

Characteristics of Over-ocean Flocking by Pacific Dunlins (*Calidris alpina pacifica*)

by

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Abstract

In 'over-ocean flocking' (OOF) shorebirds fly at high tide in place of traditional ground-based roosting. I used radar, theodolite, and video to study OOF by Pacific dunlins (*Calidris alpina pacifica*) wintering at Boundary Bay, British Columbia. OOF occurred only during daytime high-tides, and did not occur in darkness. Its mean duration was 187 ± 80 (SD) min, shortened in relation to daily temperature, and did not take place when ice in the bay facilitated roosting far from shore. Flocks flew on average 666 m from the shoreline. OOF flight had much gliding (14%) and was close to the minimum power speed, while transit flights between foraging sites had little gliding (1%) and was much faster than the maximum-range speed. These results support the hypothesis that over-ocean flocking is an anti-predator behaviour involving trade-offs between minimizing energy expenditure and maximizing safety from diurnal predators.

Keywords: Dunlin; *Calidris alpina pacifica*; bird flight; predation danger; flight optimization strategy; over-ocean flocking

*For Tristan, whose first sentence,
“Bird eats flowers”, in response to a
crow feeding on a dandelion-covered lawn,
hopefully preludes a lifelong appreciation of
birds and our natural world.*

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Table of Contents

Approval.....	ii
Partial Copyright Licence	iii
Abstract.....	iv
Dedication.....	v
Acknowledgements	vi
Table of Contents.....	viii
List of Tables.....	x
List of Figures.....	xi
1. Introduction	1
1.1. References.....	5
2. Spatio-temporal attributes and environmental predictors of over-ocean flocking of Pacific Dunlin (<i>Calidris alpina pacifica</i>) at Boundary Bay, British Columbia.	7
2.1. Introduction	7
2.1.1. Predictions	8
2.2. Methods	9
2.3. Results.....	13
2.3.1. Duration of Over-ocean Flocking.....	14
2.3.2. Radar vs. Visual Observations	14
2.3.3. Nocturnal vs. Diurnal.....	15
2.3.4. Distance from Shore	15
2.3.5. Non-occurrence and Role of Weather	16
2.4. Discussion.....	16
2.4.1. Duration of Over-ocean Flocking.....	17
2.4.2. Radar vs. Visual Observations	17
2.4.3. Nocturnal vs. Diurnal.....	18
2.4.4. Distance from Shore	19
2.4.5. Non-occurrence and Role of Weather	20
2.5. Conclusion	22
2.6. References.....	24
Appendix: Tables and Figures.....	29
3. Flight Kinematics and Energetics of Dunlin in Two Different Flight Modes.....	38
3.1. Introduction	38
3.2. Methods	40
3.2.1. Study Area	40
3.2.2. Video Collection and Analysis	41
3.2.3. Wing Measurements	41
3.2.4. Mass Data.....	42

3.2.5.	Weather Data.....	43
3.2.6.	Velocity Measurements.....	44
3.2.7.	Flight Data	45
3.2.8.	Daily Energy Expenditure Requirements.....	48
3.2.9.	Statistical Methods.....	49
3.3.	Results.....	49
3.3.1.	Mass and Morphometrics.....	49
3.3.2.	Flight Kinematics.....	50
3.3.3.	Theoretical Flight Model.....	51
3.3.4.	Daily Energy Expenditure Requirements.....	51
3.4.	Discussion.....	52
3.5.	References.....	58
3.6.	Appendix. Figures	62
4.	Conclusion.....	70
4.1.	References.....	72
	Appendices.....	73
Appendix A.	Values used to calculate flight estimates in Program Flight.....	74
Appendix B.	The measured groundspeed (based on theodolite values) and resultant calculated airspeeds for all recorded dunlins in OOF or transit flights.....	76

List of Tables

Table 2-1	Linear stepwise regression results for OOF duration.....	29
Table 2-2	Logistic stepwise regression results for OOF occurrence vs. non-occurrence	29
Table 3-1	Symbols, names, units and default values (if applicable) of variables used in formulas in text.	45
Table 3-2	Percent increase to daily energy expenditure of flying costs at four flight speeds plus the over-ocean flocking speed that incorporates gliding cost savings. Percent increases are shown for three flight durations corresponding to minimum, mean, and maximum over-ocean flocking durations, for upper (207.9 kJ/d) and lower (142.5 kJ/d) estimates of daily energy expenditure.	52

List of Figures

Figure 1-1	The effect of over-ocean flocking intensity on survival in wintering dunlins. Survival depends on the effect on predation (red line) and starvation (blue line). The optimal over-ocean flocking intensity depends on this trade-off, and occurs where the probability of surviving both depredation and starvation is maximized (black line). Adapted from Brodin and Clark (2007).	3
Figure 2-1	Radar screenshot overlaid on Google Earth image of study area. The triangular shape near the centre of the image is the Boundary Bay airport. Large red “blobs” surrounded by blue are the radar visualization of over-ocean flocking dunlins (see Fig. 2-2).....	30
Figure 2-2	Typical radar signatures of dunlin over-ocean flocking (top) and waterfowl flights (bottom). In both screenshots, distance between red lines is 0.5 nautical miles. The large orange region extending out from the centre of the rings represents land and vegetation cover. The orange shapes surrounded by blue are birds, the blue colour is an “echo” illustrating where bird targets had been recorded during the previous minute. Note the very large, dense structure of OOF, and the somewhat linear shape of the “finger” stretching out towards the shore. Waterfowl targets differ in being smaller and typically splay out offshore (left targets) before disappearing as birds land on the water.	31
Figure 2-3	Start timing of over-ocean flocking when high tide was near sunrise. Flocking commenced at or after twilight on all dates.	32
Figure 2-4	End timing of over-ocean flocking when high tide was near sunset. Flocking ended before twilight on all dates.....	33
Figure 2-5	Mapped locations of over-ocean flocks. Darker regions correspond to increased detection frequency. The green polygon denotes the subset of data points that were used in the analysis. Area between the two dashed lines indicates the radar blindspot. The black star indicates the location of the radar set-up.....	34
Figure 2-6	Average flock distance from shore binned in half-hour periods before (negative values) and after (positive values) high tide. Error bars represent 95% confidence intervals.....	35
Figure 2-7	Average flock distance from shore at four tide height categories. Error bars represent 95% confidence intervals.....	36

Figure 2-8	Over-ocean flocking duration declines with decreasing air temperatures. Days with 0 minutes duration are presented at the bottom of the graph, but were not included in the regression. Days are represented by one of 4 symbols showing whether foreshore ice, strong winds, or heavy rain were present. Several of these days met more than one criterion. Other days held none of those criteria, and are labeled as “Normal”	37
Figure 3-1	Histogram of calculated airspeeds for over-ocean flocking (top) and transit (bottom) flights. Long interval bars refer to airspeed measurements calculated from inter-point time intervals of greater than two seconds (see text). Short interval bars are for airspeeds calculated from inter-point intervals of one to two seconds.....	62
Figure 3-2	Histogram of measured groundspeeds for over-ocean flocking (top) and transit (bottom) flights. Long interval bars refer to groundspeeds measured from inter-point time intervals of greater than two seconds (see text). Short interval bars are for groundspeeds calculated from inter-point intervals of one to two seconds.	63
Figure 3-3	Chemical and mechanical power curves and associated minimum power (V_{mp}) and maximum range (V_{mr}) speeds. The dashed lines in the mechanical power graph indicate uncertainty bands around the estimates.	64
Figure 3-4	The sink rate of a gliding dunlin at various airspeeds. Rate of sink increases with increasing speed above the minimum sink speed. The speed at which glide distance is maximized is indicated as the best glide speed (V_{bg}).....	65
Figure 3-5	The cost of flight as a function of time for the four different flight speeds plus over-ocean flocking flight where there is no requirement to maintain speed or height in a glide. The minimum-power speed and the speed of over-ocean flocking are similar, and represent the most energetically inexpensive flight speeds per unit time. Transit flight speed is noticeably more expensive than all other flight speeds.	66
Figure 3-6	The cost of flight as a function of time for the four different flight speeds plus over-ocean flocking flight when there is no requirement to maintain speed or height in a glide. The maximum-range speed and the speed of over-ocean flocking with negligible glide losses are similar, and represent the most energetically inexpensive flight speeds per unit distance. The minimum power speed and over-ocean flocking flight that incorporates the need to maintain compensate for glide losses are the most expensive modes of flight.	67

Figure 3-7 Power curve showing power output with airspeed flown. Predicted minimum-power (V_{mp}) and maximum range (V_{mr}) speeds are shown, along with measured OOF (V_{oof}) and transit flights ($V_{transit} \pm 1$ standard deviation)..... 68

Figure 3-8 Power curve showing power output with airspeed flown for speeds up to the maximum-range speed. Predicted minimum-power (V_{mp}) and maximum range (V_{mr}) speeds are shown, along with measured OOF speed (V_{oof}). This is the same curve as Fig. 3-7, but the airspeed is limited to lower speeds to better illustrate the characteristic U-shaped power curve predicted by aerodynamic theory..... 69

1. Introduction

A cost-benefit trade-off underlies many behaviours we observe in nature. These trade-offs can be found in all aspects of avian ecology, from sexual selection to seasonal migrations. In one classic example, the peacock's display involves multiple costs. There are costs in growing and maintaining elaborate and conspicuous feathers used in display, costs associated with potentially reduced survivability owing to such plumage, and energetic costs associated with the burden of these elongated feathers. In exchange, peacocks with the biggest, brightest and most well-maintained feathers receive the benefit of increased reproductive success. The timing and destination of migratory flights for birds also involves trade-offs balancing speed, profitability of foraging locations, atmospheric and weather conditions, moult, predation risk and other factors, which vary among species, and even among age and sex classes of a single species. Thus, juvenile sharp-tailed sandpipers may make a 2300 km detour from their natal site in north-eastern Russia to western Alaska before undertaking apparently non-stop trans-oceanic flights to the wintering grounds, whilst adults follow a completely different continental route south (Lindström et al. 2011). Regardless of the specific nature of the behavior being observed, the behaviour with the greatest net benefit should be displayed.

While less extravagant than the peacock's courtship display or days-long non-stop migrations, flocking and communal roosting are also important behaviours incorporated into the life-history strategies of many species. Here the benefits of group-living (e.g. increased predator detection, thermal cover) must outweigh the costs (e.g. competition for food, increased conspicuity) for these behaviours to have become so prevalent, especially amongst the shorebirds. On the wintering grounds many shorebird species occur in large, mixed-species flocks, and it has been hypothesized that predation danger (*sensu* Lank and Ydenberg 2003) is a major selective force in the formation and maintenance of these flocks (Page and Whitacre 1975; Ydenberg et al. 2010). During high-tide, these flocks will move to sandbars, marshes, fields, or other

available habitats to rest until the tide recedes. While the trade-offs involved in flocking and communal roosting are similar, roosting has generally received less attention than flocking (but see Rogers 2003; Dias et al. 2006; Rogers et al. 2006a; b; Rosa et al. 2006). Generally, roost locations should be chosen that minimize both predation risk and energy expenditure; though it is often not possible to minimize both simultaneously (Rogers 2003; Rogers et al. 2006a).

