

**THE INFLUENCE OF THE PREDATOR LANDSCAPE  
ON MIGRATORY DECISIONS  
IN TWO SHOREBIRD SPECIES**

by

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## **Abstract**

I tested predictions about foraging decisions and stopover durations based on a mortality-minimizing migratory model in two shorebird species on southward migration. Semipalmated and adult western sandpipers migrate early, under low predation danger and are predicted to make behavioural decisions that allow them to avoid exposure to the seasonal increase in abundance of their main predator, peregrine falcons. Juvenile western sandpipers migrate later, experiencing higher predation danger. They are predicted to make decisions that reduce vulnerability to falcons. Early migrants seasonally lowered vigilance and adjusted stopover duration, increasing migratory speed to remain ahead of the approaching migratory falcons. Late migrants had higher vigilance, and stopover duration trends fitting reduced vulnerability at the expense of migratory speed. Flight initiation distance and spatial usage were not consistent with predictions. These species appear to make decisions that depend on spatial and temporal proximity to predator migrations, as predicted by a mortality-minimizing migration model.

**Keywords:** western sandpiper; semipalmated sandpiper; migration; vigilance; flight initiation distance; spatial usage; length of stay; predator landscape; peregrine falcon; predation danger; optimal migration; mortality-minimizers

## **Dedication**

*To my mother,*

*Stephanie Hyde*

*Throughout this degree I have drawn strength and  
determination from your fortitude.*

*I am inspired by your constant commitment to  
improvement.*

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# **1: Introductory Chapter**

## **1.1 Theoretical Background**

Long distance avian migration is largely influenced by the selective forces of time, energy, and predation (Alerstam and Lindström, 1990). Life history stage and seasonality can influence the relative importance of these factors and lead individuals to adjust behaviour. Most previous work has focused on placing migrants into the category of time-minimizer or energy-minimizer (Hedenström and Alerstam, 1997; Lindström and Alerstam, 1992). However, the influence of predation has begun to attract research and theoretical attention (Dierschke, 1998, 2003; Lank et al., 2003; Lind and Cresswell, 2006; Pomeroy, 2006; Schmaljohann and Dierschke, 2005; Ydenberg et al., 2007; Ydenberg et al., 2004). Here I explore decisions to minimize mortality while on migration based on current and future predation danger.

To explore a migrant's effort to minimize time, energy or mortality I relate these tactics to changes in migratory speed between groups and throughout the migratory season. Migratory speed is defined here as the potential flight range based on fuel load at departure divided by the time required to travel that range, including the stopover time necessary to load the fuel. We will avoid looking at decisions that influence flight velocity and instead focus on decisions that influence potential flight range and time spent at a stopover site. Time spent on migration is allocated 7:1 to stopovers versus migratory flight and energy spent on migration is 2:1 to stopovers versus flight between stopovers and therefore changes in flight speed outside those influenced by fuel load

should have relatively little influence on time on migration (Alerstam and Lindström, 1990; Hedenström and Alerstam, 1997). Potential migratory speed is therefore defined as being a function of fuel load, which influences potential flight range and time spent fuelling; fuelling rate, which influences time spent fuelling; and time spent at a stopover before fuel accumulation begins. (Alerstam and Lindstrom, 1990; Houston, 1998)

Migrants may attempt to minimize the time spent migrating to a given breeding or non-breeding ground. This is likely to be selected for if there is a cost to late arrival or an increasing cost as time spent on migration increases. The costs could include lost breeding opportunities, reduced quality of available territories, increased predation danger, or reduced food abundance (Lindström et al., 2002; Lindström and Alerstam, 1992; Scheiffarth et al., 2002). At stopovers, time-minimizers should make decisions that increase their migratory speed. Under the assumption that increasing the rate of fuel loading allows for increased migratory speed, time-minimizers should express behaviours that shift priority towards loading fuel such as foraging in areas of higher food abundance, reducing vigilance, allowing closer predator approach, or increasing the time spent foraging. (Schmaljohann and Dierschke, 2005; Beauchamp, 2009; Duijns et al., 2009).

In addition, time-minimizers should depart from a stopover site at the optimal, speed-maximizing fuel load (Alerstam and Lindström, 1990). This is the fuel load at departure that for a given fuel loading rate gives the highest migratory speed. As migrants fuel load, potential flight range increases, initially allowing an increase in migratory speed. Eventually, the cost of a high fuel load outweighs the benefit in range, and speed decreases with high fuel loads. The fuel load/stopover time providing the maximum

migratory speed is considered ‘optimum’ for time-minimizers (Alerstam and Lindström, 1990). Migrants with a given refuelling rate should depart at the time-minimizing optimum, but if there are changes in refuelling rate throughout the season, time-minimizers with higher refuelling rates should depart earlier, as it takes less time to reach the time-minimizing optimum at higher fuelling rates (Alerstam and Lindström, 1990).

Energy-minimizers attempt to minimize the energy expended while on migration, which would benefit migrants that experience either low food availability at migratory stopover sites, a cost to arriving exhausted at non-breeding or breeding grounds, or energetically demanding pre-migratory conditions (Scheiffarth et al., 2002). Theoretically, energy-minimizers depart stopover sites with a fuel load that minimizes drag, while providing sufficient fuel to reach the next stopover (Alerstam and Lindström, 1990). Therefore, energy-selected migrants should have departure fuel loads that are much lower than time-minimizers. If the refuelling rate of energy-minimizers changes throughout the season, such as due to decreasing food abundance, the residence time should adjust to reflect the time taken to reach the optimal departure fuel load. If there was a decrease in food abundance throughout the season, energy-minimizing stopover time should lengthen.

This thesis refers to migrants that attempt to minimize the probability of mortality on migration as “mortality minimizers”. These individuals should attempt to minimize the cumulative probability of mortality over the entire migration. This does not necessarily refer only to mortality from predation. If a migrant has a choice of strategy that results in no predation danger, but means that the migrant will starve on migration, mortality minimizers should accept the increased predation danger in order to reduce

probability of mortality. Mortality minimizers could be migrants that experience high predation danger throughout their migratory distance or migrants that are attempting to avoid predators in time or space. To reduce mortality probability, migrants should make decisions that become more cautious as predation danger increases. Some examples of mortality minimizing decisions, or tactics, include: avoiding habitat and/or stopover sites with high predation danger, increasing vigilance, reducing fuel load to decrease wing-loading and therefore increase escape performance, and shortening residence times (Pomeroy, 2006; Pomeroy et al., 2006; Burns and Ydenberg, 2002; Lank et al., 2003; Ydenberg et al., 2002; Ydenberg et al., 2004; Sansom et al., 2009).

If predation danger varies throughout the migratory period, this complicates predictions about appropriate tactical decisions. Migrants that are migrating under low predator abundance should attempt to avoid any temporal or spatial increases in predator abundance (Lank et al. 2003), leading to avoidance of areas with high predation danger or attempting to increase migratory speed in order to stay ahead of migrating predators. Migrants avoiding temporal increases in predation danger may behave more similarly to time-minimizers compared with mortality-minimizers that are migrating under higher predator abundance.

While most mortality-minimizers should have departure fuel loads below the speed-maximizing optimum (Houston, 1998), individuals that are able to fuel under sufficiently safe conditions may attempt to load fuel beyond the speed-maximizing point, slowing migration. High fuel loads provide sufficient fuel to perform long flights, allowing these migrants to avoid the predation danger associated with future stopover sites. Increased predation danger while fuelling reduces the benefit of this behaviour as

the high fuel load required increases vulnerability through decreased escape performance (Burns and Ydenberg, 2002; van den Hout et al., 2010).

## 1.2 Study Species

To test predictions of stopover behaviour based on the mortality-minimizing migration model, this thesis examines the southward migration of adults and juveniles of two small sandpiper species, the western and semipalmated sandpipers (*Calidris mauri* and *Calidris pusilla*). For both species' southward migrations, the adults depart the breeding grounds about a month before the juveniles (Butler et al., 1987; Gratto-Trevor, 1992) and are hypothesized to arrive at the non-breeding grounds with sufficient time to moult their flight feathers in safety before the arrival of migratory peregrine falcons (*Falco peregrinus*) (Lank et al., 2003). This often results in reduced parental care for late-hatching clutches (Ruthrauff et al., 2009). Juveniles do not moult flight feathers in their first year, but are constrained in that they grow to full size before departing on migration (Stein and Williams, 2006). Western sandpiper migrants depart from the breeding grounds in western Alaska and make a direct flight from southern Alaska to the Fraser River Delta, British Columbia. From there, they migrate southwards, either along the coast or pushing eastwards as they move south (Butler et al., 1987). Their non-breeding grounds stretch from northern California to South Carolina to Peru, with the highest concentrations in California, Mexico and Panama (Wilson, 1994). Semipalmated sandpipers have a breeding area that stretches from western Alaska to Northern Baffin Island and Labrador, and non-breeding sites that lie between the Caribbean, Central America and the northern and central coasts of South America (Gratto-Trevor, 1992). Eastern birds migrate by flying to eastern North America and then performing a single

over-ocean flight to the Caribbean or South America. Western and central birds fly down mid-continental North America and then across the Caribbean (Gratto-Trevor and Dickson, 1994; Lank, 1979).

Peregrine falcons (*Falco peregrinus*) migrate from their breeding grounds in a spatially and temporally clustered front (Lank et al., 2003; Ydenberg et al., 2007). Falcons arrive at west coast sites of similar latitude 4-6 weeks earlier than on the east coast (Worcester and Ydenberg, 2008). There is substantial between-season variation in the timing of peregrine migration, resulting in falcons migrating more synchronously with sandpiper migrations in some years (Niehaus and Ydenberg, 2006).

### **1.3 Predictions for Mortality Minimizers**

If Semipalmated and Western Sandpipers are behaving as mortality minimizers, we can make predictions about their decisions on migration and how these decisions shift throughout the season and with age. Migrants that are ahead of the peregrine falcon front in time and space should increasingly make decisions at stopovers that speed migration. The closer they are to the front, the greater the effort to increase speed should be, with the highest speeds occurring just ahead of the peregrine front. Where the age groups overlap, adults should attempt to obtain higher migratory speeds than juveniles because adults that arrive late at the non-breeding grounds experience higher vulnerability associated with moulting flight feathers under increasing predator abundance (Lank et al., 2003). As peregrine and sandpiper migrations begin to overlap in space and time, mortality-minimizing migrants must make decisions that reduce predation danger. This increasing caution should decrease potential migratory speed. This thesis examines behaviours that influence this trade-off between migratory speed and predation danger.

## 1.4 Thesis Overview

In Chapter 2, I explore the influence of the approach and arrival of the predator front on migratory stopover behaviour of adult and juvenile western sandpipers. Under the assumption that a higher fuelling rate allows for a faster migratory speed, adults migrating under low predation danger should accept greater predation danger in order to increase their fuel loading rate, and therefore also their migratory speed to meet the approaching dangerous moult period deadline. Juveniles migrating under higher predation danger should attempt to migrate safely, thereby decreasing their fuelling rate and migratory speed. To explore this, I look at the proportion of time spent vigilant, the flight initiation distance, and the relative spatial usage with respect to food abundance and predation danger.

In Chapter 3, I explore different strategies to minimize mortality on migration in adult and juvenile western and semipalmated sandpipers by looking at residence times of migrants at stopover sites in western (Sydney Island), central (Sibley Lake) and eastern (Kent Island) North America. Migrants ahead of the falcon front should have higher migratory speeds the closer they are to the falcon front. We expect adult and juvenile western sandpipers to load fuel below the time-minimizing optimum. Semipalmated sandpipers should fuel above the optimum in order to make a predator-free transatlantic flight in the east and insure against an uncertain future at central sites. Therefore, residence time should increase in adult western sandpipers and decrease in juveniles and both adult and juvenile semipalmated sandpipers.

Overall, this study helps to determine the extent to which migrants are attempting to minimize mortality while on migration. We expect different decisions based on the different annual cycle requirements and constraints for each age group and species.

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## **2: Behavioural Decisions of Western Sandpipers (*Calidris mauri*) at a Migratory Stopover Vary with Age and Position on a Predator Landscape**

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David D. Hope collected all data, performed analyses and wrote the paper. Dr. Ydenberg generated hypotheses that this work is based on, aided in planning of data collection, worked on interpretation of results and drafting of final version of the chapter. Dr. Lank assisted in generating hypotheses that were the basis of the project, provided substantial input into the planning of the project, and helped put together the final version of the chapter.

## 2.1 Abstract

Migratory decisions are governed by the influence of time, energy and predation. Differing annual cycle requirements lead to different time and predation pressure for adult and juvenile western sandpipers (*Calidris mauri*) on southward migration. Adults migrate under increasing time pressure as they attempt to reach non-breeding grounds and moult under low predation danger conditions. Juveniles migrate under increasing predation danger as migratory peregrine falcons (*Falco peregrinus*) move south alongside or just behind them. Several aspects of stopover behaviour were examined to explore if stopover behaviour decisions of adults and juvenile are related to position on the predator landscape. Adults spent a decreasing proportion of time vigilant throughout the migratory period and had lower overall vigilance than juveniles, supporting the prediction that adults reduce anti-predator behaviour in order to increase migratory speed, while juveniles are more vigilant presumably due to higher predation danger. There was no difference in spatial usage between groups and contrary to our prediction flight-initiation distance to an approaching human was greater in adults. Adults and juveniles appear to be attempting to minimize mortality on migration in different ways, adults by temporally avoiding high predation and juveniles by increasing anti-predatory behaviour.

## 2.2 Introduction

Most migratory avian species spend a large portion of their life travelling between breeding and non-breeding areas. Decisions made during migration can influence all aspects of the annual cycle and affect population growth rate (Newton, 2006; O'Hara et al., 2005). Life history priorities select for migratory strategies that attempt to optimize tradeoffs among time, predation danger, and energy expended over the migratory distance. Different priorities result in weighting one factor more than the others (Alerstam and Lindström, 1990). Traditionally, studies of optimal migration have focused on tradeoffs between migration speed and energy expenditure, leading certain species to be referred to as time- or energy- “minimizers” (Chernetsov et al., 2004; Danhardt and Lindstrom, 2001; Erni et al., 2002; Farmer and Wiens, 1999; Lindström and Alerstam, 1992). Fewer studies have looked at the influence of predation danger on migratory behaviour and these have mostly focused on the influence of immediate predation danger (Cimprich et al., 2005; Dierschke, 1998, 2003; Duijns et al., 2009; Lank et al., 2003; Moore, 1994). I introduce the term probability of mortality-minimizers (hereafter mortality minimizers) as a potential migratory strategy and use this to make and test predictions of stopover behaviour in migrants travelling in different positions on a predator landscape.

Time-minimizing migrants are predicted to adopt migratory behaviour and tactics that attempt to increase migratory speed. I use the term “migratory speed” to represent the outcome of decisions made at a stopover that influence the total time spent on a given migration. The term “speed” in this thesis refers to the potential flight range based on fuel load at departure divided by the time required to cover that range, including the stopover

time necessary to load the fuel. Migrants can reduce time on migration by increasing migratory speed or by reducing migratory distance. The distance to be travelled may be controlled by variables outside those examined by this study (Mathot et al., 2007; Nebel, 2005, 2006). Therefore, time spent on migration is defined here, as a function of speed alone, not distance travelled. It is assumed that decisions made that affect time spent on migration occur at stopovers and that migratory flight speed is primarily influenced by fuel load decisions. Because time spent on migration is allocated 7:1 to stopovers versus migratory flight and energy spent on migration is 2:1 to stopovers versus flight between stopovers, changes in flight speed outside those influenced by fuel load should have relatively little influence on time on migration (Alerstam and Lindström, 1990; Hedenström and Alerstam, 1997).

Migratory speed can be potentially increased by increasing the rate of fuel loading (Alerstam and Lindström, 1990; Houston, 1998). This allows migrants to increase their migratory speed, by either increasing the fuel load reached over a given time at a stopover or by reducing the time to reach a given departure fuel load (Figure 2.1 b and c). Alternatively, migrants with a higher loading rate could maintain the same migratory speed, but reduce stopover time and departure fuel load (Figure 2.1d). This occurs at individual stopover sites that are more dangerous, as has been seen with western sandpipers (Ydenberg et al., 2002).

Migrants that are behaving as time-minimizers or attempting to increase migratory speed should shift behaviours towards ones that increase fuel-loading rate, potentially increasing their vulnerability from predators (Houston et al., 1993; Lima and Dill, 1990; Quinn and Cresswell, 2004; Ydenberg et al., 2002). This often results in a

trade-off, whereby an individual accepts greater predation danger in order to increase food intake (Cresswell, 1994; Elgar, 1989; Pomeroy, 2006; Pomeroy et al., 2006). Increasing the fuel loading rate can be accomplished in many ways, including, decreasing vigilance, avoiding competitors, adjusting spatial usage towards habitat with higher food abundance or increasing time spent foraging, foraging efficiency, or digestive efficiency (Cowlshaw et al., 2004; Heise and Moore, 2003; Pomeroy, 2006; Stein et al., 2000).

Energy minimizers are expected to minimize energy expended both by departing with the fuel load that optimally reduces drag and by minimizing energy expended during fuel loading (Alerstam and Lindström, 1990; Scheiffarth et al., 2002). Energy minimizers have been shown to be less sensitive to changes in fuelling rate and accept less predation danger when choosing foraging habitats than time-minimizers (Duijns et al., 2009). There are no predicted seasonally changing patterns of behaviour for energy-minimizers. If food abundance decreases throughout a migratory period, refuelling rate would be expected to decline, but there would not be predicted behavioural changes to compensate for this.

Optimal migration theory describes “predation-selected” migrants as those that attempt to minimize the probability of being depredated per unit of distance travelled (Alerstam and Lindström, 1990; Houston, 1998). This thesis expands upon that by describing “mortality-minimizers” as migrants that attempt to maximize the likelihood of surviving migration through minimizing the cumulative probability of mortality over the entire migration. This allows migrants to choose tactics that provide sufficient fuel for survivorship and transport with minimal predation danger. This may result in lower

prioritization of the total time taken for the migration or total energy consumption as selective factors.

Mortality-minimizers should attempt to reduce predation danger through both avoidance of predators in space and time and adjusting behaviour to reduce vulnerability to predators encountered on migration. If predation danger varies throughout a migratory season, predicted mortality-minimizing behaviour should change. Individuals migrating under relatively low predation danger should attempt to remain under low predator conditions, while migrants experiencing high predation danger on migration should adjust behaviour at stopovers to reduce vulnerability.

I compared stopover behaviour of juvenile and adult western sandpipers (*Calidris mauri*) on southward migration with predictions of expected mortality-minimizing tactics. Predicted tactics were based on individual temporal proximity to the migration of their predator, the peregrine falcon (*Falco peregrinus*). *C. mauri* has age-specific migration timing, with adults departing southward about a month before juveniles (Butler et al., 1987). Adults abandon their offspring and depart early from the breeding grounds, which enables them to migrate with lowered predation danger and with enough time to reach the non-breeding grounds and moult their flight feathers before the arrival of the migratory peregrine falcons (*Falco peregrinus*) (Lank et al., 2003). Adult sandpipers moult their primaries in a short period of time, which reduces their flight performance as the new feathers grow in (Hedenström and Sunada, 1999). The reduced flight performance could increase the chances that a predatory attack would be successful. As predator avoidance has been suggested to be the most effective means of antipredator

behaviour (Sansom et al., 2009), adults should be selected to avoid predators during this period of increased vulnerability (Lank et al., 2003).

Juvenile sandpipers do not experience the constraint of having to moult their flight feathers in their first year, but are constrained in that they grow to full size before migration (Stein and Williams, 2006). They thus migrate later in the season, just ahead or at the same time as the falcons, which travel southward in a spatially and temporally clustered “wave” with some migratory falcons becoming resident to winter at various latitudes (Fuller et al., 1998; Lank et al., 2003; Ydenberg et al., 2007). The pattern of relative predator abundance in time and space is referred to as a “predator landscape” (Ydenberg et al., 2007). If western sandpipers are behaving as mortality-minimizers, differential constraints and priorities of adult and juvenile sandpipers lead to differential placement within the predator landscape, which leads to different predicted mortality-minimizing behaviour (Lank et al., 2003; Ydenberg et al., 2007). I hypothesize that a migrant’s age and position within the predator landscape influences stopover behaviour. My hypotheses and predictions are described in the paragraphs that follow.

Figure 2.2 outlines predictions of mortality-minimizing migratory tactics in relation to proximity to the falcon front. Migrants ahead of the falcon front should attempt to maintain a migratory speed that keeps them ahead of the falcon front. The closer a migrant is to the falcon front the more an individual make decisions that increase their migratory speed. Migrants within the falcon front should attempt to migrate increasingly cautiously as predator abundance increases.

Figure 2.3 outlines the predicted trajectory of migration for adult and juvenile sandpipers in relation to the falcon front. Early migrants (entirely adults) have a large

temporal window ahead of the falcon front and can migrate slowly (and therefore more safely) and still arrive at the non-breeding area with time to complete their moult under lower predation danger. Late migrants (entirely juveniles) must migrate slowly also, due to increased predation danger when migrating within the falcon front. Increasing predation danger increases the amount of time/energy that must be put into predator avoidance behaviour, and should therefore slow migration. As predator and prey migrations approach overlap, the migration speed of late adults and some very early juveniles should be higher as migrants try to gain safety in distance between them and the falcon front. Where age groups overlap, adults should behave more like time-minimizers than juveniles, since adults face greater danger if they do not reach the moulting grounds with sufficient time to moult before the arrival of migratory falcons (Lank et al., 2003). Very late adults may experience the arrival of the first of the migratory falcons, but should decrease rather than increase vigilance in response. Migratory speed is expected to be highest just ahead of the falcon front and should drop when the front arrives as migrants attempt to gain safety by migrating more cautiously. Based on these predictions and assuming that other relevant environmental factors such as food supply do not vary greatly, I can predict how patterns of change in potential antipredator behaviours during these periods. Specifically, I examine the proportion of time spent vigilant by migrants, the distance from which birds fly from an approaching predator, and how the spatial usage of migrants varies throughout the adult and juvenile migratory periods. I discuss predictions for these behaviours below.

Under the assumption that time spent being vigilant is time that cannot be used to load fuel, migrants that spend more time being vigilant spend less time loading fuel and

therefore likely have a lower fuelling rate, but with the benefit of an increased chance of detecting a predator (Elgar, 1989). Given the predator landscape envisioned in Figure 2.3, adults should have lower vigilance than juveniles. Through the migratory period, vigilance should decrease until falcons arrive (to allow for higher fuelling rates), then increase to allow for greater caution (at the expense of fuelling rate).

As a predator approaches, individuals must not only identify the threat, but also assess the threat in relation to the costs and benefits of staying or leaving (Ydenberg and Dill, 1986). As the cost for a slow migration speed increases in adults, I predict that the benefits of staying at a foraging location to avoid lost time foraging increases. If juveniles are attempting migrate cautiously to reduce predation danger, they should view the benefits of staying as lower than adults. Therefore, juveniles should initiate flights at greater distances than adults.

Using dropping (faecal) density as a proxy for spatial usage, Pomeroy (2006) found that northward migrants trade off predation danger against food abundance (both higher closer to shore) while foraging. I predict that adult and juvenile migrants have different priorities and therefore adjust this trade-off in spatial usage to reflect these priorities. Adults foraging closer to shore are able to increase fuelling rates, but experience greater predation danger. Juveniles are expected to take fewer risks and forage further from shore at the potential cost to their fuelling rate.

The timing of peregrine arrival at stopover sites on migration varies between years and is positively correlated with the date of arctic snowmelt. This is not observed for sandpiper migration (Niehaus and Ydenberg, 2006). Therefore, in years with earlier dates of snowmelt, adult sandpipers should experience more time pressure to reach the

moulting grounds and be expected to try to increase their migratory speed and take more risks at stopover. Since stopovers become more dangerous earlier in these years, juveniles are predicted to increase anti-predator behaviour to manage this increase in danger, at the expense of fuelling rate. This results in a slower migratory speed.

