaches in Delaware Bay, especially for 5 cm sampling (Pooler et al. 2003). There is considerable variation in the food available at the other stopover sites as well (Herring unpublished data, Weber and Haig 1997, O'Harra 2001). We might expect a high correlation of food availability from day to day, but at Merritt Island, the impoundments' water level can change rapidly from day to day due to winds and spring tides (Collazo et al. 2002).

Modeling intensity of feeding each day as a decision variable may also have added to this model. This would have allowed me to model predation as a function of feeding intensity and mass (Weber 1998b). It would allow the model to include the cost

of the extra hours of feeding required at the first two stopover sites, which had lower energy gain rates.

The mass, flight, and feeding and metabolic rate parameters of this model could be adjusted to apply the model to other shorebirds. A different set of stopover sites could be used to apply the model to birds flying through other areas, or using different stopover sites within the same area. The model could be adjusted so that birds can choose to skip sites completely, which would allow a more detailed analysis of how birds choose stopover sites. Including a wintering site and allowing the model birds to decide when they arrive at Merritt Island could also be a useful addition to the model.

How This Model Could Be Tested With Field Data

Some of the parameters that were derived by tuning the model could be tested using field studies. A large-scale radio transmitter study at a stopover site would not only provide information about how the birds are using the stopover site spatially and temporally, but also could provide an estimate of the predation rate at that site. A study of Semipalmated Sandpipers at Merritt Island could provide estimations of when birds are arriving there and with how much energy. Further invertebrate sampling at Merritt Island, during the Semipalmated Sandpiper migration period, could provide a better estimate of the food availability there. Some of the parameters that the model results were most sensitive to, such as the air speed (v_a) and other flight parameters, are unfortunately difficult to test.

The primary output of a stochastic dynamic programming model is the strategy or decision matrix. As with other stochastic dynamic programming models (Hutchinson and McNamara 2000), the decision matrix of this model generates several testable

predictions. At Merritt Island, it predicts that the birds will be mostly likely to leave on the first day between May 16 and June 20 with favorable winds at some altitude. At Yawkey, it predicts that the birds will leave on any day with favorable winds as long as they have a sufficient energy to make it to Pea Island. At Pea Island, the birds will leave any day after April 18 when there is favorable wind and they have enough energy to make it to Delaware Bay. At Delaware Bay, they will stay until they have at least 500 kJ of stored energy and the date is between June 4 and June 22, with birds that have more stored leaving earlier within that period. If these predictions do not prove correct, either the parameters are incorrect or there is a problem with the model assumptions.

How This Model Could Be Used In an Adaptive Management Framework

This model can be used as part of a larger model of how management decisions at refuges affect migrating shorebirds. The next part that is needed is a model of how changes in water levels of wetlands affect prey density and availability. It should incorporate the population biology of various prey items, effects of water level on prey numbers and mass, effects of shorebird predation on prey, and which prey items are available at different water levels. If how particular draining schedules affect water levels is known, then the models can be combined to show how different draining schedules might affect shorebird use of a managed wetland and the overall fitness of the average Semipalmated Sandpiper. This could then inform the decision as to which draining schedule to choose (Figure 24).

As my model can, with simple changes, be applied to other shorebirds, the larger model could be run several times to see how different draining schedules affect different

species. To accommodate the different species, different draining schedules may be required for impoundments within a stopover site or between nearby stopover sites.

A stated goal of the Southeastern Coastal Plains – Caribbean Regional Shorebird Plan is to coordinate monitoring, research, and management efforts between refuges and other sites shorebirds use (Hunter et al. 2000). This model represents a preliminary step in coordinating such efforts, as it both ties together data from multiple sources and predicts how changes at different stopover sites could affect shorebird fitness in different ways.

Table 1: Model Variables and Parameters.

Parameter	Description
a	Flight constant
b	Another flight constant
B	Number of unfavorable ground speeds
BMR	Basal Metabolic Rate
c	Exponent used in flight equation
C	Prey consumption rate (s^{-1})
d	Prey density (m^{-2})
D	Distance traveled (relative to ground) (km)
D _{air}	Air distance traveled (relative to wind) (km)
f	Energy capacity of birds stored reserves (kJ/g)
F	Lifetime reproductive fitness
g	Average mass of prey items (g)
G	Number of possible ground speeds
h	Number of hours birds feed per day
H	Handling time per prey item (s)
J	Energy consumed per unit distance in flight (kJ/km)
k	Energy stored (kJ/hour)
l _c	Culmen length (mm)
l _t	Tarsus length (mm)
l _w	Wing length (mm)
LM	Lean mass (including all muscle) (g)
m _b	Total mass of a bird (g)
m _l	Adjusted lean mass (not including muscle used for storing energy) (g)
n	Energetic value of prey (kJ/g)
p _s	Predation rate at stopover site s (day^{-1})
P	Energy consumed per unit time in flight (W)
r _{max}	Reproductive output (number of female offspring that survive to beginning of spring migration) of a bird that arrives at breeding ground under optimal conditions
R ₀	Average lifetime reproductive fitness of a bird at the beginning of spring migration
s	Stopover or breeding site (0-4)
S _{max}	Site number of the breeding site
S _{roy}	Survival rate through the rest of the year (not spring migration)
S _{spr}	Survival rate through spring migration
t	Date (0-90, 0=April 1)
t _{0max}	Last possible date of arrival at first stopover site
t _{0min}	First possible date of arrival at first stopover site
t _c	Length of time a flight takes (days)
t _{max}	Last possible day of arrival at breeding site for breeding
t _{open}	Opening date for the breeding site
t _{opt}	Optimal date for arrival at the breeding site

Table 1: Model Variables and Parameters, continued.

u	Flight constant
v_a	Air speed (km/hour)
v_g	Ground speed (km/hour)
V_{go}	The fitness of a bird that decides to fly to the next site
V_{stay}	The fitness of a bird that decides to stay at the current site
w	wind speed (km/hour)
x	Stored energy level of a bird (kJ)
x_{0max}	Highest possible energy level at arrival at first stopover site (kJ)
x_{0min}	Lowest possible energy level at arrival at first stopover site (kJ)
x_b	Stored energy before a flight (kJ)
x_c	Energy consumed in a flight (kJ)
x_e	Energy remaining after a flight (kJ)
x_{gain}	Amount of energy a bird stores in a day of feeding (kJ)
$x_{gainmax}$	Maximum amount of energy a bird can store in a day (kJ)
$x_{gainmin}$	Minimum amount of energy a bird will store in a day at these stopover sites (kJ)
x_{max}	Maximum amount of energy a bird can store (kJ)
x_t	Threshold level of stored energy required at arrival on breeding site for optimal reproduction (kJ)
Y	Maximum flight range of a bird
z	Wing span (m)
α	Assimilation efficiency
θ	Angle between wind vector and intended direction of flight
φ	Current year reproductive output of a bird
φ_e	Effect of breeding site arrival energy on reproductive output
φ_t	Effect of breeding site arrival date on reproductive output
ζ	Fat storage efficiency

Table 2: Prey Base at the Stopover Sites. The Merritt Island data is from G. Herring (unpublished data), the Yawkey data is from Weber (1994) and Weber and Haig (1997), the Pea Island data is from O’Harra (2001), and the Delaware Bay data is from Botton et al. (1994), Weber (2001, 2003), and Smith et al. (2002).

Site	Potential Prey Items	Dates	Average Density of Prey (ind./m ²)	Average Biomass of Prey (g/m ²)
Merritt Island	Amphipods (Aoridae, Gammaridae, Corophiidae), Tanaids (Paratanaidae), Oligochaete spp, Polychaetes (Nereidae, <i>Hobsonia florida</i> , <i>Scoloplos fragilis</i> , <i>Manyunkia</i> spp., Flabelligeridae), Coleoptera, Corixidae, Chironomidae	Apr 1 - Jun 30	2474.89	0.6549
Yawkey	Polychaetes (incl. <i>Capitella capitata</i> , <i>Laeonereis curveri</i> , <i>Stenonereis martini</i> , <i>Hobsonia florida</i> , & <i>Streblospio benedicti</i>), Chironomidae, Oligochaeta, Hydrophilidae larvae	Apr 1 - Apr 17 Apr 18 - May 9 May 10 - May 20 May 21 - Jun 30	33982.78 47333 18558.16 13587.44	4.534 6.315 2.476 1.813
Pea Island	Tanaidacea (<i>Tanais cavolini</i> and <i>Leptochelia repax</i>), Amphipoda (<i>Ampithoe</i> spp.), Polychaeta (Phyllodocidae), Chironomidae, Corixidae (<i>Trichocorixa</i> spp.), & Cyprinodontidae (<i>Cyprinodon variegates</i> and <i>Lucania parva</i>)	Apr 1 - Apr 7 Apr 8 - Apr 14 Apr 15 - Apr 21 Apr 22 - Apr 28 Apr 29 - May 5 May 6 - May 12 May 13 - May 19 May 20 - May 26 May 27 - Jun 2 Jun 3 - Jun 9 Jun 10 - Jun 30	401.32 1516.24 619.10 545.68 846.16 2669.85 1659.28 2671.26 7504.51 3544.17 1552.28	0.4979 1.881 0.7681 0.6770 1.050 3.312 2.059 3.314 9.310 4.397 1.926
Delaware Bay	Horseshoe crab eggs	Apr 1 - Apr 19 Apr 20 - May 3 May 4 - May 17 May 18 - Jun 2 Jun 3 - Jun 18 Jun 19 - Jun 30	0 60.75 2964.27 3774.36 19876.53 705.47	0 0.2261 11.04 14.05 74.00 2.626

Table 3: Energy Gain Rates at Stopover Sites.

Site	Dates	Energy stored foraging (kJ/hr)
Merritt Island	Apr 1 - Jun 30	10
Yawkey	Apr 1 - Apr 17	10
	Apr 18 - May 9	11
	May 10 - May 20	10
	May 21 - Jun 30	9
Pea Island	Apr 1 - Apr 7	12
	Apr 8 - Apr 14	34
	Apr 15 - Apr 21	17
	Apr 22 - Apr 28	15
	Apr 29 - May 5	22
	May 6 - May 12	48
	May 13 - May 19	36
	May 20 - May 26	48
	May 27 - Jun 2	75
	Jun 3 - Jun 9	56
Jun 10 - Jun 30	35	
Delaware Bay	Apr 1 - Apr 19	0
	Apr 20 - May 3	3
	May 4 - May 17	89
	May 18 - Jun 2	100
	Jun 3 - Jun 18	160
	Jun 19 - Jun 30	33

Table 4: Weather stations for wind data at sites.

Site	Weather Station	Distance (km)
Merritt Island NWR, FL	Cape Kennedy, FL	23.84
Yawkey Reserve, SC	Charleston, SC	83.46
Pea Island NWR, NC	Morehead City, NC	162.01
Delaware Bay (DE and NJ)	Wallops Island, VA	140.03
La Pérouse Bay, MB	Churchill, MB	37.69

Table 5: Targets for migration peaks.

Stopover Site	Start	End
Yawkey Reserve, SC	16-May (45)	25-May (54)
Pea Island NWR, NC	21-May (50)	28-May (57)
Delaware Bay (DE and NJ)	27-May (56)	5-Jun (65)

Table 6: Parameter Values.

Parameter	Value	Source
B	3	-
BMR	29.5	Castro and Myers 1993
c	0.35	Kvist et al. 2001
f	36.85	Jenni and Jenni-Eiermann 1998
G	9	-
H	0.45	Stillman et al. 2003
LM	21	Lyons and Haig 1995b
m _b	25	Lyons and Haig 1995b
m _l	20	Lyons and Haig 1995b
n	16.748	Cummins 1967
R ₀	1.0	-
S _{max}	4	-
t _{0min}	0	-
t _{max}	90	-
t _{open}	47	Gratto and Cooke 1987
u	0.7409	Kvist et al. 2001, Norberg 1996
X _{0min}	0	-
X _{gainmax}	100	Lank 1983, Alexander and Gratto-Trevor 1997
X _{max}	1150	Lyons unpublished
z	0.3	Burns pers. comm., Chandler 1989
α	0.73, 0.69	Kersten and Piersma 1987, Castro et al. 1989
ζ	0.88	Kersten and Piersma 1987

Table 7: Sample parameter tuning results.

Parameter	Values	Migration Peaks				Fits?	Mortality	Fits?	Fat Levels RSSD				Sum	Cells
		1	2	3					0	1	2	3		
t_{0Max}	25	51	52,53	62,63	yes	0.1188	yes	0.148371	0.055681	0.043455	0.082453	0.329961	17	
	30	50,51	52	62,63	yes	0.1153	yes	0.120128	0.053304	0.046453	0.085086	0.304971	17	
	35	50,51	52	61,62,63	yes	0.1049	yes	0.092949	0.053452	0.043735	0.08401	0.274145	17	
	40	50	51,52	62,63	yes	0.1038	yes	0.087668	0.047984	0.042134	0.079705	0.257491	17	
	45	50	51	62,63	yes	0.0987	yes	0.087357	0.047738	0.041904	0.075244	0.252243	17	
X_{0Max}	200	49	51	61,62,63	yes	0.1015	yes	0.043878	0.23922	0.049544	0.070926	0.403568	18	
	250	50	51,52	61,62,63	yes	0.1002	yes	0.064233	0.213487	0.048095	0.072662	0.398476	18	
	300	50	51	62,63	yes	0.0962	yes	0.087483	0.181814	0.038186	0.076068	0.383551	18	
	350	50	52	62,63	yes	0.0978	yes	0.112961	0.183609	0.041302	0.078023	0.415895	18	
	400	50,51	52	62,63	yes	0.0966	yes	0.140673	0.188695	0.040698	0.079756	0.449822	18	
$X_{gainmin}$	4	48	49	62,63	no	0.1033	yes							
	6	48	50	61,62,63	yes	0.1011	yes	0.031703	0.4556	0.098382	0.076124	0.661809	18	
	8	49	51	62,63	yes	0.1018	yes	0.055223	0.221153	0.044849	0.076093	0.397317	18	
	10	50	52	61,62,63	yes	0.0991	yes	0.087828	0.183422	0.039377	0.075669	0.386297	18	
	12	51	52,53	62,63	yes	0.0978	yes	0.124786	0.255028	0.048857	0.075566	0.504237	18	
h	2	49,50	51,52	61,62,63	yes	0.0975	yes	0.087615	0.101185	0.052282	0.074429	0.315512	18	
	3	50	51,52	61,62,63	yes	0.1	yes	0.087579	0.183217	0.040637	0.076409	0.387842	18	
	4	50	51,52	61,62,63	yes	0.0991	yes	0.08733	0.229808	0.03397	0.081573	0.43268	18	
	5	50	52	61,62,63	yes	0.0986	yes	0.087414	0.241737	0.032699	0.082523	0.444374	18	
	6	50	52	61,62,63	yes	0.0988	yes	0.087651	0.229748	0.031959	0.082328	0.431686	18	
p	{0.001,0.001,0.001,0.001}	11-46	18	57-63	no	0.0539	no							
	{0.002,0.002,0.002,0.002}	11-46	18	57-63	no	0.0907	yes							
	{0.002,0.002,0.003,0.003}	47	52,53	61,62,63	yes	0.0958	yes	0.25344	0.196927	0.04802	0.019455	0.517842	15	
	{0.002,0.003,0.002,0.003}	45,46	56-59	63	yes	0.0907	yes	0.263803	2.133488	0.720541	0.000366	3.118198	15	
	{0.002,0.003,0.003,0.003}	50	51,52	62,63	yes	0.0998	yes	0.087782	0.18195	0.041848	0.021896	0.333477	15	
	{0.005,0.005,0.005,0.005}	11-46	18	53-62	no	0.1827	no							

Table 7: Sample parameter tuning results, continued.

Parameter	Values	Migration Peaks				Fits?	Mortality	Fits?	Fat Levels RSSD				Sum	Cells
		1	2	3					0	1	2	3		
v_a	28	48	50,51	61,62	yes	0.1117	yes	0.087746	0.060634	0.061267	0.060752	0.270399	17	
	32	50	51,52	61,62,63	yes	0.099	yes	0.087511	0.051509	0.043125	0.075775	0.257921	17	
	36	50	52	62,63	yes	0.0931	yes	0.087383	0.141422	0.028333	0.106212	0.36335	17	
x_t	350	51	53	61,63	yes	0.0975	yes	0.087553	0.075786	0.104611	0.048698	0.316648	17	
	400	50,51	52	62,63	yes	0.0992	yes	0.087367	0.05398	0.067301	0.061465	0.270113	17	
	450	50	52	62,63	yes	0.0971	yes	0.087381	0.047178	0.053995	0.067491	0.256045	17	
	500	50	51,52	61,62,63	yes	0.0976	yes	0.087171	0.046042	0.041978	0.073897	0.249087	17	
	550	50	51,52	61,62,63	yes	0.0985	yes	0.087625	0.058288	0.035034	0.083405	0.264352	17	
t_{opt}	63	47	48,49	59	no	0.0907	yes							
	64	48	50	60	yes	0.0945	yes	0.08761	0.194	0.018358	0.120355	0.420323	17	
	65	49	51	61	yes	0.0963	yes	0.087634	0.076781	0.026043	0.091379	0.281837	17	
	66	50,51	52	62	yes	0.1001	yes	0.087572	0.051577	0.071886	0.060843	0.271878	17	
	67	52	53,54	63,64	yes	0.1012	yes	0.087716	0.154098	0.181456	0.033694	0.456965	17	

Table 8: Lengths of stay and percentage skimmed.

Stopover Site	Peak Date	Average Length of Stay	Percentage Skimmed
0: Merritt Island	5/16	26 days	<1%
1: Yawkey	5/21	3 days	38%
2: Pea Island	5/22	2 days	50%
3: Delaware Bay	6/3	11 days	<1%

Table 9: Elasticities. Shows the elasticities (percent change in response variable divided by percent change in parameter) of lengths of stay and fitness to positive and negative changes in various parameters. The effect of raising the parameter from a lesser value to the base value is on the left; the effect of raising it from the base value to a higher value is on the right. Most parameters were changed by 10% in each direction.