Shorebirds are most commonly preyed upon by raptors. In North American and Europe many raptor populations have rebounded following the banning of DDT in the early 1970s and active conservation and re-introduction programs for these species (Cade et al. 1988; Ydenberg et al. 2004). This has increased the overall level of danger for shorebirds, led to shifts in predator-prey interactions, and has been implicated in perceived declines of some prey populations (e.g. Ydenberg et al. 2004; Bell et al. 2010). As a result there has been a reduction in roost safety for wintering shorebirds, and corresponding shifts in the payoffs that certain behaviours entail. Under these circumstances, behavioural changes can be expected. Carrying less winter fat, roosting at more distant sites, and other anti-predator tactics have all been shown by shorebirds worldwide (Ydenberg et al. 2010).

Over-ocean flocking (OOF) is one such behaviour recently expressed, most notably among dunlins (*Calidris alpina*), and is characterized by flocks of shorebirds spending the majority or the entirety of a high-tide period in continuous flight above the mudflats ((Dekker 1998; Ydenberg et al. 2010). Over-ocean flocking has been most extensively documented in Pacific dunlins (*C. a. pacifica*) at Boundary Bay, in British Columbia, Canada. It has been observed here regularly since the mid-1990s, and now occurs with most winter, diurnal high-tides (Ydenberg et al. 2010). It has been shown that peregrine falcons (*Falco peregrinus*) have lower attack success rates when hunting dunlin in over-ocean flocking compared to dunlin closer to the saltmarsh (Dekker and Ydenberg 2004). However, like the peacock's tail, OOF seems extravagant. Over-ocean flocking, I hypothesize, involves trade-offs between minimizing energy-expenditure and minimizing predation risk (Figure 1-1).

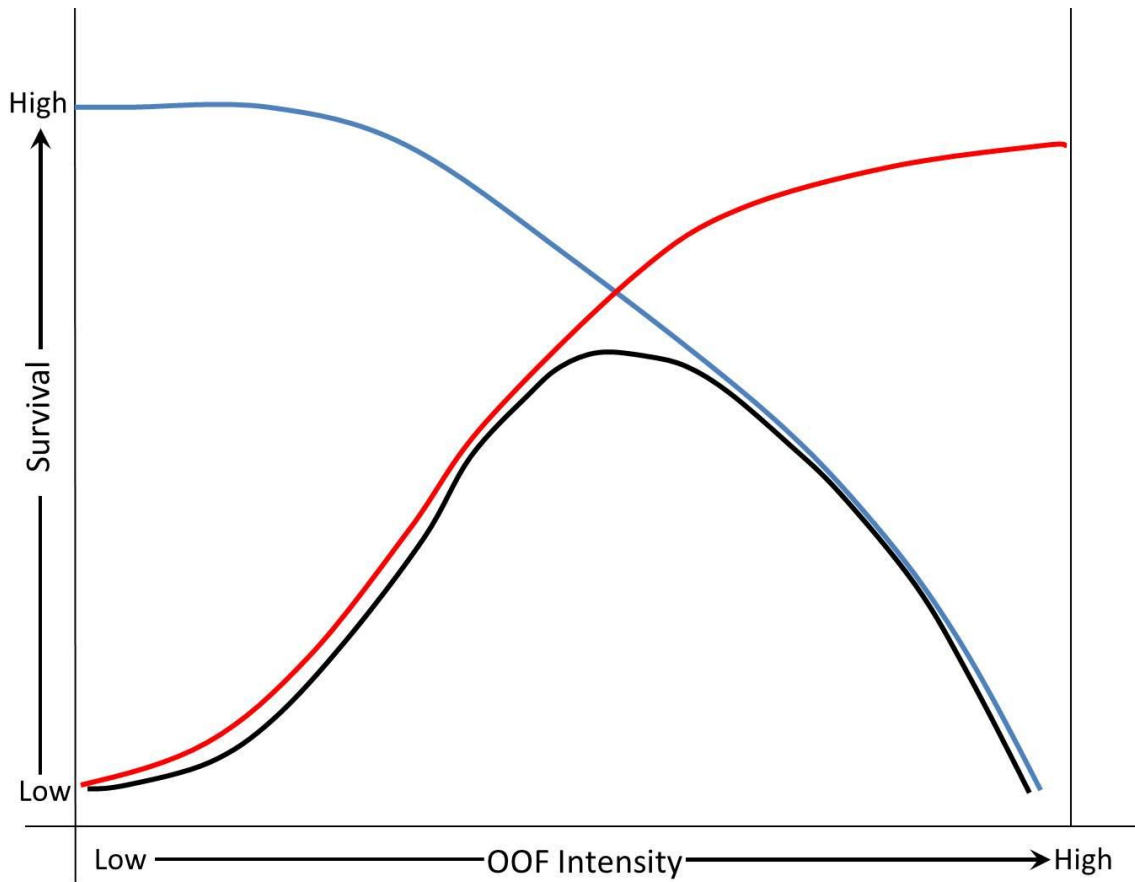


Figure 1-1 *The effect of over-ocean flocking intensity on survival in wintering dunlins. Survival depends on the effect on predation (red line) and starvation (blue line). The optimal over-ocean flocking intensity depends on this trade-off, and occurs where the probability of surviving both depredation and starvation is maximized (black line). Adapted from Brodin and Clark (2007).*

This study was conducted at Boundary Bay, on the southern edge of the Fraser River estuary in British Columbia, Canada. Boundary Bay is both an Important Bird Area and a Western Hemisphere Shorebird Reserve Network site of hemispheric importance. During winter the highest tides usually occur during daylight hours, and inundate all intertidal mudflats and most of the narrow strip of saltmarsh, which is covered with low vegetation. Boundary Bay supports wintering populations of many waterfowl species, shorebirds (especially dunlins and black-bellied plovers [*Pluvialis squatarola*]), and raptors (including peregrine falcon and merlin [*Falco columbarius*]).

In the following data chapters I describe how I investigated aspects of over-ocean flocking by dunlins (*Calidris alpina pacifica*). I analysed over-ocean flocks through use of a marine radar system, visual observations, digital theodolite, and video-camera, and by using a geographic information system. Field-work was conducted between November 2009 and January 2011.

Given the trade-off hypothesis framework underlying this thesis, I investigate the following predictions throughout the data chapters:

1. As falcons are diurnal predators and not generally active at night, I predict that OOF is a strictly diurnal activity.
2. Given that peregrine falcons had significantly lower attack success rates beyond the saltmarsh zone, and that predation danger appears to decrease with distance from shore (Dekker and Ydenberg 2004), I predict that OOF should likewise occur well beyond the saltmarsh zone and far from the nearest shoreline.
3. Under the trade-off hypothesis that dunlins balance predation and starvation dangers, I expect that over-ocean flocking will be reduced when environmental conditions increase energetic expenditure, or make food more difficult to obtain. Cold temperatures in particular should have a clear effect, because they increase energetic expenditure and also make prey harder to find, but the effects of rainfall and wind are more difficult to predict. Windless conditions make flight more expensive, but the effects of heavy winds are less clear. Heavy rainfall undoubtedly increases energetic expenditure, but the effects of lighter rains are less clear. I examine the data for the effects of wind and rain, but have no strong *a priori* predictions.
4. Individuals in over-ocean flocks should incorporate flight strategies that minimize energy expenditure, including flying at the minimum-power speed; and
5. Individuals in transit flights should fly at or faster than the maximum-range speed to minimize energy spent per unit distance flown.

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2. Spatio-temporal attributes and environmental predictors of over-ocean flocking of Pacific Dunlin (*Calidris alpina pacifica*) at Boundary Bay, British Columbia.

2.1. Introduction

Flocking and communal roosting at migratory stopovers and non-breeding sites are important components of many shorebirds' life-history strategies. It has been hypothesized that predation danger (sensu Lank and Ydenberg 2003) is a major selective force favouring the formation and maintenance of flocking of wintering shorebirds (Page and Whitacre 1975; Ydenberg et al. 2010). Roosting has generally received less attention than flocking, though recently the importance and characteristics of roosts have become a greater focus in the literature (Rogers 2003; Dias et al. 2006; Rogers et al. 2006a; b; Rosa et al. 2006) . Several hypotheses have been advanced for the purpose of communal roosting in birds, such as facilitating foraging efficiency through information transfer or conspecific attraction, decreasing predation risk through increased group vigilance, dilution effects and predator confusion, and reduced thermoregulation costs (review in Beauchamp 1999). Two underlying principles behind high-tide roost selection are minimizing predation risk, and minimizing energy expenditure; though often meeting one criterion comes at the expense of the other (Rogers 2003; Rogers et al. 2006a).

Raptors are the most important predators of shorebirds, and their populations across many parts of North America and Europe have rebounded following the banning of DDT in the early 1970s (Cade et al. 1988; Ydenberg et al. 2004). This has increased the overall level of danger for shorebirds, led to shifts in predator-prey interactions, and has been implicated in perceived declines of some prey populations (e.g. Ydenberg et al. 2004; Bell et al. 2010). One consequence of this shift is a reduction in roost safety for

wintering shorebirds. In extreme cases, there may be no safe roosting option available during high-tides, so that shorebirds must adopt other anti-predator tactics, such as carrying less winter fat, roosting at more distant sites, or ‘over ocean flocking’ in place of roosting. Such behavioural changes have already been identified, most notably among dunlins (*Calidris alpina*), at several sites globally (Dekker 1998; Hötter 2000; Buehler 2002; Ydenberg et al. 2010; Dekker et al. 2011). Over-ocean flocking, also labeled “roosting on the wing” (Prater 1981), “high-tide flight” (Brennan et al. 1985), “airborne roosting” (Hötter 2000), “over-sea flocking” (Hötter 2000), “over-water flying” (Conklin and Colwell 2007) and “over-ocean flocking” (Dekker 1998, and used here), is characterized by flocks of shorebirds spending the majority or the entirety of a high-tide period in continuous flight above the inundated mudflats.

Over-ocean flocking (OOF) has been most extensively documented in Pacific dunlins (*C. a. pacifica*) at Boundary Bay, in British Columbia, Canada. It has been observed here regularly since the mid-1990s, and now occurs during most winter daytime high-tides (Ydenberg et al. 2010). The duration of OOF has been reported to be about 3 h/day by Dekker (see Ydenberg et al. 2010). Ydenberg et al. (2010) also found that dunlins lowered their midwinter fat reserve by several grams as falcon populations increased between the 1970s and 1990s. Decreased mass increases escape performance and lowers flight costs (Hedenström 1992; Burns and Ydenberg 2002), facilitating OOF. Over-ocean flocking has previously been shown to increase safety from predators (Dekker and Ydenberg 2004), matching the hypothesis that it is an anti-predator behaviour.

In this paper I describe in detail the spatial and temporal attributes of over-ocean flocking of Pacific dunlins at Boundary Bay. My purposes are to test additional predictions from the hypothesis that its occurrence is specifically linked to predation danger posed by falcons, and to identify environmental variables that may influence OOF.

2.1.1. Predictions

As falcons are diurnal predators and not generally active at night, I predict that OOF is a strictly diurnal activity. Previous observations of radio-tagged dunlins indicate

that although nocturnally active, dunlins were not involved in sustained night-time flights (Shepherd 2001). More recently, visual observations (pers. obs.) of OOF at first-light or continuing through dusk suggest that it may occur in darkness. I developed the use of a marine radar, and employed this at night to monitor for nocturnal OOF by dunlins.

Given that peregrine falcons had significantly lower attack success rates beyond the saltmarsh zone, and that predation danger appears to decrease with distance from shore (Dekker and Ydenberg 2004), I predict that OOF should likewise occur well beyond the saltmarsh zone and far from the nearest shoreline.