## **2.3 Methods**

### **2.3.1 The Western Sandpiper**

The western sandpiper is a small shorebird, which migrates annually between neotropical non-breeding grounds ranging from California to South Carolina and Florida to Peru and the breeding areas of western Alaska (Wilson, 1994). The northward migration consists of a series of stopovers up the coast of Central and North America, though there is some movement further inland. The timing of migration is relatively condensed with the majority of birds passing through a stopover within two or three weeks (Butler et al., 1987). The southward migration is much more protracted, with adults beginning their migration about a month before the juveniles (Butler et al., 1987; Lank et al., 2003; Niehaus and Ydenberg, 2006). The adult southward migration is slightly more condensed than the juvenile migration, but each covers about a month at stopover sites with only about a week or so of overlap between age groups (Butler et al., 1987). The western sandpiper migration was chosen for investigation for several reasons. *C. mauri* has been well studied both in terms of life history and physiology (Butler et al., 1987) (Fernández and Lank, 2007; Stein and Williams, 2003). This allows us to eliminate some hypotheses, which might help us understand age-specific migratory behaviour. Having the age classes temporally separated eliminates the impact of competition

between the age classes and allows us to examine each group's behaviour independently of the direct influence of the other. The western sandpiper is also the one of the most abundant shorebirds in North America, although the population is thought to be in decline (Bishop et al., 2000; Fernández et al., 2006). During migration, large numbers pass through several important stopover points, allowing for easy assessment of stopover behaviour of large numbers of individuals. Of these stopover locations, one of the most significant to western sandpipers is the Fraser River Delta in British Columbia.

### **2.3.2 Study Site**

Data were collected between 1 July and 10 September in 2007 and 2008 at Boundary Bay on the Fraser River Delta, British Columbia (49° 4'N 122°58'W). Boundary Bay consists of a large sandy mudflat, approximately 60 km<sup>2</sup> at low tide (Pomeroy, 2006). The Fraser River delta has been designated a site of hemispheric importance by the Western Hemispheric Shorebird Reserve Network, partially due to its importance to western sandpiper migration. Boundary Bay is the site of several previous studies on the western sandpiper, allowing the present study to build upon the knowledge gained from these earlier studies. Each spring, thousands of *C. mauri* use Boundary Bay as a refuelling point in their migration to the breeding grounds (Butler et al., 1987). In the summer/fall, the Fraser River delta and the mudflats in northern Washington State are the first major stopover points for birds that make the direct flight from the south slope of Alaska, some 2400 km away. This means that a large proportion of the population uses the Fraser River delta/Boundary Bay as a key stopover point on the southward migration. Adult sandpipers migrate through predominantly in July while juveniles pass through in August and early September (Butler et al., 1987).

### **2.3.3 Vigilance**

Under the assumption that fuel loading is incompatible with vigilance, migrants that spend a greater proportion of their time vigilant would spend less time foraging (Elgar, 1989). Therefore, for migrants that are foraging equally efficiently, those that spend more time foraging would load fuel faster. Given these assumptions, birds with lower proportion of time vigilant would have higher fuel loading rates and therefore migrate more quickly.

To determine the proportion of time individual migrants spent vigilant, individually selected birds were observed. Flocks were selected opportunistically due to the low density of flocks at the site. Upon selection, flocks were approached to about fifty meters. An individual focal bird was chosen from the flock after waiting a minimum of five minutes to lessen potential influences of the initial approach. Before starting measurements of vigilance, observational parameters were recorded quantifying characteristics of the flock and individual. These parameters and other variables used in the analysis are summarized in Table 2.1. The size of the flock was estimated if it was judged to be below 200 birds; flocks larger than 200 birds were grouped into one class. For analysis, two other groups were formed: one smaller than 20 birds and one between 20 and 200 birds. Flock size was not estimated above 20 birds because little or no effect of group size on vigilance has been shown in groups of 20 or larger (Elgar, 1989). Distance of the flock from cover was recorded as this has been shown to affect vigilance (Pomeroy, 2006). The following variables shown to affect vigilance were also recorded: the position of the bird in the flock (categorized as edge if within three birds of the edge); the estimated average distance from the focal bird to its five nearest neighbours (Elgar,

1989); and the date, time and geographic location. The focal bird was identified either as a juvenile or adult based on plumage characteristics (Wilson, 1994). Each bird was observed for a two-minute interval using a Bausch and Lomb 15 - 45x60 spotting scope, during which time the total amount of time the bird was vigilant was measured. Vigilance was defined as any time that the individual's beak was parallel to the ground (Pomeroy, 2006). This included time spent running between foraging bouts, if the beak was parallel to the ground. Vigilance time was recorded using a stopwatch. If the focal bird flew before two minutes passed, the observation time was noted, and the data were included in the analysis if the observation period was longer than 30 seconds. The procedure was then repeated up to twice more on different individuals in the flock. Observations were only repeated on the same flock if it could be ensured that the same individual would not be sampled again. Upon completion of vigilance observations, the flight initiation test (see below) was initiated or the distance to the focal bird was recorded using a Global Positioning System (Garmin etrex Legend Cx). Using the time of day and date of the observations, the tidal state, onshore/offshore wind vector, and cloud cover were obtained from Vancouver Airport and Tsawwassen observation stations on the Environment Canada and Fisheries and Oceans Canada websites ([http://www.weatheroffice.gc.ca/city/pages/bc-74\\_metric\\_e.html](http://www.weatheroffice.gc.ca/city/pages/bc-74_metric_e.html); <http://www.waterlevels.gc.ca/english/Canada.shtml>). These variables were included as they have either been shown or were suspected to have an influence on vigilance behaviour (McGowan et al., 2002).

#### **2.3.4 Flight – Initiation Distance**

Upon detection of a threat, a foraging individual must decide whether to flee or ignore it. Decisions are made based on the relative costs and benefits of staying versus leaving (Ydenberg and Dill, 1986). Migrants that are attempting to increase speed of migration have a greater benefit of remaining to avoid lost foraging opportunities, and different predator landscapes may influence the decision to depart.

Following vigilance observations, flight-initiation distance (FID) was measured on the same flock. The parameters used in the analysis are described in Table 2.2. They include most of the variables described for vigilance. However, wind strength was included instead of the wind vector, since in the context of predatory escape, wind strength in general is predicted to increase the cost to flight, as opposed to wind from a particular direction. The FID test was started no less than 10 minutes after the observer's arrival, to reduce the influence of the initial approach.

A preselected bird was approached at the constant rate of 0.5m/s, which is the rate used in previous FID studies (Blumstein, 2003; Cooper, 2005; Frid and Dill, 2002). Eye contact was maintained with the focal bird until flight was initiated. When the bird began to move a marker was dropped and when the bird took flight a second marker was dropped. The time from the initiation of approach until the point when the bird flew was recorded using a stopwatch. Using a GPS and the dropped markers, the initial distance from to the bird (Starting Distance), the distance when the focal bird first reacted to being approached (Reaction Initiation Distance) and the distance when the bird flew away (Flight Initiation Distance) were measured. This test was performed only once per day on a given flock, unless at least one hour had passed since the flock was last disturbed and

the flock size was large enough to virtually eliminate the possibility of testing the same bird twice (greater than about 500 birds). The time of day and date of the observations, the tidal state, and wind strength from the Vancouver Airport and Tsawwassen observation stations on the Environment Canada and Fisheries and Oceans Canada websites were noted for each trial ([http://www.weatheroffice.gc.ca/city/pages/bc-74\\_metric\\_e.html](http://www.weatheroffice.gc.ca/city/pages/bc-74_metric_e.html); <http://www.waterlevels.gc.ca/english/Canada.shtml>).

### **2.3.5 Spatial Usage**

Pomeroy (2006) found that migrants trade off increased predation danger and food abundance close to shore. Migrants that are attempting to increase speed of migration are expected to take more risks than migrants that are attempting to migrate cautiously.

Spatial usage data was collected following the methodology of Pomeroy (2006). A transect was run perpendicular to the salt marsh and shoreline, starting at the edge of the salt marsh and running 1000 meters out from cover. Points were marked with rebar and a GPS every 50 meters from zero to 600 meters and every 100 meters beyond this. The transect was kept in the same place in the mudflat between years. A single transect was used because it has been shown that there is no significant difference in dropping and invertebrate food density at multiple sites across the mudflat (Pomeroy, 2006). The transect was walked daily at low tide. At each marker, fifteen 1-m<sup>2</sup> quadrats constructed of ½ inch PVC piping were laid down and the number of western sandpiper droppings with at least part of their area inside each were counted. The quadrats were placed by throwing a marker 15 times in a circle around the rebar and placing down the quadrat in the direction of approach with the bottom-left corner over the marker. Throwing the

marker in a circle allowed for a consistent coverage of the area around the rebar, but ensures that the small-scale placement of the quadrat is random. Time and date were also recorded and these were used with tidal data from the Fisheries and Oceans Canada Tsawwassen tidal observation station (<http://www.waterlevels.gc.ca/english/Canada.shtml>) to calculate the time that each distance from shore was last covered and from that the exposure time. Dropping counts were then standardized for area and exposure time.

### **2.3.6 Data Analysis**

#### **2.3.6.1 Vigilance**

Using an information-theoretic approach, I generated 30 candidate models to examine the importance of age and predation danger throughout the migration period (Table 2.3). All models were selected to test the relative importance of day of the year, and day squared, year, and age on the proportion of time vigilant. Variables shown to influence vigilance or flight distance but not part of the hypotheses being tested were defined as BASE variables and included together in all models. The BASE variables included in the analysis of vigilance are described in Table 2.1. Models were also included with interaction between distance from cover and tidal position; distance from cover and age; and a three-way interaction between distance to cover, age and tidal position. These interactions in BASE variables were added post-hoc and were only added to the previously top model. These interactions served to test for differences in behaviour between age groups at different distances. Variables were examined for covariance before inclusion in the analysed models.

Generalized Linear Models were run in SAS 9.1 using the “proc genmod” procedure (SAS Institute 2005). Vigilance data were transformed using a  $\log_{10}(x+0.001)$  transformation and models were run using a normal distribution. Log-likelihoods, sample sizes, and the number of parameters from each model were used to calculate an Akaike Information Criterion (AIC) value (Burnham and Anderson, 2002). AIC values were used to calculate weighted AIC values, which show the relative support for the model, given the data. AIC values were converted into Quasi AIC (QAIC) values, which correct for overdispersion (Burnham and Anderson, 2002). QAIC values allowed us to demonstrate which models were supported by the data, and also to create weighted parameter estimates. Weighted parameter estimates were calculated from all models with the amount of support for a model determining how much influence that model’s parameter estimate has on the final weighted parameter estimate with an accompanying unconditional standard error.

#### **2.3.6.2 Flight-Initiation Distance (FID)**

For the FID analysis, 27 candidate models were constructed to test the influence of age, day of year and year and control for starting distance and the environmental variables (Table 2.5). The following BASE variables were included: tidal state, wind strength, distance to cover, flock size and the distance to the focal bird’s three closest neighbours (Table 2.2).

Generalized Linear Models were run in SAS 9.1 using the “proc genmod” procedure (SAS Institute 2005). FID models were run using a normal distribution with a log link function. As with the vigilance analysis, calculated QAIC values were used them to weigh models based on their proportion of support from the data. Weighted parameter

estimates and unconditional standard errors were also calculated to examine effect size of particular parameters.

### **2.3.6.3 Spatial Usage**

To control for effect of the tidal cycle, which did not always cover the entire mudflat daily and therefore did not always remove all droppings with each tidal cycle, raw dropping counts were divided by the number of 1 m<sup>2</sup> quadrats and the number of minutes that that area of mudflat had been exposed. The droppings/m<sup>2</sup>/min were summed for each day to determine the daily proportion of droppings found at a particular distance. The mean of these daily proportions was calculated for each age and year group. R (version 2.8.1, The R Foundation for Statistical Computing 2008) was used to run a two-sample Kolmogrov-Smirnov goodness-of-fit test (Zar, 1999) to compare the distributions of proportion of droppings between adults and juveniles with distance from shore. Dates where age groups overlapped were removed from the analysis. This test uses cumulative frequencies of each group and measures the greatest distances between distributions to determine if this difference is significant.

## **2.4 Results**

### **2.4.1 Vigilance**

The proportion of time spent vigilant by sandpipers varied between 0 and 0.93 with an average ( $\pm$  SE) of  $0.0492 \pm 0.0024$  ( $n = 781$ ). Based on the global model results, a  $\hat{c}$  of 1.0303 was used in the analysis. The model that initially had almost all of the support from the data included all of the BASE variables, age, day of year, day of year squared, year, and the interactions between both day of year and day of year<sup>2</sup> with age ( $\omega_i$

= 0.996). Very little support was shown for any of the other models when compared to the top model. When the interaction terms with age, distance to cover and tide were included, the top model included the age and distance to cover term ( $\omega_i = 0.392$ ), with support for the model that included the interaction with tide as well ( $\omega_i = 0.365$ ). Support for the previously top model fell, but there was still substantial support for it ( $\omega_i = 0.217$ ) (Table 2.3).

Model fit increased dramatically with the inclusion of squared day of year term and its interaction with age. The inclusion of the BASE variables also increased the support for the models. The weighted parameter estimates and unconditional standard errors were calculated using the AIC weights from all models. The estimates and associated SE showed that there was a strong effect of year, onshore/offshore wind vector, flock size, cloud cover, distance to shore, position of bird in flock, age, and day of year (Table 2.4). The influence of tidal position, cloud cover, distance to bird, and nearest neighbour, was minimal because the SE of the effect size crossed zero, though the interaction between tidal position and distance to shore showed a stronger effect.

In adults, vigilance was high early in migration and declined quadratically with date. In juveniles, vigilance was higher than in adults, even during the short period when the two age classes overlapped in time, but was more constant throughout the migratory period (Figure 2.5) Vigilance was higher overall in 2007 than in 2008.

There was a negative correlation between distance from shore and vigilance, though the effect size was close to zero on an incoming tide (Figure 2.4). When the interaction with age was included, juveniles showed a stronger decline from a higher initial vigilance closer to shore on outgoing tides, while on incoming tides, vigilance

slightly declined in adults and remained constantly higher in juveniles, though this interaction did not have much support from the model estimates. Vigilance was higher when the wind was blowing towards shore and when it was mainly clear, though the 95% CI crossed zero. Vigilance was higher for flocks of fewer than 20 birds, and for birds on the edge of flocks.

#### **2.4.2 Flight-Initiation Distance**

FID varied between 5 and 89 m with an average ( $\pm$  SE) of  $19.59\text{m} \pm 0.97$  ( $n = 180$ ). Based on the global model output a  $\hat{c}$  of 1.0909 was used in the analysis. The top-supported model included the BASE variables plus age and year, with moderately strong support for models including date, and age and date as well as the base variables and year (Table 2.5). The top model received over 3 times the support of the next model ( $\Delta_i = 3.17$ ). The sum of all Akaike weights of models containing the BASE, year, and age variables were 0.98, 0.85, and 0.87 respectively, suggesting these variables were important in influencing FID. Because there was not one model with overwhelming support, weighted parameter estimates and unconditional standard errors were used (Table 2.6). These showed that the variables that did not have 95% CI crossing zero were starting distance to the bird, tidal state, and flock size. FID increased with starting distance and was shorter on incoming tides and in flocks between 20 and 200 compared with those larger than 200. While the 95% CI of most other parameters broadly crossed zero, distance of the bird to cover and the influence of a focal bird's nearest neighbours showed some influence, as the SE did not cross zero while the CI did. FID was shorter closer to shore and in more dense flocks. Adults showed a longer flight initiation distance, however the 95%CI crossed zero, but the SE did not. Birds in 2007 had longer

FID, though again the CI crossed zero, but the SE did not. All interactions of year, date and year showed very little support, due both to their low weighted parameter estimates and large SE of the effect sizes. Figure 2.6 shows the model average predictions for age, date and year with the daily means of the data and associated SE.

### **2.4.3 Spatial Usage**

Dropping counts varied between 0 and 69 droppings per 15 quadrats with an average ( $\pm$  SE) of  $3.266 \pm 0.243$  ( $n = 1075$ ). The daily proportion of droppings at a particular distance to cover varied between 0 and 1 with a mean ( $\pm$  SE) of  $0.0772 \pm 0.0048$ . There was a general trend for adults to have slightly higher proportion of droppings close to shore, but the distribution of proportion of droppings/m<sup>2</sup>/min did not differ between adults and juveniles in either year (Figure 2.7; 2007:  $D = 0.3077$ ,  $n = 13$ ,  $p > 0.10$ ; 2008:  $D = 0.2308$ ,  $n = 13$ ,  $p > 0.20$ ). The peaks of usage were slightly further from cover for both adults and juveniles in 2007 (250m compared with 200m in 2008). There was no difference between years within adults ( $D = 0.3077$ ,  $n = 13$ ,  $p > 0.10$ ) or juveniles ( $D = 0.3077$ ,  $n = 13$ ,  $p > 0.10$ ). Pooling the years does not make a difference in the result between age groups ( $D = 0.2308$ ,  $n = 13$ ,  $p > 0.20$ ).

## **2.5 Discussion**

### **2.5.1 Supported Predictions**

Adult and juvenile anti-predator behaviour differed in some ways throughout the migratory season and between years. Based on a mortality-minimizing strategy I predicted a pattern of declining anti-predator allocation in adults throughout their

migratory season, and more cautious behaviour throughout the migratory season of juveniles.

Patterns of time allocation to vigilance fit my predictions. Among adults, earlier migrants were more vigilant than later ones. Juveniles, which migrate later, had higher vigilance than all but the earliest adults, with relatively little variation throughout their season. For the brief period that the two age classes overlapped, which controls for variation in other environmental conditions, adults were less vigilant than juveniles (Figure 2.5).

Also as predicted, higher levels of vigilance and farther flight-initiation distance occurred in 2007, a year when peregrine falcons were predicted to have bred and migrated extremely early (snowmelt day of year 115), compared with 2008, when snowmelt on the arctic breeding grounds occurred a more normal two weeks later (day 130). Niehaus and Ydenberg (2006) found that the timing of peregrine arrival on the Fraser River delta was positively correlated with timing of snowmelt in Western Alaska. Based on Niehaus and Ydenberg's (2006) calculations, this results in an approximately 20-day difference in the date of mean falcon arrival (214 vs 230), which could account for individual sandpipers behaving more cautiously in 2007.

Based on the vigilance analysis, adults appeared to be migrating with decreasing caution, potentially in order to speed up their migration as the proximity to the falcon front increased. While higher vigilance was found in flocks of fewer than 20 birds, this accounted for only 3% of all samples and these flocks were found throughout the migratory period for both age groups and therefore cannot explain this pattern. Birds with more time vigilant spend less time foraging and therefore decrease their fuel-loading rate

(Barbosa, 1997; Cresswell, 1994; Metcalfe and Furness, 1984). While this can decrease their overall migratory speed, it provides increasing safety on migration. Juvenile sandpipers appear to be using this strategy while foraging at Boundary Bay. During the juvenile migratory period, food abundance is lower overall than during the adult migration (Pomeroy, AC, pers. comm.). If juveniles were attempting to maintain a similar fuel loading rate to that of adults, they would be expected to have to decrease vigilance to compensate for lower food availability. That juveniles increase vigilance with declining food strengthens the argument that they have a lower fuel-loading rate than adults. Vigilance has been shown to positively influence survival more strongly under higher predation danger conditions (Sansom et al., 2009). As predation danger is higher for juvenile migration, this suggests juveniles can improve survival by increasing vigilance, while adults may be instead gaining fuelling advantages by reducing vigilance.

Juvenile western sandpipers have longer small intestines than adults, which could allow them to partially compensate for increased vigilance by having an increased digestive capacity (Stein and Williams, 2006). Juveniles have been found at the same site in previous years to have similar levels of triglyceride and glycerol to adults, suggesting similar fuelling loading rates (Seaman, 2003). Cresswell et al. (2003) found foragers can maintain vigilance rates with high foraging rates, however juveniles have a trend towards lower foraging rates than adults (Seaman, 2003). Lind and Cresswell (2006) stress that individuals could compensate for increased vigilance by modifying another aspect of stopover behaviour.

### **2.5.2 Unsupported Predictions**

Contrary to our predictions, adults took flight from an approaching human at further distances than did juveniles, acting more, rather than less, cautiously, at a fairly constant rate throughout the season. There are four possible reasons for this: (1) the costs of staying are higher in adults; (2) the costs of leaving are higher for juveniles; (3) the benefits of staying are lower in adults; or (4) the benefits of leaving are lower in juveniles (Ydenberg and Dill, 1986). If adults are trying to reach their non-breeding grounds as quickly as possible, the cost of leaving should be higher for them due to the greater importance to them of a loss of potential foraging time. Any time lost needs to be made up later by foraging in a more dangerous habitat, reducing vigilance, or making some other trade-off to maintain a high fuel loading rate (Lind and Cresswell, 2006). As stated above, at Boundary Bay, the trend is that overall food is more abundant during the southward adult migration, and during the juvenile migration drops to levels similar to those found in spring migration (Pomeroy, AC, pers. comm.). Therefore, the benefits of staying in a particular foraging location could be lower for adults. It could be beneficial for an adult to simply move to another feeding site earlier, rather than paying an increasing cost of reducing foraging in order to observe a predator's approach.

Relyea (2003) reviews the influence of predation danger from multiple predators and found that individuals can act to decrease danger from the more risky predator at the expense of increasing the chance of a successful attack from the less dangerous predator. Juveniles could allow closer encroachment by humans to due to higher abundance of the more dangerous falcons. This assumes that western sandpipers view peregrines as more dangerous than humans. It should also be noted that the strength of any inferences made

from the flight-initiation distance test cannot be that strong as there was little change between the log likelihoods of the top model and the null model. Varying the number of risk factors approached individuals experience, has shown to influence flight initiation results (Cooper Jr, 2009). Sandpipers experiencing different peregrine predation danger levels could cause them to view the approach of humans differently.

I found similar patterns of spatial usage to those found by Pomeroy (2006), however there were no differences between the distributions of droppings between adults or juveniles in either year. There was a slight trend of adults having relatively higher usage closer to shore. Due to higher overall prey abundance compared with juvenile migrations, adults may have less relative benefit from foraging close to shore. There is also less of a declining trend in food abundance with distance from shore for southward migration compared with northward migration (Pomeroy, 2006). This would reduce the benefit of foraging close to shore for both age groups. While the number of peregrines increases dramatically in August, there are some predators around in July, making foraging close to shore dangerous (Lank et al., 2003). Therefore, adults may be able to reach their desired rate of fuel loading by lowering their vigilance without shifting their spatial usage closer to shore. Also, as birds decrease their distance to cover, their vigilance increases, which reduces the benefit of foraging close to shore (Barbosa, 1997; Cresswell, 1994; Pomeroy, 2006). If juveniles were using more dangerous habitats due to naïveté or incompetence, as has been suggested before (Rappole, 1995), we would expect to see relatively higher spatial usage by juveniles close to shore when compared with adults. This was not found.

### 2.5.3 Alternate Hypotheses

Neither time minimization nor energy minimization hypotheses predict seasonal changes in migratory strategy as is suggested by the vigilance trends in adult western sandpipers. If juveniles were acting as time-minimizers, they would not be expected to have higher vigilance than adults. It is possible that late adults may be attempting to minimize time on migration by reducing vigilance. However a mortality-minimization strategy is a better fit for the pattern of vigilance seen throughout adult and juvenile migratory periods.