Parameter	Base Value	Site 0 Length of Stay		Site 1 Length of Stay		Site 2 Length of Stay		Site 3 Length of Stay		Fitness	
x_{0max}	300	0.038466	0.041777	-0.17176	0.220006	-0.03461	-0.05329	-0.07458	-0.187	0.006283	0.005421
x_{max}	1150	-0.21086	-	0.029801	-	0.041626	-	0.504636	-	0.037044	-
$x_{gainmax}$	100	0.250748	0.193402	-0.04276	0.054135	-0.20114	0.075372	-0.56119	-0.53311	0.010335	0.008036
a	0.7409	-0.16672	-0.15446	-0.00839	0.194395	0.139258	0.190004	0.418089	0.305434	-0.02515	-0.03162
v_a	32	0.485244	0.224269	-1.66101	-1.16615	-1.45624	-0.98531	-0.04576	-0.17115	0.115884	0.073874
c	0.35	-0.20625	-0.19757	-0.03267	0.191871	0.172892	0.065677	0.45942	0.444386	-0.02978	-0.04376
y	0.7776	0.048989	0.059498	-0.08575	-0.03397	-0.04081	-0.04395	-0.10522	-0.67822	0.727045	0.699595
h	2	0.613094	0.004049	0.004762	0.011	-0.19929	-0.00996	-1.72408	-0.00313	0.101014	0
$x_{gainmin}$	10	0.10539	0.109599	-0.20108	0.165466	-0.06935	0.069458	-0.22421	-0.3612	0.006502	0.005483
k_2	Table 3	0.032905	0.01181	-0.17965	0.117587	-0.06202	-0.00044	-0.03445	-0.06925	0.001313	0.000985
k_3	Table 3	-0.00243	-0.00127	-0.24617	-0.11808	-0.01437	0.078719	0.047256	-0.01688	1.6E-07	1.7E-07
p_0	0.002	-0.18128	-0.20957	-0.01122	0.152772	0.121306	-0.02537	0.33323	0.418958	-0.05139	-0.05019
p_1	0.003	0.019359	0.020995	-0.07713	0.199307	-0.10827	-0.04047	0.010091	-0.05637	-0.00487	-0.00482
p_2	0.003	0.306273	0.005723	-0.19333	0.084808	-28.4811	-0.06123	4.362124	-0.02202	-0.0155	-0.00283
p_3	0.003	0.270709	-0.05055	-0.17436	0.142227	-0.03858	24.70171	-0.62066	-4.58012	-0.03073	-0.01795
Γ_{max}	0.3549	-0.05837	-0.05646	-0.13125	0.011384	0.01612	0.011477	0.698746	0.139136	0.299388	0.299842
x_t	500	-0.08984	-0.08129	0.000545	0.141065	-0.04464	-0.03616	0.267221	0.227231	-0.01456	-0.01716

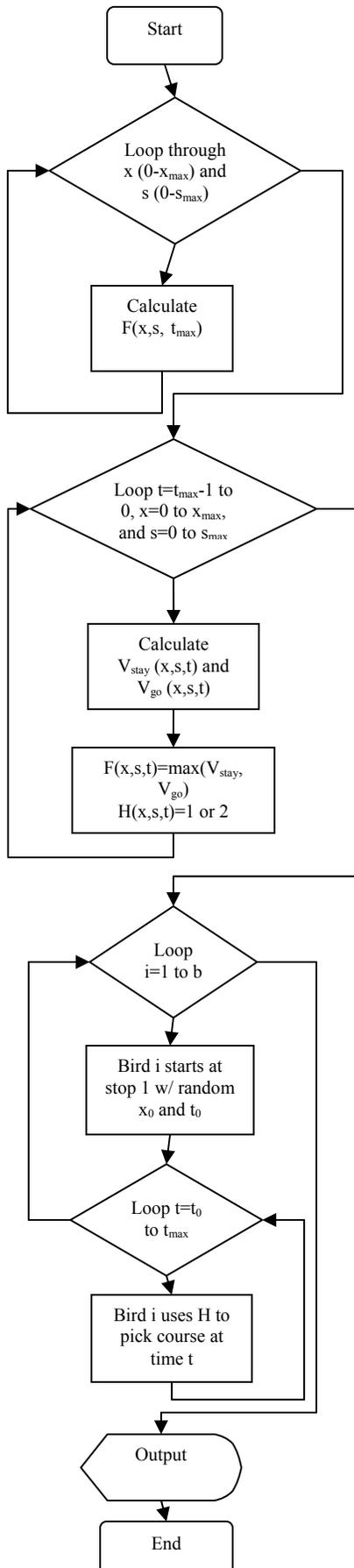


Figure 1: Flow Chart of Deterministic Model

Step 1: Develop decision matrix through backwards iteration

$F(x,s,t)$ =expected lifetime reproductive fitness
 x =energy level (x_{max} =maximum energy)
 s =site (from 0=Merritt Island to s_{max} =breeding ground)

t =date (from 0 to t_{max} , end date of spring migration)

$F(x, s_{max}, t)$ =expected current reproduction + expected future reproduction

$F(x, s < s_{max}, t_{max})$ =expected future reproduction (because they will not make it to the breeding grounds this year)

Important: Notice that we are looping backwards through time here

$V_{stay}(x,s,t)$ =fitness of staying at s for time step t

$V_{go}(x,s,t)$ =fitness of migrating to $s+1$ at time step t

Decision 1 (staying) at $t_{max}-1$ puts us at some x_1 & s at t_{max} . Decision 2 (going) at $t_{max}-1$ puts us at some x_2 & $s+1$ at t_{max} . So $V_{stay}(x,s, t_{max}-1)=F(x_1,s, t_{max})$ and $V_{go}(x,s, t_{max}-1)=F(x_2,s+1, t_{max})$ (assuming a migration step takes no more than one time step).

The bird decides the action that will maximize $F(x,s, t_{max}-1)$. The decision made at $t_{max}-2$ will be based on $F(x,s, t_{max}-1)$. $H(x,s, t_{max})$ is the matrix of these decisions.

Step 2: Simulate migration through forward iteration

b = Number of simulations/birds

There are two nested loops here – one going through each of the birds (simulations), and one going through each time step for a given bird

Each bird winds up with a final expected lifetime reproductive fitness

Step 3: Output

Where birds are when, average fitness, various statistics and variables

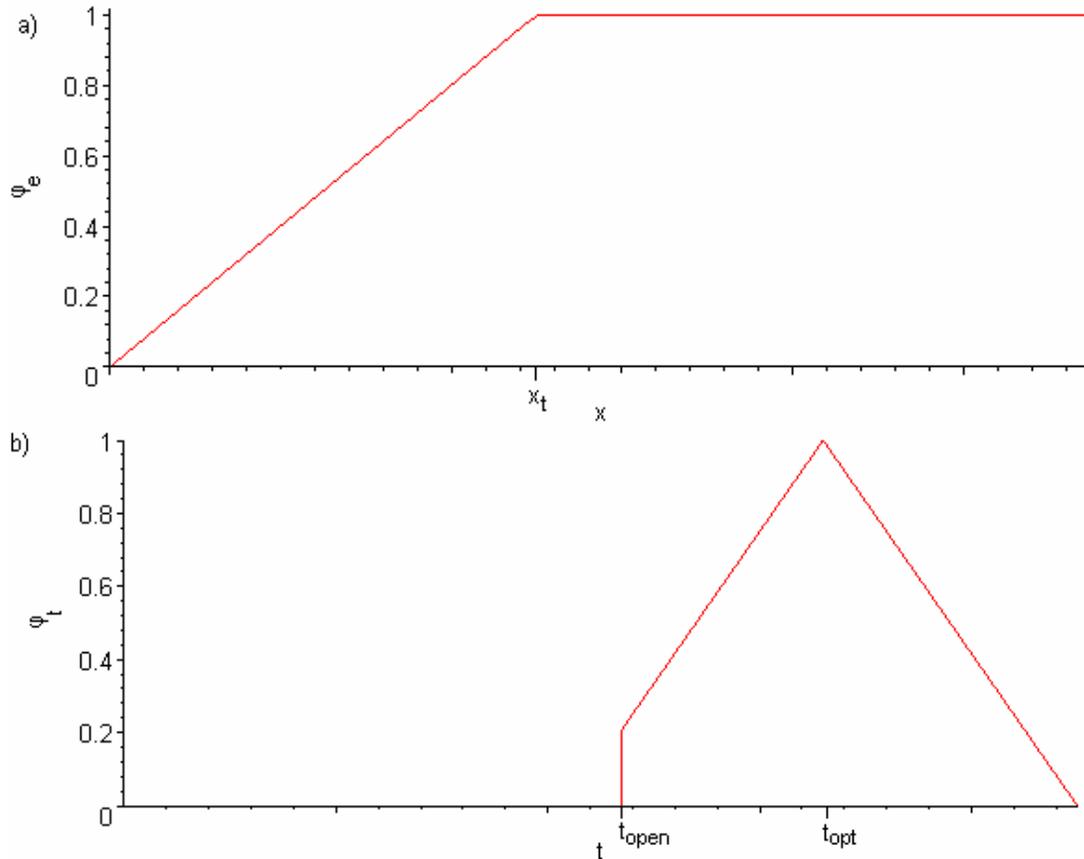


Figure 2: Reproductive factors. The current year reproductive output of a bird that reaches the breeding grounds is the product of r_{max} (the maximum reproductive output), $\phi_e(x)$ (the reproductive factor from arrival energy), and $\phi_t(t)$ (the reproductive factor from arrival date), where x is the stored energy (kJ) at arrival on the breeding grounds and t is the date of arrival on the breeding grounds. x_t is the threshold energy, above which there is no energy penalty. t_{open} is the opening date for the breeding grounds, and t_{opt} is the optimal date for arrival on the breeding grounds.

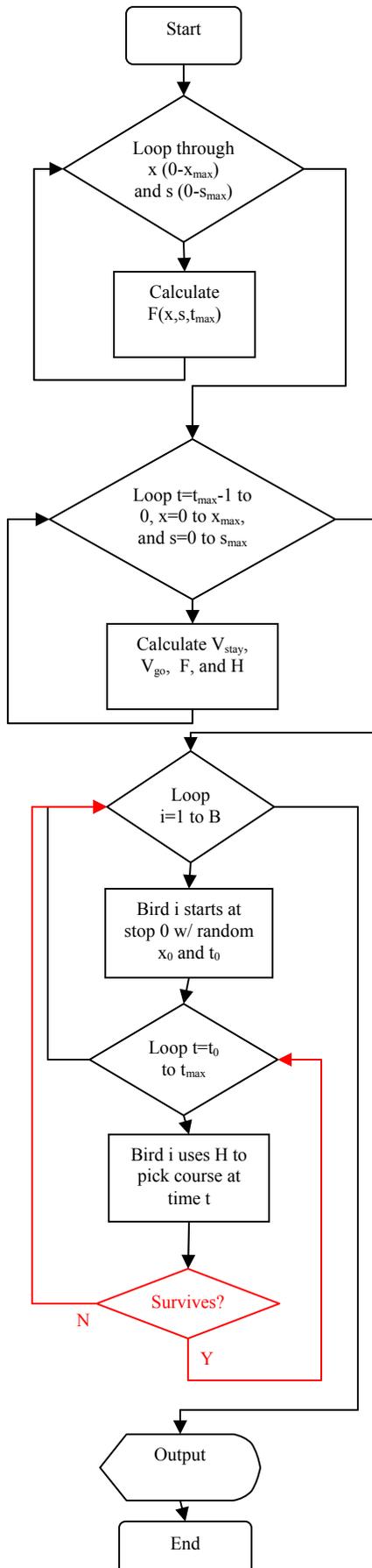


Figure 3: Flow Chart of Stochastic Model

Differences from Deterministic Model:

Step 1: Develop decision matrix through backwards iteration

Current expected reproductive success at breeding ground affected by x and t (of arrival)

V_{stay} is calculated with the new energy gain formula. For random events (winds and predation), probability of different outcomes and the resulting fitness of those outcomes are calculated into V_{stay} and V_{go} . For instance if probability of being predated at any site=0.003/day, then $V_{stay}(x,s,t) = 0.003*0 + 0.997*oldV_{stay}$ (without predation).

Step 2: Simulate migration through forward iteration

Because this model is more stochastic, more simulations are necessary. At each time step, a bird could die of starvation or predation. This is recorded and the program goes on to the next bird.

Step 3: Output

Where birds are when, average fitness, average survival, various statistics and variables

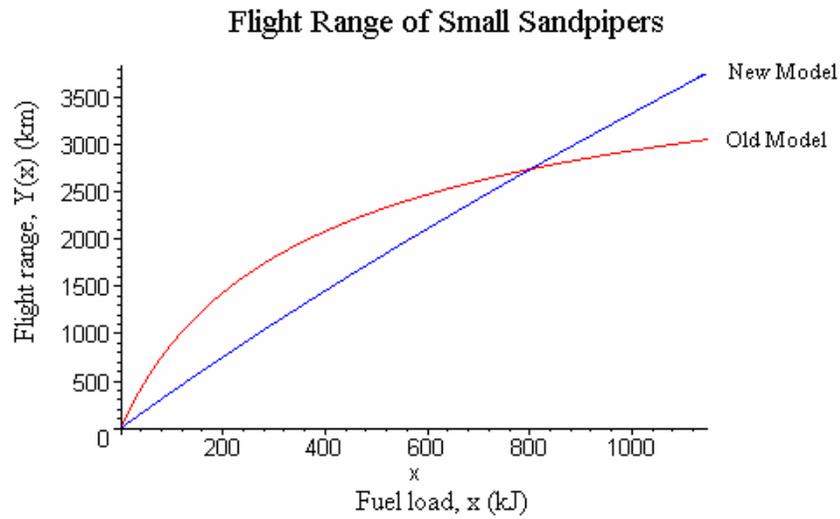


Figure 4: Two flight models. The old model uses Equation 18 to determine the flight range (maximum distance a bird can travel on the energy it has stored), and the new model uses Equation 22.

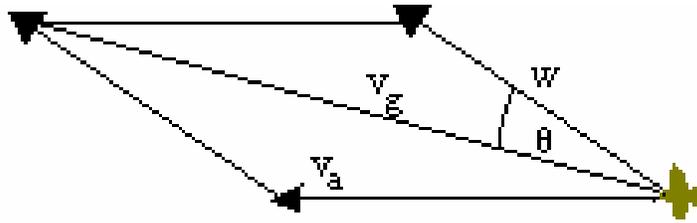


Figure 5: Wind, bird air velocity, and bird ground velocity vectors. The ground velocity vector (\mathbf{v}_g) is the sum of the air velocity vector (\mathbf{v}_a) and the wind vector (\mathbf{w}). (Bold indicates vectors; the same terms without bold are the magnitudes or speeds.) θ is the angle between the wind vector and the direction the bird intends to travel.

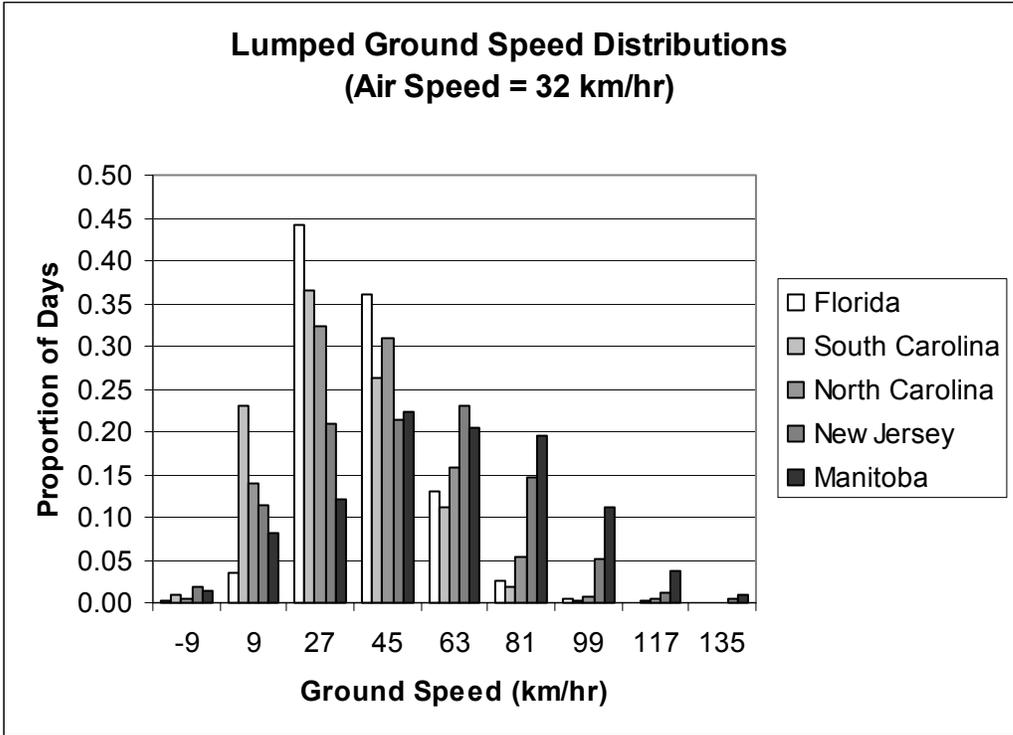


Figure 6: Resulting grounds speeds with wind factored in.