Under the trade-off hypothesis that dunlins balance predation and starvation dangers, I expect that over-ocean flocking will be reduced when environmental conditions increase energetic expenditure, or make food more difficult to obtain. Cold temperatures in particular should have a clear effect, because they increase energetic expenditure and also make prey harder to find, but the effects of rainfall and wind are more difficult to predict. Windless conditions make flight more expensive, but the effects of heavy winds are less clear. Heavy rainfall undoubtedly increases energetic expenditure, but the effects of lighter rains are less clear. I examine the data for the effects of wind and rain, but have no strong *a priori* predictions.

2.2. Methods

This study was conducted at Boundary Bay, on the southern edge of the Fraser River estuary (49°05'N, 123°00'W) in British Columbia, Canada. The bay is 16 km across and the intertidal zone is roughly 4 km wide at the lowest ebb. The tidal rhythm is semi-diurnal. During winter the highest tides usually occur during daylight hours, and inundate all intertidal mudflats and most of the narrow strip of saltmarsh, which is covered with low vegetation, above a height of about 3.8 m. A dyke protects adjacent low-lying agricultural fields. Boundary Bay supports a variable wintering population of up to ~40,000 dunlins and 1700 black-bellied plovers, and is the main wintering site for dunlin in British Columbia (Butler and Vermeer 1994). Birds of prey are common, with peregrine falcons (*Falco peregrinus*) and merlins (*Falco columbarius*) the most frequently encountered diurnal shorebird predators.

Monitoring timing and locations of over-ocean flocks was achieved with a marine radar set-up. The radar was fixed in a stationary position, mounted on the flat roof of a municipal pumphouse at a height of about 5.7 m above the saltmarsh/high-tide mark, oriented to geographic north and left in place for the duration of the study. The view from the pumphouse allowed simultaneous visual and radar observations across most of the bay. I used a Furuno FR-7112 X-band marine radar (peak power 12 kW, horizontal/vertical beamwidths 1.9°/22°, antenna rotation 24 rpm) connected to a radar monitor. The radar screen and human operator were stationed inside the enclosed pumphouse. The radar was operated continuously for typically 2-3 h before and 2-3 h after the daily tidal maximum. Occasionally the radar was run for longer periods (>4 h before or after high tide), or terminated sooner after high tide when mudflats were exposed and all birds were again foraging. The radar range was set at 1.5 nautical miles (NM), with occasional range adjustments from 0.5 NM to 3 NM to ensure all flocks were detected. At a range setting of 1.5 NM, only large targets could be detected, thereby eliminating interference from individual birds. Over-ocean flocking was distinct from other flight modes in shape and behavior, and identified on the radar based on these distinct target signatures (see results for description). For each over-ocean flock, a distance and an angle from the radar unit were manually recorded, along with time of day. These measurements were made to the geometric centre of each flock as estimated by eye. Observations were recorded whenever a noticeable movement in flock position occurred, a new flock emerged, or every 2-3 minutes. The start time of OOF was defined as the moment at which one or more flocks matching the visual signature of OOF became apparent on the radar screen. The appearance of OOF flocks on the screen occurred rapidly. OOF end time was defined as the moment in which large flocks were no longer apparent. Cessation of OOF was not instant, rather flocks approached shore and “blinked” on and off the radar screen as individuals began to land on exposed mudflats or foreshore vegetation while others would again take flight in a seemingly nervous manner. Occasionally large flocks could be seen moving along the shorelines, but these targets always disappeared rapidly and were not considered to be in over-ocean flocks. Radar monitoring was not possible during periods of heavy rain or dense fog due to signal scatter.

Flocks were also monitored visually by a separate observer, from roughly four hours before until four hours after high tide, using the methods described by Dekker (2003). Observations were made from a dyke alongside the bay using 8x30 binoculars and a 20x60 spotting scope. In poor weather conditions, observations were conducted from a car parked at a vantage point along the dyke. At the start of an observation period, notes were made on the time of day, cloud cover, occurrence of precipitation, and an estimation of the tide height. Changes to these variables during the observation period were also noted. The observation period generally ended at dusk. The start of over-ocean flocking was defined as the moment that a flock left land with constant speed, and stayed in the air for more than 10 minutes. Just before over-ocean flocking completely terminated, the flocks that had already landed tended to be chaotic and agitated, appearing ready to start over-ocean flocking again at any moment. Due to this behaviour, the end of OOF was defined when all birds were on land for at least 10 minutes, and no more hovering flocks could be detected. The start and end times of over-ocean flocking were recorded, as well as any interruptions to flocking behaviour.

Flock locations (centre of flocks) determined from the radar were converted into UTM coordinates using trigonometric functions, and entered into a geographic information system (ArcGIS 9.3, ESRI Inc.). Distance between flocking locations and the nearest shoreline were obtained using the Point Distance function in ET GeoWizards 10.0 (<http://www.ian-ko.com>). A subset of points was used in determining distance from shore, due to potential biases resulting from a blindspot in the radar view (see Fig. 2-5), caused by tall trees growing along a segment of the dyke. To eliminate this bias in the analyses, flocking points in which the closest distance to shore passed over this blindspot were removed.

To determine which environmental factors influenced the occurrence and duration of over-ocean flocking, I used a stepwise regression analysis using both “forwards” and “backwards” selection methods. OOF occurrence utilized a logistic regression model (presence/absence) with independent variables of mean temperature, mean wind speed, total precipitation, maximum tide height, and a temperature x wind speed interaction. The OOF duration model, which excluded days with no recorded OOF, used a linear regression with independent variables of mean temperature, mean wind speed, total precipitation, maximum tide height, and a temperature x wind speed

interaction. Tide height was included in the duration model; however, due to local and varying wind conditions, the predicted tide heights may only roughly approximate actual height (which was not measured). Thus, any significance (or lack thereof) with this variable in the model may reflect sampling conditions rather than true tidal influences. In both models I used a stepwise probability of 0.05 for entry and 0.10 for removal. Temperature and wind speed values were calculated from hourly averages over the OOF period for each date. On dates in which no OOF occurred, temperature and windspeed averages were based on the values from 3 hours before to 3 hours after the daytime high tide, to match the average time period in which these values were calculated on days with OOF. Precipitation was measured as the cumulative total for a given date, and tide values were based on the tidal maximum for the daytime high tide. Predictor variables were assessed for collinearity using Pearson's correlations (r) and variance inflation factors (VIF). Variables were considered as not collinear when Pearson's r was below 0.6, VIF values were below 10, and mean VIF scores were not considerably greater than 1 (Chatterjee et al. 2000). Statistical analyses were performed using R 2.13.1 (R Development Core Team 2011), except for the stepwise logistic regression which was run in SPSS 15.0 (SPSS Inc. 2006). Error estimates are standard errors unless otherwise noted.

A 2x2 contingency table was used to statistically compare the proportion of days with strong winds or heavy rainfall to days in which there were neither strong winds nor heavy rain, for days in which OOF occurred and days that it did not. A similar 2x2 contingency table was used to compare days with light winds against those without light winds, for both OOF and non-OOF days. Fisher's Exact Test was implemented for both these analyses to calculate a p-value. Strong winds were defined as average wind speeds ≥ 19 m/s, which approximates the Environment Canada criteria for issuing a wind warning. Similarly, Environment Canada issues a heavy rainfall warning for this region when cumulative precipitation equals 55 mm over a 24 hour period. As precipitation may not accumulate evenly over the day, I defined heavy rainfall as daily precipitation ≥ 25 mm. Light wind was defined as winds ≤ 9.2 m/s, based on the predicted value of the minimum-power airspeed for dunlin flight (see Chapter 2).

The tidal level was obtained from Environment Canada for the Tsawwassen tide station (<http://www.waterlevels.gc.ca>). Weather data were obtained from Environment

Canada for the Vancouver International Airport weather station (<http://www.weatheroffice.gc.ca>). This weather station is on the Fraser estuary 15 km NW of Boundary Bay.

2.3. Results

Dunlin flocking was monitored on 62 days between 09 November 2009 and 26 January 2010, comprised of 26 days with radar observations and 55 days with visual observations, including 18 days with both. On two of the 55 days, the visual observer recorded OOF during two separate high tide periods in a single day, though based on the tidal cycle, usually only one high tide period could be observed per day.

Over-ocean flocking had distinct characteristics that distinguished it from other dunlin flight modes and other species, both visually and on the radar screen (Fig. 2-2). In accord with other descriptions (summarized in Ydenberg et al. 2010) over-ocean flocks were large (up to 2 km in length), irregularly-shaped (often globular or ribbon-like), and relatively slow-moving. Directional changes, while frequent, were not rapid, such that a single flock often lingered in one general area. In contrast, escape flights were characterized by tightly-clustered flocks that rapidly changed shape and direction in response to a direct predatory attack, while general transit flights were long and linear, with birds flying in a “stream” with apparent constant speed and direction.

When over-ocean flocking occurred, the vast majority of individuals participated. A small percentage of birds were observed flying away from the bay around the time of OOF commencement on most days. On days when a limited amount of vegetation remained exposed, some birds would roost in dense concentrations, but with continuous shuffling between land and the over-ocean flocks beyond.

Over-ocean flocking by dunlin observed on the radar screen could be distinguished from flights by gulls (*Larus* spp.) and waterfowl (*Anas* spp.) that were also common in the study area. Gull flocks were a recognition challenge during the early morning period, when several hundred birds occasionally circled in one area of the bay for extended periods of time. Although the shape and extent emulated over-ocean

flocking, it differed in not being as dense as a typical dunlin flock, and it remained in one specific area much longer than dunlin flocks were ever observed to do. Ducks could be seen with the radar as they entered the bay from nearby agricultural fields before dawn every morning. These targets could easily be distinguished from dunlin OOF as they moved quickly and soon disappeared out over the bay as the ducks settled on the water. Flights of ducks (usually flushed by eagles) during the day were occasionally evident, but differed from dunlin in that the leading edge of these flocks always showed a splayed-out pattern, and the target moved in one general direction fairly rapidly, and soon disappeared.

2.3.1. *Duration of Over-ocean Flocking*

The complete OOF sequence was captured by the radar observer on each of the 13 days OOF was detected by that method. In contrast, the visual observer was not present for either the start or end time of OOF 14 times on 13 of 40 days with visual OOF detections. Duration was documented by both observers on 6 of 18 days, with an additional 3 days in which OOF end time was noted by both observers, but for which the visual observer was not present to witness OOF start. An additional 5 of 18 days had no OOF detected by either observer. The complete duration of OOF was recorded 35 times on 34 days. In total, OOF was detected 46 times on 44 days.

The mean duration of OOF was 187 ± 14 min (range 75 - 390 min). Considering only OOF flights that were not truncated by dawn or dusk (i.e. the tidal maximum occurred >1 h from a period of darkness) the mean flight time was 234 ± 20 min (range 89 - 390 min).

On days when the tidal maximum occurred >1 h from a period of darkness (i.e. over-ocean flocking was not truncated by twilight), the duration of OOF before and after the high tide did not differ significantly ($t = -0.823$, $df = 25$, $p = 0.42$).

2.3.2. *Radar vs. Visual Observations*

On days with simultaneous observations, the measured OOF duration was strongly correlated between radar and visual observations (Pearson's $r = 0.85$). The duration as measured via radar was slightly greater than that simultaneously made by

the visual observer (mean difference = 10.0 ± 4.9 min, range = 0.3 – 29.8 min, n = 6). Over-ocean flocking start and end times were also strongly correlated between observers (Pearson's $r = 0.94$ and 0.98 respectively). In general, the radar observer detected the start of OOF after the visual observer, and OOF end times later as well (mean differences = 18.4 ± 9.0 min, n=6, and 19.1 ± 6.1 min, n=9, respectively). Both observers always equally categorized OOF as being present or not detected, except on one date when flocking occurred entirely out of the radar's view.