Incompetence and naïveté in juveniles has also been used to explain differences in vigilance between adults and juveniles. Despite a wide variety of positive and negative correlations with age, Caro (2005) describes the possibility that juveniles are less competent than adults, making vigilance less profitable. He relates this to the possibilities that they might fail or be slower to notice dangerous predators, or even recognize them as a threat. Other studies have found that adults have higher vigilance than their juvenile offspring, but in these cases the juveniles and adults were together (Alonso and Alonso, 1993; Bildstein et al., 1991). Our findings do not support the idea that juveniles behave less cautiously due to lack of experience with predators; though it is possible they could have increased vigilance to compensate for entering novel habitats. It is possible that juveniles were compensating for increased diurnal vigilance by increasing their night time foraging activity, as has been found for other migrating birds experiencing higher predator abundance (Fransson and Weber, 1997). However, it is just as likely that birds are already foraging at levels similar to those during the day, as found in semipalmated sandpipers and dunlin (McCurdy et al., 1997; Mouritsen, 1994). While these hypotheses

cannot be eliminated, the general trend within adults, follows the predictions that changes in predation-danger landscapes and moult timing lead to differing vigilance levels in adults and juveniles and that the decreasing vigilance in adults represents an attempt to increase their speed of migration.

Another hypothesis associated with migration strategies is that adults depart early in order to take advantage of high food abundance and juveniles migrate quickly to avoid migrating in very low food conditions (Schneider and Harrington, 1981). As discussed by Lank et al. (2003), there is not a decline in all prey species abundance, meaning late migrants would still have enough food for foraging. While invertebrate abundance is overall lower for juveniles, it still remains overall higher than in the spring when birds migrate northward (Pomeroy AC, Pers. Comm.). This hypothesis predicts juveniles should have lower vigilance as they compensate for declining food abundance. Juveniles are also predicted to shift spatial usage to higher food abundance closer to shore and allow closer approach by humans, with this trend increasing throughout their migratory period. The data did not support these predictions for vigilance or spatial usage and there was no trend for decreasing FID throughout the juvenile migration period. Therefore this hypothesis was only supported by FID result, but the studies described above make this factor unlikely to have a strong effect on this system.

#### **2.5.4 Other Influential Variables**

Outside of the predation danger hypothesis, the results show that other variables influence vigilance and flight-initiation distance. That vigilance was higher when the wind was blowing towards shore is not easily explained and could be a result of the wind being more likely to be blowing towards shore on an incoming tide (pers. obs.). The

influence of tide is discussed below. McGowan et al. (2002) found that flocks became more flighty as temperature increased, which might explain why birds were more vigilance when there was less cloud cover. The weather was mostly clear for 46% of samples, so this may have biased the data as well.

Weighted parameter estimates show that vigilance declined much more dramatically on outgoing tides for juveniles compared with adults (Figure 2.4). This fits with the prediction that the cost of being close to shore should be higher for juveniles and that adults have the most to benefit from lowering vigilance in the more dangerous, near-cover area. As distance from cover increased, the danger decreased and the proportion of time vigilant between the age groups converged (Dekker and Ydenberg, 2004; Pomeroy, 2006). On an incoming tide, across distances from cover, the level of vigilance remained near that of birds that were foraging close to shore on an outgoing tide. In adults there was even a slight decline from higher vigilance far from shore. This would suggest that sandpipers view incoming tides to be equally dangerous across distances to cover (Sansom et al., 2009). This could be due to the increasing number of falcon attacks that come as the tide is incoming (pers. obs.). While Dekker and Ydenberg (2004) found that kill rate is actually higher after high tide, this does not mean that the birds are not being disturbed by unsuccessful falcon attacks and by the tide pushing them closer to shore. Further research may illuminate this issue.

Shorter FID on incoming tides and closer to shore fits well with the multiple predator hypothesis, suggesting that these birds are allowing closer approach by less dangerous humans, potentially to increase survival probability from peregrine attacks (Relyea, 2003). This finding is similar to the comparison between adults and juveniles,

with the incoming tide inducing similar reactions to that of juveniles across the migratory period, whereas the falling tide had similar results to that found by adults.

### **2.5.5 Future Studies**

Extending our findings to other stopover locations based on the predation danger hypothesis, sites that are further south would be expected to have more dramatic changes in stopover behaviour occurring throughout the season. If adults have not gained enough ground on the peregrine front, they would be predicted to increase their migratory speed through changes in their stopover behaviour (Ydenberg et al., 2007). The closer to the front the more dramatic the changes in behaviour are. With juveniles, attempts to maximize immediate safety increases as the front arrives or passes. Further exploration of behaviour at other stopover sites may elucidate the different migratory strategies.

Length of stay can be used to infer changing patterns of speed of migration and this is explored further (Chapter 3). This avoids the complication of observing behaviours that may influence fuel loading rate, but that can be compensated for by shifting other behaviours and therefore may not affect overall migration speed (Lind and Cresswell, 2006). The interactions between behaviours are often unknown, and without experimental manipulation drawing inferences from observed behaviour can be difficult. Length of stay, and direct estimates of fuel loading rate and departure fuel load are hard to obtain, especially at large sites such as the Fraser River delta, however such data could be collected with enough catching and resighting effort (Duijns et al., 2009).

My results illustrate the complexity of understanding how stopover decisions influence migratory speed. Migrants may trade-off behaviours, resulting in little change

in fuelling rate between groups or individuals (Lind and Cresswell, 2006). Changing environmental conditions throughout and between migratory periods can make inferring migratory speed decisions difficult. Despite these qualifications, I conclude that adults are lowering vigilance as the season progresses, presumably to increase fuelling rate, even though they are behaving more cautiously towards approaching humans. Departing a month before juveniles may provide enough of a time window that adult migrants do not need to adjust multiple aspects of stopover behaviour in order to achieve their desired mortality-minimizing migratory speed. The FID and vigilance changes in years of earlier peregrine migration, suggests that all migrants may perceive danger in these years differently. Adult and juvenile sandpipers are adjusting some behaviours throughout the season while other behaviours appear to be more static. Adults may forage more intensely, but be more sensitive to disturbance. This study highlights the importance of looking at variables outside of those an individual is currently experiencing in attempting to understand animal behaviour.

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## 2.7 Tables

Table 2.1 Variables used in creating models for analysis of proportion of time vigilant. BASE variables are in bold.

Predictor variable	Description	Units	Data Distribution		Source	Reference
			Mean / Group	Range / %		
Age	Hatch year birds (first migration) or after hatch year birds	Categorical	Adult Juvenile	42% 58%	Visual assessment	Elgar 1989
Day of Year	Date of vigilance observation		218.19	184-251	Calendar from GPS	Lank et al 2003
Year	Year of observation	Categorical	2007 2008	53% 47%	Calendar GPS	Niehaus and Ydenberg 2006
<b>Tidal State</b>	Whether the tide was falling or rising	Categorical	Incoming Outgoing	38% 62%	Digitized tidal chart	Pers Obs, Pomeroy (Pers. Comm)
<b>Onshore/Offshore Wind Vector</b>	Strength of wind from the north(+)/south(-)	km/hr	5.45	-17.85 - 38.11	Environment Canada Website	Pers Obs
<b>Cloud Cover</b>	Categorical evaluation of cloud cover based on weather	Categorical	Mainly Clear Partially Cloudy Cloudy or Rain	46% 27% 27%	Environment Canada Website	Elgar 1989
<b>Distance to Cover</b>	Distance of bird to cover	m	312.61	0 -1500	GPS	Pomeroy 2006b
<b>Flock Size</b>	Number of birds within a group ending when birds are more than 10m apart	Small, <20; 20< Medium <200; Large > 200	Small Medium Large	3% 39% 58%	Visual assessment	Elgar 1989
<b>Position in Flock</b>	Edge - within 3 birds from edge	Position Categories	Edge Middle	50% 50%	Visual assessment	Elgar 1989
<b>Distance to Bird</b>	Distance from observer to focal bird	m	60.35	10-195	GPS	Elgar 1989
<b>Nearest Neighbours</b>	Mean distance from focal bird to closest 3 birds	m	1.59	0-6	Visual assessment	Elgar 1989
<b>Time</b>	Proportion of Day Passed		0.48	0.233-0.792	Clock	Elgar 1989

Table 2.2 Variables used to create models in analysis of Flight-Initiation Distance. Variables other than Age, Day of Year, and Year are included as BASE variables.

Predictor variable	Description	Units	Data Distribution		Source	Reference
			Mean / Group	Range / %		
Starting Distance	Distance from observer to focal bird before approach	m	65.36	21 - 197	GPS assessment	Blumstein 2003
Age	Hatch year birds (first migration) or after hatch year birds	Categorical	Adult Juvenile	46% 54%	Visual assessment	
Day of Year	Date of vigilance observation		215.79	188-251	Calendar	Lank et al 2003
Year	Year of observation	Categorical	2007 2008	57% 43%	Calendar	Niehaus and Ydenberg 2006
Tidal State	Whether the tide was falling or rising	Categorical	Incoming Outgoing	37% 63%	Digitized tidal chart	Pers Obs, Pomeroy (Pers. Comm)
Wind Strength	Strength of wind blowing (no directionality)	km/hr	15.13	0 - 44	Environment Canada Website	McGowan et al. 2002
Distance to Cover	Distance from bird to cover on shoreline	m	333.78	0 - 1100	GPS assessment	Pomeroy 2006
Flock Size	Number of birds within a group ending when birds are more than 10m apart	Small<20 20<Medium<20 0 Large> 200	Small Medium Large	3% 34% 63%	Visual assessment	
Nearest Neighbours	Average distance from focal bird to closest 3 birds	m	1.68	0 - 5	Visual assessment	

Table 2.3 Summary of results and models from AIC analysis of generalized linear models of proportion of time vigilant.  
 Global model includes all variables and interactions included in other models. A  $\hat{c}$  of 1.0303 was used in the analysis. Parameter estimates included +1 for the intercept, +1 for the model variance, and +1 because Quasi-AIC values were used. McFadden's  $R^2$  are listed to show improvement of model fit between null and fitted model.

Model	N obs	K	Log Likelihood	Delta QAICc	QAICw	Pseudo-R <sup>2</sup>
BASE AGE DATE DATE <sup>2</sup> YEAR AGExDATE AGExDATE <sup>2</sup> D2CxAGE	781	21	-509.17	0.00	0.39	0.20
BASE AGE DATE DATE <sup>2</sup> YEAR AGExDATE AGExDATE <sup>2</sup> D2CxAGExTIDE	781	22	-508.16	0.14	0.37	0.20
BASE AGE DATE DATE <sup>2</sup> YEAR AGExDATE AGExDATE <sup>2</sup>	781	20	-510.87	1.19	0.22	0.19
GLOBAL	781	25	-507.64	5.54	0.02	0.20
BASE AGE DATE DATE <sup>2</sup> YEAR AGExDATE	781	19	-517.96	12.84	0.00	0.18
BASE AGE DATE DATE <sup>2</sup> YEAR AGExDATE	781	18	-524.37	23.17	0.00	0.17
BASE AGE YEAR	781	16	-527.89	25.82	0.00	0.17
BASE AGE DATE YEAR	781	17	-527.75	27.65	0.00	0.17
BASE AGE DATE YEAR AGExDATE	781	18	-527.05	28.38	0.00	0.17
BASE AGE DATE YEAR DATExYEAR	781	18	-527.10	28.47	0.00	0.17
BASE AGE DATE YEAR AGExYEAR	781	18	-527.42	29.10	0.00	0.17
BASE AGE	781	15	-539.52	46.31	0.00	0.15
BASE AGE DATE AGExDATE	781	17	-537.55	46.67	0.00	0.15
BASE AGE DATE	781	16	-539.06	47.51	0.00	0.15
AGE YEAR	781	5	-550.85	47.76	0.00	0.13
AGE DATE YEAR	781	6	-550.80	49.70	0.00	0.13
AGE DATE YEAR AGExDATE	781	7	-550.19	50.54	0.00	0.13
AGE DATE YEAR DATExYEAR	781	7	-550.68	51.49	0.00	0.13
AGE DATE YEAR AGExYEAR	781	7	-550.68	51.51	0.00	0.13
BASE DATE YEAR	781	16	-547.08	63.08	0.00	0.14
AGE	781	4	-567.97	78.96	0.00	0.10
AGE DATE AGExDATE	781	6	-566.35	79.89	0.00	0.11
AGE DATE	781	5	-567.96	80.98	0.00	0.10
BASE DATE	781	15	-557.98	82.15	0.00	0.12
DATE YEAR	781	5	-571.38	87.61	0.00	0.10
DATE	781	4	-587.77	117.41	0.00	0.07
BASE YEAR	781	15	-578.33	121.65	0.00	0.09
BASE	781	14	-583.89	130.37	0.00	0.08
YEAR	781	4	-625.00	189.68	0.00	0.01
NULL	781	3	-633.98	205.09	0.00	0.00

Table 2.4 Model Likelihoods, weighted parameter estimates, unconditional standard errors and 95% confidence interval for AIC results of proportion of time vigilant.

Nominal parameters listed are additive above those included in the intercept. Intercept groupings include: Juveniles, outgoing tidal position, cloudy, birds in the middle of a flock, flocks larger than 200 birds, and 2008. Parameter estimates are in log<sub>10</sub> scale. Day of year is the day number after day number 180.

<i>Parameter</i>	<i>Model Likelihood</i>	<i>Weighted Parameter Estimate</i>	<i>Unconditional SE</i>	<i>95CI</i>
Intercept*	1.0000	-0.3307	0.5904	1.1572
Adult	1.0000	-0.6054	0.5961	1.1683
Day of Year	1.0000	-0.0490	0.0232	0.0455
Day of Year * Adult	0.9994	-0.0482	0.0280	0.0548
2007	1.0000	0.1472	0.0460	0.0901
Adult 2007	0.0246	0.0072	0.0172	0.0336
Day of Year*2007	0.0246	0.0001	0.0003	0.0005
Day of Year <sup>2</sup>	1.0000	0.0005	0.0002	0.0004
Day of Year <sup>2</sup> *Adult	0.9994	0.0015	0.0004	0.0008
Day of Year*Adult 2007	0.0246	-0.0002	0.0004	0.0009
Incoming Tide	1.0000	-0.0318	0.0537	0.1053
Onshore/Offshore Wind	1.0000	-0.0034	0.0021	0.0041
Mainly Clear	1.0000	0.0535	0.0449	0.0881
Partially cloudy	1.0000	0.0126	0.0469	0.0920
Distance from Cover	1.0000	-0.0005	0.0001	0.0003
Flock Size <20 birds	1.0000	0.2543	0.1038	0.2034
Flock Size 20 – 100 birds	1.0000	-0.0215	0.0383	0.0750
Position of Bird - Edge	1.0000	0.0761	0.0363	0.0711
Distance to Bird	1.0000	0.0004	0.0007	0.0013
Nearest Neighbour	1.0000	0.0085	0.0166	0.0325
Distance from cover – Incoming Tide	1.0000	0.0005	0.0002	0.0003
Distance from cover - Adult	0.7826	0.0002	0.0002	0.0003
Distance from cover – adult – incoming tide	0.3901	-0.0001	0.0002	0.0003
Scale	1.0000	0.4644	0.0118	0.0231

Table 2.5 Summary of results and models from AIC analysis of generalized linear models of flight initiation distance.

Global model includes all variables and interactions included in other models. A  $\hat{c}$  of 1.0909 was used in the analysis. Parameter estimates include +3 for the intercept, the model variance, and the Quasi-AIC values. McFadden's  $R^2$  are listed to show improvement of model fit between null and fitted model.

<i>Model</i>	<i>N</i>	<i>K*</i>	<i>Log Likelihood</i>	<i>Delta AICc</i>	<i>QAICw</i>	<i>Psuedo-R<sup>2</sup></i>
Base Age Year	180	12	-672.69	0.00	0.41	0.06
SD Base Age Date Year	180	13	-672.68	2.31	0.13	0.06
SD Base Date Year	180	12	-674.25	2.87	0.10	0.06
SD Base Age	180	11	-675.71	3.24	0.08	0.06
SD Base Age Date Year	180	14	-672.10	3.61	0.07	0.06
Age*Date	180	14	-672.13	3.66	0.07	0.06
SD Base Age Date Year	180	14	-672.13	3.66	0.07	0.06
Date*Year	180	14	-672.30	3.97	0.06	0.06
SD Base Age Date Year	180	14	-672.30	3.97	0.06	0.06
Age*Year	180	12	-675.71	5.53	0.03	0.06
SD Base Age Date	180	11	-677.13	5.85	0.02	0.06
SD Base Date	180	11	-677.13	5.85	0.02	0.06
SD Base Age Date Age*Date	180	13	-674.94	6.45	0.02	0.06
SD Year Age	180	6	-684.45	8.19	0.01	0.05
SD Base Year	180	11	-678.47	8.30	0.01	0.05
Global With Base	180	17	-670.76	8.38	0.01	0.06
SD Age Date Year	180	7	-684.45	10.35	0.00	0.05
SD Age Date Year Age*Year	180	8	-683.51	10.82	0.00	0.05
SD Age Date Year	180	8	-683.52	10.84	0.00	0.05
Date*Year	180	8	-683.52	10.84	0.00	0.05
SD Year Date	180	6	-685.98	10.99	0.00	0.04
SD Age	180	5	-687.56	11.74	0.00	0.04
SD Age Date Year Date*Age	180	8	-684.25	12.17	0.00	0.05
SD Base	180	10	-682.24	12.95	0.00	0.05
Age + Date +SD	180	6	-687.53	13.84	0.00	0.04
SD + Date	180	5	-688.73	13.89	0.00	0.04
SD Age Date Age*Date	180	7	-687.31	15.59	0.00	0.04
Global Without Base	180	11	-682.84	16.31	0.00	0.05
SD Year	180	5	-692.47	20.74	0.00	0.03
SD	180	4	-695.05	23.36	0.00	0.03
Null	180	3	-716.87	61.27	0.00	0.00

Table 2.6 Model Likelihoods, weighted parameter estimates, unconditional standard errors and 95% confidence interval for AIC results of flight-initiation distance.

Nominal parameters listed are additive above those included in the intercept. Intercept groupings include Juveniles, outgoing tidal position, flocks larger than 200 birds and 2008. Parameter estimates are in log<sub>10</sub> scale. Date parameter is the day of year number after 180.

<i>Parameter</i>	<i>Parameter Likelihoods</i>	<i>Weighted Parameter Estimates</i>	<i>Unconditional SE</i>	<i>95% CI</i>
Intercept	1.00	2.504	2.83E-1	5.54E-1
SD	1.00	6.284E-3	8.71E-4	1.71E-3
Age Adult	0.87	2.920E-1	1.92E-1	3.76E-1
Date	0.50	4.117E-5	3.43E-3	6.71E-3
Year 2007	0.85	1.782E-1	1.26E-1	2.47E-1
Tide Incoming	0.98	-1.921E-1	9.48E-2	1.86E-1
Wind	0.98	-4.514E-3	5.31E-3	1.04E-2
D2C	0.98	2.450E-4	1.46E-4	2.85E-4
Flock 0	0.98	-1.776E-1	2.77E-1	5.42E-1
Flock 1	0.98	-2.520E-1	9.18E-2	1.80E-1
NN	0.98	-5.976E-2	3.91E-2	7.66E-2
Date*Age Adult	0.09	-9.164E-4	2.31E-3	4.54E-3
Age*Year Adult	0.06	1.621E-2	3.74E-2	7.33E-2
Date*Year 2007	0.07	-3.212E-4	8.93E-4	1.75E-3
Date*Age*Year	0.01	-2.083E-4	4.68E-4	9.18E-4
Scale	1.00	10.20	0.548E-1	1.07

## 2.8 Figures

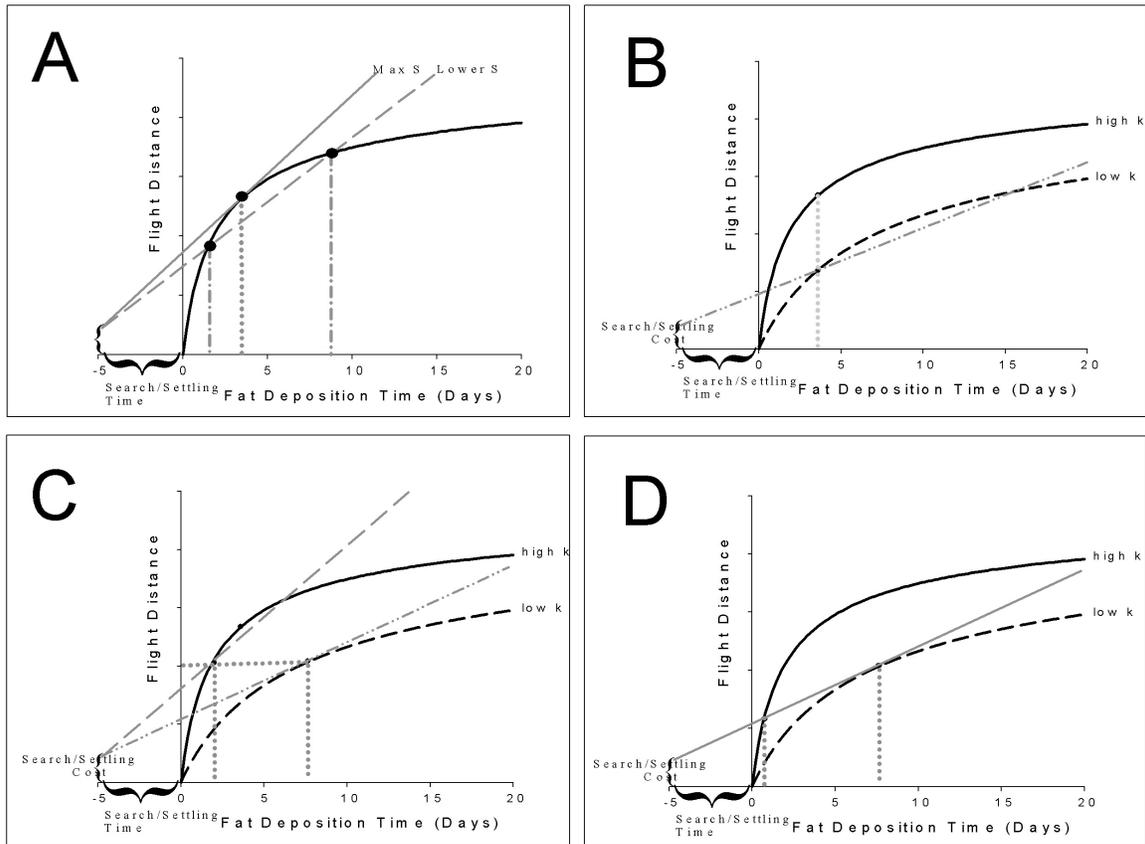


Figure 2.1 Migratory speed based on fuel loading rate and departure decisions (solid and dashed lines).

Vertical lines represent length of stay at departure. Speed of migration ( $S$ ) is the slope of the line that intercepts the search/settling point and touches the departure point for a given fuel loading rate ( $K$ ) (A) Optimal departure decisions for a given loading rate. Higher fuel loading rate could give (B) a higher fuel load at departure, (C) an earlier departure or (D) the same speed of migration with earlier departure and fuel load. Formulas from (Alerstam and Lindström, 1990).