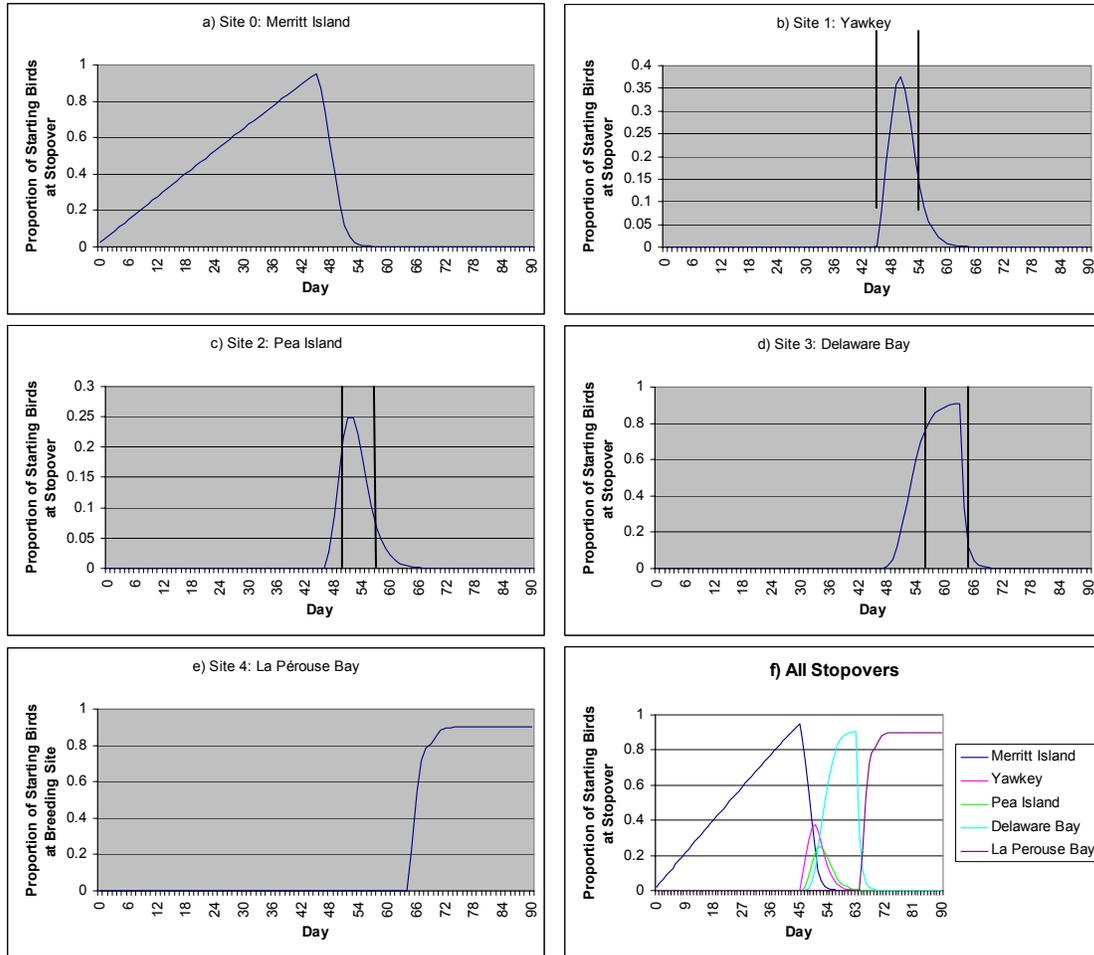


Figure 7: Movement through stopover sites in base model. Proportion of the birds that started the migration at each stopover site (and the breeding site) by day of the migration season. The vertical lines represent the targets for the peaks of migration (see Table 5). Results are the average of 10,000 iterations.

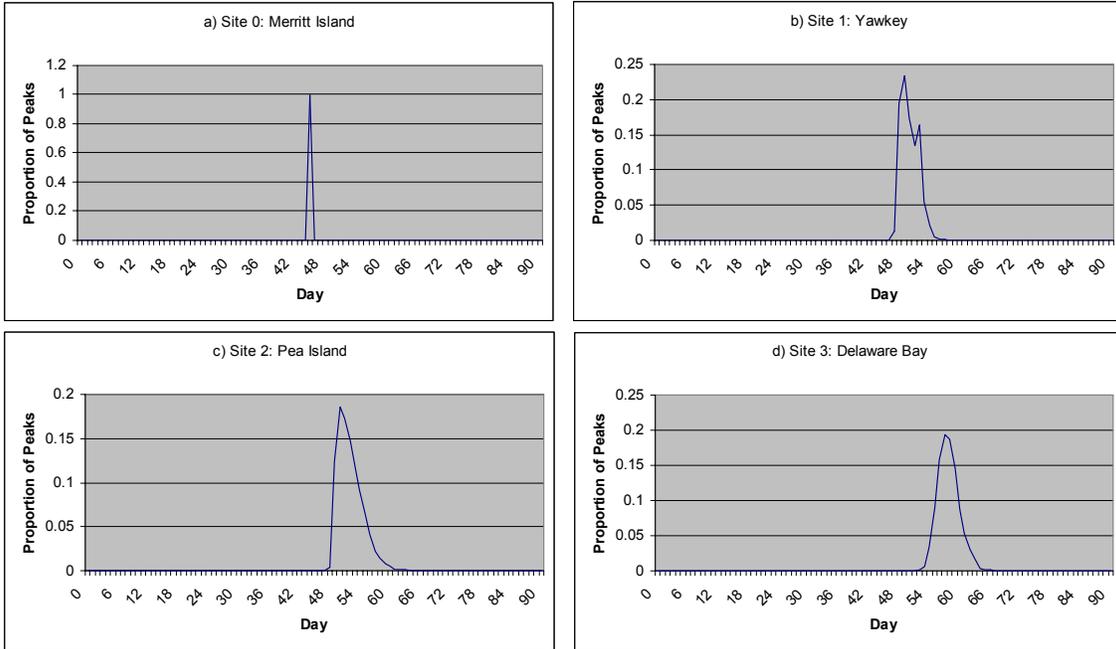


Figure 8: Distribution of peaks. The proportion of iterations where the peak falls on each day for each of the four stopover sites.

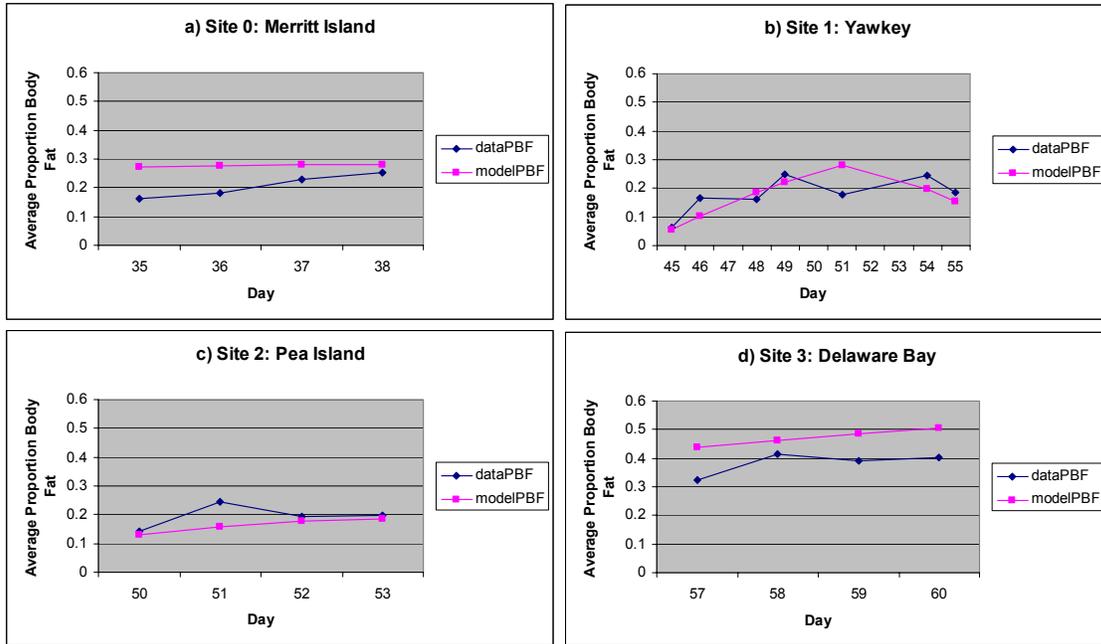


Figure 9: Proportions of body fat. Average estimated proportion body fat of birds measured at stopover sites and average proportion body fat of birds in model, for dates where both values exist. Day 0=April 1.

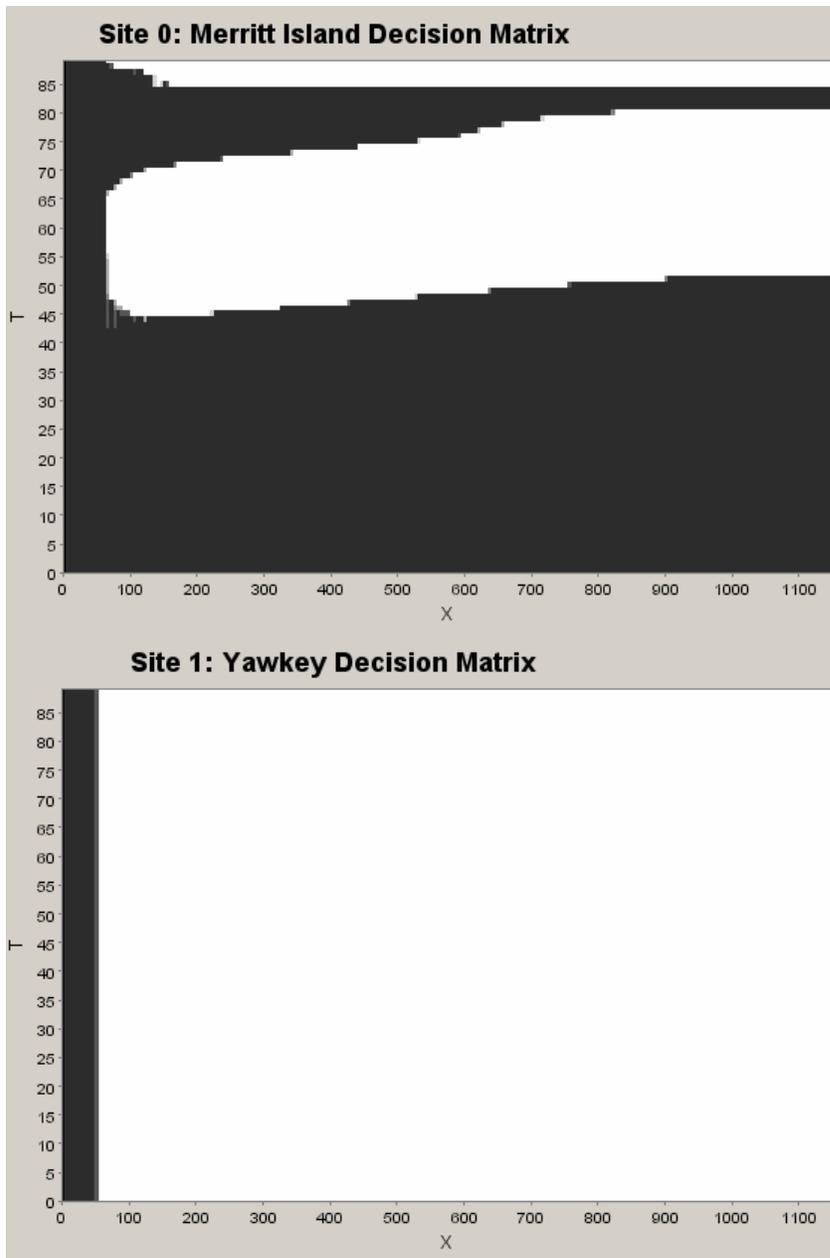


Figure 10: Decision matrix. The panels are the stopover sites, and time is on the y axis and energy is on the x axis. Each time unit is displayed; the average across 5 energy units is displayed. Black represents the decision to stay, white represents the decision to go, and shades of gray represent an average of stay and go decisions.

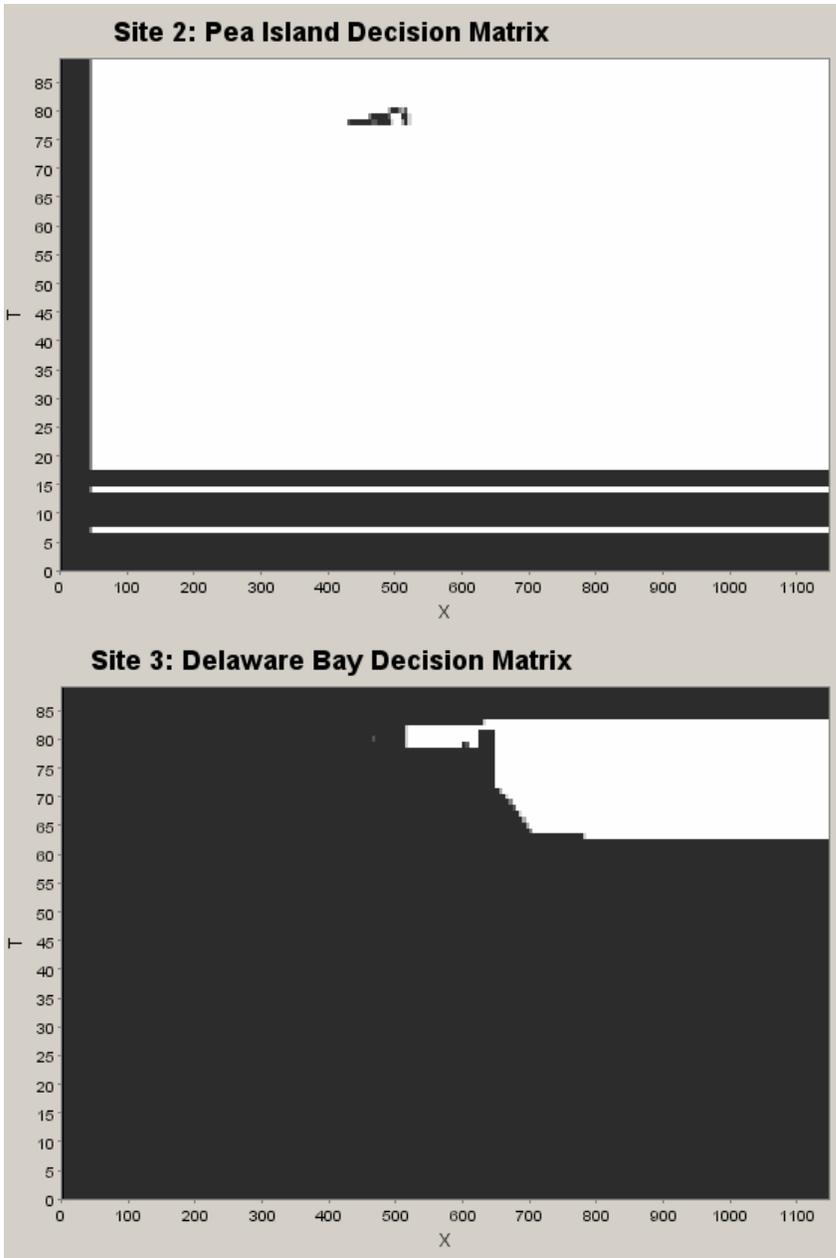


Figure 10: Decision matrix, continued.

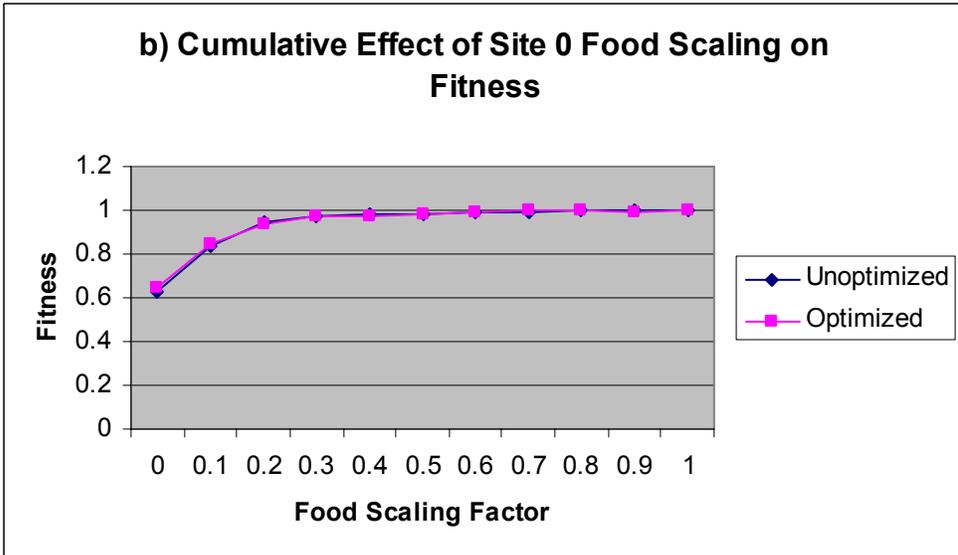
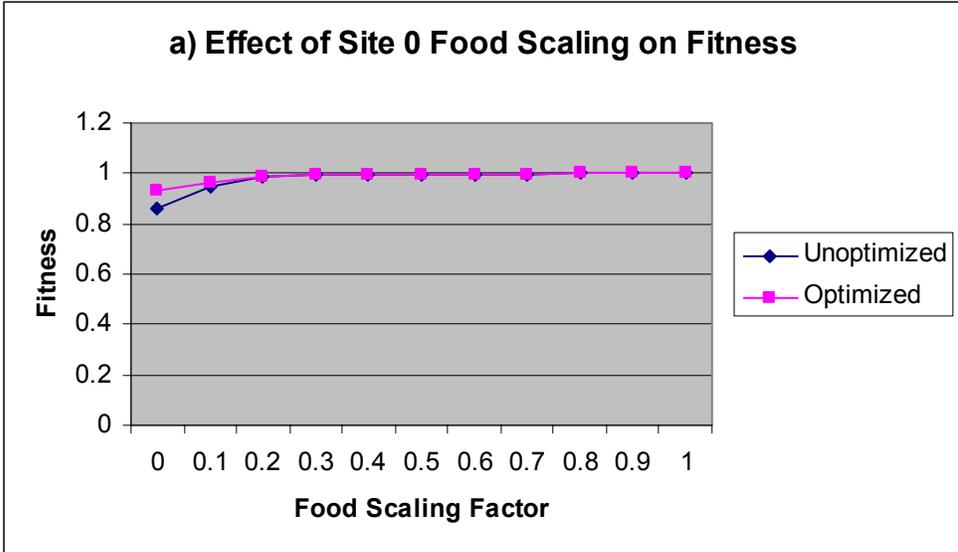


Figure 11: Effect of scaling $x_{gainmin}$ down at Site 0 (Merritt Island) on fitness. Part a shows the effect of one season's change on fitness, for birds that have adapted to the change (optimized) and those that have not (unoptimized). Part b show the effect on fitness if every spring migration has the same change. Figures 11, 13, 15, and 17 are not scaled the same.