2.3.3. *Nocturnal vs. Diurnal*

Over-ocean flocking often started abruptly near sunrise, or ended abruptly near sunset, even when it was expected to start earlier or end later based on tidal height (Figs. 2-3 and 2-4). No OOF was detected during darkness on the 16 days in which the radar was run for any amount of time between midnight and sunrise (total radar time = 23 h 15 min) or between sunset and midnight (total radar time = 2 h 7 min).

2.3.4. *Distance from Shore*

A total of 1556 over-ocean flocking locations were mapped. Of these, 491 were used in the analysis of distance to shore, representing 11 different observation days. Due to the flock sampling method, multiple flock locations were sometimes mapped for a single flock, and multiple flocks were sometimes recorded per day. Of the 491 flock locations used in the analysis of distance to shore, an average of 45 locations per day were recorded (range = 1 to 134 locations/day). Flocks ranged from 2 to 4402 m from the closest shoreline, with a mean of 771 ± 31 m. The extreme value of 4402 m occurred on 22 January, 2010, and was an outlier lying 9 standard deviations from the mean distance of 666 ± 19 m excluding this date. Over-ocean flocks usually remained in the vicinity of their foraging area (Fig. 2-5), and did not move large distances within the bay during a single OOF period.

The mean distance from shore before high tide was 931 ± 50 m compared to 549 ± 19 m after high tide (Fig. 2-6). This trend was retained, though reduced, when excluding data from the most extreme date (22 January 2010) when birds flew furthest from shore (737 ± 29 m and 569 ± 21 m before and after high tide respectively). Over-

ocean flocking also occurred significantly closer to shore when the tide height was >4.1 m high (Fig. 2-7).

2.3.5. *Non-occurrence and Role of Weather*

No over-ocean flocking was detected on 18 of 62 days. Nine of these occurred during or immediately after days of cold temperatures when foreshore ice was present. Neither wind speed nor heavy rainfall appeared to affect either the occurrence or duration of OOF. There was no difference in the proportion of days with strong winds or heavy rainfall between days with OOF and those without ($p=0.76$) or in the proportion of days with light winds ($p=1$). A stepwise regression retained only mean temperature as a variable for predicting OOF presence or absence ($p<0.001$, Nagelkerke $R^2=0.34$; Table 2). Mean temperature was also the only variable retained in the duration model, being positively correlated ($p<0.001$, $R^2=0.44$; Table 1; Fig. 2-8). Nonetheless, it was noted on a couple occasions by the visual observer that OOF was interrupted during periods of heavy rainfall, even though these were days that otherwise measured average total precipitation.

2.4. Discussion

The main hypothesis for OOF put forth previously is that it is an anti-predator behavioural response (Dekker and Ydenberg 2004; Ydenberg et al. 2010). Ydenberg et al. (2010) established that OOF was rare to absent in this study area prior to the 1990s, increasing in occurrence in tandem with predator densities, especially those of the peregrine falcon. Dekker and Ydenberg (2004) have shown a considerably lower success rate for peregrine falcons attacking OOF dunlins versus birds in the saltmarsh, further indicating a strong anti-predator benefit to this behaviour. My observations support this view, with OOF being performed by the majority of individual dunlins, but only during the day when falcons were a threat. The flights lasted the two to four hour duration of the high-tide period, when dunlin would otherwise be concentrated close to shore, and therefore most at risk of predation. Birds moved offshore by typically less than 1 km, flying in a zone of relative safety, but remaining in the general vicinity of their foraging grounds. However, this study also identified environment-mediated constraints

placed on OOF by dunlin. Both OOF occurrence and duration were most influenced by temperature. This indicates that dunlin make a trade-off between predation and starvation risk that determines the use of this behaviour in a dynamic environment.

2.4.1. *Duration of Over-ocean Flocking*

The start timing of OOF was abrupt and rapid, with most birds simultaneously commencing over-ocean flocking. In contrast, much shuffling of birds between ground and air after high tide led to a more prolonged time to complete termination of OOF. Despite the different flight commencement and flight termination characteristics, there was no statistical difference in number of minutes before high tide that OOF started and minutes after high tide that it finished on days in which the tidal maximum occurred >1 h after sunrise or before sunset. When all dates are considered, OOF lasts much longer after high tide, but this is due to a bias in a greater number of early morning observations when the start of OOF was truncated by darkness. The temporal symmetry of flocking around high-tide is contradictory to work previously conducted at the same site, which found that birds both started and ended OOF earlier than predicted by tide height alone (Dekker and Ydenberg 2004). Dekker and Ydenberg argued that falcon hunting activity altered the timing of OOF. Using similar techniques to Dekker and Ydenberg, a visual study by Out (2010) conducted concurrently with mine found no difference in raptor abundance or attack rates between those studies, albeit with a smaller sample size than that of Dekker and Ydenberg (2004). Thus, methodological differences are not likely to account for the difference in findings. It is possible that predation risk differed between the studies, or that dunlins were favouring a slightly more risk-prone strategy.

2.4.2. *Radar vs. Visual Observations*

Radar observations and visual observations closely match with respect to assessing OOF occurrence and duration. Radar is clearly the preferred method when nocturnal observations are required, precise location data are sought, or flocks occur far from shore and are thus difficult to detect with the naked eye. The visual observer, however, is unhindered by visual obstructions resulting from a stationary set-up, or by an inability to track during periods of rain (though the ability to detect and follow flocks is undoubtedly then also lessened). One main limitation of the radar data is the potential to

lose flocks when they drop to extremely low altitudes above the water surface (1-2 m). OOF flocking dunlins do not stay at these heights for long, but this behaviour caused the radar observer to temporarily lose track of flocks. Start and end times of OOF as noted by the radar and visual observers, though highly correlated, were consistently recorded earlier by the visual observer. I believe this was due to a spatial mismatch between the observer locations, as the visual observer frequently was positioned within the radar's blindspot, rather than any true difference in detection abilities. The visual observer was in a location where the saltmarsh was narrow or absent, and thus tidal inundation started and ended slightly earlier than the saltmarsh zone adjacent to the radar location.

2.4.3. Nocturnal vs. Diurnal

Over-ocean flocking was only observed during the day, as expected based on falcon behaviour. Regardless of the time or amplitude of night-time high tides, dunlins were relieved from falcon predation danger during the night. Though nocturnal predators (e.g. owls) are present, these may be of lesser threat. Short-eared (*Asio flammeus*), barn (*Tyto alba*) and great horned (*Bubo virginianus*) owls were all encountered in the general study area. While these species undoubtedly catch dunlins on occasion, they likely focus on mammalian prey (Houston et al. 1998; Wiggins et al. 2006; but see Page and Whitacre 1975). Zharikov et al. (2009) never observed barn or great horned owls over mudflats on a nearby estuary. Snowy owls (*Bubo scandiaca*) may be a greater threat in years when these sporadic visitors are present. They have been observed attacking dunlin, and were responsible for shifting habitat use by dunlin both within and outside of the mudflats (Zharikov et al. 2009). However, these sporadic visitors, present in variable numbers during some winters, were not encountered during my study.

Dunlins utilize different anti-predator tactics in dealing with diurnal vs. nocturnal predators. On the ground, dunlins by day were described as being "...congregated in a few large mobile flocks..." while "...in small, broadly dispersed groups..." by night (Zharikov et al. 2009, p.136). Mouritsen (1992) also describes looser flock structures, increased incidence of "freezing" behaviour, and decreased call rates in night-feeding dunlin.

An alternative hypothesis to explain the lack of nocturnal OOF is that due to visual limitations, dunlins are not capable of performing OOF, regardless of predation risk. This could explain the abrupt start and end times observed around twilight. Night-time observations of dunlins have found birds feeding in softer sediments and with more probing action (Mouritsen 1994), indicating a switch from visual to tactile foraging. Mouritsen also documented an increased night-time *Corophium* density. This fits a general pattern of decreased predation and disturbance rates at night, with a corresponding increase in food availability (Beauchamp 2007). It is also worth noting that in this study area, winter night-time high-tides are usually lower than their daytime counterparts. Whether visual limitations, increased foraging profitability, decreased predation risk, or some combination of the above result in no OOF at night remains untested.

Differing diel predation risks may explain temporal patterns of estuarine vs. agricultural usage. Agricultural fields are considered riskier habitats than mudflats (Shepherd 2001), yet a substantial proportion of dunlin diets can come from terrestrial origins (Evans Ogden et al. 2006). Dunlins are frequently detected in agricultural fields at night or towards periods of darkness (Shepherd 2001; Shepherd and Lank 2004; Evans Ogden et al. 2006; Zharikov et al. 2009). On several nights, I heard dunlin calling from nearby fields adjacent to the mudflats, while none were encountered there during the day. Decreased predation risk at night allows birds to disassemble large flock structures and move into habitats that are unsafe during the day. I thus conclude that dunlins are plastic in their behaviour and habitat usage and utilize context-dependent anti-predation strategies. Over-ocean flocking is likely not implemented at night as less costly anti-predator strategies exist which allow for increased foraging opportunities in areas that are perceived as too dangerous during the day.

2.4.4. Distance from Shore

Dunlin OOF averaged less than 1 km from the nearest shoreline, only rarely being detected much further out into the bay. Previous work at Boundary Bay documented peregrine falcon hunting success rates of up to 44% in the shoreline-saltmarsh zone (the width of which varies along the bay, but is generally within 100 m of shore), compared with 10-11% in the mudflat-ocean zones beyond the saltmarsh

(Dekker and Ydenberg 2004). Thus, OOF predominantly occurs within this “safe” zone, beyond the saltmarsh. Although there do not appear to be increased survival advantages the further out into the safe zone birds move, there may be additional benefits. Flocks that occur further out have increased predator detection time, and can move in any horizontal direction while simultaneously remaining in the safe zone. They may also gain knowledge of the locations of known predators, such as falcons that have made previous attacks. OOF gives dunlin an advantage in being able to continuously monitor their foraging grounds. Flocks ranged somewhat within the bay, but their distribution was not random, being concentrated in areas where mudflats and/or vegetation were first exposed on the falling tide. Due to frequent onshore winds, the timing of mudflat exposition can be difficult to predict, and birds that remain in the area have the advantage of knowing precisely when feeding opportunities are again present.

I observed Dunlin flying further from shore both before the high tide maximum and at lower high-tide heights. Segments of the flocks would often break off and approach shore, especially later in an OOF cycle. If vegetation was exposed, a proportion would attempt to land, either abandoning the attempt, or displacing other grounded birds. Birds would then re-join an over-ocean flock, creating a continuous shuffling of grounded and flying individuals. I believe that before high tide, most birds began over-ocean flocking and moved offshore, as little or no foraging or safe roosting habitat was available, or would be available as the incoming tide continued. After several hours of flight some birds may become physically or energetically strained, altering the state-dependent trade-off balance in favour of landing. As some individuals moved closer to shore to prospect or compete for exposed land as the tide receded, the flocks in general moved closer to shore. Decisions regarding remaining in flight or landing on dangerous exposed habitat patches may have reflected individual states (McNamara and Houston 1996; Gill et al. 2001; Beale and Monaghan 2004).