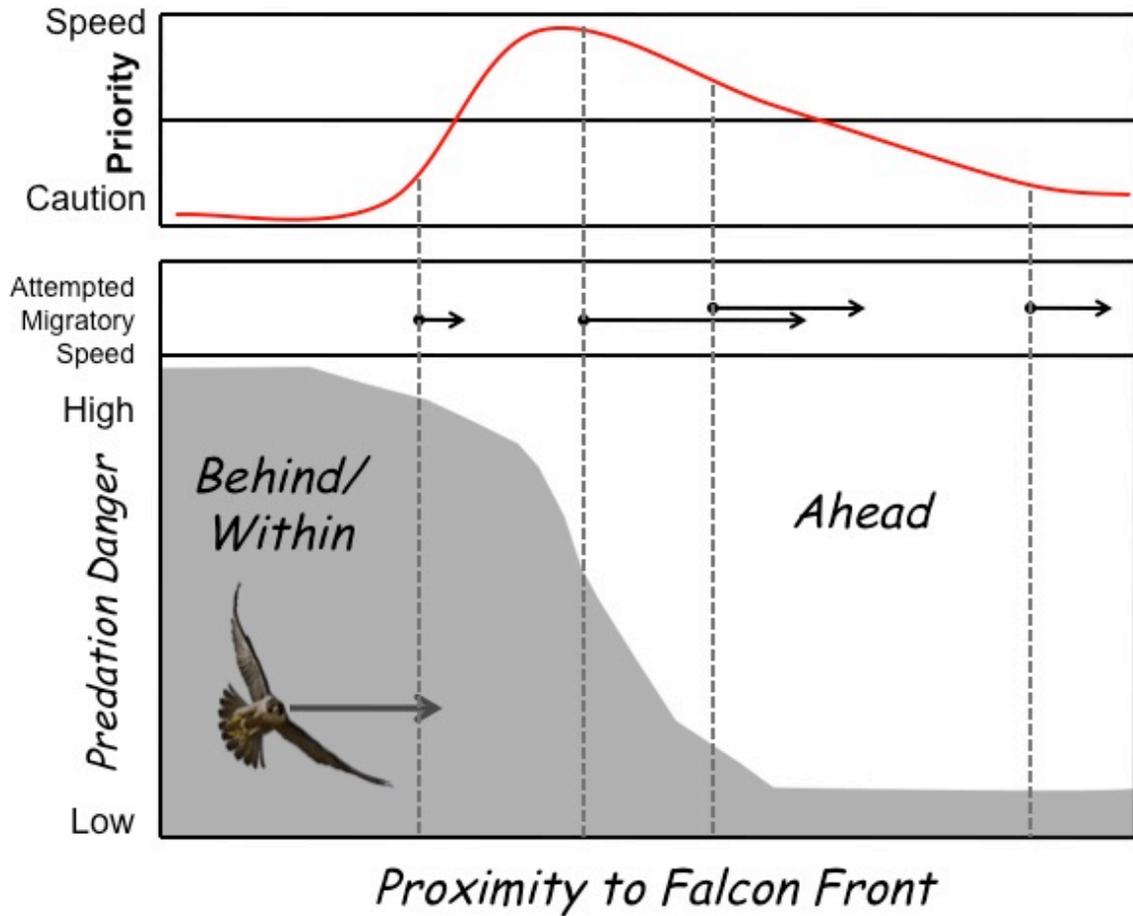


Figure 2.2 Predicted seasonal variation in migration tactics of sandpipers at a particular stopover site relative to the falcon front.

Shifts in priority (top curve) are expected to shift from caution (below line) to speed (above line) as the predator front (solid arrows) becomes increasingly closer in space and time. As predation danger (grey shading) increases sandpiper priority should shift back to caution. Migrants at various proximities (vertical dashed lines) to the falcon front should have different tactics and different attempted migratory speeds (horizontal dashed arrows). Migrants ahead of the falcon front should have higher speeds than those behind the front. Falcon arrival varies between years (solid arrows) and migrants attempting to stay ahead of the falcon front must have speeds higher than the falcon front (estimated at 170km/day (Fuller et al., 1998; Worcester and Ydenberg, 2008)) Falcon front based on Figure 1, Lank et al. (2003). Photo credit: bairdphotos.com.

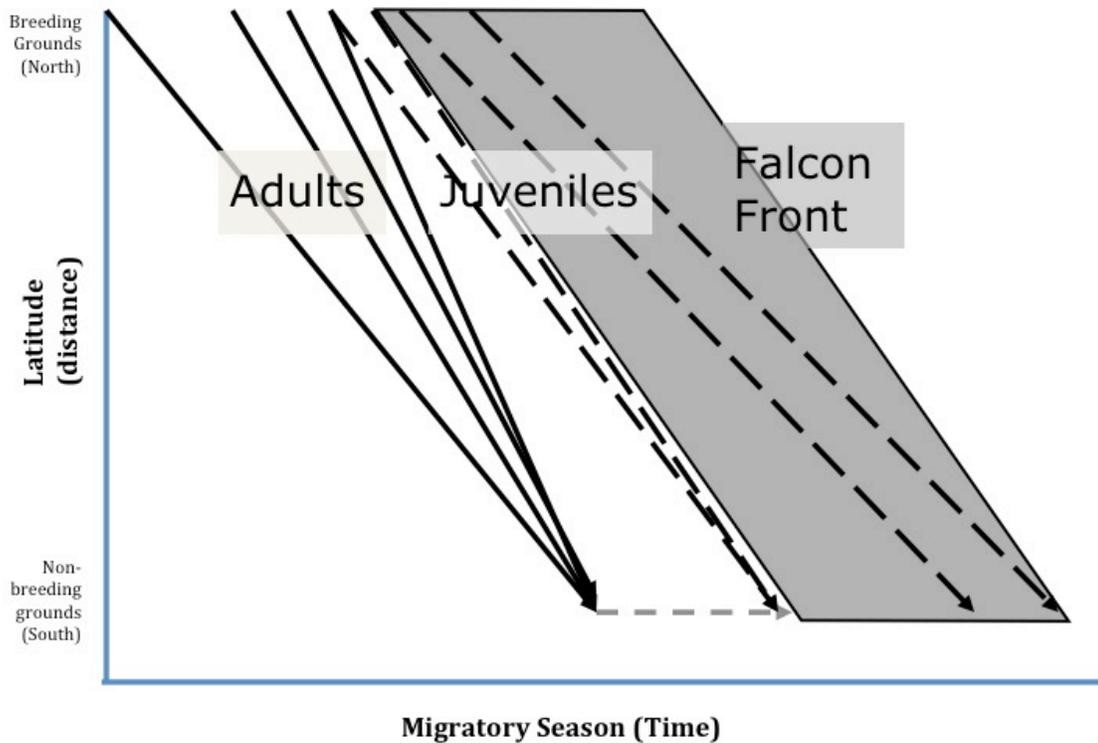


Figure 2.3 Graphical representation of predicted migration trajectories for adult (solid) and juvenile (dashed) western sandpiper and peregrine falcon (grey box) migrations. The steeper the arrow, the faster an individual is migrating. Late adults migrate faster than early migrants, while juveniles are predicted to migrate more slowly. The light grey dashed line represents required time for moulting.

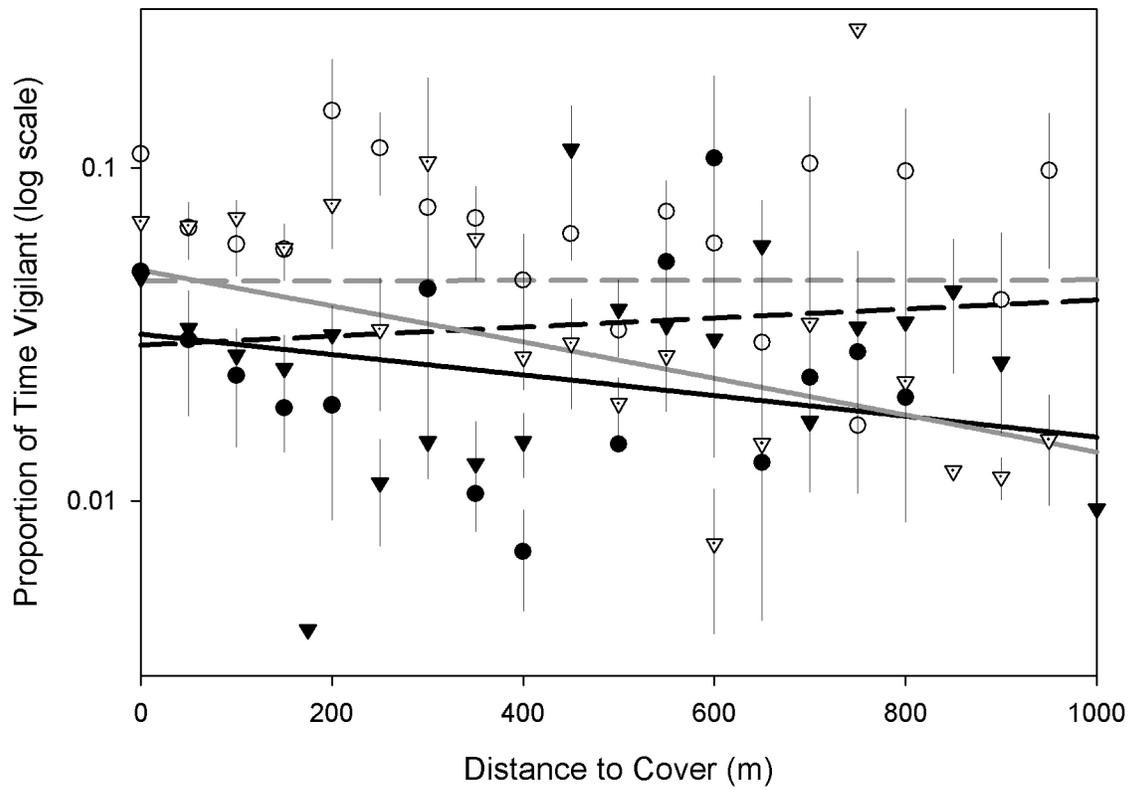


Figure 2.4 Weighted model outputs for log of the proportion of time vigilant with increasing distance from cover. The points represent averages for each distance from cover for adults (solid) and juvenile (open) on incoming (circles) and outgoing (triangles) tides with accompanying standard errors. The lines are adult (black) and juvenile (grey) vigilance levels on incoming (dashed) or outgoing (solid) tides as predicted by the weighted parameter estimates from an AIC analysis.

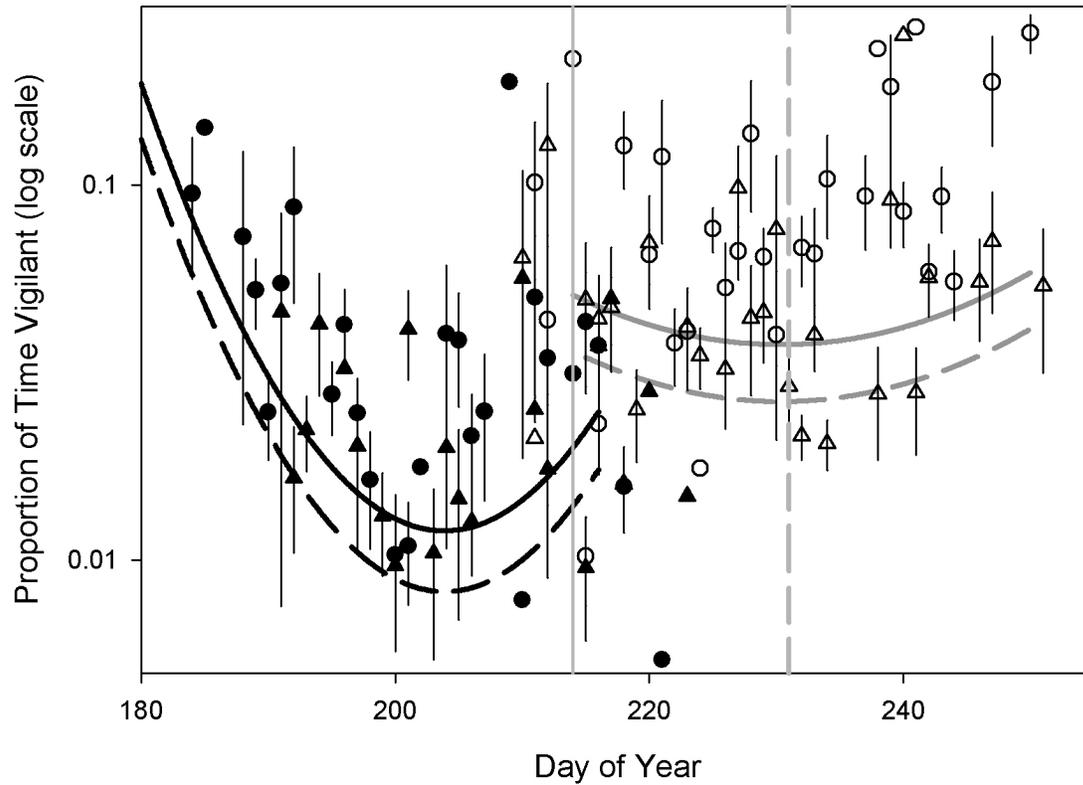


Figure 2.5 Weighted model outputs for proportion of time vigilant with day of year. The points represent averages with SE for each day for adults (solid) and juvenile (open) in 2007 (circles) and 2008 (triangles). The lines are adult (black) and juvenile (grey) vigilance levels in 2008 (dashed) or 2007 (solid) as predicted by the weighted parameter estimates from an AIC analysis. Grey vertical lines indicate predicted 50% falcon arrival dates for 2007 (solid) and 2008 (dashed).

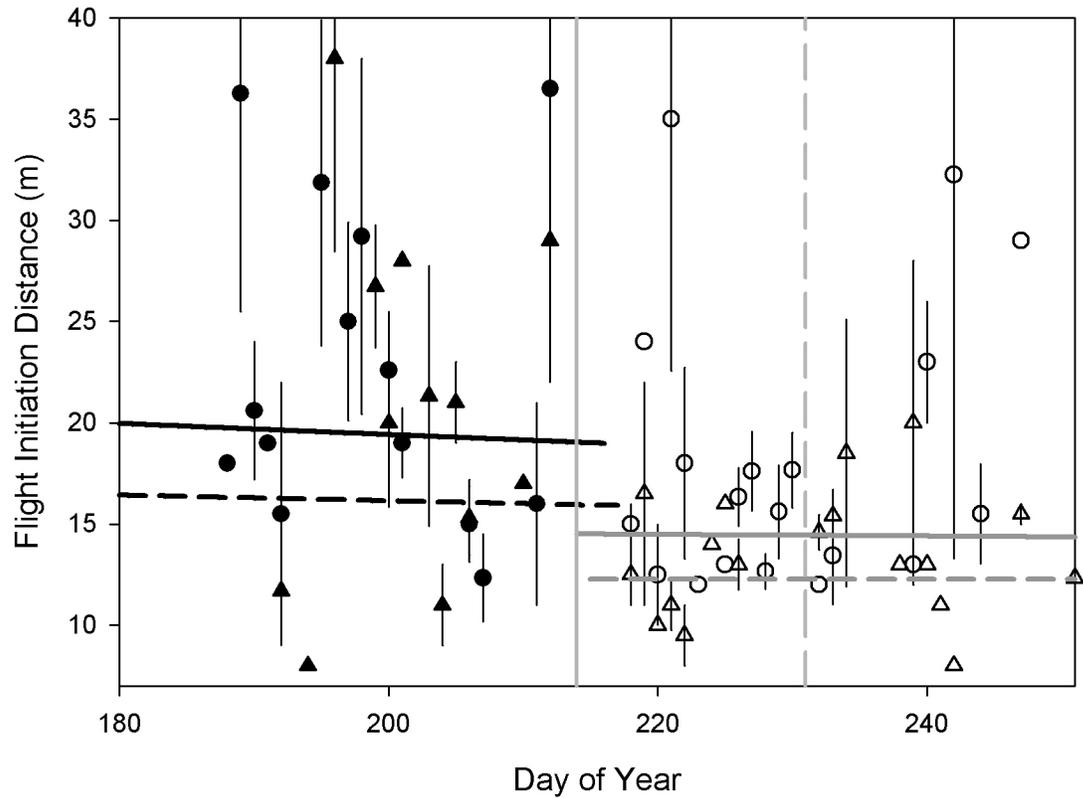


Figure 2.6 Weighted model outputs for flight-initiation distance with day of year. The points represent averages with SE for each day for adults (solid) and juvenile (open) in 2007 (circles) and 2008 (triangles). The lines are adult (black) and juvenile (grey) vigilance levels in 2008 (dashed) or 2007 (solid) as predicted by the weighted parameter estimates from an AIC analysis. Vertical lines indicate predicted 50% falcon arrival dates for 2007 (solid) and 2008 (dashed). Based on Neihaus and Ydenberg (2006).

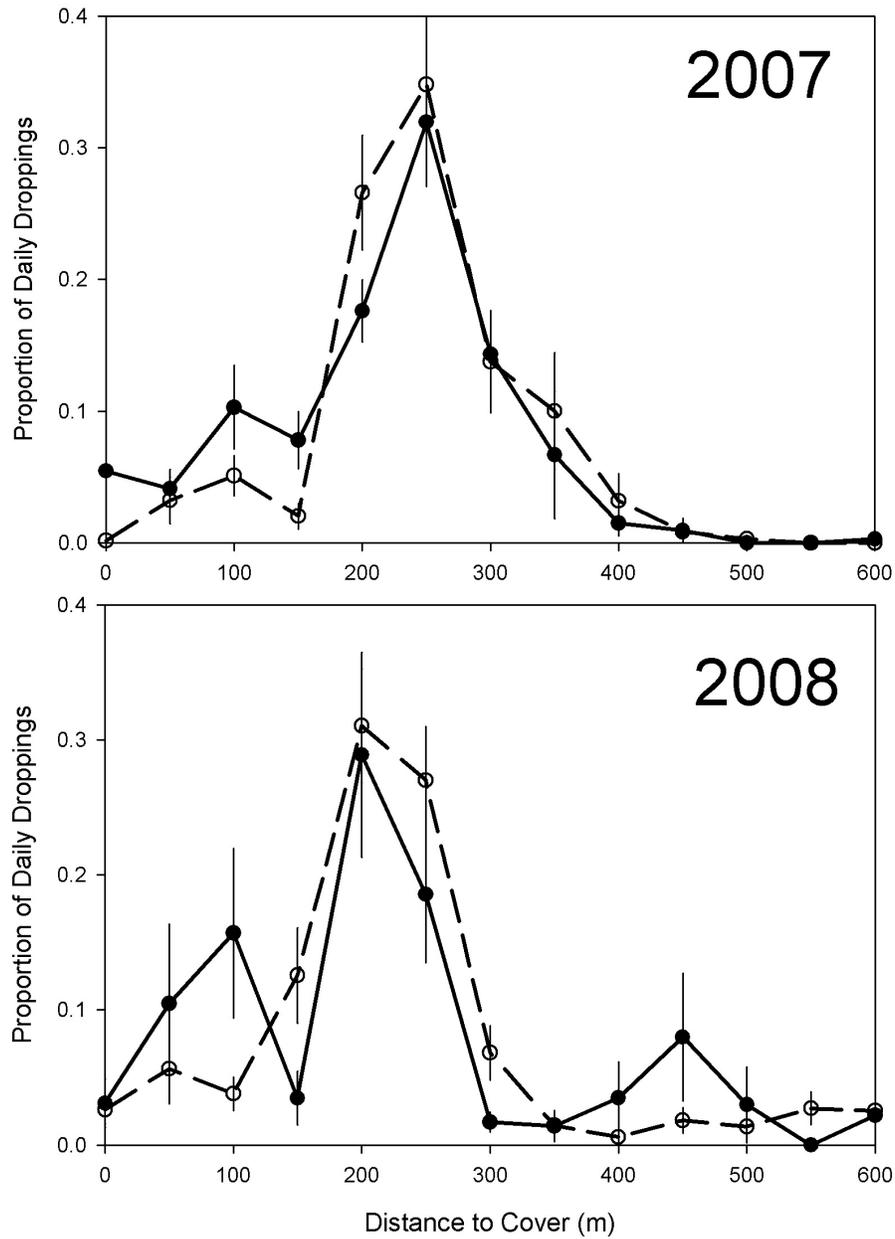


Figure 2.7 Average values of proportion of daily droppings with SE for each distance from cover in 2007 and 2008. Adults are solid lines and juveniles are dashed.

### **3: Mortality-Minimizing Strategies of Residence Times of Two Calidrid Sandpiper Species Vary With Positions on Predator Landscapes**

To be submitted with the following authors:

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David D. Hope performed analysis of semipalmated sandpiper data, and wrote the chapter. Dr. Ydenberg generated the hypotheses that this work is based on, worked on interpretation of results and drafting of final version of the chapter. Dr. Lank collected semipalmated data, assisted in generating hypotheses, provided substantial input into the planning of the project, worked on interpretation of results and helped put together the final version of the chapter. Dr. Butler collected western sandpiper recapture data. Dr. Smith performed residence time analysis of western sandpiper data and assisted in drafting the chapter.

### **3.1 Abstract**

We examined migratory departure decisions of two shorebird species with respect to age-class and position on predator landscapes. Relative predator abundance increases in a short period of time at stopover sites, due to the arrival of migrating peregrine falcons. Semipalmated sandpipers and adult western sandpipers pass through stopover sites while predator abundance is relatively low. However, juvenile western sandpipers migrate under higher predation danger, as their migration overlaps with that of the peregrine falcon. As time spent fuelling lengthens, migratory speed will increase to a theoretical maximum and then start to decrease as migrants continue to load fuel stores. Western sandpipers loaded fuel below the optimum and adults seasonally increased whereas juveniles decreased stopover length. Eastern semipalmated sandpipers loaded fuel past the speed-maximizing point with lengths of stays decreasing for both adults and juveniles. Semipalmated sandpipers travelling along an overland migration route loaded less fuel and had shorter stays time than those preparing for a transoceanic flight. Migrants ahead of the falcon front appear to be attempting to migrate quickly, while those experiencing higher predation danger appear to be attempting to increase safety at stopovers. This study highlights three separate tactics that all appear to attempt to minimize mortality on migration.

## 3.2 Introduction

### 3.2.1 Theoretical Background

Migration strategies in birds are governed by the influences of time, energy and predation (Alerstam and Lindström, 1990). As time at stopover sites represents the majority of the total time spent on migration, decisions made about stopover duration have a large influence on migration speed, energy expenditure, and predation danger (Hedenström and Alerstam, 1997). Alerstam and Lindström (1990) showed how migrants can adjust their migration speed by changing the rate at which they load fuel or by adjusting the size of fuel load at departure. “Migratory speed” is defined here as the potential migratory flight range based on fuel load at departure divided by the time required to cover that range, including the stopover time necessary to load the fuel.

As time spent fuelling at a stopover site increases, fuel load accumulates, which in turn increases the flight range. Drag increases with fuel load, causing flight efficiency to decrease, which in turn gives diminishing returns in flight range (Figure 3.1; Pennycuick, 1975). At a given fuel-loading rate, migratory speed moves towards a maximum as fuel load increases, and then begins to fall past this point. For migrants minimizing the time spent on migration, the maximum migration speed is by definition ‘optimal’. At higher fuel loads, the flight range is greater, but migratory speed lower (Alerstam and Lindström, 1990). These migrants are considered to be ‘loading past the optimum’.

An alternative strategy outlined by Alerstam and Lindström (1990) is to minimize energy expenditure during the entire migration. Energy-minimizers should have departure fuel loads that minimize drag, but provide sufficient fuel to reach the next available

stopover site. They should depart with lower fuel loads than birds that are time-selected and migrate in short hops from stopover to stopover without skipping any sites.

Higher fuel loading rates reduce the time needed to reach an optimal departure fuel load, but can result in increased predation danger while foraging. For a given fuel loading rate, birds loading below the time-minimizing optimum migratory speed by departing heavier and staying longer. Migrants loading past the optimum increase migratory speed by shortening stopover times (Figure 3.1; (Alerstam and Lindström, 1990; Houston, 1998). Migrants that load past the optimum have no benefit in terms of migratory speed because the same speed could be achieved by departing earlier. However, high fuel loads can be selected for if a large ecological barrier must be crossed making time minimization a low priority (Bairlein, 1992; Dunn et al., 1988; Holmgren et al., 1993; Richardson, 1979; Wichmann et al., 2004).