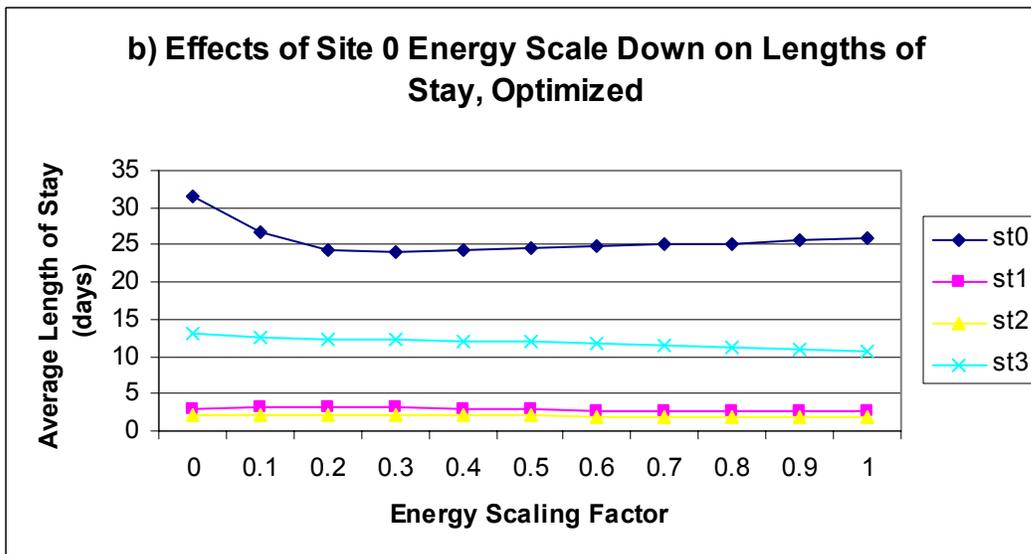
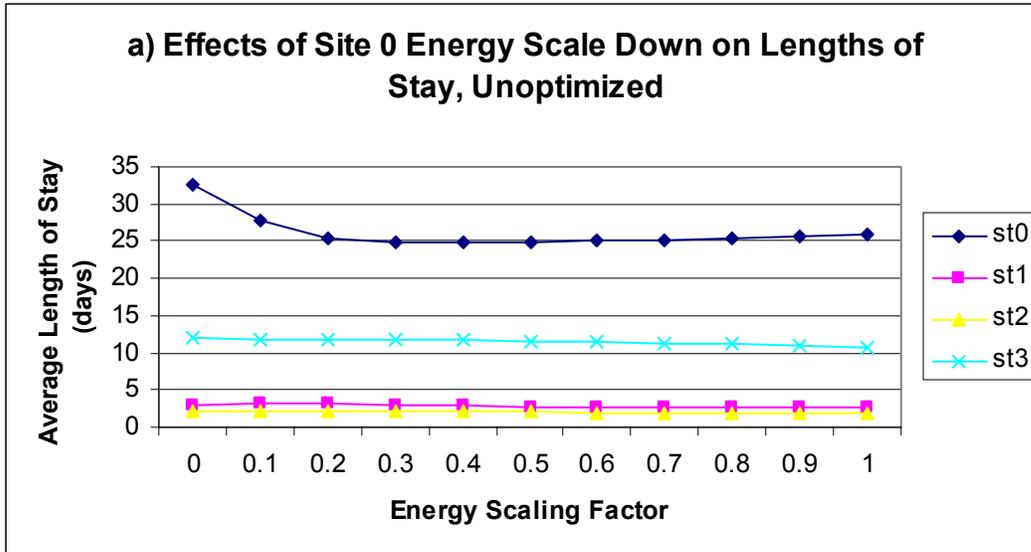


Figure 12: Effects of scaling x_{gainmin} down at Site 0 (Merritt Island) on average lengths of stay. Diamonds represent the length of stay at Site 0, squares the length of stay at Site 1 (Yawkey), triangles the length of stay at Site 2 (Pea Island), and Xs the length of stay at Delaware Bay (Site 3). x_{gainmin} at Site 0 is multiplied by the energy scaling factor. Part a shows the effects on birds that have not adapted to the change (unoptimized), and part b shows the effects on those that have (optimized).

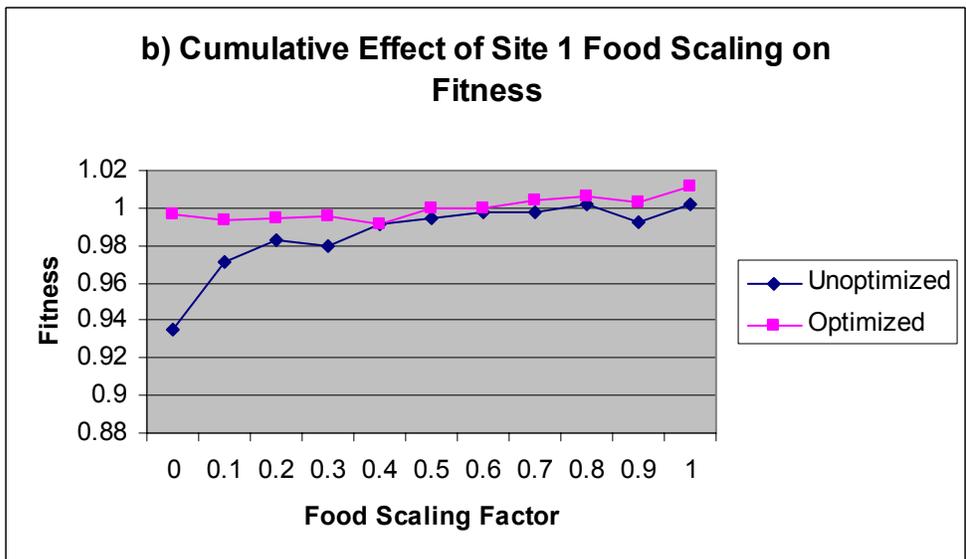
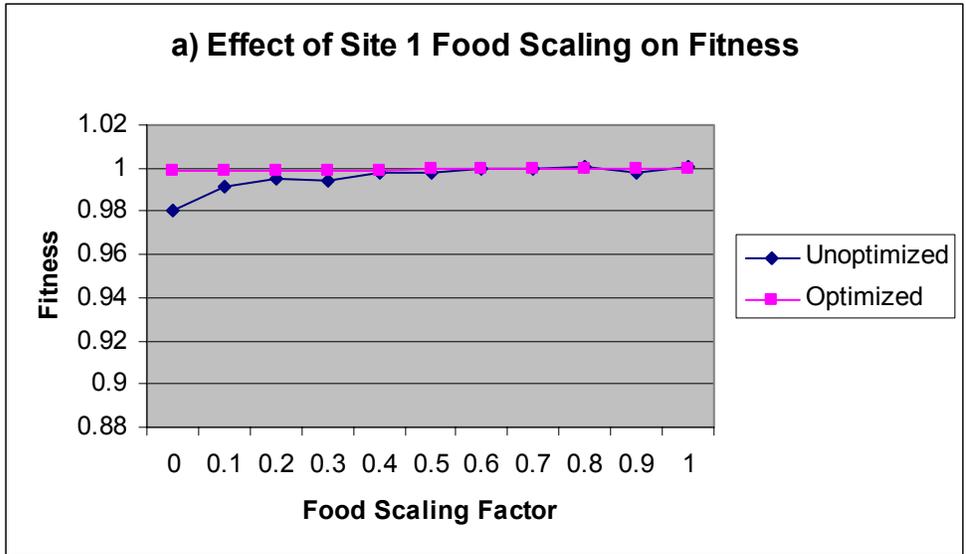


Figure 13: Effect of scaling $x_{gainmin}$ down at Site 1 (Yawkey) on fitness. Part a shows the effect of one season's change on fitness, for birds that have adapted to the change (optimized) and those that have not (unoptimized). Part b show the effect on fitness if every spring migration has the same change. Figures 11, 13, 15, and 17 are not scaled the same.

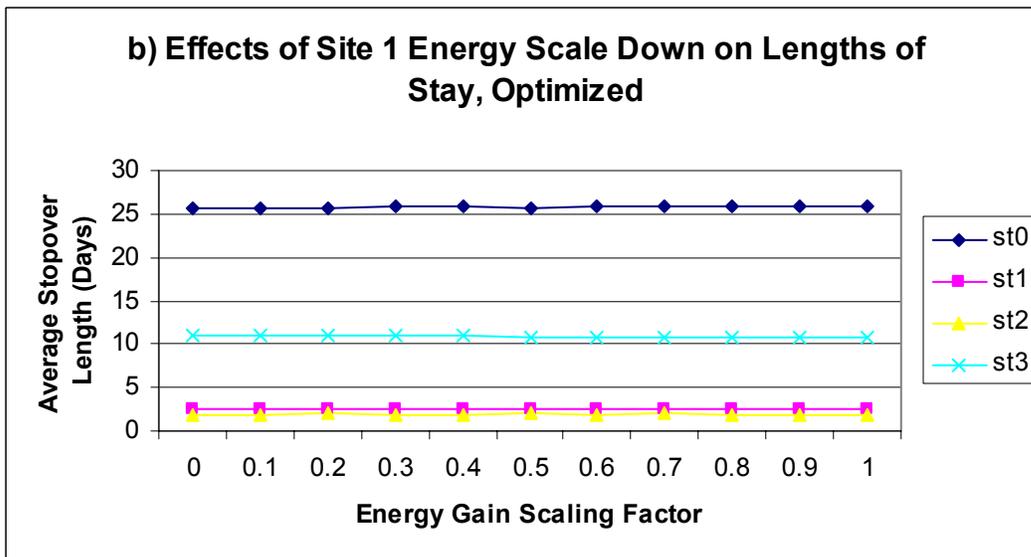
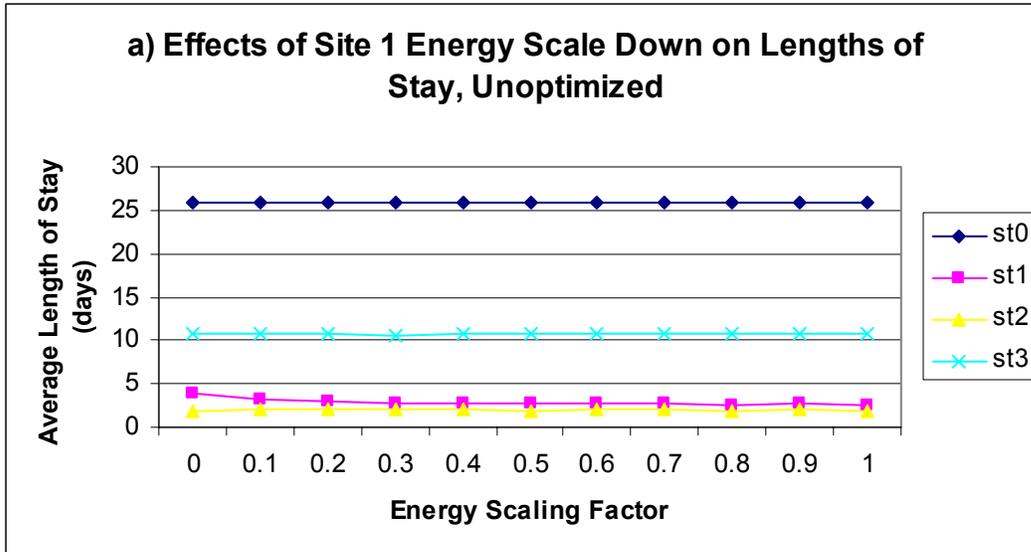


Figure 14: Effects of scaling x_{gainmin} down at Site 1 (Yawkey) on average lengths of stay. Diamonds represent the length of stay at Site 0 (Merritt Island), squares the length of stay at Site 1, triangles the length of stay at Site 2 (Pea Island), and Xs the length of stay at Delaware Bay (Site 3). x_{gainmin} at Site 1 is multiplied by the energy scaling factor. Part a shows the effects on birds that have not adapted to the change (unoptimized), and part b shows the effects on those that have (optimized).

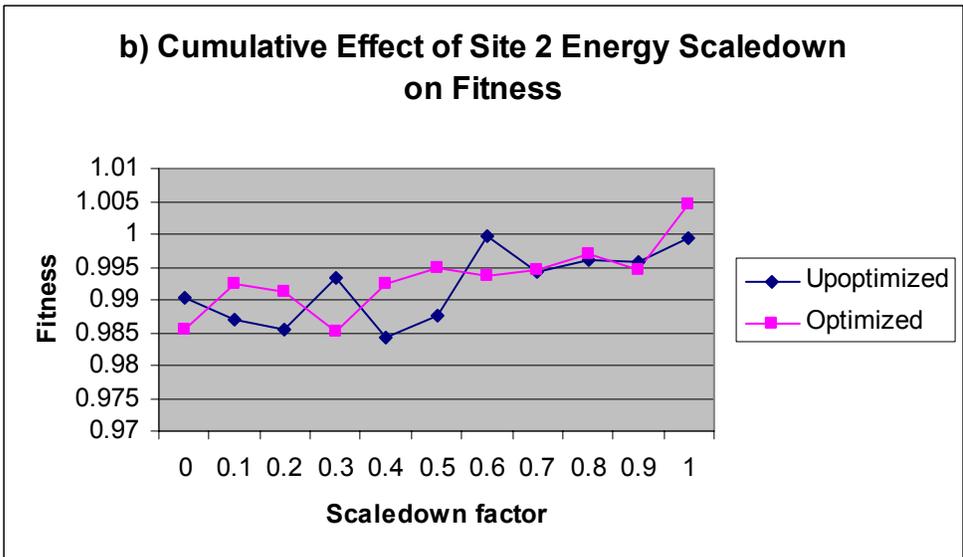
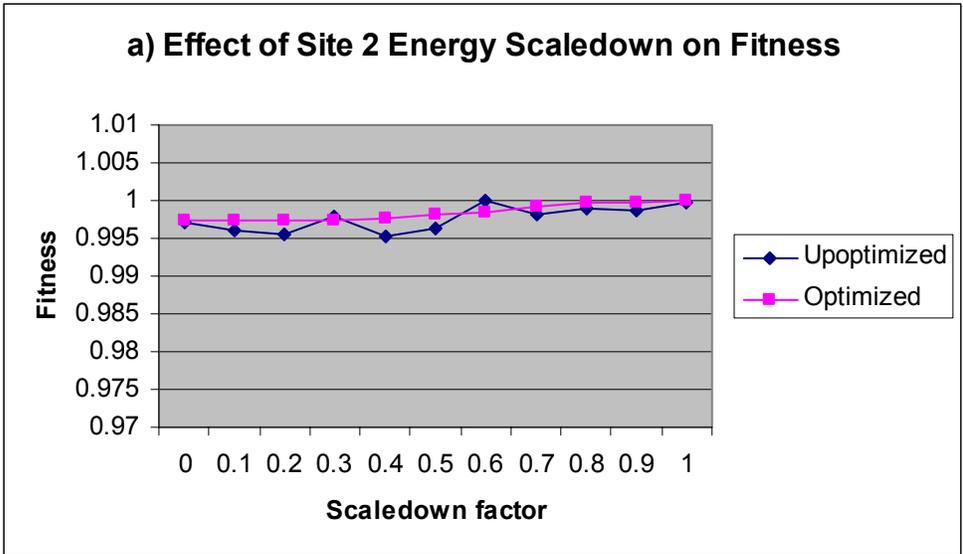


Figure 15: Effect of scaling hourly energy gain rates (k) down at Site 2 (Pea Island) on fitness. Part a shows the effect of one season's change on fitness, for birds that have adapted to the change (optimized) and those that have not (unoptimized). Part b show the effect on fitness if every spring migration has the same change. Figures 11, 13, 15, and 17 are not scaled the same.

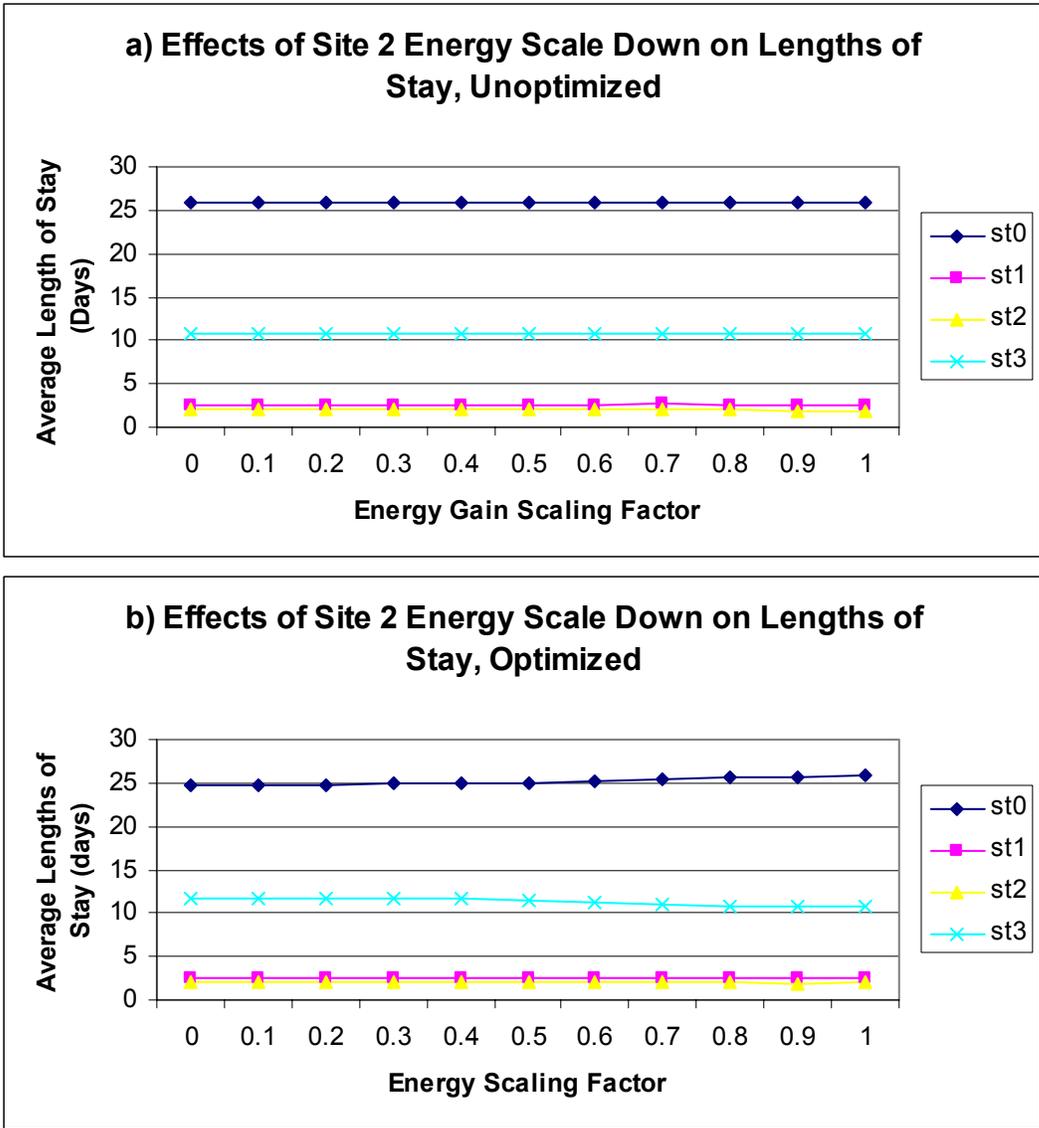


Figure 16: Effects of scaling hourly energy gain rates (k) down at Site 2 (Pea Island) on average lengths of stay. Diamonds represent the length of stay at Site 0 (Merritt Island), squares the length of stay at Site 1 (Yawkey), triangles the length of stay at Site 2, and Xs the length of stay at Delaware Bay (Site 3). The k values at Site 2 are multiplied by the energy scaling factor. Part a shows the effects on birds that have not adapted to the change (unoptimized), and part b shows the effects on those that have (optimized).