2.4.5. *Non-occurrence and Role of Weather*

Temperature had a significant inverse effect on OOF occurrence and duration. A trade-off between predation and starvation risks appears to underlie this pattern. Increased basal metabolic rate and food consumption are both related to decreases in air temperature below thermoneutrality (Kersten and Piersma 1987), which for dunlin

appears to be 20°C (Kelly 2000). At low temperatures, dunlins may not be able to recover energetic costs incurred by prolonged OOF, or might be able to do so only by resorting to foraging in riskier situations. Alternatively, birds may refrain from OOF to increase body mass in preparation for winter storms. Temperate shorebirds typically retain only 1.5-4 days of reserve energy (Castro et al. 1992; Piersma et al. 1994). Theoretically, body mass should be regulated to compensate for the risk of starvation, due to negative conditions persisting on time-scales longer than the individual's fasting capacity, against a higher risk of predation entailed with heavier body mass (Boyce 1986; Lima 1986; McNamara and Houston 1990; Houston and McNamara 1993; Biebach 1996; Kelly et al. 2002). Daily body mass increases related to decreased air temperatures have been documented in some species (Nolan Jr. and Ketterson 1983; Ekman and Hake 1990; Gosler 1996; Lilliendahl et al. 1996; but see Dawson and Marsh 1986). Within dunlins there is inconsistency in this trend, with some studies supporting (Pienkowski et al. 1979; Kelly et al. 2002 (captive birds)), and others showing the opposite (Mascher 1966; Kelly et al. 2002 (free-living birds)). The seemingly contradictory mass trends in dunlins may reflect site-specific differences in predation risk, food availability, or other variables. Other authors have identified stronger correlations with different environmental variables, such as wind speed (e.g. Dugan et al. 1981; Zwarts et al. 1996) or rainfall (Kelly et al. 2002). What is clear is that shorebirds are able to regulate body mass based on short-term factors rather than just on long-term seasonal averages, and the importance of those factors likely varies between sites. During this study, a period of sub-zero minimum temperatures lasted for 13 days, with 8 of those days having a mean temperature below 0° C. This same period also held the longest stretch without OOF being detected (9 days). For the two days immediately after temperatures (both mean and minimum) had ascended back above 0° C, there was still no observation of OOF.

The days with sub-zero temperatures were a good case-study of why dunlins may reduce flights at lower temperatures to conserve energy or to increase foraging time, despite potentially increased predation risk. Foreshore ice had built-up on the surface layer of the water, remaining as a frozen layer regardless of tide height, extending hundreds of metres out into the bay. Nearby agricultural fields were also frozen, restricting foraging opportunities and limiting the ability for an individual to

compensate for the energetic costs that OOF entail. However, whether the cold temperatures and associated thermodynamic and foraging costs was the cause of OOF cessation is confounded by several other attributes of this cold period. Sea ice, by virtue of extending hundreds of metres out into the bay, simultaneously limited access to mudflats and offered a temporary safe roosting site for dunlins, which were regularly observed there. Perhaps at risk of starvation, about 20,000 dunlins temporarily left the study area during this time, followed by a reduction in diurnal raptor detections. Birds returned shortly after temperatures warmed to the seasonal average. This pattern of fewer total dunlins roosting on the ice was also noted by Dekker (1998), along with a return of dunlins back to former numbers and a resumption of OOF once temperatures increased. He makes further mention of greatly reduced avoidance reactions in response to hunting falcons during this time period. Furthermore, in both studies, attacks on dunlins by glaucous-winged gulls (*Larus glaucus*) were noted during the freezing period, an atypical interaction and perhaps adding additional strength to the hypothesis that dunlins experience great energetic stress during these periods. The question of whether reduced predation risk or increased starvation risk was the primary driver of forfeiting OOF during this cold period requires further research, but I believe that current observations support the latter.

Dekker and Ydenberg (2004) report that when dunlins commence OOF, some will instead fly inland, especially during or after heavy rain. My analysis did not identify rain as a significant predictor of OOF duration or occurrence. However, it was noted on one date that OOF was suspended during a brief period of especially heavy rainfall, and resumed when rainfall lightened. Most data during heavy rainfalls rely on visual observations, as the radar cannot isolate targets out of the rain scatter. The extent to which precipitation limits OOF is unknown, but certainly this behaviour is not deterred under average or even moderate rainfalls.

2.5. Conclusion

Overall, dunlins in my study area appear to perform OOF as an anti-predator behaviour, recently expressed in the Fraser River Delta in response to increased falcon

abundance beginning in the 1990s. OOF allows dunlins to remain in close contact with their foraging grounds, providing access to high quality feeding opportunities as soon as mudflats are exposed. It occurs frequently, and seems to be shortened or halted only during cold temperatures. I expect over-ocean flocking to be witnessed at an increasing number of sites globally, as raptor populations rebound and sites become unsafe for traditional roosting.

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Appendix: Tables and Figures

Table 2-1 *Linear stepwise regression results for OOF duration*

Model					
	Sum of Squares	df	Mean Square	F	P-value
Regression	100825.7	1	100825.70	27.9	<0.001
Residual	119274.5	33	3614.38		
Total	220100.2	34			
Coefficients	Unstandardized Coefficients		Standardized Coefficients		
	B	S.E.	Beta	t-value	p-value
Constant	52.21	27.49		1.90	0.07
Temperature	20.68	3.92	0.68	5.28	<0.001

Table 2-2 *Logistic stepwise regression results for OOF occurrence vs. non-occurrence*

	B	S.E.	df	p-value	Odds Ratio
Temperature	0.383	0.117	1	0.001	1.467
Constant	-1.124	0.636	1	0.073	0.325



Figure 2-1 Radar screenshot overlaid on Google Earth image of study area. The triangular shape near the centre of the image is the Boundary Bay airport. Large red “blobs” surrounded by blue are the radar visualization of over-ocean flocking dunlins (see Fig. 2-2).

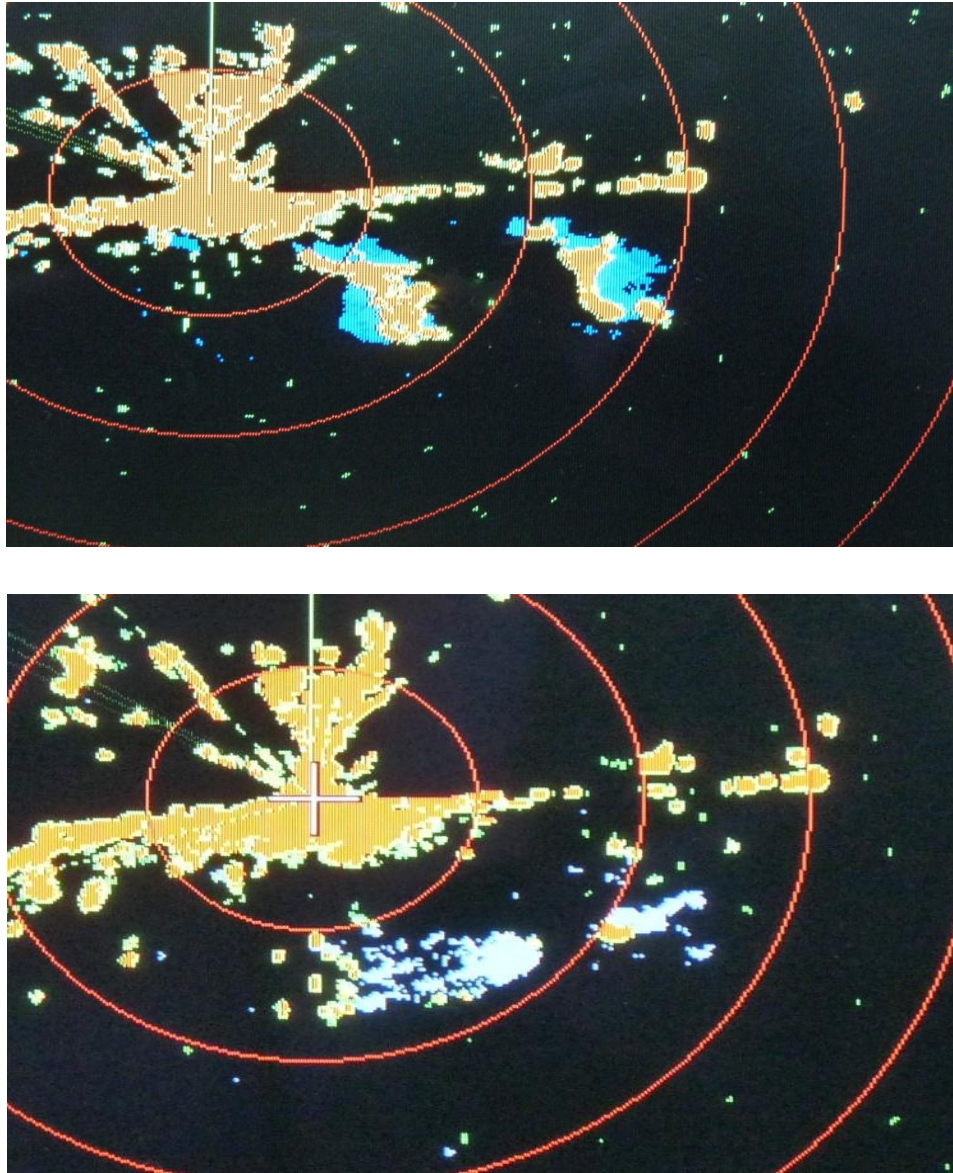


Figure 2-2 *Typical radar signatures of dunlin over-ocean flocking (top) and waterfowl flights (bottom). In both screenshots, distance between red lines is 0.5 nautical miles. The large orange region extending out from the centre of the rings represents land and vegetation cover. The orange shapes surrounded by blue are birds, the blue colour is an “echo” illustrating where bird targets had been recorded during the previous minute. Note the very large, dense structure of OOF, and the somewhat linear shape of the “finger” stretching out towards the shore. Waterfowl targets differ in being smaller and typically splay out offshore (left targets) before disappearing as birds land on the water.*

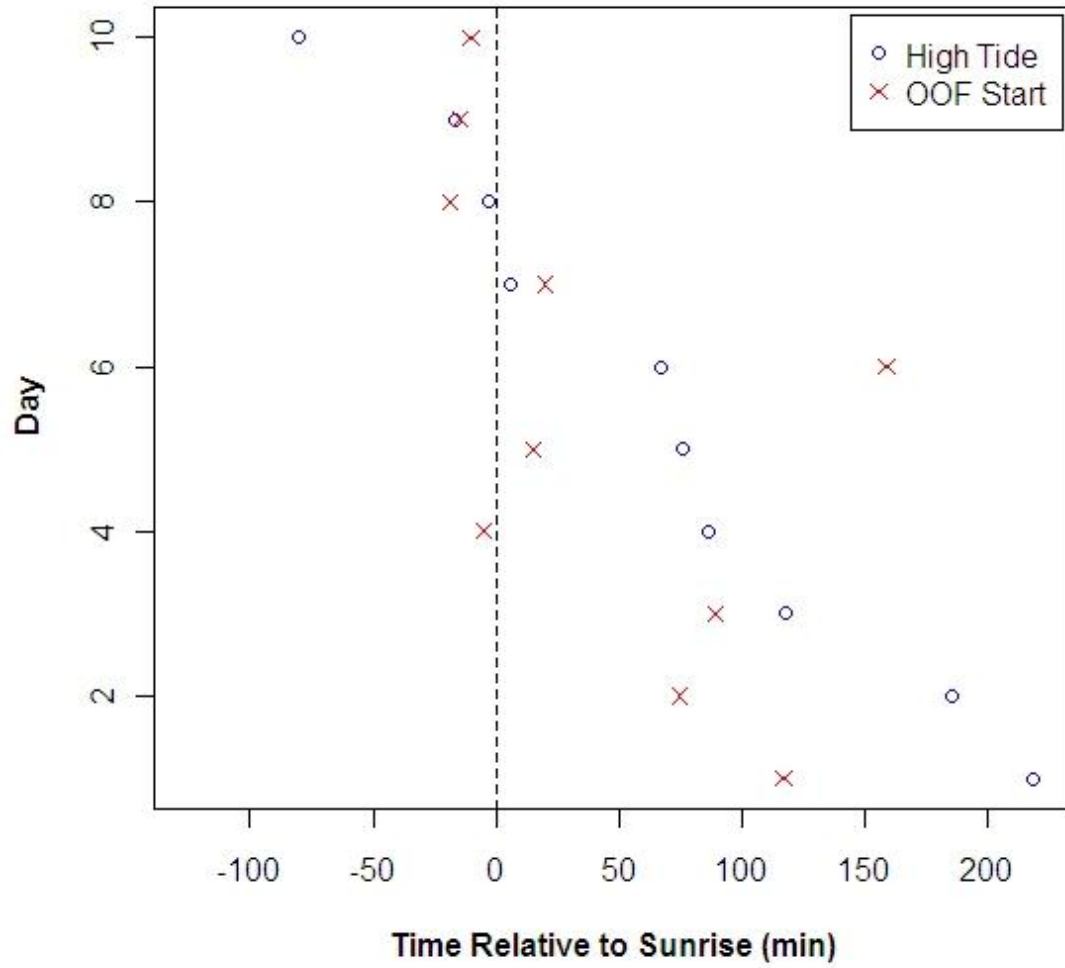


Figure 2-3 *Start timing of over-ocean flocking when high tide was near sunrise. Flocking commenced at or after twilight on all dates.*