Most studies on migration strategies have tried to categorize a particular species as either a “time-minimizer” or an “energy-minimizer” (Chernetsov et al., 2004; Danhardt and Lindstrom, 2001; Erni et al., 2002; Farmer and Wiens, 1999; Lindström and Alerstam, 1992). Migrants may alternatively attempt to maximize the likelihood of surviving migration through minimizing the cumulative probability of mortality over the entire migration. We will refer to these migrants as probability of mortality-minimizers, hereafter “mortality-minimizers”. Under similar conditions and if birds with higher fat loads have a greater chance of being successfully depredated, mortality-minimizing migrants should have lower departure fuel loads and slower speeds of migration than time-minimizers (Burns and Ydenberg, 2002; Houston, 1998, Figure 1). In general, mortality-minimizers should avoid migration routes, habitats, or sites that have higher

predation danger, even if they provide a higher fuel-loading rate (Figure 3.2; Alerstam and Lindström, 1990). This final prediction is complicated if predation danger at sites varies throughout the migratory season. Under the mortality-minimizing strategy, migrants that are migrating under low predator abundance should attempt to avoid any temporal or spatial increases in predator abundance (Lank et al. 2003). While most mortality-minimizers should have departure fuel loads below the speed-maximizing optimum (Houston, 1998), individuals that are able to fuel under sufficiently safe conditions may attempt to load fuel beyond the speed-maximizing point, which will also slow migration. High fuel loads provide sufficient fuel to perform long flights, allowing these migrants to avoid the predation danger associated with future stopover sites. However, since the high fuel load required increases vulnerability through decreased escape performance (Burns and Ydenberg, 2002), the benefit of this behaviour should be reduced if predation danger increases.

### **3.2.2 Mortality-minimizing predictions**

To explore the use of different tactics for minimizing mortality while on migration, this study looks at the age-specific residence time patterns of the western sandpiper (*Calidris mauri*) and semipalmated sandpiper (*Calidris pusilla*) on southward migration. It examines predictions made based on the mortality minimizing strategy for migrants in two different life-history stages, in the two species, based on their relative positions on their predator landscapes.

In both the western sandpiper and semipalmated sandpiper migrations, adults depart southward about a month before juveniles (Butler et al., 1987; Page and Middleton, 1972). Western sandpipers travel down the western half of North America

from their breeding grounds in western Alaska. Semipalmated sandpipers migrate either through the centre of the continent and across the Caribbean, or to southeastern Canada or the northeastern United States and make a single transoceanic flight to the Caribbean or South America (Figure 3.5; Gratto-Trevor and Dickson, 1994). Adults of both species moult their flight feathers upon arrival at the wintering grounds, during which time they have a reduced flight capacity (Hedenström and Sunada, 1999; Lank et al., 2003). Juveniles do not moult flight feathers in their first year.

The pattern of relative predator abundance in time and space is referred to as a “predator landscape” (Ydenberg et al., 2007). The peregrine falcon (*Falco peregrinus*) is hypothesized to be the most important predator influencing the migratory behaviour of western and semipalmated sandpipers (Ydenberg et al., 2007). Peregrines migrate in a temporally and spatially clustered front that spreads southward and eastward from their breeding grounds in the Arctic (Enderson, 1965; Fuller et al., 1998; Lank et al., 2003; McGrady et al., 2002; Mueller et al., 2000; Worcester and Ydenberg, 2008; Ydenberg et al., 2007). As the front moves southward, falcons drop out and winter at various latitudes, causing predator numbers to remain higher than prior to the falcons’ passage (Fuller et al., 1998; Lank et al., 2003). The falcon front on the west coast occurs arrives 4-6 weeks earlier than on the eastern seaboard (Worcester and Ydenberg, 2008). Western falcons migrate ahead or just behind juvenile western sandpipers, while eastern falcons appear to be migrating just behind juvenile semipalmated sandpipers (Lank et al., 2003).

Figure 3.3 presents predicted migration tactics for mortality-minimizing migrants in relation to proximity to the falcon front. Migrants ahead of the falcon front should attempt to maintain a migratory speed that keeps them ahead of the falcon front. The

closer a migrant is to the falcon front, the more an individual should attempt to increase their migratory speed. In contrast, migrants within the falcon front should attempt to migrate increasingly cautiously as predator abundance increases

Figure 3.4 portrays age-specific migratory speed predictions for mortality minimizing southward migrants in relation to the falcon front. In adults, the timing of increased speed allows for their higher vulnerability with late arrival at primary moulting grounds, while juveniles, which do not moult, only face increasing danger if they fail to stay ahead of the front. Where the age groups overlap, adults should thus have higher migratory speeds than juveniles. Migrants within, or behind, the front should migrate with increasing caution as peregrine abundance increases.

### **3.2.3 Site Specific Predictions**

We made predictions of mortality minimizing tactics by comparing sandpiper behaviour at four migratory stopover sites with different attributes, and tested them with data on migrants' mass and residency times. They are in western (Sidney Island and Boundary Bay), central (Sibley Lake), and eastern (Kent Island) North America at about the same latitude (Figure 3.5).

Sidney Island, British Columbia is a relatively small site with high predation danger and food abundance, attracting lightweight migrants and allowing high refuelling rates (Pomeroy et al., 2008; Ydenberg et al., 2002). Ydenberg et al. (2004) showed previously that mean capture masses and lengths of stay declined steadily during the 1990s, which they related to increases in predation danger as falcon populations increased. We predict that birds should not load past the optimum, because the site has

high danger and some predators are present throughout July and August. As Figure 3.1 shows, for migrants that load below the time-minimizing optimum, increasing the length of stay should increase migratory speed (Alerstam and Lindström, 1990; Lank et al., 2003). We predicted that within seasons, adults are expected to have longer stopover times as the predator front approaches and the benefit to reducing time spent on migration to avoid increased danger on migration and late arrival on the moulting grounds increases. Juveniles' lengths of stays should decrease as peregrines arrive, and the cost of being at a high danger site increased (Ydenberg et al., 2004). Shorter residence times will be expected to lead to a decrease in departure fuel load, thus slowing migration.

Boundary Bay is a large (16km<sup>2</sup>) sandy mudflat on the Fraser River Delta. Migrants here have been shown to have lower fuelling rates due to lower food density compared with Sidney Island (Ydenberg et al., 2002). The site has lower predation danger, so adults should be migrating at close to the maximum speed for their fuelling rate, while at Sidney Island migrants should have to trade-off the high predation danger and therefore have lower than maximum speed for their fuelling rates. Seasonal patterns of lengths of stays could not be examined at this site because mark recapture studies are not practical at such a large site

Kent Island, New Brunswick is very similar to Sidney Island in that it is a small, highly productive stopover site with cover close to shore (Lank, 1983). However, at Kent Island the predator front arrives 4-6 weeks later than on the west coast, allowing many migrants to prepare for a long flight directly to South America (Dunn et al., 1988; Lank et al., 2003; McNeil and Cadieux, 1972; Morrison, 1984; Richardson, 1979). We predict that adults have high fuel loads in order to make this trans-Atlantic flight. As the predator

front approaches, newly arriving adult migrants should have been selected to increase migratory speed, in order to reach the non-breeding grounds and moult safely. Changing departure decisions should reduce the amount of fuel loading past the optimum to increase migratory speed. The length of stay of adults is therefore predicted to shorten throughout the season. The earliest juveniles likely experience low predation danger conditions, as with adults, and may prepare for the long over-ocean flight. However, large fuel loads should be selected against as peregrines arrive so they should switch to the shorter length of stays more quickly than adults. We expect most juveniles not to attempt this large over ocean flight and instead migrate in hops down the coast.

At Sibley Lake, North Dakota, migrants are expected to have shorter residence times than their relatives at Kent Island. Interior habitat is very patchy, both spatially and temporally (Skagen and Knopf, 1994), and the cost of being unprepared for unexpected gaps in stopover sites can be very high (Skagen, 2006; Skagen et al., 2008). Interior migrants are thus predicted to load past the optimum in order to ensure against uncertain future stopover site availability, but to a lesser extent than at Kent Island, as they do not have as large or absolute a barrier to cross. The pattern in residence time throughout the season should be similar to that at Kent Island, with migrants attempting to increase speed and safety by reducing fuel load as the predator front approaches.

Sibley Lake and Kent Island data were collected in 1977 and 1978, when peregrine numbers were extremely low in central and eastern North America. Since then, the banning of DDT and various recovery strategies have resulted in recovering numbers of the falcons (Hoffman and Smith, 2003; Ydenberg et al., 2002). We predict that sandpipers caught at these sites in the 1970s would have had much higher fuel load and

therefore higher body masses than those caught during the late 1990s or in the last decade. As Kent Island is very similar to Sidney Island in predation danger, we would expect overall abundance to be lower and length of stay to be lower for those birds that are there.

### **3.3 Methods**

To examine the role placement within predator landscapes in shaping migratory strategies I examined residence time in the western and semipalmated sandpipers at three sites across the North America. I also compared estimates of migratory speed, based on stopover behaviour at these sites and at one additional site, Boundary Bay.

#### **3.3.1 The Western Sandpiper**

The western sandpiper is a small sandpiper that migrates annually between neotropical non-breeding grounds ranging from California to Peru to South Carolina and Florida and the breeding areas of southwestern Alaska (Wilson, 1994). Their northward migration consists of a series of stopovers up the coast of North America, though there is some movement further inland. The timing of the northward migration is relatively condensed, with the majority of birds passing through a stopover within a two or three week period (Butler et al., 1987). The southward migration is much more protracted, with adults beginning their migration about a month before the juveniles (Butler et al., 1987; Lank et al., 2003; Niehaus and Ydenberg, 2006). The adult southward migration is slightly more condensed than the juvenile migration, but both cover about a month at stopover sites with only about a week or so of overlap between age groups (Butler et al., 1987).

The western sandpiper migration was chosen for investigation for several reasons. *C. mauri* has been very well studied both in terms of life history and physiology ((Butler et al., 1987; Fernández and Lank, 2007; O'Hara et al., 2006; Stein et al., 2005). Having the age classes temporally separated eliminates the potential impact of competition between them and allows us to examine each group's behaviour independent of the direct influence of the other. The western sandpiper is also one of the most abundant shorebirds in North America (Bishop et al., 2000; Fernández et al., 2006; Morrison et al., 1994). During migration, large numbers pass through several important stopover points, allowing for easy access to the stopover behaviour of large numbers of individuals. Of these stopover locations, one of the most significant to western sandpipers is the Fraser River Delta and surrounding Strait of Georgia in British Columbia.

The collection of western sandpiper capture and resighting data at Sidney Island was previously described in Ydenberg et al. (2004), which analysed annual trends in sandpiper residency time with respect to changes in falcon numbers. Sidney Island, British Columbia is in the Strait of Georgia, which is the first major stopover area for migrants making the direct flight from southern Alaska (Butler et al., 1994) and has been shown to have more available food, but also to be more dangerous than other nearby mudflats, such as Boundary Bay on the Fraser River estuary (Pomeroy et al., 2008; Ydenberg et al., 2002). Migrants at this site should therefore be more sensitive to the time/danger tradeoff and its changes through the migratory season when compared with birds at Boundary Bay.

Adult and juvenile southward migrants were trapped using mist nets at Sidney Island (48°38' N, 123°20' W). Captured sandpipers (n = 282 adults and 1021 juveniles)

were weighed, measured, and individually colour banded and searched for daily using a telescope (Ydenberg et al., 2002; Ydenberg et al., 2004). Trapping and resighting was performed every year from 1992-2001 between 3 July and 3 September with varying survey effort each year.

To determine patterns of residence time in adult and juvenile migrants, resighting data were binned into 7-day segments for analysis. Conditional weekly residence times were calculated using Cormack-Jolly-Seber mark-recapture methodology (Lebreton, 1992; Ydenberg et al., 2004). These estimates were conditional on the assumption that we can only know the residence time since first capture. Varying the effect of week and year on the two age classes generated several candidate models (Table 3.1 and Table 3.2). Adults and juveniles models were run and analysed separately. Models were then ranked based on Akaike's Information Criterion (AIC) (Burnham and Anderson, 2002). The AIC weights of the models for adults and juveniles were used to generate model averages which produced predictions of mean residence times ( $1/\ln[\text{daily local residence}]$ ) and the trends within seasons and across years. True survival was assumed to be 100% over the residency period.

### **3.3.2 Semipalmated Sandpiper**

The semipalmated sandpiper (*Calidris pusilla*) is in many respects the eastern equivalent of the western sandpiper in morphology, breeding ecology and population abundance. It migrates annually between breeding grounds that stretch from western Alaska to Northern Baffin Island and Labrador, and non-breeding sites that lie between the Caribbean, Central America and the northern and central coasts of South America (Gratto-Trevor, 1992). There are two primary elliptical migration routes taken by birds

(Gratto-Trevor and Dickson, 1994). During the northward migration, most central and western birds migrate through the middle of the continent, directly to their breeding sites, while eastern birds migrate up the east coast of America (Gratto-Trevor and Dickson, 1994; Lank et al., 2003). Western and central breeders migrate southward through central North America towards Florida and the Gulf Coast, whereas adult eastern breeders migrate to the Bay of Fundy and the northeastern American Coast. Here they load up on fuel and depart into the Atlantic, and make a direct trans-Atlantic flight to the eastern Caribbean or north coast of South America (Dunn et al., 1988; Lank, 1979; Lank et al., 2003; McNeil and Cadieux, 1972; Morrison, 1984; Richardson, 1979). Many eastern juvenile semipalmated sandpipers shift their migration further south and head towards Virginia or the Carolinas (Lank, 1979; Lank et al., 2003; Morrison, 1984). The semipalmated sandpiper migration presents an interesting contrast to the western sandpiper as the species are similar in many respects such as abundance and body sizes, but have different migratory timing, destinations, and strategies with respect to making longer versus shorter flight segments. In both migrations adults migrate about a month before the juveniles.

Semipalmated sandpipers were caught by David Lank at two stopover locations (Lank, 1979, 1983; Lank et al., 2003). Sibley Lake, North Dakota (46°57'N, 99°43'W) is a permanent saline lake with several smaller lakes surrounding it on the western edge of the mid-continental semipalmated sandpiper flyway. Kent Island, New Brunswick (44°35'N, 60°27'W) is a small island with coastal tidal flats on the eastern coast of North America. Sibley Lake was studied between 13 July and 27 September 1978 and Kent Island between 11 July and 23 September 1977. During the 1970s, both sites hosted up to

5000 semipalmated sandpipers at one time, but generally held 300-1000 daily (Lank, 1983). Migrants were caught using mist nets at both sites and walk-in traps at Sibley Lake, banded, weighed, assigned an age class as juvenile or adult based on plumage, and marked with wing tags (Lank, 1979). Each day, sites were censused for total numbers of semipalmated sandpipers and for resighting marked individuals (Lank, 1983). At Sibley Lake, 636 adults and 800 juveniles were caught with 4637 resightings. At Kent Island 1172 adults and 281 juveniles were caught with 3245 resightings. Additional capture data on mass were available from semipalmated sandpipers captured at Kent Island by Lank in 1972 (N=305) and by Katie O'Reilly in 1996 (N= 69) and from birds captured by O'Reilly in 1999 (N= 24) at Johnson's Mills, New Brunswick (45°48'N, 64°31'W), a large mainland coastal mudflat in the upper Bay of Fundy. Data are used here with their permission.

To determine patterns of residence time in adult and juvenile migrants, capture and resighting data from Sibley Lake and Kent Island were digitized, pooled into 26 and 25 three-day periods respectively, and entered into Program MARK (White and Burnham, 1999). The sites were analysed independently because there are separate hypotheses for each site and the data were collected from the two sites in different years. Varying the effect of 1<sup>st</sup> capture, age and date generated several candidate models (Table 3.3 and Table 3.4). Juvenile daily residence and resighting probabilities were fixed at 1 for those dates early on, before any birds were caught. Models with a mass covariate were included to test the importance of mass at capture in determining length of stay. Models were ranked based on Akaike's Information Criterion (AIC) (Burnham and Anderson, 2002). Based on the AIC weights, Program Mark calculated weighted daily

residence and resighting probability estimates, with accompanying unconditional standard errors. The daily residence probability estimates were converted into mean conditional residence times for each time-interval and age group ( $1/\ln[\text{daily local residence}]$ ). True survival was assumed to be 100% over the residency period.

### 3.3.3 Migratory speed

Using capture data from Sibley Lake, Kent Island, Sidney Island and Boundary Bay (see below for description of this site) the age and site specific mean migratory speed ( $S$ ) were calculated using the following formula from Alerstam and Lindström (1990):

$$S = \frac{c (1 - (1+f)^{-0.5})}{t_e + f/k}$$

Refuelling rates ( $k$ ) were calculated from values of weight gain and mean fat-free weights for the two species (Guglielmo and Williams, 2003; Lank, 1983; Page and Middleton, 1972; Ydenberg et al., 2002). We were unable to find age-specific refuelling rates, so the average rate across fall migration at each site was used. Mean mass at capture was calculated for the semipalmated sandpiper sites and taken from previous mean capture data for Sidney Island and Boundary Bay (Lank, 1983; Ydenberg et al., 2002). Relative fuel loads ( $f$ ) were taken from mean mass at capture for each age group at each site and the fat-free weight of the species (Guglielmo and Williams, 2003; Lank, 1983; Page and Middleton, 1972; Ydenberg et al., 2002). The flight constant ( $c$ ) was set at 15000 for all calculations and the search/settling time ( $t_e$ ) was set for 0.5 days for all calculations. These were arbitrarily set to give realistic migration speeds, but are will not influence the comparisons between groups.

Boundary Bay is on the Fraser River Delta, British Columbia (49° 4.1'N 122°58.0'W) about 50 km east of Sidney Island. Boundary Bay consists of a large sandy mudflat, approximately 60 km<sup>2</sup> at low tide (Pomeroy, 2006). As the area is the first major stopover points for birds that make the direct flight from the south slope of Alaska, a large proportion of the population uses the Fraser River Delta/Boundary Bay as a key stopover point on the southward migration. It is a safer site than Sidney Island, but has lower food abundance (Pomeroy et al., 2008; Ydenberg et al., 2002).

## **3.4 Results**

### **3.4.1 Western Sandpiper**

The top ranked model predicting daily residence time of adults at Sidney Island showed times increasing linearly within seasons and decreasing across years ( $\omega_i = 0.465$ ). There was moderate support for quadratic changes both within seasons and across years (Table 3.1). In juveniles, the top model included quadratic terms that decreased both within seasons and across years ( $\omega_i = 0.554$ ). Moderate support was also found for models with a linear term either within seasons or across years, but not both (Table 3.2). Within years, the averaged models were used to generate predictions of conditional residence times for adults and juveniles (Figure 3.6). Adult residence time increased from a low at the start July to a high in the first week of August, which is the latest adults were seen in the Fraser River Delta (Butler et al., 1987). Juvenile residence time declined throughout their migratory period from a maximum, which was similar to that of adults to a minimum at the end of August (Figure 3.6). As previously described by Ydenberg et al. (2004), residence time decreased between 1992 and 2001 for both adults and juveniles.

### **3.4.2 Semipalmated Sandpiper**

#### **3.4.2.1 Sibley Lake**

Residence time declined for adults from a maximum at the start of the migratory period. The model with the most support from the data included a linear change in daily residence probability for adults over the migratory period and a quadratic change for juveniles ( $\omega_i = 0.33$ ). There was nearly equal support for a model in which daily residence probability changed linearly with time ( $\omega_i = 0.28$ ). A capture effect was constant for adults and changed linearly or quadratically for juveniles (Table 3.3; Figure 3.8). For juveniles, residence time increased early in the migratory period and then decreased after the 15 of August (Figure 3.7). Juvenile residence time was higher than adults for most of the migratory period. The inclusion of mass as a covariate did not improve model fit.

#### **3.4.2.2 Kent Island**

Residence time decreased dramatically for both adults and juveniles throughout their migratory period (Figure 3.9). The models with strong support from the data included linear changes in daily residence both for adults and juveniles ( $\omega_i = 0.34$  and  $0.20$ ; Table 3.4). The inclusion of mass as a covariate did not increase support for these models ( $\omega_i = 0.09$  and  $0.09$ ). The effect of capture varied linearly for adults and there was equal support a linear ( $\omega_i = 0.34$ ) and quadratic ( $\omega_i = 0.20$ ) trend for capture survival in juveniles (Figure 3.10).

Date-specific masses for birds caught at Kent Island in 1972 match those caught in 1977, however birds caught in 1996 were much lighter than birds caught on the same

day of year in 1997 (Figure 3.11). At Johnson's Mills, the large, mainland mudflat site, birds had weights similar to those at Kent Island in 1977, but were heavier than those found at Kent Island in 1996.

### **3.4.3 Migratory Speed**

Figure 3.12 shows the mean migratory speed for each age group and site based on the mean relative fuel load and fuelling rate. At Sidney Island, where fattening rates were estimated at 1.0 g/day (Ydenberg et al., 2002), both adults and juveniles were migrating below their theoretical maximum migratory speed, due to loading less than the optimum for their fuelling rate. They appear to have been migrating close to the mortality-minimizing point (Houston, 1998). Both estimates of fuel loading rates on the Fraser River Delta (0.3 and 0.7 g/day, Ydenberg et al., 2002) suggest that migrants there were migrating at close to their maximum potential speed. Due to the higher fuel-loading rate at Sidney Island, the migratory speed was still faster at the smaller Sidney Island site, even though these migrants were migrating at below their maximum potential speed. Estimates of juvenile migration speeds were slightly higher than adults at both sites.

The overall migratory speed was higher at Kent Island due to the higher estimated fuelling rate (2.0 g/day vs 1.3 g/day at Sibley Lake, Lank et al., 2003). Birds at Kent Island had the highest migratory speed, but appeared to be loading past the optimum and therefore migrating at below their maximum migratory speed. Juveniles had much lower fuel loads, but were migrating faster due to carrying fuel loads closer to the speed maximizing point. At Sibley Lake, birds also were loading past the optimum, but to a lesser extent than at Kent Island. Juveniles had slightly higher fuel loads and lower speeds of migration than adults.

### 3.5 Discussion

Western and semipalmated sandpipers showed distinct patterns of age-specific residence times throughout their migratory seasons. Based on the mortality-minimizing strategy, migrants should choose the tactic that minimizes the cumulative probability of mortality over the entire migration. We predicted that migrants experiencing low predation danger on migration, and seasonally increasing predation danger attempt to increase their migratory speed ahead of the higher predation danger by adjusting their residence time. To increase speed, migrants that load fuel past the time-minimizing optimum should reduce length of stay, while those loading below the optimum should increase length of stay (Alerstam and Lindström, 1990). Individuals experiencing higher predation danger on migration, but little cost to late arrival on the non-breeding grounds, were expected to migrate safely by reducing departure fuel loads and therefore having shorter lengths of stay (Houston, 1998).

We found that adult and juvenile semipalmated sandpipers loaded fuel past the optimum and decreased residence time ahead of the seasonal arrival of migrating peregrine falcons. Western sandpipers loaded below the optimum with adults increasing residence time ahead of the falcon front and juveniles decreasing residence time as the front arrived. As predicted, migrants of both species that were ahead of the falcon front appear to be endeavouring to increase migratory speed by altering residence time, while those within the front appear to increase caution by reducing departure fuel load. Differential placement on the predator landscape across different longitudes may influence the different mortality-minimizing tactics between western and semipalmated sandpipers. We discuss these strategies below.