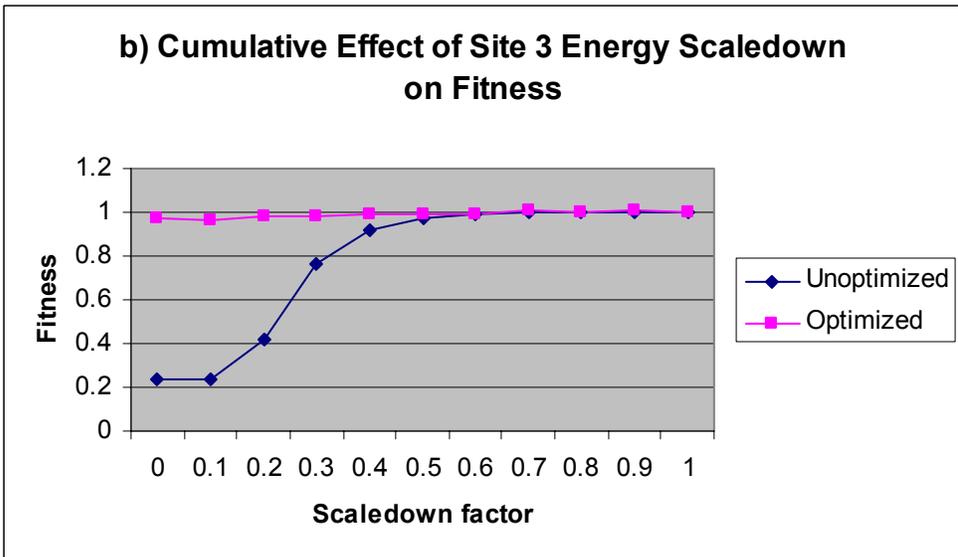
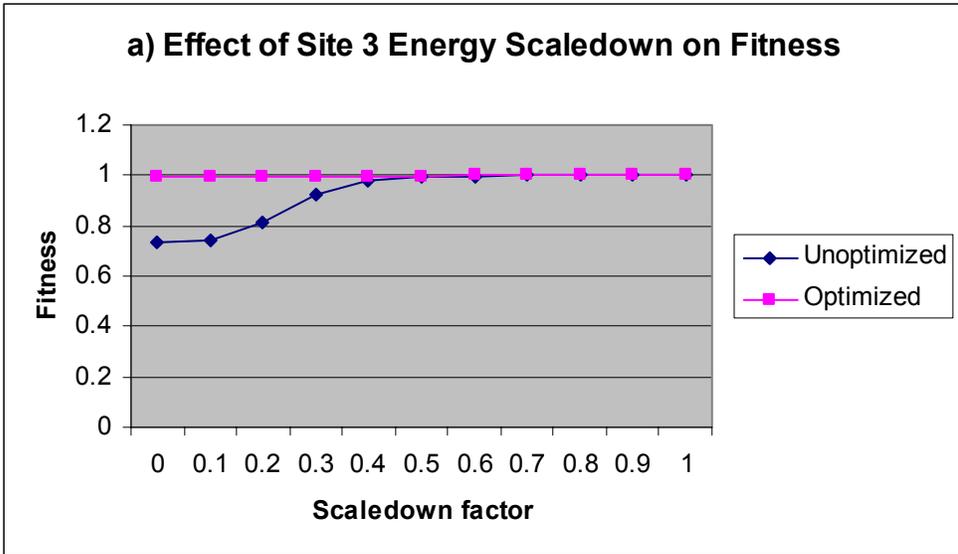


Figure 17: Effect of scaling hourly energy gain rates (k) down at Site 3 (Delaware Bay) on fitness. Part a shows the effect of one season's change on fitness, for birds that have adapted to the change (optimized) and those that have not (unoptimized). Part b show the effect on fitness if every spring migration has the same change. Figures 11, 13, 15, and 17 are not scaled the same.

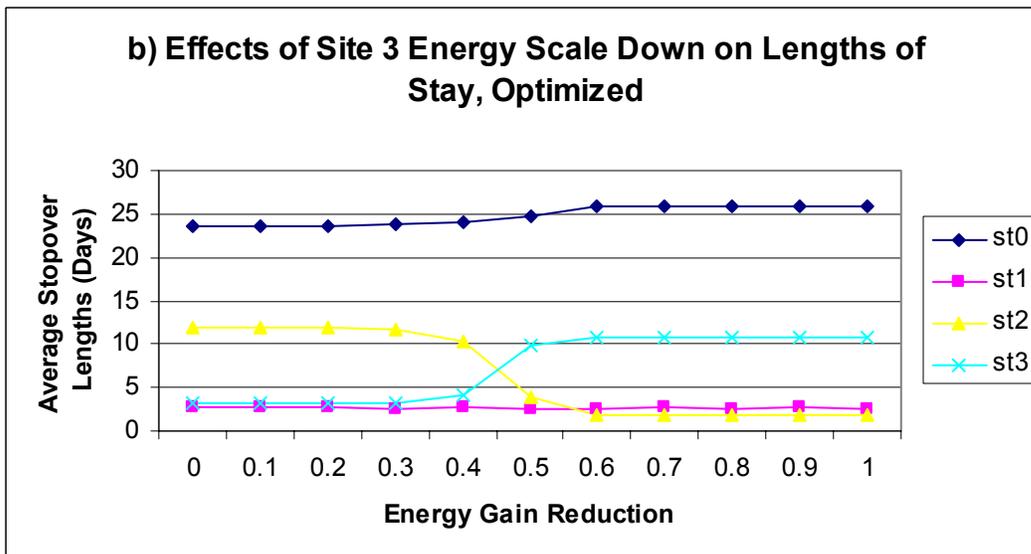
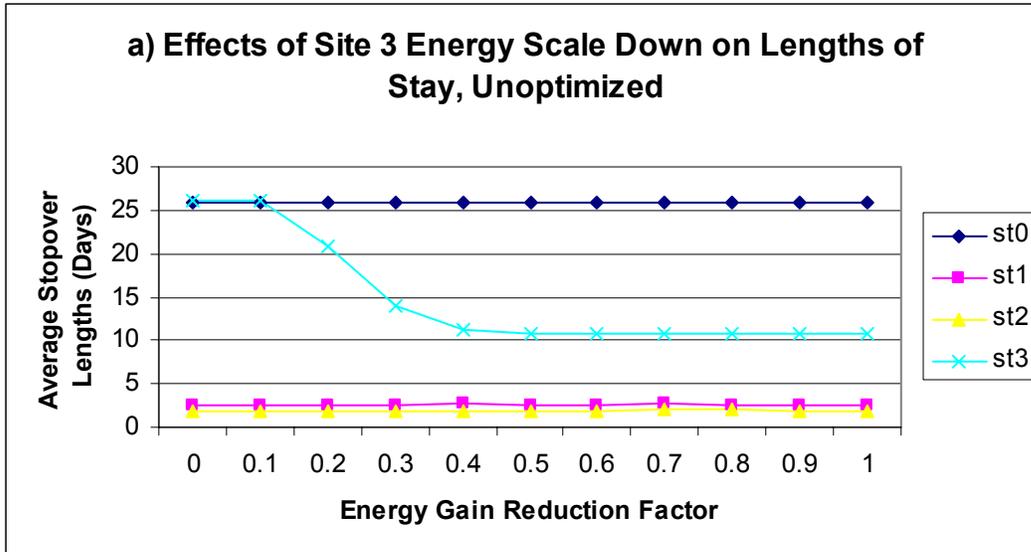


Figure 18: Effects of scaling hourly energy gain rates (k) down at Site 3 (Delaware Bay) on average lengths of stay. Diamonds represent the length of stay at Site 0 (Merritt Island), squares the length of stay at Site 1 (Yawkey), triangles the length of stay at Site 2 (Pea Island), and Xs the length of stay at Site 3. The k values at Site 3 are multiplied by the energy scaling factor. Part a shows the effects on birds that have not adapted to the change (unoptimized), and part b shows the effects on those that have (optimized).

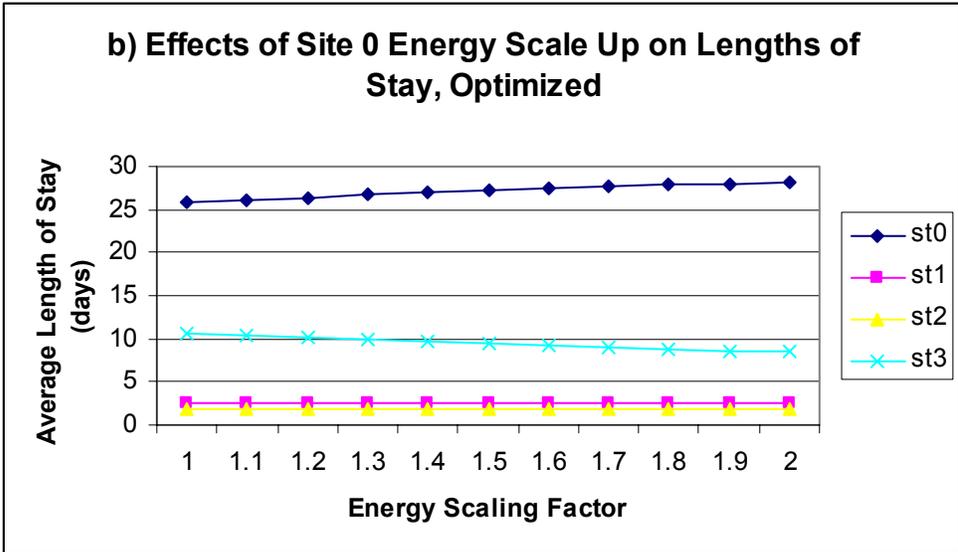
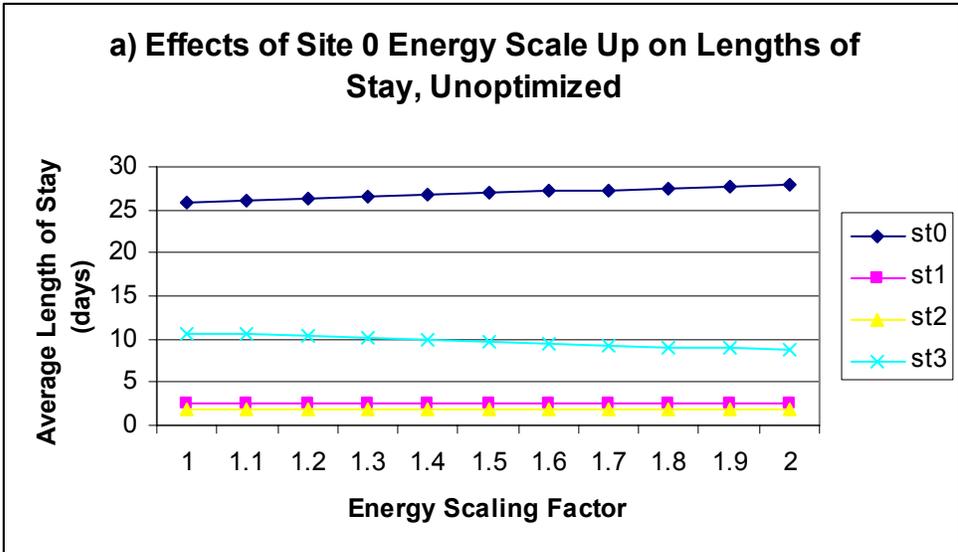


Figure 19: Effects of scaling x_{gainmin} up at Site 0 (Merritt Island) on average lengths of stay. Diamonds represent the length of stay at Site 0, squares the length of stay at Site 1 (Yawkey), triangles the length of stay at Site 2 (Pea Island), and Xs the length of stay at Delaware Bay (Site 3). x_{gainmin} at Site 0 is multiplied by the energy scaling factor. Part a shows the effects on birds that have not adapted to the change (unoptimized), and part b shows the effects on those that have (optimized).

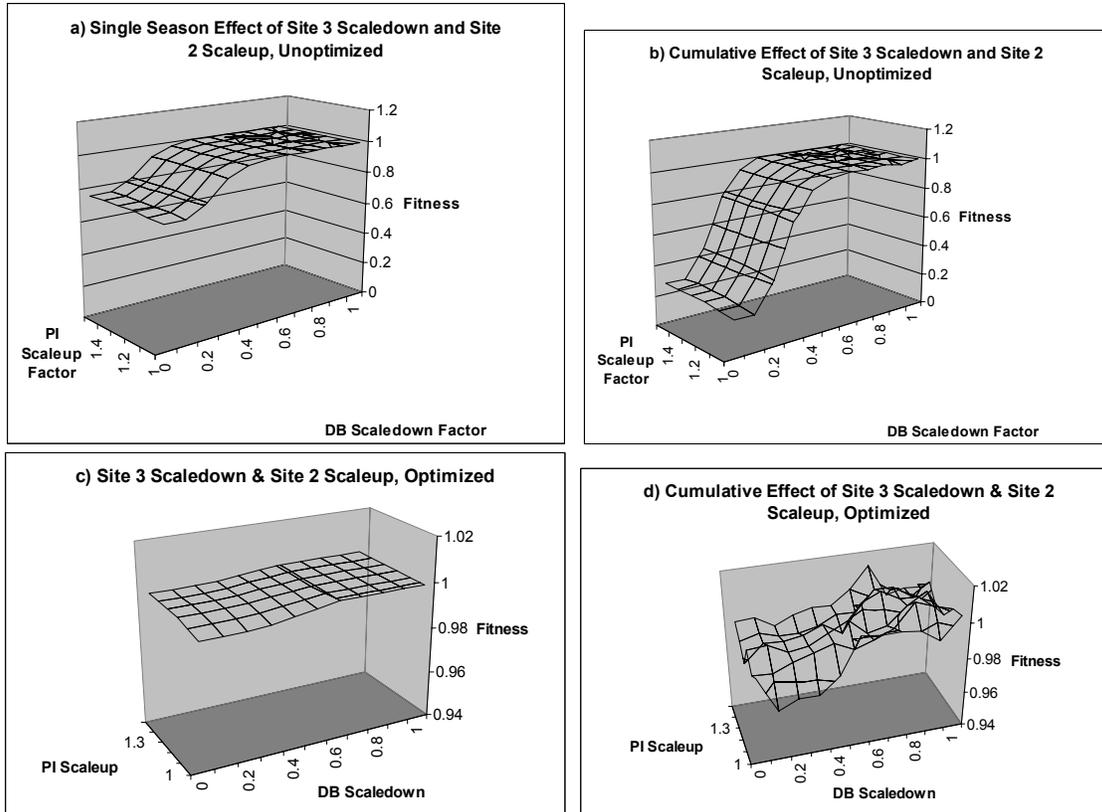


Figure 20: Effects of scaling down the hourly energy gain rates at Site 3 (Delaware Bay) and scaling up the hourly energy gain rates at Site 2 (Pea Island) on fitness. Graphs a and c show the effect of a single season of change on fitness, graphs b and d show the effect of the change continuing into the future on fitness. Graphs a and b show what happens when the birds don't adapt to the change, and graphs c and d show what happens when they do adapt. Graphs are not all to the same scale.

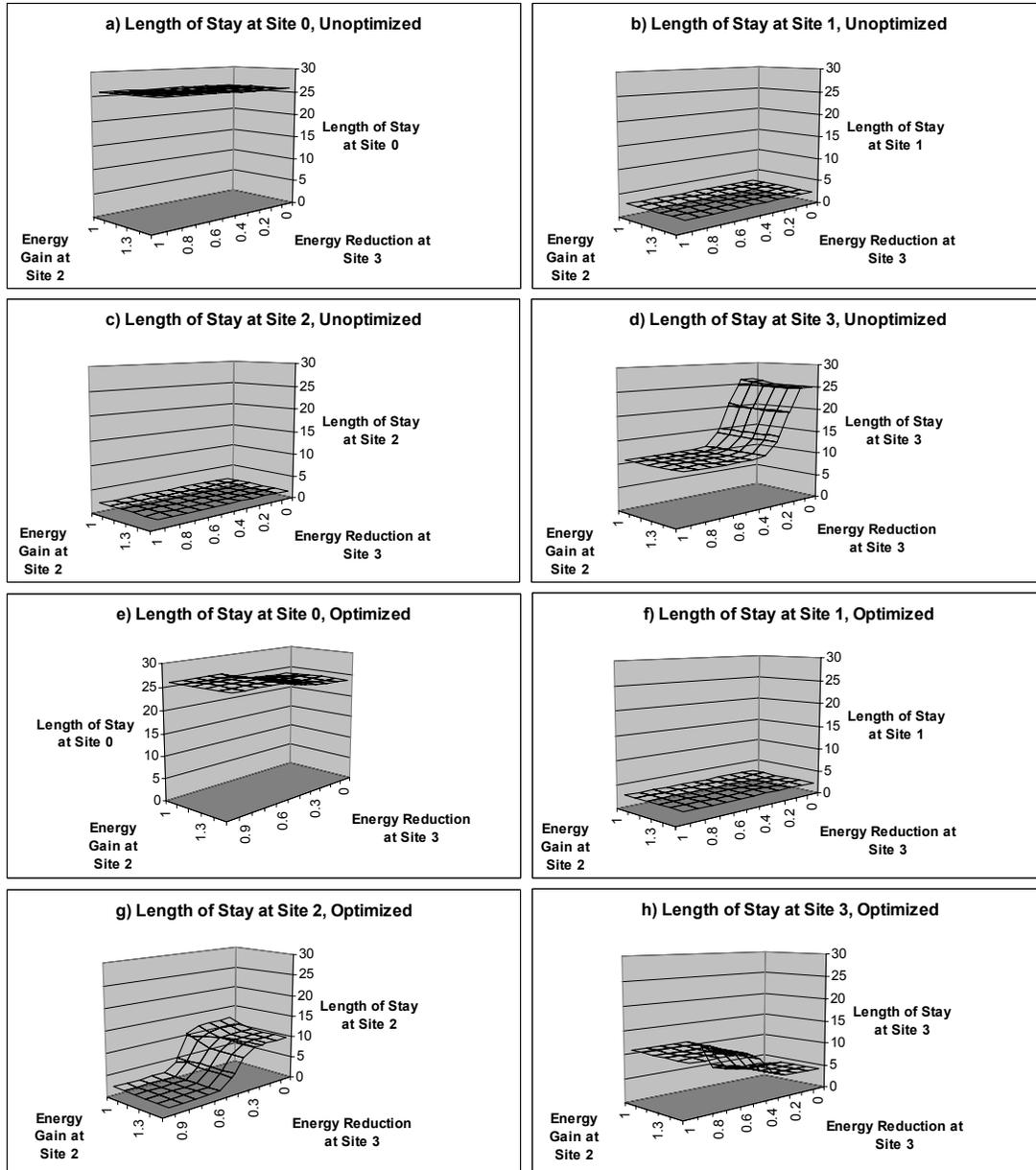


Figure 21: Effects of scaling down the hourly energy gain rates (k) at Site 3 (Delaware Bay) and scaling up k values at Site 2 (Pea Island) on average lengths of stay at the stopover sites. Parts a-d show the effects on birds that are not optimized (following the old strategy) and parts e-h show the effects on birds that are optimized (following a new strategy, based on the changes). k values at Site 3 are multiplied by a factor between 0 and 1, while k values at Site 2 are multiplied by a factor between 1 and 1.5.