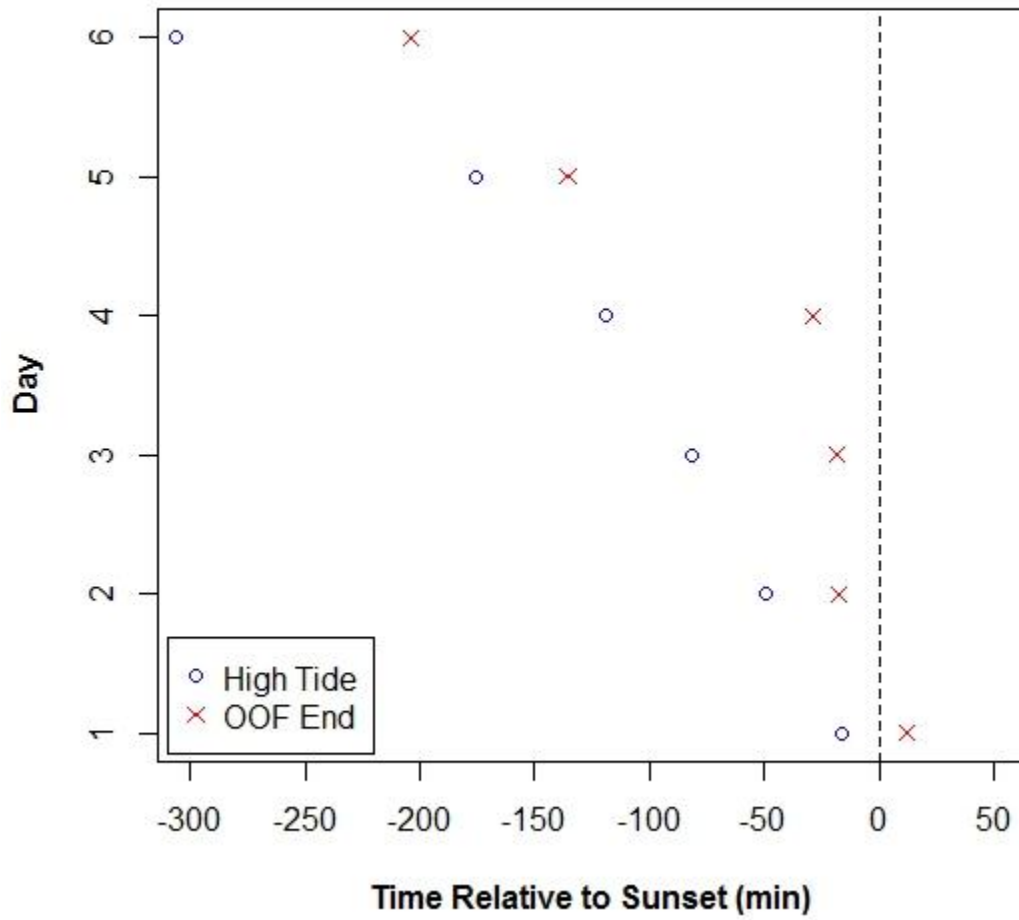


Figure 2-4 *End timing of over-ocean flocking when high tide was near sunset. Flocking ended before twilight on all dates.*

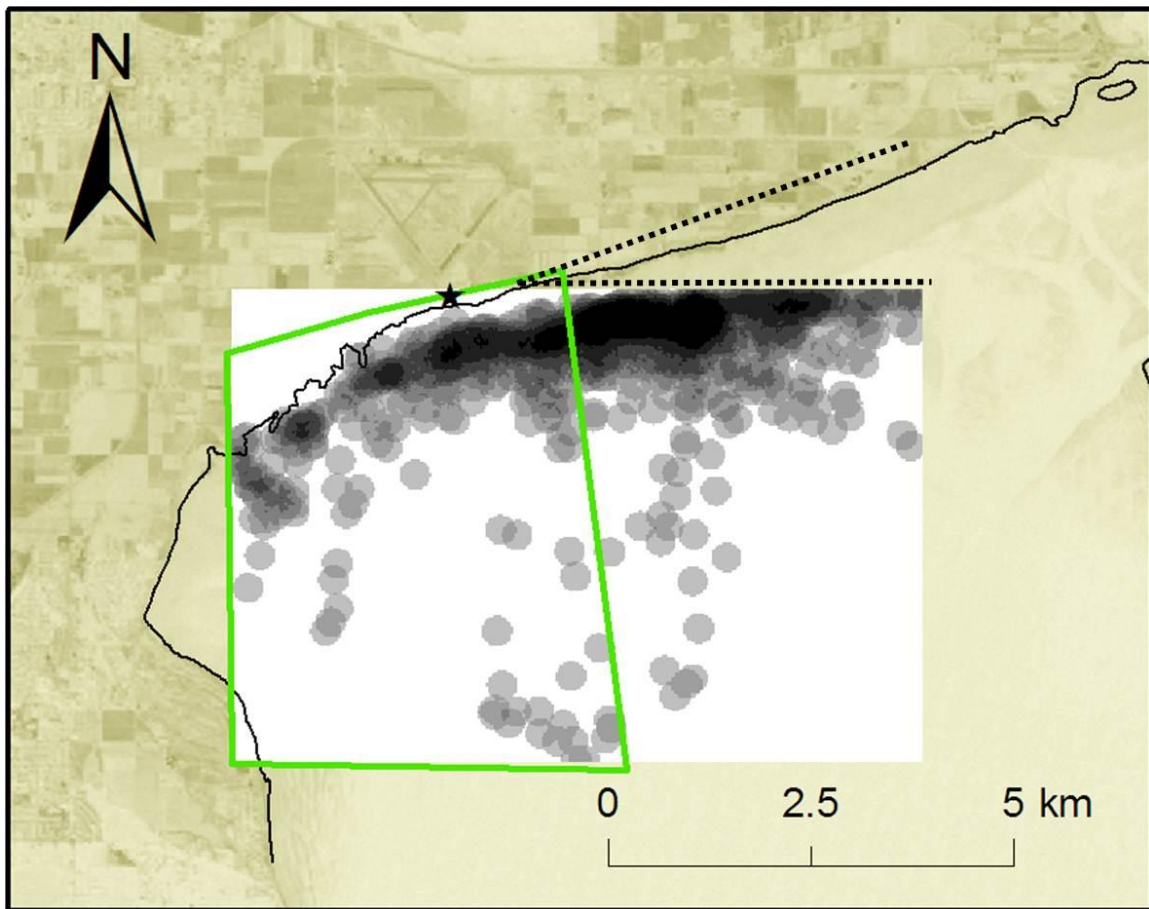


Figure 2-5 *Mapped locations of over-ocean flocks. Darker regions correspond to increased detection frequency. The green polygon denotes the subset of data points that were used in the analysis. Area between the two dashed lines indicates the radar blindspot. The black star indicates the location of the radar set-up.*

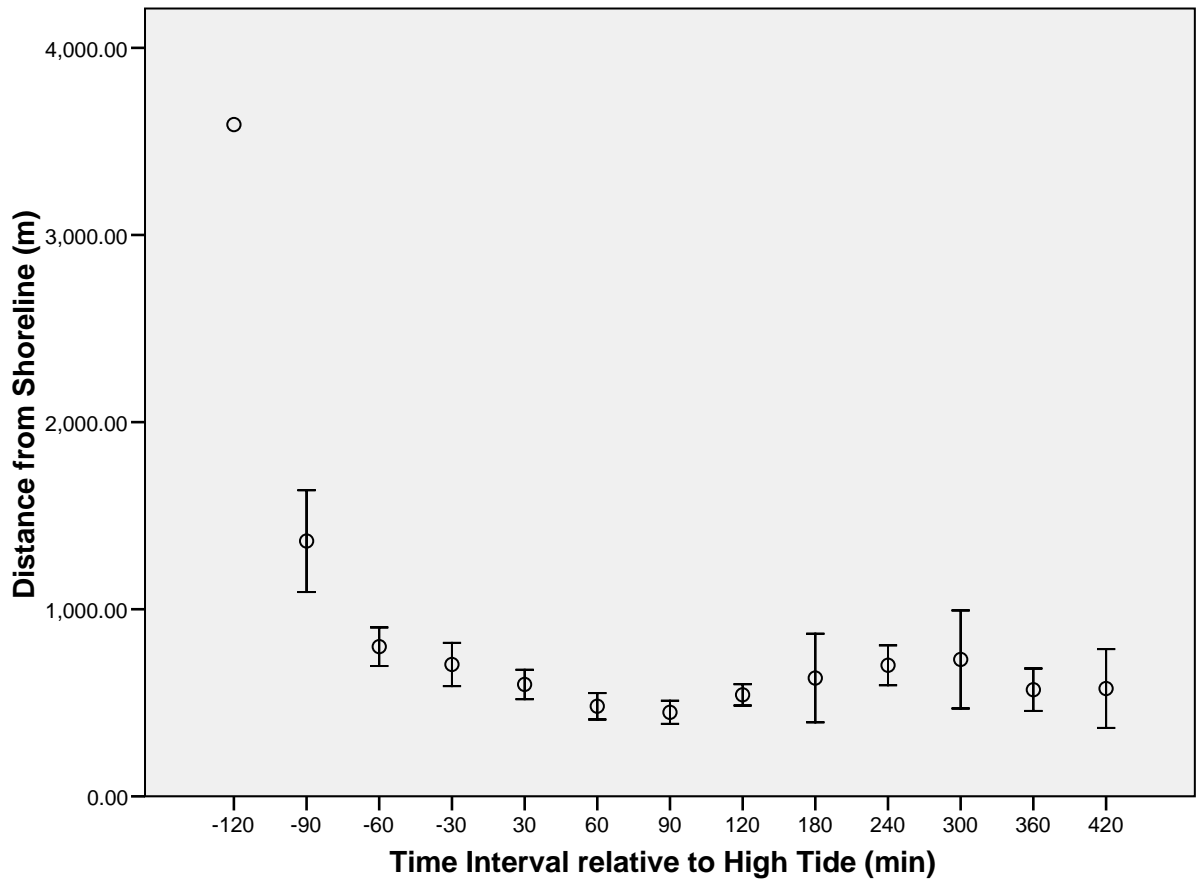


Figure 2-6 Average flock distance from shore binned in half-hour periods before (negative values) and after (positive values) high tide. Error bars represent 95% confidence intervals.