### 3.5.1 The Western Sandpiper

Ydenberg et al. (2004) showed that the mean lengths of stay of migrant western sandpipers at Sidney Island decreased steadily between 1992 and 2001, and attributed this change to simultaneously increasing danger as falcon populations recovered. Their explanations for this pattern focused on local food-danger tradeoffs, and did not consider effects on overall migration speed or strategies, the focus of this study. We now show that within each year, western sandpiper residence time at this small, food rich, but relatively dangerous stopover site differed with age class and throughout the migratory season. For adults, conditional residence time increased throughout the migratory season, but it decreased with the later-migrating juveniles. Migrants who stop at Sidney Island have higher fuel loading rates than others at nearby, less dangerous sites, and are hypothesized to use this site as a location to refuel quickly, but at the cost of increasing their immediate danger (Pomeroy et al., 2008; Ydenberg et al., 2002). Figure 3.12 shows that birds at Sidney Island were migrating below the optimal time minimizing speed, but still potentially faster than those at the nearby, larger and safer site on the Fraser River Delta. Our length of stay results suggest that adults moved closer to the maximum potential migratory speed throughout the season as their residence time increased (Figure 3.12). Juveniles appear to have decreasing migratory speed from an early peak until the end of the season. The peak length of stays occurred just as peregrine numbers begin to increase in the area (Figure 3.6; Lank et al., 2003, Figure 3; Niehaus and Ydenberg, 2006). Food abundance does not change dramatically at this site over the migration period, and if anything increases in some prey species (Lank et al., 2003).

### 3.5.2 Semipalmated Sandpiper

Semipalmated sandpipers have evolved a different strategy from western sandpipers to minimize mortality when travelling through their predator landscape (Lank et al., 2003). In the east, falcons arrive 4-6 weeks after they have arrived at similar latitudes on the west coast, giving sandpipers sufficient time to safely load enough fuel to make a flight directly from northeastern North America to South America (Lank et al., 2003; McNeil and Cadieux, 1972; Morrison, 1984; Worcester and Ydenberg, 2008). At Kent Island, the predicted 50% falcon passage date is 1 October, which is after all birds had left the site. Early adults and juveniles spent extremely long periods of time at Kent Island, but this dropped dramatically as the season progressed (Figure 3.9). These results, and the migratory speed estimates, suggest that early migrants accumulate high fuel loads, potentially at a cost to their migratory speed, but an over-ocean flight allowed adults to avoid potential future predation along the migratory route. For later adults, the flight may not provide the speed required to reach the non-breeding grounds with time to moult. These adults cut short their stopover and likely switched to short hop flights, potentially moving southwestward to increase their migratory speed and gain additional time on the falcon front. Lank (1979, 1983) obtained direct resightings of marked birds from sites along the coast.

Juveniles have a shorter time window before the arrival of the predator front, and therefore shorten lengths of stays more quickly than adults. The estimated fuelling rate (2.0 g/day) from Lank (1983) would allow the lightest bird (18 g) caught to load fuel to reach the mass of the heaviest bird caught (49 g) in 15.5 days. The mean 50% arrival date (1 October) is the date when 50% of all migratory peregrines have passed this site.

However, peregrines begin passing through 15-30 days before this date (Worcester and Ydenberg, 2008). Therefore, the cost to carrying high fuel loads should increase for late migrants, reducing the benefit of building up the fuel loads required for the over-ocean flight. To determine when the change in migration tactic occurs, we worked backwards from the estimated 50% falcon arrival date for Kent Island. Considering the 15 days before the 50% arrival date and the 15.5 days required to reach maximum fuel load, gives an estimated date (1 September) which coincides with a drop in juvenile residence time (Figure 3.9). Changes in residence time at Kent Island were not due to direct encounters with falcons; Lank (1979) noted the complete absence of raptor disturbance on shorebirds throughout the sampling period. Juveniles that are arriving or are still light around this date may therefore be shifting strategies to shorter migratory hops down the coast.

Juveniles were overall much lighter than adults at this site, resulting in different estimated flight ranges and migratory speeds. There were also relatively few juveniles at Kent Island compared with sites further inland or further south (Dunn et al., 1988; Gratto-Trevor and Dickson, 1994; Lank et al., 2003; Morrison, 1984; Page and Middleton, 1972). Juveniles appear to be more likely to move directly south to the east coast of the central and southern United States and perform short-hop migration down the coast. As in the present study, Dunn et al. (1988) found that juveniles stayed for shorter periods along the coast of Maine, and carried significantly less fat than adults, suggesting juveniles may not have the fuel loads at departure to make the >3200 km trans-Atlantic trip to the Caribbean or South America in one flight. Pfister et al. (1998) found a similar trend of decreasing lengths of stay for semipalmated sandpipers throughout the season in both 1985 and 1986 at Plymouth Beach, Massachusetts.

While this seasonal pattern in residence time differs from those shown by western sandpipers, we believe it is because semipalmated sandpipers appeared to be loading past the optimum, while western sandpipers were underloading or migrating at their theoretical maximum migratory speed. *C. pusilla* had high fuel loads early in the season, presumably in order to have enough fuel to make the long over-ocean flight (Dunn et al., 1988; Pfister et al., 1998). Adults of both species appear to attempt to increase speed to stay ahead of the falcon front. Eastern juvenile semipalmated sandpipers appear to have enough of a time window to attempt to stay ahead of the falcon front.

The predominant migration strategy for birds at Kent Island appears to have shifted over the past 4 decades. The substantially lower weight of birds caught in 1996 parallels the well-documented decline in mass at capture throughout the 1990s found at Sidney Island (Figure 3.11; Ydenberg et al., 2002; 2004). This, and that birds found at a larger mainland coastal site retained similar weights as the 1970s at Kent Island, suggest that during the 1990s migrants did not remain at small, now more dangerous sites as they became heavier. As expected under this model, censuses of semipalmated sandpipers done during the summer of 2003 using the same protocols as Lank (1983), counted less than a tenth of the 1977 daily levels (Lank, DB, pers. comm.). Migrants may have shifted towards higher use of less dangerous fuelling sites. It is expected that length of stay at Kent Island would be much shorter now.

At Sibley Lake, semipalmated sandpipers also appeared to be loading past the optimum, despite not facing an over-ocean flight (Figure 3.7). Conditional residence times and speed estimates in Figure 3.12 were much lower than at Kent Island, suggesting that migrants were not loading fuel to the same extent and likely had lower

potential flight distances at departure. Based on daily changes in masses of captured samples, Lank (1983) concluded that fuel loads at departure were about 10% lower at Sibley Lake than at Kent Island. The birds appear to have been preparing in a relatively safe location and time window for lengthy flights, perhaps to provide insurance against an uncertain quality and quantity of future stopovers (Skagen et al., 2008; Skagen and Knopf, 1994). The residence time decline throughout the season matches our predictions. Juveniles could be carrying lower fuel loads due to increasing predation danger, which would lower their residence time and have the effect of speeding up migration. We are unable to differentiate if adults and juveniles were departing earlier for different reasons. The mean 50% falcon arrival date is much earlier for birds at Sibley Lake than at Kent Island and there were still birds present at this time (Figure 3.7). However, because peregrine numbers were so low in the 1970s, birds may have adjusted their tactics accordingly. We would predict that they do not now load fuel to the same extent and juveniles may not load fuel past the optimum at all.

### **3.5.3 Limitations and Assumptions**

As with most length of stay analyses there are several caveats to our findings. Our lengths of stays are the estimated time between capture and departure. Our interpretations of them assume that lengths of stays prior to first capture were constant across groups (Schaub et al., 2001). The probability of selecting migrants that have been at a stopover site before capture may increase as migrant numbers at a site declines, This may cause perceived residence time to decline and the time a migrant has spent at the site before capture to increase. The probability that a migrant has already been caught and banded increases through this period as well.

At Kent Island the within season trends are so dramatic that we do not feel that they are only caused by changes in capture bias. At Sidney Island, the trends in adults are opposite to what would be expected based on changing pre-capture residence. This means the trends seen there could be stronger than observed. With respect to juveniles at Sidney Island and semipalmated sandpipers at Sibley Lake, it is possible that the results are entirely due to changes in pre-capture residence. We pooled dates at all sites and estimated first capture effect at Sibley Lake and Kent Island, which may reduce such an influence on the results. Migrants that left in less than 3 days after capture, were accounted for in the first capture effect, but 1<sup>st</sup> capture effect was separated from residence time discussions. These migrants were more likely to be migrants that had spend longer pre-capture at the site. The proportion of migrants at a site that have been previously banded will also influence this effect. If a large proportion of total birds are banded, then the effect should be smaller as the probability of selecting an old bird that hasn't already been banded should be lower. Estimating the pre-capture residence time trends should help elucidate this potential bias in results (Schaub et al., 2001).

It is also assumed that survival was 100% over the stopover period. There were some mortality events in the analysis of semipalmated sandpipers, but these individuals were removed from the analysis (Lank, 1979, 1983). In the semipalmated sandpiper analysis the confidence intervals were extremely large for juveniles at Kent Island, and early on at Sibley Lake (Figure 3.7; Figure 3.9) due to small sample sizes.

The effect of capture was larger in juveniles at both sites, with adults being more likely to be resighted after banding. If juveniles are less willing to expose themselves to danger, then they would be more likely to move on from a dangerous site where they are

captured. Adults may accept greater danger if a high refuelling rate can be maintained and would be expected to remain at a site after capture.

Migration speed appears to be higher in juveniles than in adults at Sidney Island, Sibley Lake, and Boundary Bay, due to higher capture weights for juveniles at these sites. This difference may not be real as the same fuelling rate was used for adults and juveniles, and this may not be the case as different stopover behaviour has been observed for adult and juvenile western sandpipers (Chapter 2). Seaman (2003) found that the trend of body masses differed between years, with adults having higher mass at capture in one of the two years in the study. The differences in mass could be alternatively related to feather wear differences between adults and juveniles. Adults are migrating for the second or third time, while juveniles are migrating with newly grown wings (Wilson, 1994). This could lead to differences in wing loading, which would allow juveniles to carry more weight safely (Burns and Ydenberg, 2002; Ydenberg et al., 2004).

#### **3.5.4 Alternate theories**

The influence of energy-minimizing behaviour was not focused on by this study. However, energy-minimizers try to optimize the total fat consumption during migration, and therefore should not have changing departure fat loads throughout the season, unless, for example, there were trends in the direction and strength of prevailing wind. While residence time and departure load were influenced by weather, a trend in weather throughout the season was not found for the semipalmated sandpiper at either site (Lank, 1983); this has not been examined for the western sandpiper. Energy-minimizers would also change departure load with the fat-loss during search/settling time, so if juveniles took longer to start fuelling, we would expect them to stay longer than adults (Alerstam

and Lindström, 1990). Since neither of these predictions were met in our analyses, we find no support for an hypothesis that southward migrants are attempting to minimize energy expenditure over the migration.

Support for time-minimization strategy appears to have limited support as well. That semipalmated sandpipers loaded past the time-minimizing optimum, shows they are not behaving as optimal migration theory would predict for time minimizers. While migrants just ahead of the falcon front do appear to be attempting to increase and potentially maximize speed, the mortality-minimizing strategy better explains the trends found with all groups of migrants studied.

Our findings and hypotheses counter the traditional view that differences in migration behaviour and routes in juveniles are solely due to inexperience rather than strategy. Several studies have found that adult and juveniles in different wader species express different migratory behaviour (Dierschke, 1996; Dierschke, 1998; Lindström et al., 2002). Juveniles have been found using more dangerous habitat, having lower fuel stores, and having shorter lengths of stay. These authors and others state that juveniles were naïvely choosing high predation sites (Dierschke, 1998, 2003; Rosner, 1990). Low fuel loads have been suggested to result in juveniles exposing themselves to greater predation danger (Wichmann et al., 2004), despite evidence that heavier birds are less able to escape predators and no evidence that these juveniles are not simply strategically choosing to migrate with lower fuel loads (Burns and Ydenberg, 2002). In passerines, the effect of age on stopover behaviours is often different for different species, but similar conclusions are drawn as with waders (Moore, 1994; reviewed in Woodrey, 2000; Woodrey and Moore, 1997).

Neophobia is another suggested explanation that has been given for age-specific differences in foraging behaviour (Woodrey, 2000). We are not denying that there is competition between adults and juveniles in these species, or that juveniles are less experienced than adults. We do, however, suggest there should be strong selection pressure for juvenile migrants that choose the migration route and strategy that gives them the highest chance of survival over the annual cycle. Looking at potential fitness benefits of choosing these different strategies should help elucidate the issue more than simply writing off any differences due to inexperience.

### **3.5.5 Future steps**

To further explore these results, it would be helpful to collect additional contemporary data at the Sibley Lake and Kent Island sites. If the length of stay patterns that we documented were the historical result of low peregrine numbers, behaviour should shift to look more like Sidney Island as new tactics are favoured. This appears to have been the case based on the limited data now available from Kent Island and the mainland Bay of Fundy sites. The amount of plasticity in migration decisions might be further revealed through a comparison of eastern and central semipalmated sandpiper reactions to interannual differences in timing of peregrine migration (Niehaus and Ydenberg, 2006). This study has shown that different migratory strategies have evolved to assist adult and juvenile western sandpipers to deal with the predator landscape. The influence of the west to east timing of peregrine migration appears to influence the migratory strategies of the prey species differentially across the longitudinal gradient. This work provides new information on the importance of predators in the life-history

decisions of prey species. Much more work needs to be done on a variety of species across the globe to completely understand the scope of predator influence.

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### 3.7 Tables

Table 3.1 Summary of results and models from AIC analysis of survival for adult western sandpipers at Sidney Island, British Columbia.

Model names are listed as year (g) and week (w). Possible trends are linear (L), quadratic (Q), free (independent estimate for each group and/or week) (f), or null (0). A  $\hat{c}$  of 1.268 was used in the analysis. Parameter estimates included +1 for the intercept, +1 for the model variance, and +1 because we used Quasi-AIC values.

Model	-2ln[L]	N	K	QAIC	Delta AIC	LikelihoodAIC	AICw
g L w L	1193.409	489	13	967.974	0.000	1.00	0.46
g L w Q	1192.424	489	14	969.317	1.343	0.51	0.24
g Q w L	1193.405	489	14	970.090	2.116	0.35	0.16
g Q w Q	1192.417	489	15	971.440	3.466	0.18	0.08
g L w 0	1202.858	489	12	973.315	5.341	0.07	0.03
g 0 w L	1204.588	489	12	974.680	6.705	0.03	0.02
g 0 w Q	1204.502	489	13	976.722	8.748	0.01	0.01
g 0 w 0	1220.702	489	11	985.286	17.312	0.00	0.00
g F w F	1160.337	489	36	993.018	25.044	0.00	0.00

Table 3.2 Summary of results and models from AIC analysis of survival for juvenile western sandpipers at Sidney Island, British Columbia.

Model names are listed as year (g) and week (w). Possible trends are linear (L), quadratic (Q), free (independent estimate for each group and/or week) (f), or null (0). A  $\hat{c}$  of 1.186 was used in the analysis. Parameter estimates included +1 for the intercept, +1 for the model variance, and +1 because we used Quasi-AIC values.

Model	-2ln[L]	N	K	QAIC	Delta AIC	LikelihoodAIC	AICw
g Q w Q	7193.397	2415	15	6093.613	0.000	1.00	0.55
g L w Q	7198.082	2415	14	6095.537	1.924	0.38	0.21
g Q w L	7198.280	2415	14	6095.704	2.091	0.35	0.19
g L w L	7204.425	2415	13	6098.861	5.247	0.07	0.04
g F w F	7119.692	2415	55	6113.898	20.285	0.00	0.00
g L w 0	7241.001	2415	12	6127.669	34.056	0.00	0.00
g 0 w Q	7239.559	2415	13	6128.475	34.862	0.00	0.00
g 0 w L	7246.584	2415	12	6132.375	38.762	0.00	0.00
g 0 w 0	7291.373	2415	11	6168.109	74.496	0.00	0.00

Table 3.3 Summary of results and models from AIC analysis of survival for adult and juvenile semipalmated sandpipers at Sibley Lake, North Dakota. Possible model effects are adults and juveniles with mass as a covariate. The probability of resighting varied with time in all models. Possible trends are linear (l), quadratic (q), cubic, (c), free (t), or null (.). A  $\hat{c}$  of 3.1083 was used in the analysis. Parameter estimates included +1 for the intercept, +1 for the model variance, and +1 because we used Quasi-AIC values.

Model	QAICc	Delta QAICc	QAICc Weights	Model Likelihood	Num. Par	QDeviance
Adults(./l) Juveniles(l/q)	4192.70	0.00	0.33	1.00	34	4124.16
Adults (./l) Juveniles(q/l)	4193.07	0.36	0.28	0.83	34	4124.52
Adults(./l) Juveniles (q/q)	4193.22	0.52	0.25	0.77	35	4122.65
Adults(./l) Juveniles (l/l)	4194.75	2.04	0.12	0.36	33	4128.24
Adults (l/l) Juveniles (l/q)	4200.44	7.74	0.01	0.02	35	4129.87
Adults(l/l) Juveniles(q/l)	4200.83	8.13	0.01	0.02	35	4130.26
Adults(l/l) Juveniles(q/q)	4201.01	8.31	0.01	0.02	36	4128.41
Adults(l/l) Juveniles(q/q) mass(no int)	4202.62	9.91	0.00	0.01	37	4127.98
Adults(l/l) Juveniles(l/l)	4203.80	11.10	0.00	0.00	34	4133.88
Adults(q/q) Juveniles(l/l)	4205.73	13.03	0.00	0.00	36	4133.13
Adults(q/q) Juveniles(q/q)	4206.24	13.54	0.00	0.00	38	4127.54
Adults(l/l) Juveniles(q/q) mass	4208.69	15.99	0.00	0.00	40	4127.94
Adults(c/c) Juveniles(c/c)	4211.08	18.38	0.00	0.00	42	4126.26
Age + Time	4211.57	18.86	0.00	0.00	51	4108.36
Time	4219.23	26.52	0.00	0.00	50	4116.67
Adults (t) Juveniles (t) no 1st Capture	4224.81	32.11	0.00	0.00	67	4087.33
Adults(./t) Juveniles(t/t)	4230.58	37.87	0.00	0.00	81	4065.53
Adults(./. ) Juveniles(./. )	4233.33	40.63	0.00	0.00	30	4171.54
Null	4240.61	47.91	0.00	0.00	27	4184.90
Age	4242.10	49.39	0.00	0.00	28	4184.36
Adults(t/t) Juveniles(t/t)	4248.72	52.89	0.00	0.00	90	4066.67

Table 3.4 Summary of results and models from AIC analysis of survival for adult and juvenile semipalmated sandpipers at Kent Island, New Brunswick. Possible model effects are adults and juveniles with mass as a covariate. The probability of resighting varied with time in all models. Possible trends are linear (l), quadratic (q), cubic, (c), free (t), or null (.). A  $\hat{c}$  of 2.9075 was used in the analysis. Parameter estimates included +1 for the intercept, +1 for the model variance, and +1 because we used Quasi-AIC values.

Model	QAICc	Delta QAICc	QAICc Weights	Model Likelihood	Num. Par	QDeviance
Adults l/l Juveniles l/l	3945.77	0.00	0.34	1.00	33	3877.84
Adults l/l Juveniles q/l	3946.79	1.03	0.20	0.60	34	3876.12
Adults l/l Juveniles l/l Mass (No Interactions)	3948.42	2.65	0.09	0.27	34	3877.75
Adults l/l Juveniles l/l Mass	3948.49	2.72	0.09	0.26	37	3873.74
Adults q/q Juveniles l/l	3948.78	3.01	0.08	0.22	35	3876.07
Adults l/l Juveniles q/q	3948.79	3.02	0.08	0.22	35	3876.08
Adults q/l Juveniles q/q	3949.53	3.76	0.05	0.15	36	3874.79
Adults l/q Juveniles q/q	3950.07	4.30	0.04	0.12	36	3875.33
Adults q/q Juveniles q/q	3950.26	4.49	0.04	0.11	37	3874.18
Adults q/q Juveniles q/q Mass	3955.57	9.80	0.00	0.01	41	3870.61
Adults l/l Juveniles q/t	3971.28	25.51	0.00	0.00	45	3878.14
Adults (l) Juveniles (l) No 1st Capture effect	3973.02	27.25	0.00	0.00	29	3913.23
Adults l/l Juveniles t/t	3973.40	27.64	0.00	0.00	50	3870.00
Adults (t) Juveniles (t) No 1st Capture	3979.52	33.75	0.00	0.00	56	3864.46
Adults ./t Juveniles ./t	3985.22	39.45	0.00	0.00	63	3855.71
Age + Time (No Interaction or 1st Capture	3987.83	42.06	0.00	0.00	48	3889.23
Adults(t/t) Juveniles (t/t)	3990.83	45.06	0.00	0.00	74	3838.49
Time (No Group or 1st Capture	3991.93	46.17	0.00	0.00	49	3889.23
Mass	4011.82	66.05	0.00	0.00	26	3957.42
Adults (.) Juveniles (.)	4012.75	66.98	0.00	0.00	27	3954.99
Time   Mass	4013.16	67.39	0.00	0.00	68	3872.58
Adults (./.) Juvenile (./.)	4014.27	68.50	0.00	0.00	29	3952.45
Null	4015.82	70.05	0.00	0.00	26	3960.09
Adults (t/.) Juveniles (t/.)	4026.34	80.58	0.00	0.00	47	3929.80

### 3.8 Figures

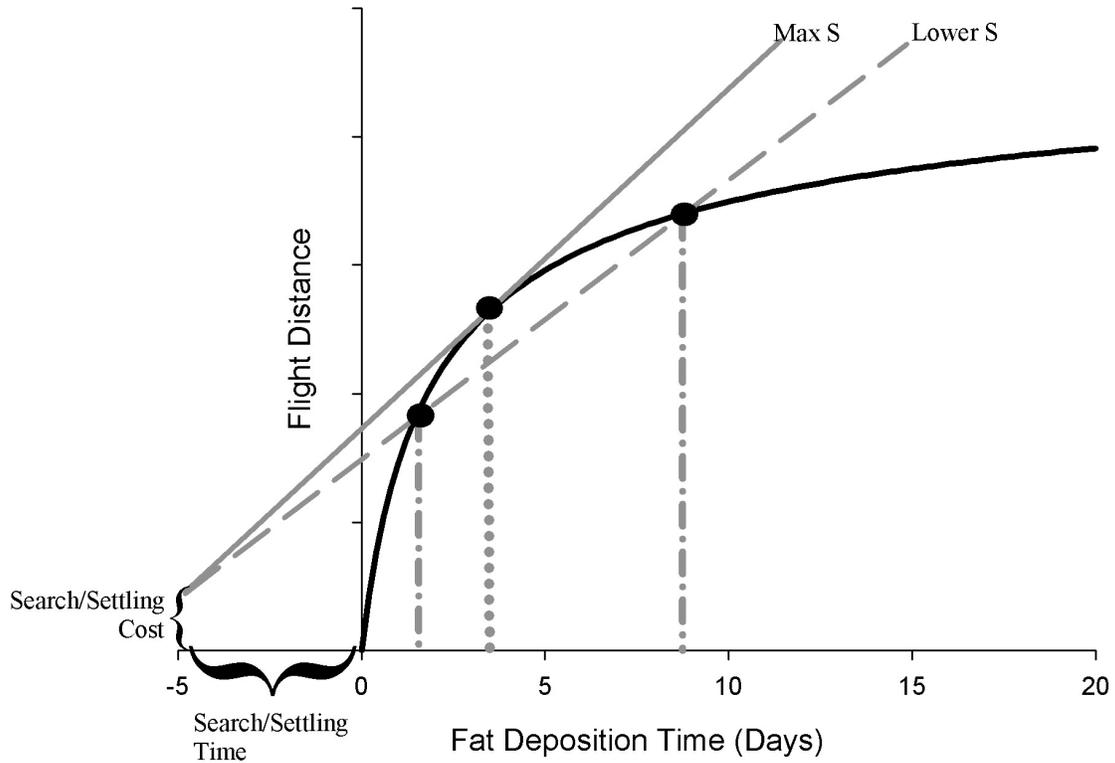


Figure 3.1 Speeds of migration ( $S$ ) varying with increasing length of stay under diminishing return of flight distance. Individuals with a given fuel-loading rate (black curve) can maximize their migratory speed by departing where their migratory speed is the highest (solid grey line). They could also depart earlier, but with a lower migratory speed (dashed grey line). There is no benefit to migratory speed for loading fuel past the speed maximizing point. Formulas from Alerstam and Lindström (1990)

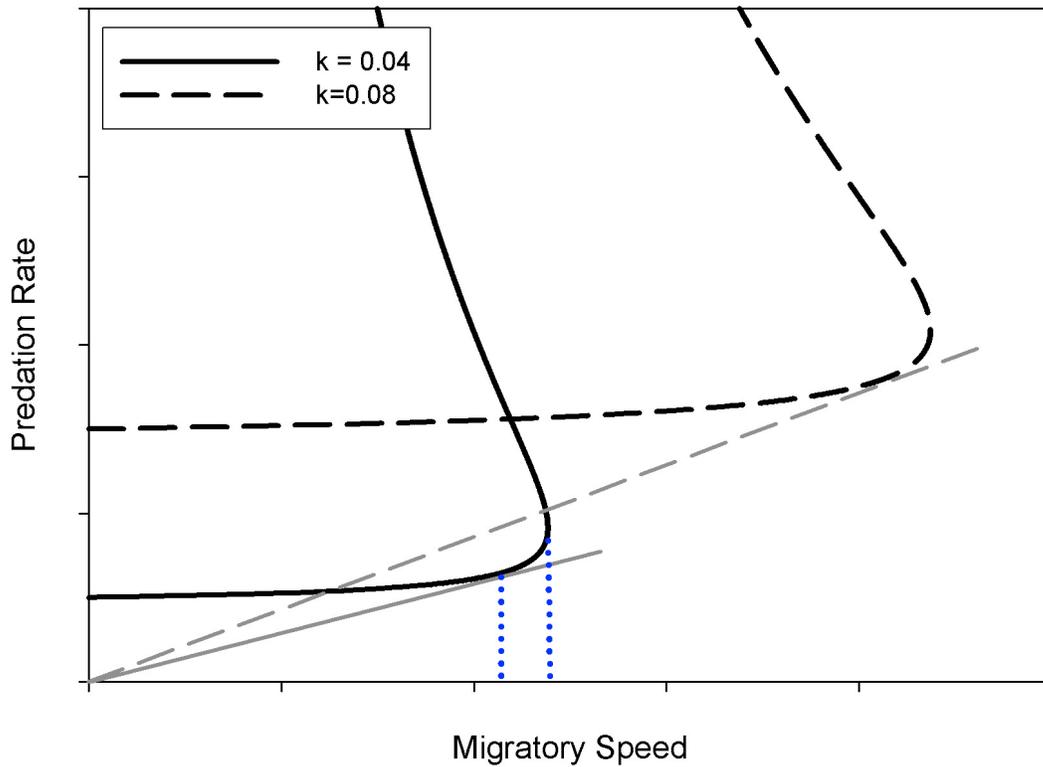


Figure 3.2 Differences in predicted migratory speed between time and mortality minimizers.