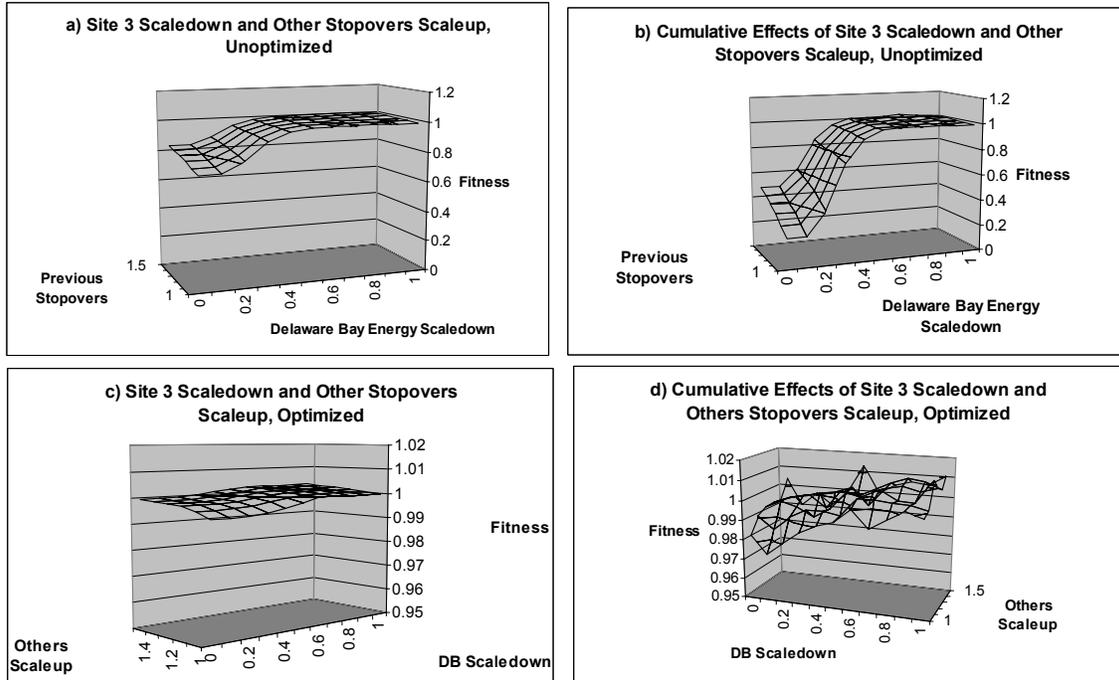


Figure 22: Effects of scaling down the hourly energy gain rates at Site 3 (Delaware Bay) and scaling up the hourly energy gain rates at Site 2 (Pea Island) and $x_{gainmin}$ at Sites 0 and 1 on fitness. Graphs a and c show the effect of a single season of change on fitness, and graphs b and d show the effect of the change continuing into the future on fitness. Graphs a and b show what happens when the birds don't adapt to the change, and graphs c and d show what happens when they do adapt. Graphs are not all to the same scale.

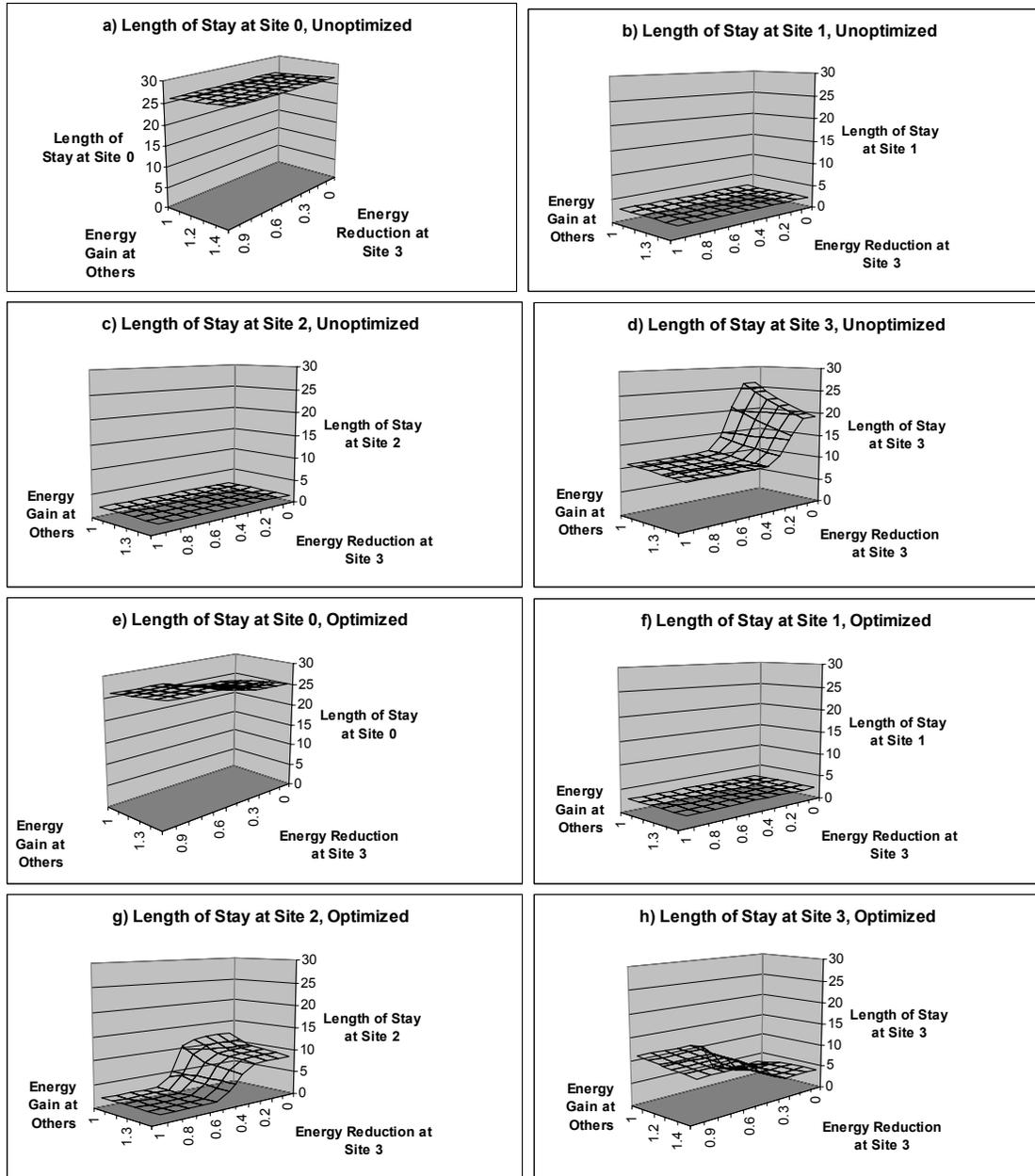


Figure 23: Effects of scaling down the hourly energy gain rates (k) at Site 3 (Delaware Bay) and scaling up k values at Site 2 (Pea Island) and x_{gainmin} at Sites 0 and 1 on average lengths of stay at the stopover sites. Parts a-d show the effects on birds that are not optimized (following the old strategy) and parts e-h show the effects on birds that are optimized (following a new strategy, based on the changes). k values at site 3 are multiplied by a factor between 0 and 1, while k values at site 2 and x_{gainmin} at Sites 0 and 1 are multiplied by a factor between 1 and 1.5.

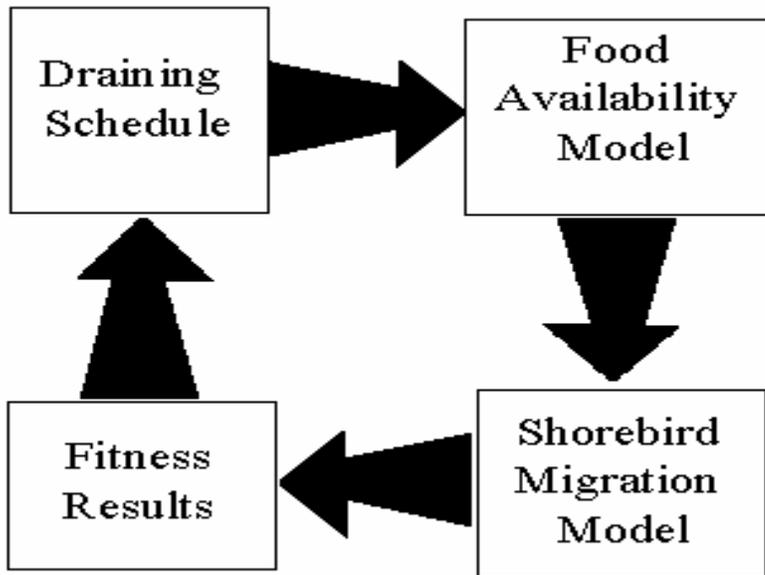


Figure 24: How the shorebird migration model will fit into the rest of the adaptive management plan for managed wetlands.

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APPENDICES

APPENDIX 1: SELECTED SOURCE CODE

```
File Options.java:
//These are the two choices the birds can make
interface Options
{
    int STAY=1, GO=2;
}

File EnergyGainModes.java:
//How energy gain rate at a stopover is defined (DATE was used)
interface EnergyGainModes
{
    int CONSTANT=0, DATE=1;
}

File PredationModes.java:
//Possible predation models (SIMPLE was used)
interface PredationModes
{
    int NONE=0, SIMPLE=1, EFFORT=2, WEIGHT=3, BOTH=4;
}

File SESA.java:
import java.util.*;
/* Semipalmated Sandpipers=SESA. Several species specific parameters below*/
class SESA extends Bird
{
    /*Interface*/
    public static final int TRADITIONAL=0;
    public static final int NEW=1;

    /* Bird or Global Parameters*/
    public static int xMax=1150; //based on NJ data and my best calculations
    public static int tMax=90; //using 6/30
    public static double avFlightSpeed=32; //tuned parameter

    public static double a=0.7409198;
    /*a was calculated by setting Pmet from Norberg 1996 equal to Pmet from Kvist et
    al. 2001
    using an average weight for both models of 25.3 g (Lyons and Haig 1995b) and
    wingspan of 30 cm (Chandler 1989).
    */
    public static double b=0.001; // no longer used

    public static double fuelValue=36.850394; //kJ/g, based on 39 kJ/g for fat, 18
    kJ/g for protein,
    /*and estimate that they get 5% of energy from protein (Jenni and Jenni Eiermann
    1998) */

    public static double expectedFutureReproduction=0.777636939; //actually
    expectedFutureReproduction=1*expectedSurvivalUntilNextSpring

        //Adjusted to make spring survival*rest of year survival=0.7

    public static double avLeanMass=20.109944; //From Lyons and Haig 1995b, corrected
    to not include protein energy

    public static double flightExponent=0.35; //From Kvist et al. 2001

    public static int xMaxGain=100; //maximum kJ/day energy bird can store

    public static int flightModel=NEW;
    /* Constructor for SESA. Call to super calls Bird constructor. */

    SESA (int xSet, int sSet, int tSet, int sMax)
    {

        super(xSet, sSet, tSet, xMax, tMax, avFlightSpeed, a, fuelValue, avLeanMass, flightExponent
        , sMax);
    }
}
```

```

    }

}

From the file Bird.java:
import java.util.*;

// This is the base class for all birds. The birds used are SESA
class Bird
{
    final int xMax, tMax; //maximum level of energy, and number of days in migration
season
    static double avFlightSpeed; //We're assuming constant speed in calm air
    int x, s, t; //current energy level, location, and date
    boolean alive;
    int[] lengthOfStay;
    double a, fuelValue, avLeanMass, flightExponent; // flight and body parameters

    //initializes new bird object
    Bird (int xSet, int sSet, int tSet, int xMaxSet, int tMaxSet, double
flightSpeedSet, double aSet, double fuelSet,
        double leanSet, double expoSet, int sMax) {
        x=xSet;
        s=sSet;
        t=tSet;
        xMax=xMaxSet;
        tMax=tMaxSet;
        avFlightSpeed=flightSpeedSet;
        a=aSet;
        fuelValue=fuelSet;
        avLeanMass=leanSet;
        flightExponent=expoSet;
        lengthOfStay=new int[sMax];
        alive=true;
    }

    //Calculates the amount of energy used in flight. Based on my new flight model,
which is based on Kvist et al. 2001
    int flightEnergyCost(int groundDistance, double groundSpeed) {
        double reverseFlightExponent=1-flightExponent;
        double airDistance=avFlightSpeed/groundSpeed*groundDistance;
        double
term1=Math.exp(reverseFlightExponent*Math.log(avLeanMass+x/fuelValue));
        double term2=term1-
airDistance*3.6*reverseFlightExponent*a/groundSpeed/fuelValue;
        /*if (term2<0) //If the energy required to get there > energy have,
formula doesn't work right
            return x+100; //So return value that won't let the bird leave*/
        double xnew=fuelValue*(Math.exp(Math.log(term2)/reverseFlightExponent)-
avLeanMass);
        return (int) (x-xnew);
    }

    int flightEnergyCost(int groundDistance, double groundSpeed, double b) {
        double airDistance=avFlightSpeed/groundSpeed*groundDistance;
        double term1=airDistance*a*b/2.0+1/Math.sqrt(1+b*x);
        double term2=1/term1/term1;
        double xnew=(term2-1)/b;
        return (int) (x-xnew);
    }

    // How many days does it take to get there
    int flightTimeCost(int groundDistance, double groundSpeed) {
        return (int) (groundDistance/groundSpeed/24+1);
    }

    //Run a bird through migration. generateFitness must be run first.
    void migrate (PeepHerderBase topLevel) {
        while (s<topLevel.sMax && t <= tMax) {

```

```

        if (x<=0)
        {
            alive=false;
            if (topLevel.putBirdHistories)
                outputCurrentState(topLevel);
            return;
        }
        topLevel.sites[s].numberAt[t]++; //keeps track of how many birds
are at each stop
        topLevel.sites[s].averageEnergy[t]+=x; //sum up energy of birds
(divide later)
        lengthOfStay[s]++; //keeps track of how long spent at each stop
        if (topLevel.putBirdHistories)
            outputCurrentState(topLevel); //records where bird is when
        if (topLevel.decision [x] [s] [t]==Options.STAY ||
topLevel.sites[s].currentWind[t]<avFlightSpeed)
        {
            x=x+topLevel.sites[s].energyGain(x,t);
            if (topLevel.putBirdHistories)
                topLevel.prn("Energy Gain:
"+topLevel.sites[s].energyGain(x,t)+", Hours Spent Foraging:
"+topLevel.sites[s].timeSpentForaging(x,t));
            double r=topLevel.randGen.nextDouble();//Math.random();
            if (r>topLevel.sites[s].survivalRate(x,t)) {
                alive=false;
                if (topLevel.putBirdHistories)
                    outputCurrentState(topLevel);
                return;
            }
            t++;
        }
        else {
/*
            if (topLevel.sites[s].currentWind[t]<0) {
                topLevel.prn("Wind Speed
"+topLevel.sites[s].groundSpeeds[sp]+" sp "+sp+", wind num "+wind+", sumprob "+sumProb);
                alive=false;
                outputCurrentState(topLevel);
                return;
            }
            if ((s==(topLevel.sMax-1)) &&
(topLevel.sites[topLevel.sMax].windy))
            {
                if (SESA.flightModel==SESA.NEW)
                    x-
=flightEnergyCost(topLevel.sites[s].distToNext/2, topLevel.sites[s].currentWind[t]);
                //flies to next spot, uses up energy and
                else
                    x-
=flightEnergyCost(topLevel.sites[s].distToNext/2,
topLevel.sites[s].currentWind[t],SESA.b); //flies to next spot, uses up energy and
                t+=flightTimeCost(topLevel.sites[s].distToNext/2,
topLevel.sites[s].currentWind[t]); // time
                if (t>tMax)
                    break;
                if (SESA.flightModel==SESA.NEW)
                    x-
=flightEnergyCost(topLevel.sites[s].distToNext/2, topLevel.sites[s+1].currentWind[t]);
                //flies to next spot, uses up energy and
                else
                    x-
=flightEnergyCost(topLevel.sites[s].distToNext/2,
topLevel.sites[s+1].currentWind[t],SESA.b); //flies to next spot, uses up energy and
                if (topLevel.sites[s+1].currentWind[t]<0)
                {
                    alive=false;
                    if (topLevel.putBirdHistories)
                    {
                        topLevel.prn("Caught in Bad Wind!");
                        outputCurrentState(topLevel);
                    }
                }
                return;
            }
        }
    }
}

```

```

    }
    t+=flightTimeCost(topLevel.sites[s].distToNext/2,
topLevel.sites[s+1].currentWind[t]); // time
    if (t>tMax)
        break;
    }
    else
    {
        if (SESA.flightModel==SESA.NEW)
            x-
=flightEnergyCost(topLevel.sites[s].distToNext, topLevel.sites[s].currentWind[t]);
//flies to next spot, uses up energy and
        else
            x-
=flightEnergyCost(topLevel.sites[s].distToNext, topLevel.sites[s].currentWind[t],SESA.b);
//flies to next spot, uses up energy and
            t+=flightTimeCost(topLevel.sites[s].distToNext,
topLevel.sites[s].currentWind[t]); // time
        }
        s++;
    }
}
if (x<=0)
    alive=false;
if (topLevel.putBirdHistories)
{
    topLevel.pr("Final: ");
    outputCurrentState(topLevel);
}
if (alive)
    for ( int tSub=t;tSub<=tMax;tSub++) //record presense at final stop
for remainder of time steps
        topLevel.sites[s].numberAt[tSub]++;
}

void outputCurrentState(PeepHerderBase topLevel) {
    topLevel.pr("Time: "+t+", Site: "+s+", Energy: "+x);
    if (alive)
        topLevel.prn(" alive");
    else
        topLevel.prn(" DEAD");
}
}