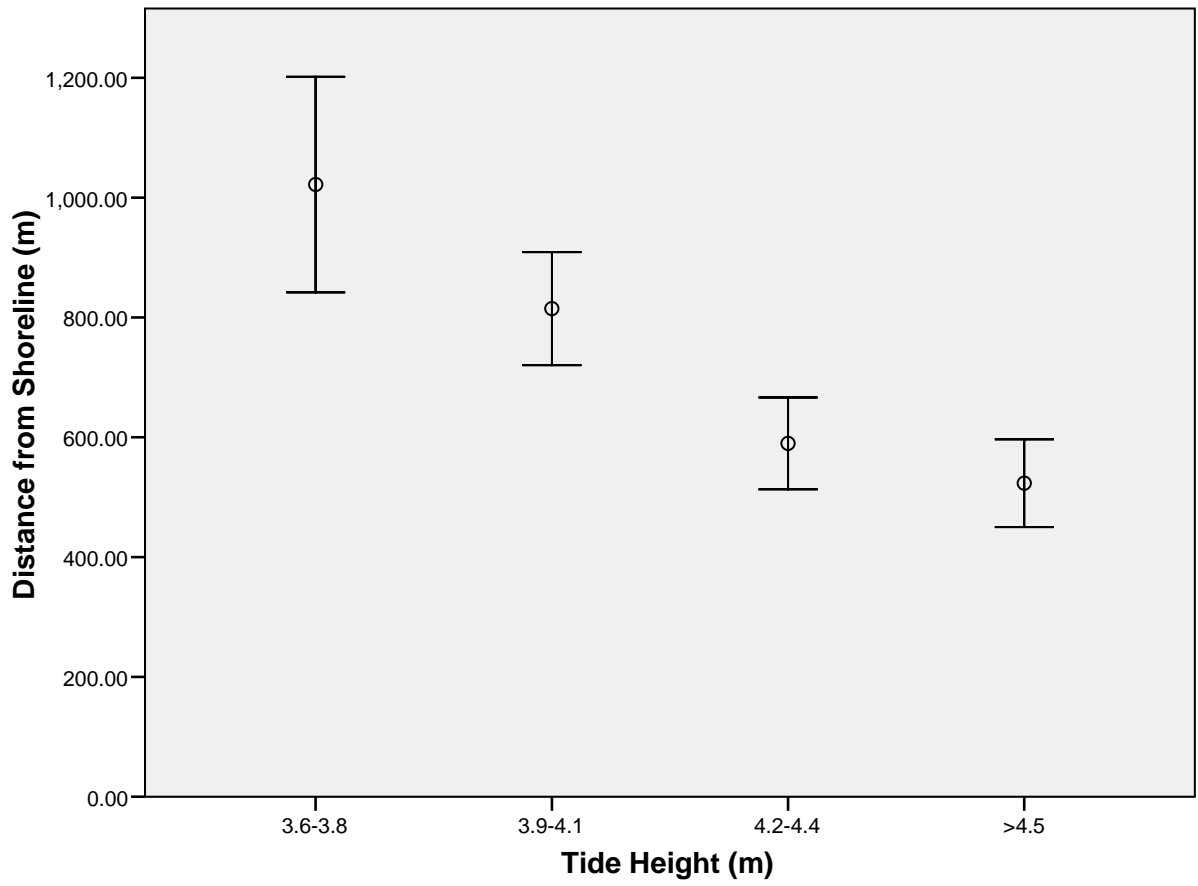


Figure 2-7 *Average flock distance from shore at four tide height categories. Error bars represent 95% confidence intervals.*

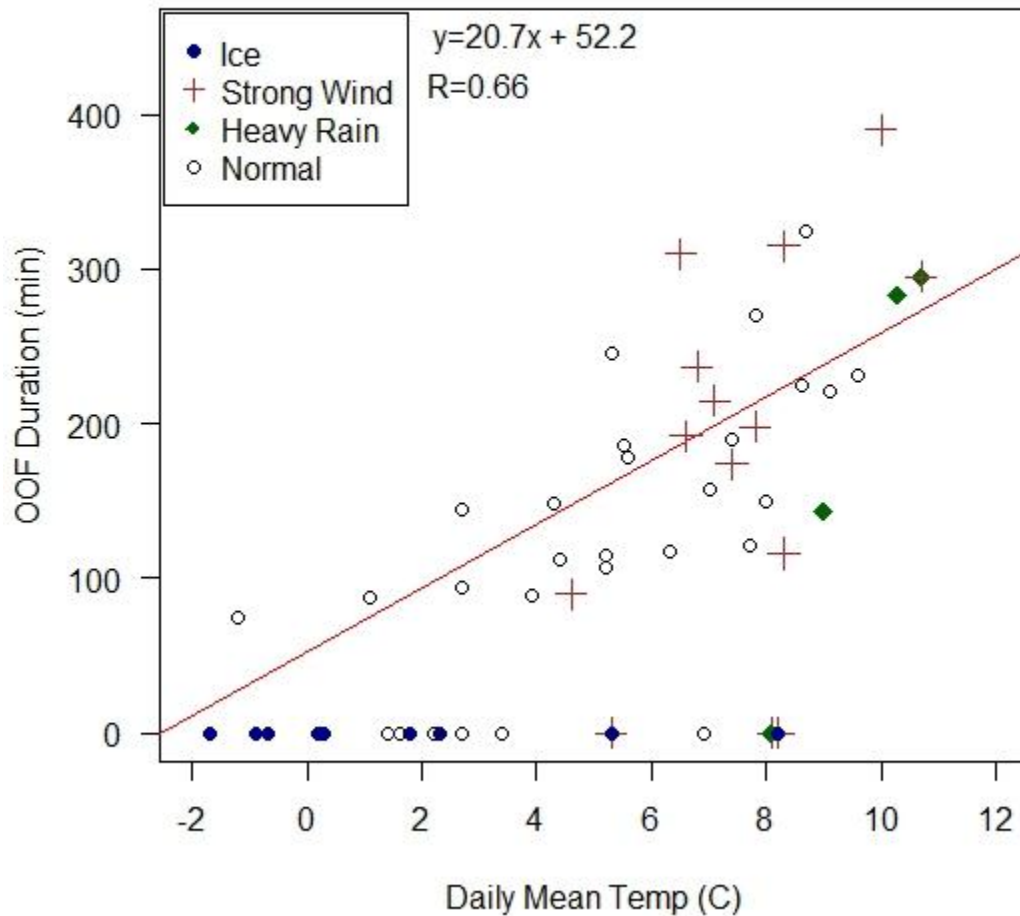


Figure 2-8 *Over-ocean flocking duration declines with decreasing air temperatures. Days with 0 minutes duration are presented at the bottom of the graph, but were not included in the regression. Days are represented by one of 4 symbols showing whether foreshore ice, strong winds, or heavy rain were present. Several of these days met more than one criterion. Other days held none of those criteria, and are labeled as “Normal”.*

3. Flight Kinematics and Energetics of Dunlin in Two Different Flight Modes

3.1. Introduction

Birds fly for a multitude of reasons, including migration, mating displays, predator evasion, transit between locations (e.g. nests, foraging patches, roosts), transporting food, and searching for resources. This ability has enabled birds to occupy a wide range of habitats, resulting in diverse life-history strategies. The contexts within which flight occurs, however, vary daily and seasonally, in response to environmental conditions, foraging opportunities, disturbances and predators. Powered flight is an energetically costly mode of transport; therefore individuals should adapt their flight attributes (e.g. speed, altitude, power) to the context and conditions in which they are travelling.

Flight attributes of different species of birds, or of different flight types within a single species, may be predicted through a well-developed aerodynamic theory of powered flight (Pennycuik 1969, 1975, 2008; Tucker 1973; Greenewalt 1975; Rayner 1979). Fundamental to this theory is a U-shaped total power curve relating the combined profile, induced, and parasite powers to true airspeed (Rayner 1999; Pennycuik 2008). From these theoretical predictions and with inputs of morphological parameters and air density, calculations of flight power, optimal flight velocities and wingbeat frequency can be obtained. Flight speed may be optimized in several ways, such as minimizing energy spent per unit time (minimum-power speed; V_{mp}) or minimizing energy spent per unit distance flown (maximum-range speed; V_{mr}). Together, these theories allow for comparative studies between species/individuals, or amongst flight types in the same species/individual. V_{mp} and V_{mr} present two benchmark speeds to which flight optimization strategies can be inferred. Despite many assumptions and occasional debate over flight model parameters (Ellington 1991; Pennycuik 1995; Alexander 1997; Rayner 1999, 2001), these theories are believed to provide the best estimates of power

and speed values — which are otherwise very difficult to measure — of birds under typical field-conditions (Dial et al. 1997; Rayner 1999, 2001; Tobalske et al. 2003; Pennycuick 2008).

During the non-breeding season, wintering shorebirds (order Charadriiformes) primarily make flights to and from foraging and roosting locations, and to escape predators. While the ideal roost is both safe from disturbances and close to the foraging grounds, these conditions are not always met (Rogers 2003). As a result, many shorebirds make frequent and sometimes lengthy flights between foraging and roosting sites (Symonds et al. 1984; Piersma et al. 1993; Drake et al. 2001; Gabbard et al. 2001; Rogers 2003; Dias et al. 2006). Long-distance commuting flights may be less energetically costly than multiple short flights (Nudds and Bryant 2000; Rogers et al. 2006b). Thus, flying to farther, safer roost sites can simultaneously decrease predation risk and decrease net energy expenditure when no nearby safe roost option exists. Conversely, birds moving between separated foraging patches may be maximizing other currencies, such as net energy intake rate (the difference between gross energy gain from food and foraging energy expenditure) or foraging gain ratio (the ratio of gross energy intake rate to the foraging cost above the resting metabolic rate) (Hedenström and Ålerstam 1995). Compared to these situations, an individual in predator-evasion manoeuvres should not be concerned with minimizing energy, and should fly in whichever manner is most likely to maximize the probability of survival, including utilizing anaerobic flight (Hedenström and Ålerstam 1995). Despite a significant literature on bird flight, few studies have compared different flight types within the same species, relating them in an ecological context.

Dunlins (*Calidris alpina pacifica*) wintering on the Fraser River estuary in southwest British Columbia, Canada, are a prime species to test flight theory predictions for different flight types. Dunlins at this location regularly fly for extended periods of time around high-tide, in a behaviour called over-ocean flocking (OOF) (see Chapter 1 for a description). Over-ocean flocking began regularly occurring in the mid-1990s, coinciding with increasing raptor populations (Ydenberg et al. 2010). It has previously been shown that over-ocean flocking significantly reduces predation risk (Dekker and Ydenberg 2004). The benefit of reducing predation risk is offset to some extent by the energetic cost of sustained flight lasting about 3 hours on average (Chapter 1). During over-ocean

flocking, birds remain near (directly overtop) their foraging site, and bide their time until tides recede and safer feeding opportunities become available. To minimize energetic costs, I predict that individuals should fly at the minimum-power speed while in over-ocean flocking. In contrast, transit flights are used for commuting between foraging and/or roosting sites. As most birds fly between V_{mp} and V_{mr} , and as it has been questioned whether birds fly faster than V_{mr} (Pennycuick 1995, 2001, 2008), I predict that individuals in transit flights will fly at the maximum-range speed to minimize energy spent per unit distance flown.