Migrants will have a maximal migratory speed for a given fuel-loading rate (or predation danger under the assumption that predation risk increases with increasing fuel load ( $k$ )). If an individual is trying to minimize mortality for a given fuel loading rate (relative fuel load/Speed, grey lines), it will have a lower migratory speed than an individual who only attempts to maximize its migratory speed (Houston 1998; Alerstam and Lindström 1990).

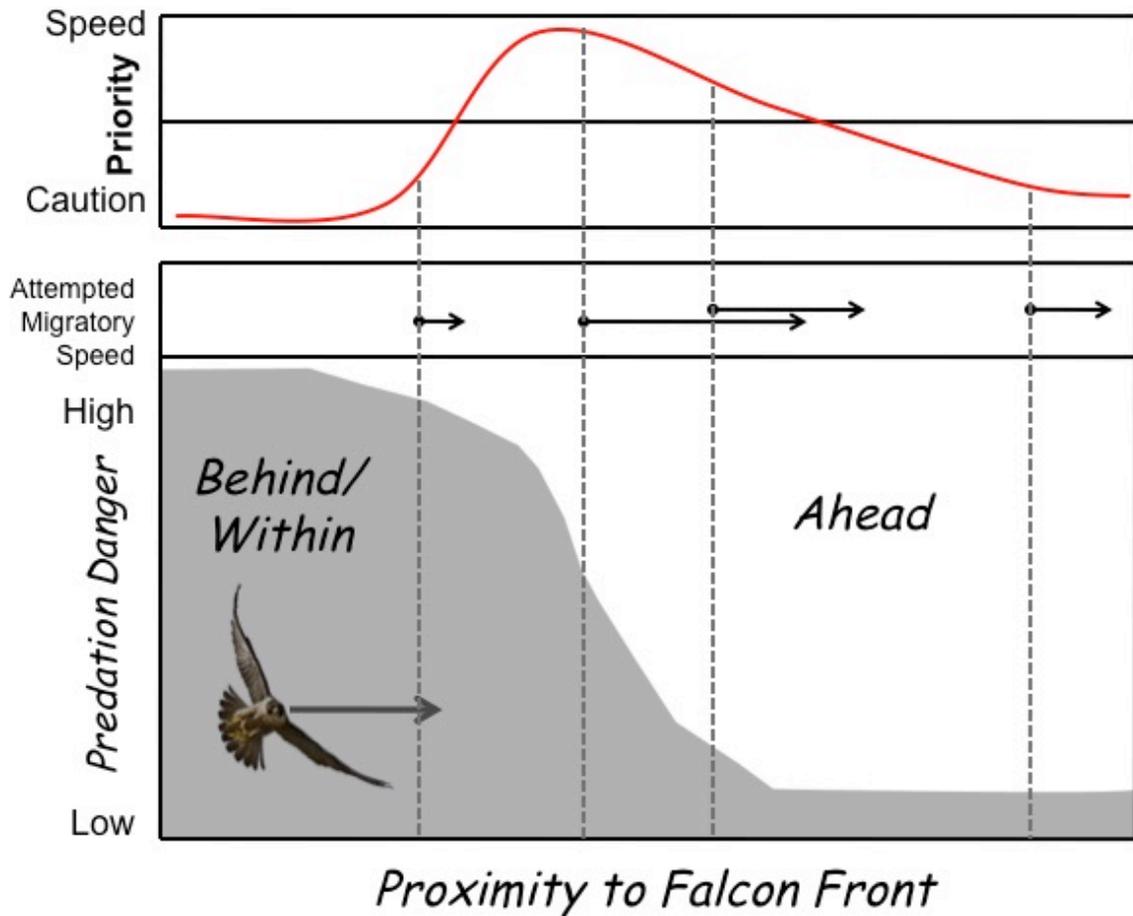


Figure 3.3 Predicted seasonal variation in migration tactics of sandpipers at a particular stopover site relative to the falcon front. Shifts in priority (top curve) are expected to shift from caution (below line) to speed (above line) as the predator front (solid arrows) becomes increasingly closer in space and time. As predation danger (grey shading) increases sandpiper priority should shift back to caution. Migrants at various proximities (vertical dashed lines) to the falcon front should have different tactics and different attempted migratory speeds (horizontal dashed arrows). Migrants ahead of the falcon front should have higher speeds than those behind the front. Falcon arrival varies between years (solid arrows) and migrants attempting to stay ahead of the falcon front must have speeds higher than the falcon front (estimated at 170km/day (Fuller et al., 1998; Worcester and Ydenberg, 2008)) Falcon front based on Figure 1, Lank et al. (2003). Photo credit: bairdphotos.com.

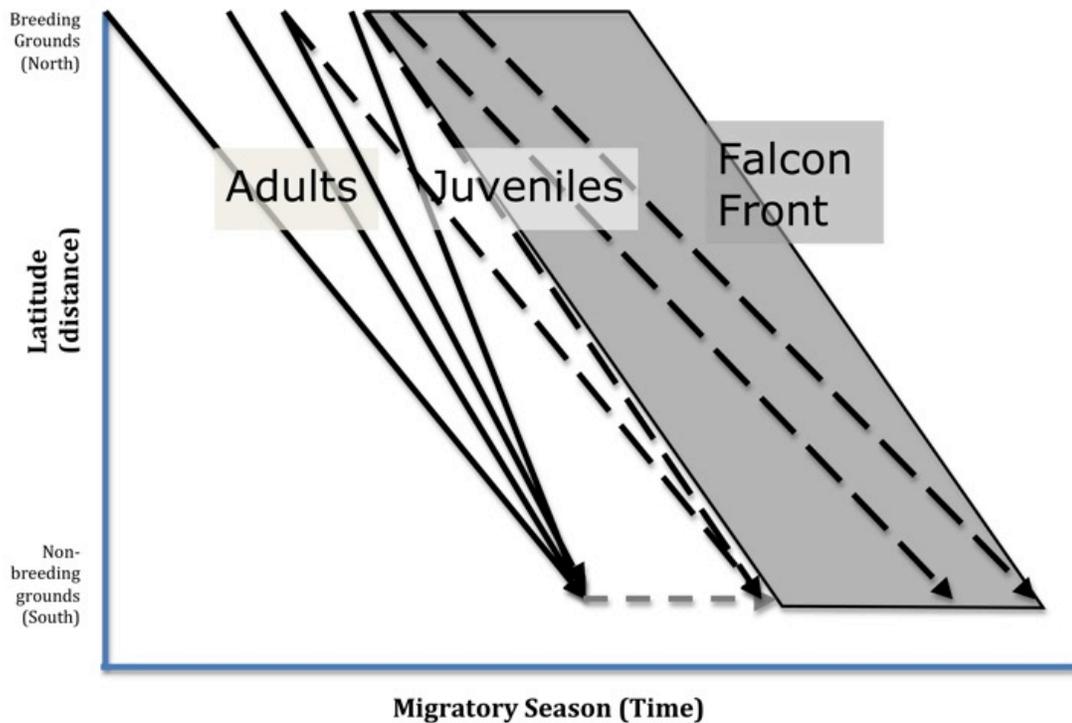


Figure 3.4 Graphical representation of predicted migration trajectories for adult (solid) and juvenile (dashed) western and semipalmated sandpiper and peregrine falcon (grey box) migrations. The steeper the arrow, the faster an individual is migrating. Migrants closer to the falcon front will have higher speeds than those far ahead or within the front. Adults should have higher speeds than juveniles, where the migrations overlap. The light grey dashed line represents required time for moulting.

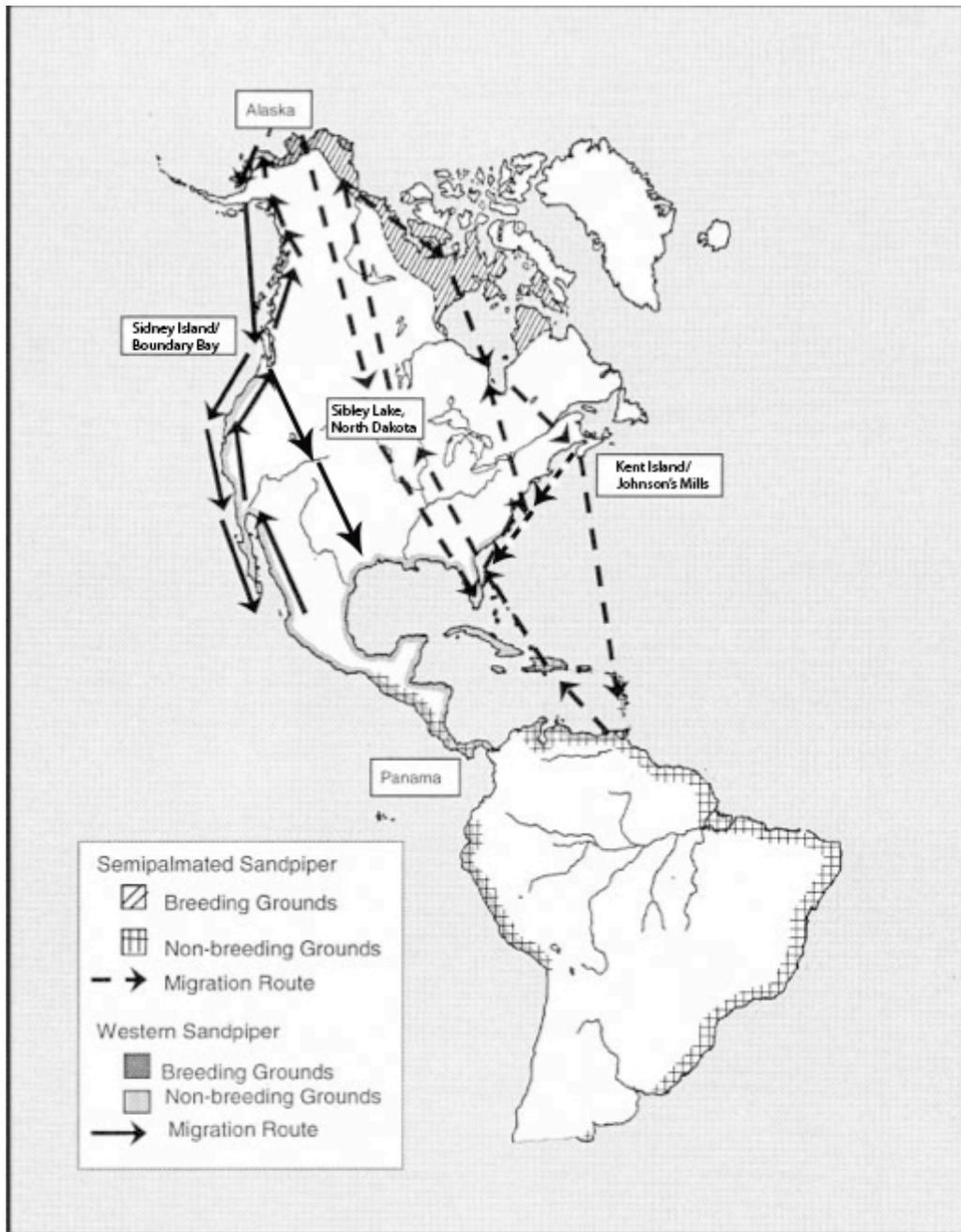


Figure 3.5 Breeding, non-breeding ranges and northward and southward migration routes of the western and semipalmated sandpipers. Study sites are described in the text. Modified from Lank et al. (2003).

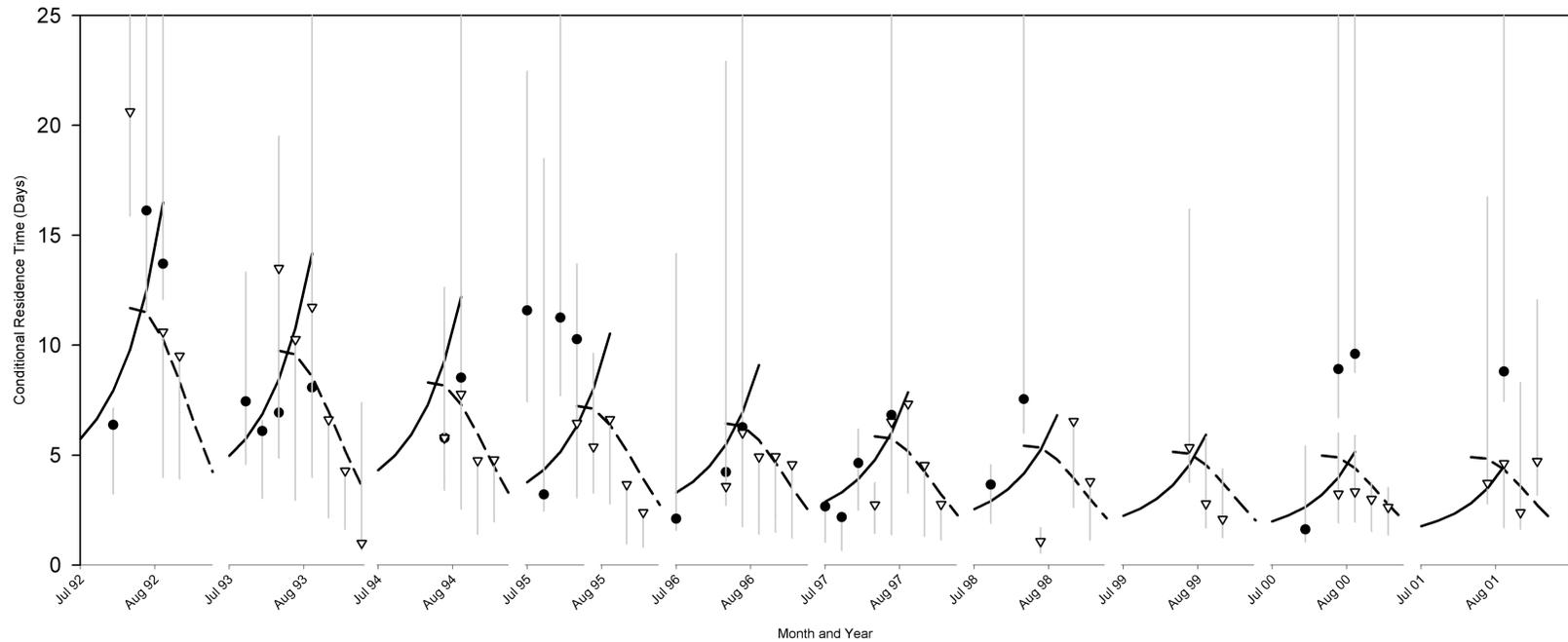


Figure 3.6 Weighted models of conditional residence time in days, over each migratory season between 1992 and 2001. Adults (black) and juvenile (dashed) models were based on QAIC weights (Table 1). Dots (black adults; open triangles juveniles) are year-week averages for residence time with associated 95% confidence intervals. Mean 50% falcon arrival date for the area occurs around the end of the adult migration (August 8), though there is substantial variation between years (Niehaus and Ydenberg, 2006).

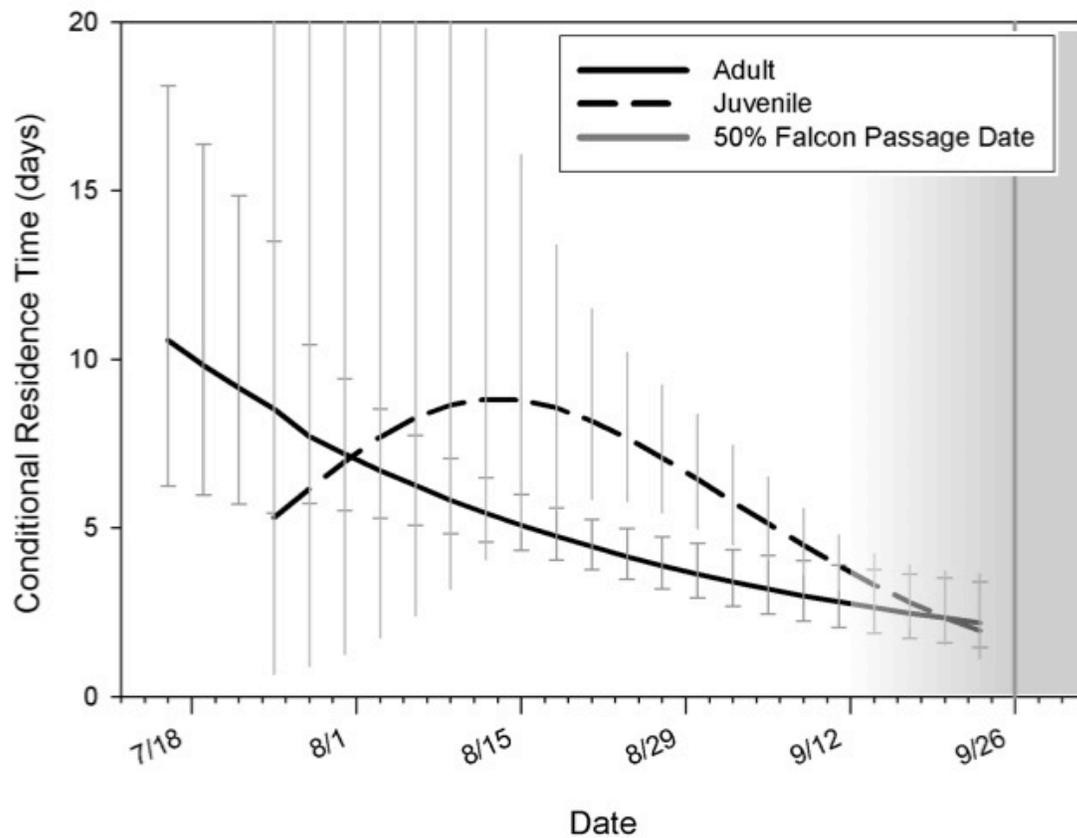


Figure 3.7 Predicted conditional residence times with 95% confidence intervals for adult (solid) and juvenile (dashed) migrants at Sibley Lake, North Dakota. Models were generated from averaged daily survival estimates based on AIC weights calculated using ProgramMARK. The estimated 50% falcon arrival date for Sibley Lake is shown (vertical grey line.) Grey shading shows increasing predator abundance ahead as migrant peregrines arrive (Worcester and Ydenberg, 2008).

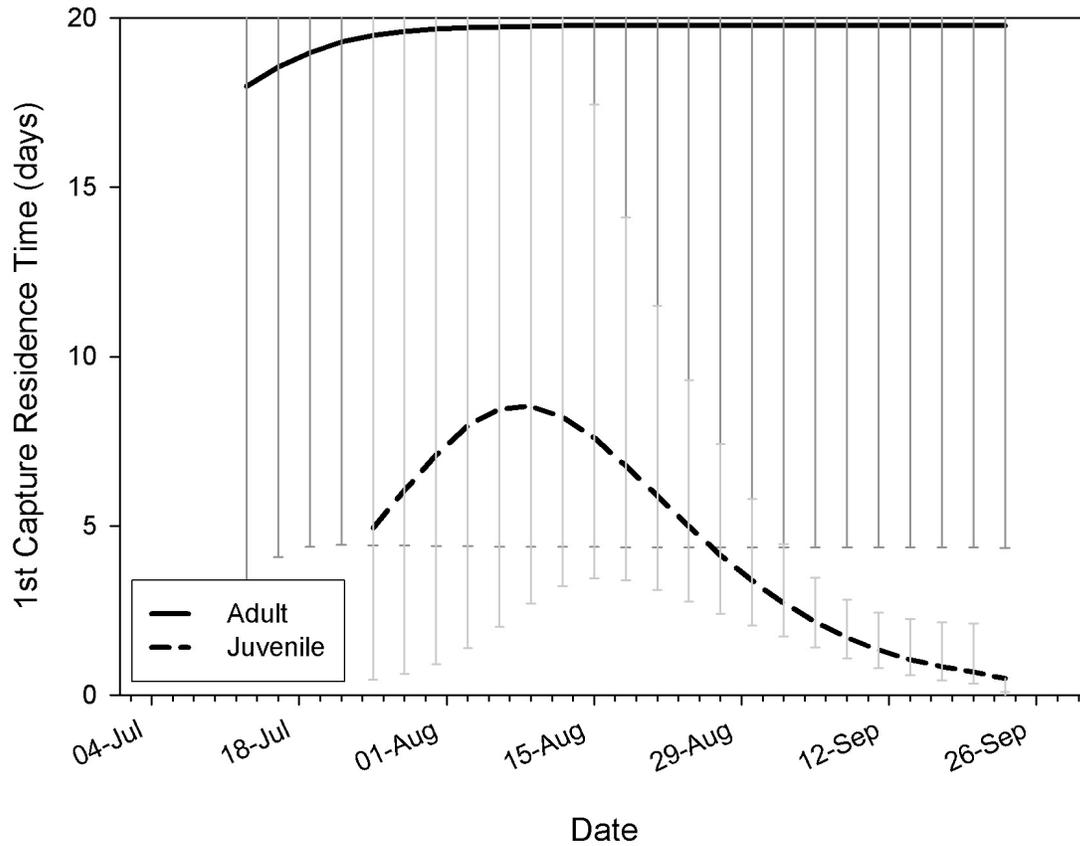


Figure 3.8 Predicted capture effect on birds at Sibley Lake with 95% confidence intervals for adult (solid) and juvenile (dashed) migrants at Sibley Lake, North Dakota. Models were generated from averaged daily survival estimates based on AIC weights calculated using ProgramMARK.