```

From BreedingSite.java:

```
import java.util.*;
```

```
/* A BreedingSite is a type of Site. It also has breeding specific parameters as well.*/
class BreedingSite extends Site
```

```
{
    int distToNext=0;
/*Breeding site parameters*/
    public double rBreeding=0.3549; //tuned to give average fitness of 1
    public int energyThreshold=500; //tuned
    public int optimalDate=66;
    public boolean energyPenalty=true;
    public boolean arrivalPenalty=true;
    public double avArrivalTime=0;
    public double avArrivalEnergy=0;
    public int [] arrivalTimeRange=new int[SESA.tMax+1];
    public int [] arrivalEnergyRange=new int[SESA.xMax+1];

```

```
BreedingSite (String nameSet, String latSet, String lonSet, int open)
{
    super(nameSet,latSet,lonSet,0,open);
    super.windy=false;
}

```

```

    BreedingSite (String nameSet, String latSet, String lonSet, int open, double
probSet[])
    {
        super(nameSet,latSet,lonSet,0,null,1,open, probSet);
        super.windy=true;
    }

    /*Set to be one x<maxEnergy/5, slope down to 0 at x=0*/
    double lowEnergyFactor(int x)
    {
        double lowEnergyPenalty=1.0/energyThreshold;
        if (energyPenalty)
            return Math.min(lowEnergyPenalty*x,1);
        else
            return 1;
    }

    /* Set to be one at optimal date, and slope down to 0 at closing date */
    double lateArrivalFactor(int t) {
        double lateArrivalPenalty=1.0/(SESA.tMax-optimalDate);
        if (arrivalPenalty)
            return Math.max(0.0,1-Math.abs(t-optimalDate)*lateArrivalPenalty);
        else
            return 1;
    }

    /* Supersedes procedure for site to give expected offspring this year*/
    double expectedCurrentReproduction(int x, int t) {
        return rBreeding*lowEnergyFactor(x)*lateArrivalFactor(t);
    }
}

From Site.java:
import java.util.*;

/* A site object is created for each stopover and the breeding site (see below). It
contains parameters unique to that site. */
class Site
{
    /*Site parameters*/
    String name;
    String lat, lon;
    int distToNext;
    int energyConst=30; //averaged together energy rates for all stopovers and
dates
    double survivalConst=1;
    double baseSurvival=1;
    double survivalIntensityExponent=2;
    double survivalWeightExponent=3;
    int openDate=0;
    double averageLengthOfStay=0;
    int[] lengthOfStayRange=new int[SESA.tMax+2];
    public int numVisited=0;
    public int numSkipped=0;
    int maxHoursForaging=3;
    int energyUsePerDay=74;
    int xMinGain=10;
    int [] numberAt=new int[SESA.tMax+1];
    double [] averageEnergy=new double[SESA.tMax+1];
    double [] currentWind=new double[SESA.tMax+1];
    double groundSpeeds[]={-9,9,27,45,63,81,99,117,135};
    double groundSpeedProbs[];
    int energyLevels[][];
    int predationModel=PredationModes.SIMPLE;
    int energyGainModel=EnergyGainModes.DATE;
    boolean windy=true;
    boolean extraEating=true;
    public static final int maxEnergyDates=13;
}

```

```

Site (String nameSet, String latSet, String lonSet, int distSet, int open) {
    name=nameSet;
    lat=latSet;
    lon=lonSet;
    distToNext=distSet;
    openDate=open;
}

Site (String nameSet, String latSet, String lonSet, int distSet, int
energySet[][], double survSet, int open, double probSet[]) {
    name=nameSet;
    lat=latSet;
    lon=lonSet;
    distToNext=distSet;
    energyLevels=energySet;
    baseSurvival=survSet;
    openDate=open;
    groundSpeedProbs=probSet;
}

int energyGain (int x)
{
    int var=energyConst*maxHoursForaging-energyUsePerDay;
    if (var<0)
    {
        int hrs=maxHoursForaging;
        while (hrs<24 && var<0)
        {
            hrs++;
            var=energyConst*hrs-energyUsePerDay;
        }
    }
    else if (var>SESA.xMaxGain)
        var=SESA.xMaxGain;
    if (var>(SESA.xMax-x))
        return SESA.xMax-x;
    else
        return var;
}
int energyGain (int x, int t)
{
    if (energyGainModel==EnergyGainModes.CONSTANT)
        return energyGain(x);
    int i=energyLevels[0].length-1;
    while (energyLevels[0][i]>t)
        i--;
    int var=energyLevels[1][i]*maxHoursForaging-energyUsePerDay;
    /*
    if (var<0 && extraEating)
    {
        int hrs=maxHoursForaging;
        while (hrs<24 && var<0)
        {
            hrs++;
            var=energyLevels[1][i]*hrs-energyUsePerDay;
        }
    }
    */
    if (var<xMinGain && extraEating)
        var=xMinGain;
    else if (var>SESA.xMaxGain)
        var=SESA.xMaxGain;
    if (var>(SESA.xMax-x))
        return SESA.xMax-x;
    else
        return var;
}

int timeSpentForaging (int x, int t)
{
    int i=energyLevels[0].length-1;
    while (energyLevels[0][i]>t)
        i--;
}

```

```

int var=energyLevels[1][i]*maxHoursForaging-energyUsePerDay;
if (var<0 && extraEating)
{
    int hrs=maxHoursForaging;
    while (hrs<24 && var<0)
    {
        hrs++;
        var=energyLevels[1][i]*hrs-energyUsePerDay;
    }
    return hrs;
}
else if (energyLevels[1][i]==0)
    return maxHoursForaging;
else
    return Math.min(
        Math.max(
            1,
            Math.abs(Math.round((SESA.xMax-
x+energyUsePerDay)/(long)(energyLevels[1][i])))),
        Math.min(
            Math.abs(Math.round((SESA.xMaxGain+energyUsePerDay)/(long)(energyLevels[1][i])),
            maxHoursForaging));
}

double survivalRate()
{
    return baseSurvival;
}

/*From Weber, Ens, & Houston 1998*/
double survivalRate(int x, int t)
{
    if (predationModel==PredationModes.NONE)
        return 1;
    else if (predationModel==PredationModes.SIMPLE)
        return survivalRate();
    double deathConst=1-survivalConst;
    double
numerator=Math.exp(survivalWeightExponent*Math.log(x+energyGain(x,t)))-
Math.exp(survivalWeightExponent*Math.log(x));
    if (predationModel==PredationModes.WEIGHT)
        return baseSurvival-
deathConst*numerator/survivalWeightExponent/(timeSpentForaging(x,t)/24.0)/energyGain(x,t)
;
    double
num2=Math.exp(survivalIntensityExponent*Math.log(timeSpentForaging(x,t)/24.0));
    if (predationModel==PredationModes.EFFORT)
        return baseSurvival-deathConst*num2;
    return baseSurvival-
deathConst*numerator/survivalWeightExponent/(timeSpentForaging(x,t)/24.0)/energyGain(x,t)
*num2;
}

void setWeather() {
    for (int t=0; t<=SESA.tMax; t++) {
        if (windy)
        {
            double wind=Math.random();
            int sp=0;
            double sumProb=0;
            do
            {
                sumProb+=groundSpeedProbs[sp];
                sp++;
            } while (wind>sumProb);
            sp--;
            currentWind[t]=groundSpeeds[sp];
        }
        else
            currentWind[t]=SESA.avFlightSpeed;
    }
}

```

```

    }
}

void clearNumbers()
{
    for (int i=0;i<numberAt.length;i++)
    {
        numberAt[i]=0;
        averageEnergy[i]=0;
    }
    for (int t=0; t<=(SESA.tMax+1); t++)
        lengthOfStayRange[t]=0;
    averageLengthOfStay=0;
    numVisited=0;
    numSkipped=0;
}

/* Unless the bird ends up at a breeding site, reproduction for that year is zero*/
/*   double expectedCurrentReproduction(int x, int t) {
    return 0;
}
*/
}

From PeepHerderBase.java:
import java.util.*;

/*The original main class, which runs the model and so on*/
class PeepHerderBase
{
    /* Array of sites. Latitude and longitude are currently not used by program.*/
    double wind1[]={1.31926121372032E-03,3.56200527704486E-
02,0.441952506596306,0.361477572559367,0.130606860158311,0.025065963060686,3.957783641160
95E-03,0,0};
    double wind2[]={9.43396226415094E-
03,0.230188679245283,0.364150943396226,0.262264150943396,0.111320754716981,1.886792452830
19E-02,1.88679245283019E-03,1.88679245283019E-03,0};
    double wind3[]={5.61797752808989E-
03,0.140449438202247,0.322097378277154,0.308988764044944,0.157303370786517,5.430711610486
89E-02,7.49063670411985E-03,3.74531835205993E-03,0};
    double wind4[]={1.89393939393939E-
02,0.113636363636364,0.208333333333333,0.214015151515152,0.231060606060606,0.145833333333
333,5.11363636363636E-02,1.13636363636364E-02,5.68181818181818E-03};
    double wind5[]={1.30841121495327E-02,8.22429906542056E-
02,0.121495327102804,0.224299065420561,0.205607476635514,0.194392523364486,0.112149532710
28,3.73831775700935E-02,9.34579439252337E-03};

    int food1[][]= {{0},{10}};
    int food2[][]=
    {
        {0,17,39,50},
        {10,11,10,9}};
    int food3[][]=
    {
        {0,7,14,21,28,35,42,49,56,63,70},
        {11,34,17,15,22,48,36,48,75,56,35}};
    int food4[][]= {{0,19,33,47,63,79},
                    {0,3,89,100,159,33}};

    public Site[] sites =
    {
        new Site ( "Merritt Island", "283859N","0804158W", 528, food1,
0.998, 0, wind1 ),
        new Site ( "Yawkey", "331331N","0791320W", 438, food2, 0.997, 0,
wind2 ),
        new Site ( "Pea Island", "354101N","0752859W", 388, food3, 0.997,
0, wind3 ),
        new Site ( "Delaware Bay", "391006N","0751053W", 2532, food4,
0.997, 0, wind4 ),
    }
}

```

```

        new BreedingSite ( "La Perouse Bay", "584500N","0932458W", 47,
wind5 )
    };

    /*Program/Simulation parameters*/
    int sMax=sites.length-1;
    public int birds=100; //how many simulations to run
    public int xStartMin=0; //Range of start values for simulations.
    public int xStartMax=300; //Energy: Tuned Result
    public int tStartMin=0; //Date: Based loosely on general info from
Jaime Collazo and tuning
    public int tStartMax=45; //Equals arrival at Merritt Island 4/1-5/16

    public boolean fitnessRun=false;
    public boolean putBirdHistories=true;
    public PeepHerder10 parent=null;
    public Random randGen=new Random();
    /*Matricies: These are all filled using generateFitness
    fitness[x][s][t] is the same as Fs(x,t) from Clark and Mangel. It is the max of
vStay and vGo
    vStay[x][s][t] is the same as V1s(x,t) from Clark and Mangel.
    vGo[x][s][t] is the same as V3s(x,t) from Clark and Mangel.
    decision[x][s][t] is the matrix of decisions the birds should make, based on
current conditions
    */
    double[][][] fitness = new double[SESA.xMax+1] [sMax+1] [SESA.tMax+1];
    double[][][] vStay = new double[SESA.xMax+1] [sMax+1] [SESA.tMax+1];
    double[][][] vGo = new double[SESA.xMax+1] [sMax+1] [SESA.tMax+1];
    int[][][] decision = new int[SESA.xMax+1] [sMax+1] [SESA.tMax+1];

    /*Stats*/
    double mortality;
    int numDead=0, numAlive=0;
    double avReproduction, numFemaleOffspring=0, avFitness=0, startFit=0;
    int reprScale=100;
    int [] offspringRange=new int[reprScale+1];

    public PeepHerderBase(PeepHerder10 par)
    {
        super();
        parent=par;
    }

    public PeepHerderBase()
    {
        super();
    }

    public double expectedFutureReproduction(int s)
    {
        return SESA.expectedFutureReproduction;
    }

    /* This is a key method. It uses backwards iteration to find fitness at different
states and generate
    a strategy for a bird to follow to maximize its fitness*/
    void generateFitness ()
    {
        /*Final time step*/
        for (int s=0; s<=sMax; s++)
            for (int x=1; x<=SESA.xMax; x++)
                fitness [x] [s] [SESA.tMax] =
expectedFutureReproduction(s);
        /*At breeding site*/
        for (int x=1; x<=SESA.xMax; x++)
            for (int t=0; t<=SESA.tMax; t++)
            {
                BreedingSite b=(BreedingSite) sites[sMax];
                // prn("x: "+x+" t: "+t+" Repro:
"+sites[sMax].expectedCurrentReproduction(x,t));

```

```

+
        fitness [x] [sMax] [t] = b.expectedCurrentReproduction(x,t)
        expectedFutureReproduction(sMax);
    }
    /*Minimum energy*/
    for (int s=0; s<=sMax; s++)
        for (int t=0; t<=SESA.tMax; t++)
            fitness [0] [s] [t] = 0;
    /*Backward iteration of all other states*/
    for (int t=SESA.tMax-1; t>=0; t--)
        for (int x=1; x<=SESA.xMax; x++)
            for (int s=0; s<=sMax; s++)
                {
                    int xNew=x+sites[s].energyGain(x,t);
                    if (xNew<=0)
                        vStay [x] [s] [t] = 0;
                    else
                        vStay [x] [s] [t] = fitness [xNew] [s] [t+1]
*sites[s].survivalRate(x,t);
                    SESAs dummyBird=new SESAs(x,s,t, sMax);
                    vGo [x] [s] [t] = 0;
                    double probBadWind=0;
                    if (sites[s].windy)
                        {
                            for (int i=0;
i<sites[s].groundSpeeds.length; i++)
                                {
                                    if
(sites[s].groundSpeeds[i]<dummyBird.avFlightSpeed)
                                        {
                                            probBadWind+=sites[s].groundSpeedProbs[i];
                                            continue;
                                        }
                                    if ((s==(sMax-1)) &&
(sites[sMax].windy))
                                        {
                                            int xCost1, xCost2, tCost1,
tCost2=0;
                                            if
(dummyBird.flightModel==SESA.NEW)
                                                xCost1=dummyBird.flightEnergyCost (sites[s].distToNext/2,
sites[s].groundSpeeds[i]);
                                                else
                                                    xCost1=dummyBird.flightEnergyCost (sites[s].distToNext/2,
sites[s].groundSpeeds[i], dummyBird.b);
                                                tCost1=dummyBird.flightTimeCost (sites[s].distToNext/2, sites[s].groundSpeeds[i]);
                                                dummyBird.x-=xCost1;
                                                for (int j=0;
j<sites[s+1].groundSpeeds.length; j++)
                                                    {
                                                        if
(dummyBird.flightModel==SESA.NEW)
                                                            xCost2=dummyBird.flightEnergyCost (sites[s].distToNext/2,
sites[s+1].groundSpeeds[j]);
                                                        else
                                                            xCost2=dummyBird.flightEnergyCost (sites[s].distToNext/2,
sites[s+1].groundSpeeds[j], dummyBird.b);
                                                        tCost2=dummyBird.flightTimeCost (sites[s].distToNext/2,
sites[s+1].groundSpeeds[j]);
                                                        xNew=x-xCost1-xCost2;
                                                        int
tNew=t+tCost1+tCost2;
                                                        if
(sites[s+1].groundSpeeds[j]>0 && xNew>0 && tNew<=SESA.tMax && tNew>=sites[s+1].openDate)

```

```

                                                                    vGo [x] [s]
[t] += fitness[xNew] [s+1] [tNew] * sites[s].groundSpeedProbs[i] *
sites[s+1].groundSpeedProbs[j];
                                                                    }
                                                                    }
                                                                    else
                                                                    {
                                                                    if
(dummyBird.flightModel==SESA.NEW)
                                                                    xNew=x-
dummyBird.flightEnergyCost(sites[s].distToNext, sites[s].groundSpeeds[i]);
                                                                    else
                                                                    xNew=x-
dummyBird.flightEnergyCost(sites[s].distToNext, sites[s].groundSpeeds[i],dummyBird.b);
                                                                    int
tNew=t+dummyBird.flightTimeCost(sites[s].distToNext, sites[s].groundSpeeds[i]);
                                                                    if (xNew>0 && tNew<=SESA.tMax
&& tNew>=sites[s+1].openDate)
                                                                    vGo [x] [s] [t] +=
fitness[xNew] [s+1] [tNew] * sites[s].groundSpeedProbs[i];
                                                                    }
                                                                    }
                                                                    vGo [x] [s] [t] = vGo [x] [s] [t] / (1-
probBadWind); //Normalizing probabilities of good winds to sum to 1
                                                                    }
                                                                    else
                                                                    {
                                                                    xNew=x-
dummyBird.flightEnergyCost(sites[s].distToNext, dummyBird.avFlightSpeed);
                                                                    int
tNew=t+dummyBird.flightTimeCost(sites[s].distToNext, dummyBird.avFlightSpeed);
                                                                    if (xNew>0 && tNew<=SESA.tMax &&
tNew>=sites[s+1].openDate)
                                                                    vGo [x] [s] [t] = fitness[xNew] [s+1]
[tNew];
                                                                    //if (x<150)
                                                                    //System.out.println("x:"+x+" s:"+s+"
t:"+t+" Stay:"+vStay [x] [s] [t] + " Go:" + vGo [x] [s] [t]);
                                                                    }
                                                                    if (vStay [x] [s] [t] >= vGo [x] [s] [t])
                                                                    {
                                                                    decision [x] [s] [t] = Options.STAY;
                                                                    fitness [x] [s] [t] = vStay [x] [s] [t];
                                                                    }
                                                                    else
                                                                    {
                                                                    decision [x] [s] [t] = Options.GO;
                                                                    if (sites[s].windy)
                                                                    fitness [x] [s] [t] = vGo [x] [s]
[t]*(1-probBadWind)+vStay[x] [s] [t]*probBadWind;
                                                                    else
                                                                    fitness [x] [s] [t] = vGo [x] [s]
[t];
                                                                    }
                                                                    }
                                                                    fitnessRun=true;
                                                                    }
                                                                    }

void setUpSites()
{
    mortality=0;
    avFitness=0;
    avReproduction=0;
    numFemaleOffspring=0;
    for (int i=0; i<=reprScale; i++)
        offspringRange[i]=0;
    numAlive=0;
    numDead=0;
    startFit=0;
    for (int s=0; s<=sMax; s++)