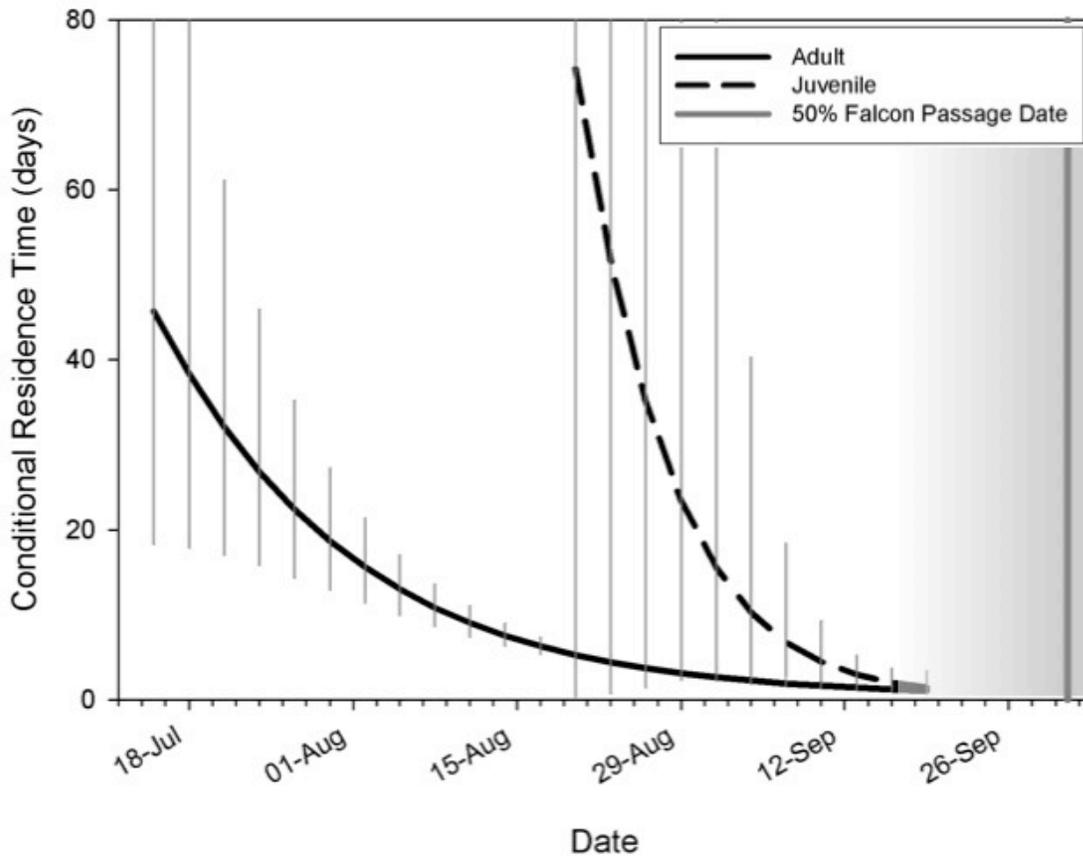


Figure 3.9 Predicted conditional residence times with 95% confidence intervals for adult (solid) and juvenile (dashed) migrants at Kent Island, New Brunswick. Models were generated from averaged daily survival estimates based on AIC weights calculated using ProgramMARK. The estimated 50% falcon arrival date for Kent Island is shown (vertical grey line). Grey shading shows increasing predator abundance ahead as migrant peregrines arrive (Worcester and Ydenberg, 2008).

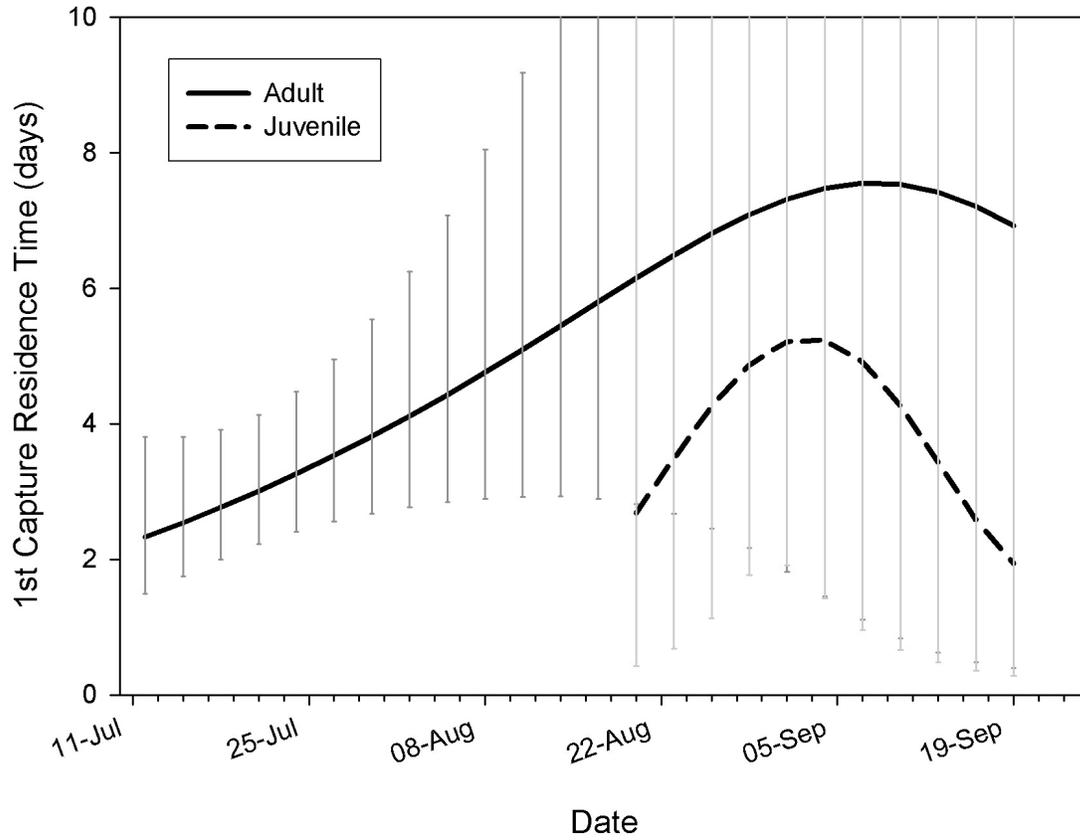


Figure 3.10 Predicted capture effect at Kent Island 95% confidence intervals for adult (solid) and juvenile (dashed) migrants at Kent Island, New Brunswick. Models were generated from averaged daily survival estimates based on AIC weights calculated using ProgramMARK.

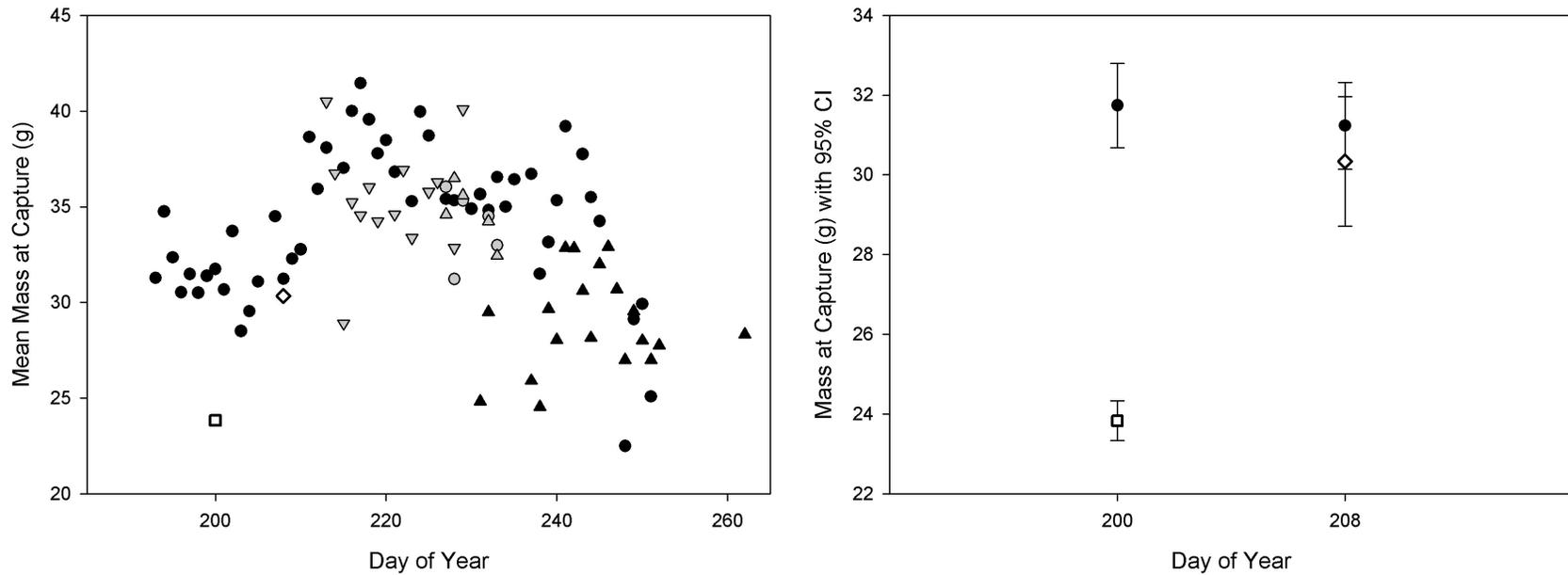


Figure 3.11 Mean mass at capture for adult and juvenile at Kent Island and Johnson’s Mills, New Brunswick in 1972,1977, 1996, and 1999.

Mean masses are shown for days caught in the 1990s with 95% confidence intervals in the right graph. Birds caught at Kent Island in 1996 (N= 69) are the open square, while those caught at Johnson’s Mills in 1999 (N= 24) are the open diamond. Birds caught in 1977 (N= 1453) are black circles (adults) and triangles (juveniles) and in 1972 (N=305) grey circles (adults), triangles (juveniles) and unknown (downwards triangles). The left hand graph represents mean daily masses of birds caught throughout the migratory season.

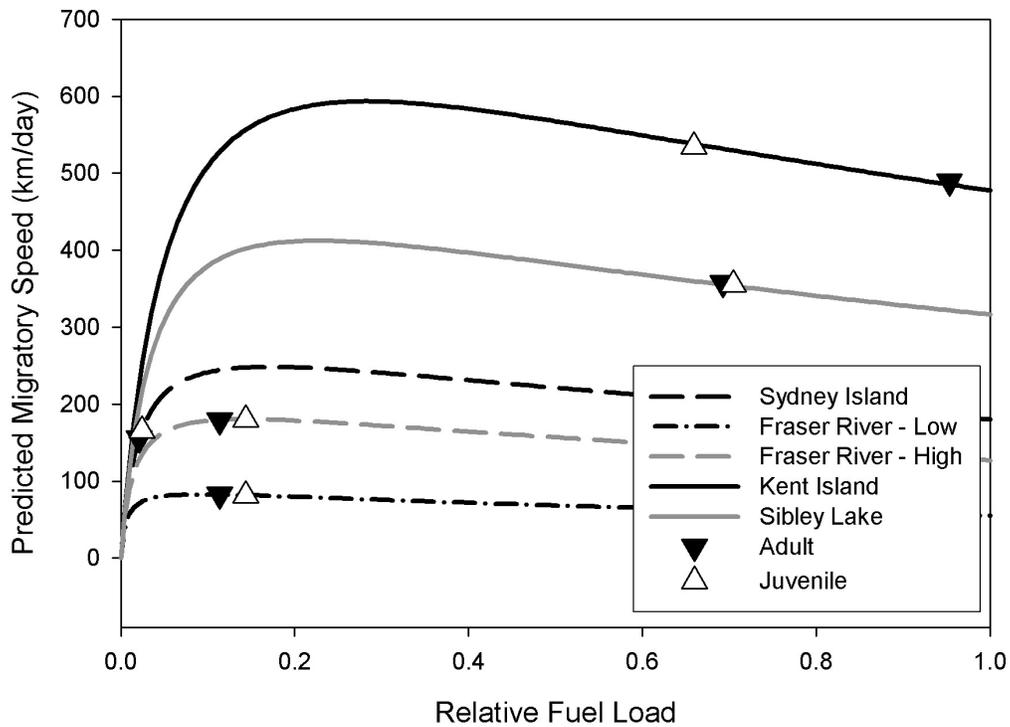


Figure 3.12 Estimated mean migratory speed for western sandpipers and semipalmated sandpipers on their southward migration. Points are calculated from Alerstam and Lindström's (1990) migratory speed formula using site-specific mean mass at capture, fuel loading estimates, and species-specific fat-free weights. Migratory speed lines are generated using fuel-loading estimates for each site.

## **4: Conclusions**

### **4.1 Summary of Findings**

Predation danger has been proposed to be an important factor in shaping the evolution of migratory decisions (Lank et al., 2003). This study has explored the mortality minimizing strategy by looking at variation in migratory tactics based on spatial and temporal dynamics of predation danger. Differential placements within the predator landscape were predicted to result in different tactics to minimize mortality on migration. Under the mortality-minimizing migration model, individuals migrating under low predation danger should attempt to avoid temporal or spatial increases in predation danger. Mortality-minimizers experiencing high predation danger should attempt to migrate as safely as possible. As decisions made at stopovers influence migratory speed and vulnerability to predation, we focused on a trade-off between foraging and vigilance behaviour, and its effect on residence time decisions in western and semipalmated sandpipers. Increasing fuel-loading rate increases the migratory speed, by decreasing the time needed to reach a given departure fuel load. At a constant rate of fuel loading, increasing length of stay to achieve a time-minimizing fuel load increases migratory speed, but loading fuel past this point, slows migration. Increases in fuel loading rate and fuel load may increase vulnerability to predation (Burns and Ydenberg, 2002; Sansom et al., 2009).

The sandpipers migrate through a landscape that varies in predation danger in space and time, with low danger early and a sharp increase as peregrine falcons migrating

southward from their breeding grounds arrive at sites. (Ydenberg et al., 2007). This “falcon front” moves southward about 4-6 weeks earlier on the west coast compared with the east coast of North America (Worcester and Ydenberg, 2008). We predicted that migrants ahead of this falcon front should attempt to increase speed. The closer they are migrating to the falcon front the more decisions should shift towards ones that increase speed (Figure 2.2). Where their migrations overlap, adults should make decisions that produce higher migratory speeds, due to the hypothesized time deadline for arrival at the non-breeding grounds (Lank et al., 2003). As the peregrine and sandpiper migrations begin to overlap, migrants should switch to migrating with increasing caution in order to increase survival while on migration. .

For western sandpipers, adult vigilance declined quadratically throughout the migration season, while juveniles overall were more vigilant and had slightly increasing vigilance with date. Adults flushed upon approach by a human at a further distance than did juveniles and there was no difference in spatial usage between age groups. Length of stay increased in adults and declined in juveniles, with the longest stays occurring around the mean 50% falcon arrival date. Adults migrate ahead of the falcon front, while juveniles migrate under increasing predator abundance (Lank et al., 2003). The vigilance and residence time results suggest adults are attempting to increase their migratory speed both by increasing their fuel-loading rate (by decreasing time spent vigilant) and by increasing their length of stay below the speed maximizing point. Juveniles appear to be adjusting vigilance behaviour to reflect the increased predation danger they are migrating through. The flight-initiation distance results do not support this hypothesis. It may be that juveniles view humans as less of an immediate threat and allowed closer approach by

humans to increase safety in to peregrine falcons (Relyea, 2003). Variation in the number of risk factors experienced has been shown to influence flight initiation results (Cooper Jr, 2009). In a year with earlier expected falcon migration (2007; Neihaus and Ydenberg, 2006), both adults and juveniles behaved more warily.

In semipalmated sandpipers, both adults and juveniles at central and eastern sites are ahead of migratory falcons. They loaded fuel past the time-minimizing optimum early at an eastern coastal site, presumably in order to fuel a single long distance flight towards non-breeding grounds. This would allow them to avoid the dangers associated with future stopover sites. As the falcon front approached, however, this flight may not provide the speed required to arrive at the moulting grounds with time to moult in safety. Because semipalmated sandpipers are loading fuel past the time-minimizing optimum, they are expected to attempt to increase migratory speed by loading less fuel and therefore shift their departure fuel load back towards the optimum. This should result in increasing the number of future stopovers. Juveniles appeared later in the season and may not have had sufficient time to load fuel to make the over-ocean flight before the arrival of the peregrine front. The change in stopover length was much more dramatic for them. Semipalmated sandpipers at a central site loaded past the speed maximizing optimum as well, but to a lesser amount than eastern birds. This is likely insurance against uncertain food abundance in and the availability of inland stopover sites further south. Both adults and juveniles increased their migratory speed by departing the stopover site earlier as the season progressed. In juveniles, lower fuel loads and early departures may be selected for, as they are migrating later when predation danger is higher.

Overall, these results provide support for predictions made based on the mortality-minimizing strategy. This suggests that sandpipers are attempting to minimize mortality on migration by ensuring they either remain spatially and/or temporally ahead of the falcon front or make decisions that reduce predation danger experienced on migration. While differences in migratory behaviour are often simply attributed to decisions based on inexperience, our results suggest the birds' behaviour is consistent with fitness maximizing strategies. Future studies should avoid dismissing age-specific differences as being solely due to inexperience and take into account differences in life-history priorities and constraints between the groups.

Our results did not provide support for predictions made under either the time-minimizing or energy minimizing strategies, the principle alternate hypotheses in the optimal migration literature (Alerstam and Lindström, 1990). A combination of the safe-moult deadline in adults and falcon arrival on migration do appear to cause migrants to attempt to reduce time on migration. However, semipalmated sandpipers loaded past the time-minimizing optimum, suggesting other factors must influence their migratory decisions. In juvenile western sandpipers, behavioural and length-of-stay decisions suggest migratory speed is actually declining throughout their migratory period. Late adults may behave as time-minimizers, but it does not appear that early adults are attempting to minimize time on migration. Energy minimizing does not predict a change in tactics throughout the migratory period or between groups, and therefore is not supported.

## 4.2 Constraints and Caveats

Changing time spent vigilant may not result in a change in fuelling rate. Cresswell et al. (2003) found that foragers can compensate for total time spent vigilant by adjusting the rate at which they raise their head. We measured total time vigilant, so if adults were compensating in this way we would expect that the total time vigilant would be the same between age classes. We tried to account for this by measuring several different behaviours, but some compensatory behaviour may not have been measured or considered.

Lower food abundance occurs during juvenile migration and this may have influenced behavioural decisions made by the age groups (Pomeroy, pers. comm.). Juveniles have longer small intestines than adults, which could partially compensate for a lower foraging rate from higher vigilance (Stein and Williams, 2006). Seaman (2003) found that there was no difference in plasma triglycerides between adult and juvenile western sandpipers, suggesting there may be little difference in fattening rate. However, as much as 40 percent of mass change is due to increased muscle mass, so it is possible that there is a difference in fuel stored as muscle (Guglielmo and Williams, 2003). It is possible that they could be increasing nocturnal foraging time to compensate for reduced diurnal foraging (McCurdy et al., 1997; Mouritsen, 1994). These physiological changes strengthen the idea that juveniles are changing behaviour to increase safety, even if there is no net change in refuelling rate. Vigilance has been shown to increase survival under high predation danger conditions, similar to those experienced by juveniles, so juveniles may achieve the desired safety even if they do not pay a cost in refuelling rates (Sansom et al., 2009).

The length of stay results from Kent Island and Sibley Lake were collected over 30 years ago, when peregrine abundance was extremely low. In western sandpipers at Sidney Island, recovering peregrine populations correlated with annual declines in sandpiper capture mass. (Ydenberg et al., 2004). As peregrine populations recover, it could be that now birds at Kent Island do not load fuel above the speed optimizing point and are now displaying residence time patterns that are similar to western sandpipers at Sidney Island. This might not occur at all eastern sites, as capture masses at a larger, safer site remain similar to birds at Kent Island in the 1970s (Figure 3.11). In addition, there is still a 4-6 week difference in peregrine arrival, which would give migrants enough time to load fuel for the long flight. Central semipalmated, sandpipers, which experience earlier falcon arrival and did not load fuel to the same amount as eastern semipalmated sandpipers, may be more likely to have changed their tactics.

This study does not examine the response of the predators to changes in prey behaviour. As peregrines are more constrained by a longer breeding season, they are thought to have less ability to adjust their breeding period to the extent adult sandpipers do (Niehaus and Ydenberg, 2006). In addition, peregrines migrate around the same period as juvenile sandpipers and many species of waterfowl. These individuals likely provide sufficient food on migration to reduce selection toward falcons that shift migration earlier.

### **4.3 Future Studies**

As stated above, some semipalmated sandpiper migration decisions may have adjusted to become similar to those found at Sidney Island for western sandpipers. Similar residence time studies need to be performed at such sites under the new predator

landscape. At these sites, updated capture and resighting data would be needed, but there is also a need for an accurate assessment of fuelling rate. Comparing results from sites further south would also help document changes in behaviour that occur as migrants approach their non-breeding grounds. The influence of falcon arrival on migratory behaviour is also something that is worth exploring further. Despite only looking at two years for our study, there appeared to be a strong effect of interannual variation in the predator landscape on vigilance and flight-initiation distance. It would be interesting to see if this interannual variation influences other migratory decisions.

While we have assumed that changing stopover behaviour influences migratory speed, there have been mixed results concerning the influence of foraging decisions and residence times on actual fuel loading rate and departure fuel load (Cresswell et al., 2003; Dunn et al., 1988; Lank, 1983). Lank (1983) found that when weather conditions favoured migratory departure, heavier adults were more likely to depart than lighter ones. Emigration probability increased above a threshold that was higher at Kent Island than at Sibley Lake. In contrast, for juveniles departure probability was not as influenced by mass. It still holds that birds that depart heavier are able to fly further, and that increasing the time spent at a stopover site decreases the migratory speed after a time-minimizing point. However, it would be interesting to further explore the relative importance of fuel-load, weather, conspecifics, predator abundance, or other credible variables on departure decisions, as was performed previously for semipalmated sandpipers (Lank, 1983). By looking at more than one variable and behaviour, we could test if individuals are compensating for changing conditions by shifting behaviour in ways that do not affect the overall speed of migration (Cresswell et al., 2003).

The location tracking technology that could help measure real migration speeds across sandpiper species and age groups is now being developed and early versions have been used to examine migratory patterns in small passerines (Stutchbury et al., 2009). Using geolocators would allow us to directly measure the relative migration speeds of individual migrants and track their migratory routes to see if there is a change throughout the migratory season. Careful tracking of predator abundance and behaviour at key stopover sites could help highlight changes in residence time and flight distance based on predator abundance on migration. As sandpipers show high breeding and wintering site fidelity, birds could easily be caught at nesting sites and recaptured the next year to download the data (Lanctot et al., 2000). If the migration departure decision was randomly manipulated by holding back some migrants, we could determine if there is a fitness cost to migrating later. With juveniles, recapture may be more difficult to accomplish, as they have lower natal philopatry compared with adult site fidelity (Gratto, 1988; Gratto et al., 1985). However, the technology to allow remote downloading from unrecaptured birds cannot be far away.

Overall, this study has helped to highlight the importance of predation danger in shaping migratory decisions. While western and semipalmated sandpipers are not legally 'at risk' species, it is important for conservation scientists to consider the role of predation in shaping life-history strategies when creating conservation plans for a species. Expanding the work done on western and semipalmated sandpipers to other species of avian migrants is important to assist in understanding the global importance of indirect predator/prey interactions in shaping migratory strategies. Some work is beginning on

shorebirds in Europe (Dierschke, 1998; Duijns et al., 2009; Van den Hout et al., 2008), but more needs to be done.

#### 4.4 References

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