```

```

        {
            sites[s].setWeather();
            sites[s].clearNumbers();
        }
        BreedingSite br=(BreedingSite) sites[sMax];
        br.avArrivalTime=0;
        br.avArrivalEnergy=0;
        for (int t=0; t<=SESA.tMax; t++)
            br.arrivalTimeRange[t]=0;
        for (int x=0; x<=SESA.xMax; x++)
            br.arrivalEnergyRange[x]=0;
    }

void computeAverageLengthOfStay(Bird b)
{
    for (int s=0; s<sMax; s++)
    {
        if (b.lengthOfStay[s]!=0)
        {
            sites[s].averageLengthOfStay+=b.lengthOfStay[s];
            sites[s].lengthOfStayRange[b.lengthOfStay[s]]++;
            sites[s].numVisited++;
        }
        if (b.lengthOfStay[s]==1)
            sites[s].numSkipped++;
    }
}

void computeStats(Bird b)
{
    if (b.alive)
    {
        numAlive++;
        avFitness+=expectedFutureReproduction(b.s);
        if (b.s==sMax)
        {
            BreedingSite br=(BreedingSite) sites[sMax];
//
            prn ("s\t"+b.x+"\t"+b.t+"\t"+br.expectedCurrentReproduction (b.x,b.t));

            numFemaleOffspring+=br.expectedCurrentReproduction (b.x,b.t);
            offspringRange[ ((int)
(br.expectedCurrentReproduction (b.x,b.t)*reprScale) ) ]++;
            avFitness+=br.expectedCurrentReproduction (b.x,b.t);
            br.avArrivalTime+=b.t;
            br.avArrivalEnergy+=b.x;
            br.arrivalTimeRange[b.t]++;
            br.arrivalEnergyRange[b.x]++;
        }
    }
    else
        numDead++;
}

void finishSiteComputations ()
{
    for (int s=0; s<sMax; s++)
    {
        if (sites[s].numVisited>0)

        sites[s].averageLengthOfStay=sites[s].averageLengthOfStay/sites[s].numVisited;
        for (int t=0; t<=SESA.tMax; t++)
            if (sites[s].numberAt[t]>0)

        sites[s].averageEnergy[t]=sites[s].averageEnergy[t]/sites[s].numberAt[t];
    }
}

void finishStatComputations ()
{
    mortality=1.0*numDead/(numAlive+numDead);
}

```

```

        avFitness=avFitness/birds;
        avReproduction=numFemaleOffspring/birds;
        BreedingSite br=(BreedingSite) sites[sMax];
//      prn("Before:"+br.avArrivalTime+", "+br.avArrivalEnergy);
        br.avArrivalTime=br.avArrivalTime/br.numberAt[SESA.tMax-1];
        br.avArrivalEnergy=br.avArrivalEnergy/br.numberAt[SESA.tMax-1];
//      prn("After:"+br.avArrivalTime+", "+br.avArrivalEnergy);

    }

    double avStartingFitness()
    {
        double fitSum=0;
        for (int x=xStartMin; x<=xStartMax; x++)
            for (int t=tStartMin; t<=tStartMax; t++)
                {
                    fitSum+=fitness [x] [0] [t];
                }
        return fitSum/(xStartMax-xStartMin+1)/(tStartMax-tStartMin+1);
    }

    /*Another key method. This performs the simulations. Notice that the migrate
    method of Bird is called to actually run
    the simulation for an individual bird*/
    void runMigrations ()
    {
        setUpSites();
        for (int i=0; i<birds; i++)
        {
//            int xStart = (int) (Math.random()*(xStartMax-xStartMin) +
xStartMin);
//            int tStart = (int) (Math.random()*(tStartMax-tStartMin) +
tStartMin);
            int xStart = randGen.nextInt(xStartMax-xStartMin+1) + xStartMin;
            int tStart = randGen.nextInt(tStartMax-tStartMin+1) + tStartMin;
            startFit+=fitness[xStart][0][tStart];
            SESA s= new SESA (xStart, 0, tStart, sMax);
            if (putBirdHistories)
                prn("Bird "+i);
            s.migrate(this);
            computeAverageLengthOfStay(s);
            computeStats(s);
        }
        startFit=startFit/birds;
        finishSiteComputations();
        finishStatComputations();
    }

    /*Output procedures*/
    void prn(String s)
    {
        if (parent!=null)
            parent.prn(s);
        else
            System.out.println(s);
    }

    void pr(String s)
    {
        if (parent!=null)
            parent.pr(s);
        else
            System.out.print(s);
    }

    /* Calls everything.
    public static void main (String[] args)

```

```
{
    PeepHerder10 peep=new PeepHerder10();
        peep.generateFitness();
        peep.runMigrations();
        peep.outputResults(args);
}*/
}
```

APPENDIX 2: SAMPLE PROGRAM RESULTS

This sample run of the program averages together 10000 years with 10000 birds per year. Energy values are in kilojoules. Days are days after April 1.

Site	Day	Average Birds	Average Energy
0	0	216	150.4904
0	1	432	155.4632
0	2	648	160.493
0	3	864	165.4968
0	4	1078	170.5027
0	5	1293	175.4653
0	6	1507	180.4256
0	7	1721	185.403
0	8	1934	190.387
0	9	2147	195.3516
0	10	2359	200.3196
0	11	2571	205.2805
0	12	2782	210.2418
0	13	2993	215.1972
0	14	3204	220.1434
0	15	3415	225.0872
0	16	3624	230.0303
0	17	3833	234.973
0	18	4042	239.9109
0	19	4251	244.8485
0	20	4459	249.7823
0	21	4667	254.7059
0	22	4874	259.6326
0	23	5081	264.5564
0	24	5287	269.4738
0	25	5493	274.3877
0	26	5699	279.295
0	27	5905	284.2021
0	28	6109	289.1034
0	29	6314	294.0036
0	30	6518	298.8938
0	31	6722	303.7897
0	32	6925	308.6838
0	33	7128	313.5698
0	34	7330	318.4565
0	35	7532	323.3403
0	36	7734	328.2101
0	37	7935	333.0843
0	38	8136	337.9524
0	39	8337	342.8194
0	40	8537	347.6876
0	41	8736	352.5505

0	42	8936	357.4055
0	43	9134	362.2581
0	44	9327	367.2812
0	45	9503	372.7182
0	46	8731	401.9397
0	47	7356	446.1562
0	48	5663	499.438
0	49	3869	561.2945
0	50	2268	626.0561
0	51	1137	652.0178
0	52	551	355.2542
0	53	259	177.799
0	54	120	88.55856
0	55	60	43.7553
0	56	31	22.07639
0	57	11	10.7161
0	58	5	5.078517
0	59	3	2.895358
0	60	1	1.057509
0	61	0	0.375879
0	62	0	0.166521
0	63	0	0.135937
0	64	0	0.038752
0	65	0	0.020367
0	66	0	0.021367
0	67	0	0
0	68	0	0
0	69	0	0
0	70	0	0
0	71	0	0
0	72	0	0
0	73	0	0
0	74	0	0
0	75	0	0
0	76	0	0
0	77	0	0
0	78	0	0
0	79	0	0
0	80	0	0
0	81	0	0
0	82	0	0
0	83	0	0
0	84	0	0
0	85	0	0
0	86	0	0
0	87	0	0
0	88	0	0
0	89	0	0

0	90	0	0
1	0	0	0
1	1	0	0
1	2	0	0
1	3	0	0
1	4	0	0
1	5	0	0
1	6	0	0
1	7	0	0
1	8	0	0
1	9	0	0
1	10	0	0
1	11	0	0
1	12	0	0
1	13	0	0
1	14	0	0
1	15	0	0
1	16	0	0
1	17	0	0
1	18	0	0
1	19	0	0
1	20	0	0
1	21	0	0
1	22	0	0
1	23	0	0
1	24	0	0
1	25	0	0
1	26	0	0
1	27	0	0
1	28	0	0
1	29	0	0
1	30	0	0
1	31	0	0
1	32	0	0
1	33	0	0
1	34	0	0
1	35	0	0
1	36	0	0
1	37	0	0
1	38	0	0
1	39	0	0
1	40	0	0
1	41	0	0
1	42	0	0
1	43	0	0
1	44	5	10.31982
1	45	27	34.33446
1	46	775	74.82764

1	47	1854	123.0974
1	48	2844	175.7442
1	49	3545	228.9732
1	50	3775	285.4973
1	51	3438	334.3349
1	52	2726	342.5438
1	53	1911	300.4383
1	54	1291	248.5246
1	55	859	199.9232
1	56	541	157.1319
1	57	350	126.7589
1	58	218	102.8145
1	59	135	69.12027
1	60	82	46.28282
1	61	44	29.4863
1	62	25	19.32166
1	63	15	12.28536
1	64	10	8.095344
1	65	5	5.510232
1	66	3	3.257329
1	67	1	1.880503
1	68	0	1.156321
1	69	0	0.725426
1	70	0	0.511379
1	71	0	0.290033
1	72	0	0.220629
1	73	0	0.06442
1	74	0	0.04512
1	75	0	0.02432
1	76	0	0.02532
1	77	0	0.02632
1	78	0	0
1	79	0	0
1	80	0	0
1	81	0	0
1	82	0	0
1	83	0	0
1	84	0	0
1	85	0	0
1	86	0	0
1	87	0	0
1	88	0	0
1	89	0	0
1	90	0	0
2	0	0	0
2	1	0	0
2	2	0	0
2	3	0	0

2	4	0	0
2	5	0	0
2	6	0	0
2	7	0	0
2	8	0	0
2	9	0	0
2	10	0	0
2	11	0	0
2	12	0	0
2	13	0	0
2	14	0	0
2	15	0	0
2	16	0	0
2	17	0	0
2	18	0	0
2	19	0	0
2	20	0	0
2	21	0	0
2	22	0	0
2	23	0	0
2	24	0	0
2	25	0	0
2	26	0	0
2	27	0	0
2	28	0	0
2	29	0	0
2	30	0	0
2	31	0	0
2	32	0	0
2	33	0	0
2	34	0	0
2	35	0	0
2	36	0	0
2	37	0	0
2	38	0	0
2	39	0	0
2	40	0	0
2	41	0	0
2	42	0	0
2	43	0	0
2	44	0	0
2	45	0	0.180106
2	46	6	5.12778
2	47	285	26.22278
2	48	858	58.02333
2	49	1530	92.01963
2	50	2116	141.3817
2	51	2463	176.7874

2	52	2473	204.6574
2	53	2292	230.7433
2	54	1835	234.0121
2	55	1366	218.9424
2	56	1009	196.0786
2	57	677	181.4579
2	58	446	162.9524
2	59	299	147.7627
2	60	201	138.088
2	61	133	120.2264
2	62	86	93.40663
2	63	47	70.98023
2	64	27	47.87374
2	65	18	31.94155
2	66	10	21.1668
2	67	7	13.47099
2	68	5	7.269861
2	69	2	3.755412
2	70	0	2.17014
2	71	0	1.588052
2	72	0	0.920653
2	73	0	0.496002
2	74	0	0.304266
2	75	0	0.186247
2	76	0	0.0688
2	77	0	0
2	78	0	0.02056
2	79	0	0
2	80	0	0
2	81	0	0
2	82	0	0
2	83	0	0
2	84	0	0
2	85	0	0
2	86	0	0
2	87	0	0
2	88	0	0
2	89	0	0
2	90	0	0
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3	1	0	0
3	2	0	0
3	3	0	0
3	4	0	0
3	5	0	0
3	6	0	0
3	7	0	0
3	8	0	0

3	9	0	0
3	10	0	0
3	11	0	0
3	12	0	0
3	13	0	0
3	14	0	0
3	15	0	0
3	16	0	0
3	17	0	0
3	18	0	0
3	19	0	0
3	20	0	0
3	21	0	0
3	22	0	0
3	23	0	0
3	24	0	0
3	25	0	0
3	26	0	0
3	27	0	0
3	28	0	0
3	29	0	0
3	30	0	0
3	31	0	0
3	32	0	0
3	33	0	0
3	34	0	0
3	35	0	0
3	36	0	0
3	37	0	0
3	38	0	0
3	39	0	0
3	40	0	0
3	41	0	0
3	42	0	0
3	43	0	0
3	44	0	0
3	45	0	0
3	46	0	0
3	47	0	0.449042
3	48	115	9.274742
3	49	521	41.90433
3	50	1292	100.6163
3	51	2397	180.2685
3	52	3667	267.6267
3	53	4934	359.4504
3	54	6129	449.5264
3	55	7066	537.5374
3	56	7744	623.7215

3	57	8262	709.7329
3	58	8605	799.7533
3	59	8810	890.7803
3	60	8936	971.6058
3	61	9015	1033.217
3	62	9055	1075.415
3	63	9076	1102.544
3	64	3323	808.9288
3	65	1243	677.043
3	66	500	635.5907
3	67	200	609.0741
3	68	92	550.1223
3	69	43	367.8231
3	70	18	222.8647
3	71	9	131.5079
3	72	4	77.15603
3	73	2	42.94064
3	74	0	24.89245
3	75	0	13.23613
3	76	0	7.08125
3	77	0	4.260414
3	78	0	3.06042
3	79	0	2.090683
3	80	0	0.822531
3	81	0	0.59465
3	82	0	0.25016
3	83	0	0.17276
3	84	0	0.18276
3	85	0	0.19276
3	86	0	0.20276
3	87	0	0.21276
3	88	0	0.22276
3	89	0	0.23276
3	90	0	0.24276
4	0	0	
4	1	0	
4	2	0	
4	3	0	
4	4	0	
4	5	0	
4	6	0	
4	7	0	
4	8	0	
4	9	0	
4	10	0	
4	11	0	
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4	24	0
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4	28	0
4	29	0
4	30	0
4	31	0
4	32	0
4	33	0
4	34	0
4	35	0
4	36	0
4	37	0
4	38	0
4	39	0
4	40	0
4	41	0
4	42	0
4	43	0
4	44	0
4	45	0
4	46	0
4	47	0
4	48	0
4	49	0
4	50	0
4	51	0
4	52	0
4	53	0
4	54	0
4	55	0
4	56	0
4	57	0
4	58	0
4	59	0
4	60	0
4	61	0

4	62	0
4	63	0
4	64	0
4	65	2202
4	66	5376
4	67	7154
4	68	7804
4	69	8060
4	70	8464
4	71	8796
4	72	8922
4	73	8973
4	74	8991
4	75	8998
4	76	9005
4	77	9006
4	78	9008
4	79	9008
4	80	9008
4	81	9008
4	82	9008
4	83	9008
4	84	9008
4	85	9008
4	86	9008
4	87	9008
4	88	9008
4	89	9008
4	90	9008

APPENDIX 3: SENSITIVITIES

Shows the sensitivities (change in response variable divided by change in parameter) of lengths of stay and fitness to positive and negative changes in various parameters. The effect of raising the parameter from a lesser value to the base value is on the left; the effect of raising it from the base value to a higher value is on the right. Most parameters were changed by 10% in each direction.

Parameter	Base Value	Site 0 Length of Stay		Site 1 Length of Stay		Site 2 Length of Stay		Site 3 Length of Stay		Fitness	
t _{0min}	0	-	-0.50644	-	0.008385	-	0.003723	-	0.037282	-	0.001089
t _{0max}	45	-0.50935	-0.44825	0.010545	0.018654	0.004879	0.004584	0.023355	-0.03271	0.0008	0.000536
X _{0min}	0	-	0.003427	-	-0.00123	-	0.000332	-	-0.00314	-	0.000135
X _{0max}	300	0.003311	0.003596	-0.00148	0.001896	-0.00022	-0.00034	-0.00267	-0.0067	2.09E-05	1.81E-05
X _{1max}	1150	-0.00473	-	6.7E-05	-	6.99E-05	-	0.004715	-	3.22E-05	-
X _{gainmax}	100	0.064751	0.049942	-0.00111	0.0014	-0.00388	0.001455	-0.06029	-0.05728	0.0001	8.04E-05
u	0.7409	-5.81075	-5.38336	-0.02927	0.678456	0.36294	0.495196	6.062762	4.42914	-0.03395	-0.04267
v _a	32	0.391577	0.180978	-0.13422	-0.09423	-0.08788	-0.05946	-0.01536	-0.05746	0.00362	0.002308
c	0.35	-15.2175	-14.5764	-0.24138	1.417587	0.953881	0.362351	14.10309	13.64159	-0.08508	-0.12502
S _{roy}	0.7776	1.626771	1.975738	-0.28515	-0.11296	-0.10133	-0.10912	-1.45379	-9.37053	0.93492	0.899616
h	2	7.915962	0.052281	0.006157	0.014222	-0.19242	-0.00962	-9.26191	-0.01683	0.05051	0
X _{gainmin}	10	0.272149	0.283019	-0.052	0.042788	-0.01339	0.013412	-0.2409	-0.38808	0.00065	0.000548
k ₀	Table 3	0	0	0	0	0	0	0	0	0	0
k ₁	Table 3	0	0	0	0	0	0	0	0	0	0
k ₂	Table 3	0.849701	0.304972	-0.46455	0.304066	-0.11976	-0.00085	-0.37017	-0.74403	0.00131	0.000985
k ₃	Table 3	-0.06271	-0.03281	-0.63656	-0.30533	-0.02775	0.152008	0.507722	-0.18136	1.6E-07	1.7E-07
p ₀	0.002	-2340.59	-2705.86	-14.5056	197.5255	117.1224	-24.4942	1790.137	2250.675	-25.6924	-25.0952
p ₁	0.003	166.6342	180.7155	-66.4816	171.7947	-69.692	-26.0466	36.13958	-201.88	-1.62174	-1.60747
p ₂	0.003	2636.293	49.25777	-166.641	73.10097	-18332.5	-39.4105	15622.45	-78.8702	-5.16656	-0.94261
p ₃	0.003	2330.17	-435.127	-150.289	122.594	-24.83	15899.81	-2222.82	-16403.2	-10.2419	-5.98338
t _{open}	47	-0.00236	0.010838	-0.00138	0.005378	0.005317	0.002476	-0.00359	-0.00999	0	0
t _{opt}	66	0.991332	0.999614	-0.02833	-0.01007	-0.01366	-0.00621	0.029719	-0.04579	-0.00163	-0.00264
Γ _{max}	0.3549	-4.24741	-4.10835	-0.95634	0.08295	0.087709	0.062447	21.15367	4.212165	0.84356	0.844839
X _t	500	-0.00464	-0.0042	2.82E-06	0.00073	-0.00017	-0.00014	0.005742	0.004883	-2.91E-05	-3.4E-05