In this chapter I compare flight kinematics data between two flight types (OOF and transit) in a wild, unrestrained dunlin population. Observed data are compared to predictions from flight theory, and these are related to the ecological context in which they occurred. I also investigate the energetic demands that these flights place on dunlins and the increase to estimated daily energy expenditure they entail.

3.2. Methods

3.2.1. Study Area

This study was conducted at Boundary Bay, on the southern edge of the Fraser River estuary (49°05'N, 123°00'W) in British Columbia, Canada. The bay is 16 km across and the intertidal zone is roughly 4 km wide at the lowest ebb. The tidal rhythm is semi-diurnal. During winter the highest tides usually occur during daylight hours, and inundate all intertidal mudflats and most of the narrow strip of saltmarsh, which is covered with low vegetation, above a height of about 3.8 m. A dyke protects adjacent low-lying agricultural fields. Boundary Bay supports a variable wintering population of up to ~40,000 dunlins and 1700 black-bellied plovers, and is the main wintering site for dunlin in British Columbia (Butler and Vermeer 1994). Birds of prey are frequently encountered, with peregrine falcons (*Falco peregrinus*) and merlins (*Falco columbarius*) being sighted multiple times daily.

3.2.2. Video Collection and Analysis

Video of dunlin flight was recorded by a professional videographer on 17 and 18 January, 2011 with a Canon XL2 standard definition camera with a 20x (5.4-108 mm, F/1.6-3.5) zoom lens at 30 fps. I attempted to capture OOF, transit, and predator-escape flights, but no predator-escape flights were filmed. Video was slowed down by 40% using Final Cut Studio Pro 7 and burned onto standard DVDs.

The slowed down video footage was reviewed frame-by-frame using WinDVD (InterVideo Inc., Fremont, CA) on a laptop computer. Individual birds in level flight were selected, and followed frame-by-frame for 300 frames. At each frame in the series I manually recorded whether the bird's wing was in an upstroke, a downstroke, or a glide. This was done for 50 birds for both the OOF and transit flights.

Wingbeat frequency was determined by dividing the total number of strokes (complete upstroke-downstroke cycle) by the period of flapping time. Flapping time was the total number of frames observed per bird minus the number of frames with gliding. The proportion of time that dunlins spent gliding was calculated as the number of frames with gliding divided by total number of frames. The average proportion of time spent gliding of all individuals was calculated for each flight type, and separately for only those individuals that had at least some gliding.

3.2.3. Wing Measurements

Wing morphometrics (wing span [B] and wing area [S_{wing}]) were measured from dunlin carcasses. These specimens were all collected by other researchers for other projects, but from the same study region. Wing span was defined as the wingtip-to-wingtip linear distance on open, spread wings, measured in centimetres. As some specimens were missing wings, or had feather damage to the primaries on one wing, the wing span was taken as the distance from the wingtip of one open, spread wing to the bird's centerline (backbone) multiplied by 2. Partial wing areas were determined by tracing the outline of one fully extended wing per bird, following methods described in Pennycuick (2008). The outline was traced from the body-wing interface on the leading edge, all the way around the wing to the body-wing interface on the trailing edge. The two edges were connected by a straight line. A transparency with a 1 mm² x 1 mm² grid

was placed over top of the tracing, and this partial area was counted up as the number of grid-squares the wing tracing occupied, measured in mm². Root area was added to the partial wing area. The root area was based on a theoretical box with top and bottom lines the distance between the bird's centerline and the wing-body interface, and with sides as the root chord (the distance between the leading edge of the wing and the trailing edge, along the body-wing interface). The area of this root box was added to the partial wing area, and the resultant area doubled to get the total wing area. Total wing area was converted to m². These values were used to calculate the mean chord (c_m) (distance from the open wing's leading to trailing edge) using the formula

$$c_m = \frac{S_{wing}}{B},$$

and the aspect ratio (R_a) using the formula

$$R_a = \frac{B^2}{S_{wing}}. \quad (2)$$

3.2.4. Mass Data

The mass of 53 dunlins was measured during late March and early April 2011 (C. T. St.Clair unpubl. data). These birds were captured at the beginning of the ebbing tide, as they began to feed in concentrated groups on the newly exposed mudflats. Dunlins were measured to the nearest gram using a Pesola scale. Fat scores were recorded on a scale of 0 to 7, where 0 was no visible fat, and 7 was bulging with fat in the furcular hollow, wingpit and/or lower abdomen. As dunlins may have begun fattening up for migration during this period, only birds with fat scores of 0 or 1 were used to calculate average mass (n=44). Additional analysis by C.T. St. Clair measured gut contents of about 1.5 g, which was considered as payload mass for flight calculations. Thus, body mass was the mean mass minus 1.5 g. Fat mass was estimated as 2 g, based on Figure 4 of Ydenberg et al. (2010).

3.2.5. Weather Data

Barometric pressure and temperature data were collated from Environment Canada (<http://climate.weatheroffice.gc.ca>) for the Vancouver International Airport (YVR) weather station for 2 pm and 3 pm on January 17th, and 2 pm on January 18th, corresponding to the time periods in which video was recorded. Air pressure was converted from kPa to millibars. These values were used to find the local air density (ρ) using Boyle's Law (see Table 1 for variable definitions):

$$\rho = 1.226 \left(\frac{p}{1013} \right) \left[\frac{288}{(T+273)} \right] \quad (3)$$

As OOF dunlin usually fly at higher altitudes than birds in transit flights, a height correction for air density was applied using the formula

$$\frac{\rho_2}{\rho_1} = \left\{ 1 - \left[\frac{0.00650 \Delta}{(273+T)} \right] \right\}^{4.256} \quad (4)$$

where h is bird height above the observer (in metres), and ρ_1 is equal to Boyle's Law equation above.

Wind data were obtained from the Automatic Terminal Information Service (ATIS: 1-877-517-2847) for the Boundary Bay Airport (CZBB), approximately 3 km west of the total station location. ATIS reports were updated regularly, and included wind direction (the direction *from* which the wind blows) to magnetic north, and wind strength (in knots). All dunlin measurements were made within 1 hr and 10 min of an ATIS update.

Air pressures were 101.89, 101.98 and 102.09 kPa respectively. Temperatures were 8.4, 7.7, and 4.3° C respectively. The average values of 101.99 kPa and 6.8° C were used to calculate a local air density of 1.27 kg/m³ (Eqn. 3). A correction was made for birds in over-ocean flocking (Eqn. 4), as these flew at higher altitudes (~100 m) than commuting birds, resulting in an air density of 1.26 kg/m³.

Wind direction was constant between ATIS updates at 253° to true north on January 17, and 263° on January 18. Wind speed varied between 6.4 and 7.7 m/s on January 17 and was 5.1 m/s on January 18.

3.2.6. *Velocity Measurements*

A Leica FlexLine TS06 reflectorless total station (Leica Geosystems AG, Heerbrugg, Switzerland) was used to record time-stamped horizontal and vertical angles between the unit and the leading dunlin in a flock. Distance measurements using the total station were made to stationary objects (e.g. driftwood or debris) as close to the dunlin locations as possible, and the distance between the observer and the dunlin were inferred from this measurement. Measurements were made only on dunlins in sustained, level flight. Angles were automatically recorded in degrees, minutes, seconds (dd.mm.ss) format. This total station model had angle measurement accuracy to 1 arc-second (0.3 mgon standard deviation), and reflectorless distance tracking measurement accuracy of 5 mm + 3 ppm with a typical measure time of 0.25 s. However, these values are for typical surveying purposes, and it is unknown what accuracy is achieved when measuring flying birds.

Universal Transverse Mercator (UTM) positions were calculated for each dunlin measurement. To determine these, horizontal angles were first converted from dd.mm.ss format to radians. These radian values were used to determine UTM eastings and northings using trigonometric functions based on the GPS-measured total station location. UTM positions were mapped in ArcGIS 10 (ESRI, California). The “movement.pathmetrics” command of Geospatial Modelling Environment 0.6.1 (Beyer 2012) generated inter-point distances and path bearings (the bird’s track). The distances between points divided by the time difference between those points yielded the bird’s ground speed in m/s. Dunlins selected for ground speed measurements were flying approximately into a headwind.

The bird’s track and ground speed were used to calculate a ground-speed vector. A wind speed vector was the wind direction minus 180° together with wind speed converted to m/s. The resulting air speed vector was solved with the law of cosines.

As some of the airspeed values for transit flight appeared unrealistically high, possible bias in the measurements was a concern. The time interval between successive speed measurements differed, and I found that groundspeed values were higher when this time interval was only 1 or 2 seconds. Thus, measurements based on time intervals of 1 or 2 seconds, and their resulting airspeeds, are presented separately.

3.2.7. *Flight Data*

Predicted values for wingbeat frequency, minimum power speed, maximum range speed, mechanical and chemical power required for flapping flight, the minimum sink and best glide air speeds, and chemical power required for gliding flight were calculated using program Flight version 1.24 (Pennycuick 2011). These values were calculated separately for OOF and transit flights, and also separately for predicted and observed wingbeat frequencies. Estimates were based on a hypothetical dunlin with average wing measurements and masses as described above. Other modifiable fields used Flight's default values, and are listed in Appendix 1.

Table 3-1 *Symbols, names, units and default values (if applicable) of variables used in formulas in text.*

Variable	Name	Units	Default Value
C_m	Mean Wing Chord	m	
S_{wing}	Wing Area	m ²	
B	Wing Span	m	
R_a	Aspect Ratio		
T	Temperature	°C	
ρ	Air Density	kg/m ³	
h	Bird height above the observer	m	
P_{mech}	Mechanical Power	W	
P_{ind}	Induced Power	W	
P_{par}	Parasite Power	W	
P_{pro}	Profile Power	W	
k	Induced Power Factor		1.2

Variable	Name	Units	Default Value
m	Mass	kg	
g	Acceleration due to gravity at the earth's surface	m/s ²	
S_D	Disc Area	m ²	
V_t	True Airspeed	m/s	
C_{Db}	Body Drag Coefficient		0.1
C_{pro}	Profile Power Constant		8.4
P_{bmr}	Basal Metabolic Rate	W	
η	Conversion Efficiency		0.23
P_{chem}	Chemical Power	W	
f_{ref}	Predicted Wingbeat Frequency	Hz	
R	Respiration Factor		1.1

The mechanical power required to fly was based on the equation:

$$P_{mec} = P_{ind} + P_{par} + P_{pro}$$

Where P_{ind} is the induced power in horizontal flight (the power that the flight muscles must provide to support the bird's weight), P_{par} is the parasite power (the rate at which work is done to overcome the drag of the body, excluding wings), and P_{pro} is the profile power (the rate at which is done to overcome the drag of the wings). Each of these respective powers was determined as follows:

$$P_{ind} = \frac{k(mg)^2}{2 \cdot \rho \cdot S_d \cdot V}$$

where S_d is the disc area calculated by the formula:

$$S_D = \frac{\pi \cdot B^2}{4}$$

Parasite power is calculated as:

$$P_{par} = \frac{(\rho \cdot V_t^3 \cdot S_b \cdot C_{Db})}{2}$$

where S_b is the body frontal area defined as:

$$S_b = 0.00813 \cdot m^{0.666}$$

Profile power is found by the formula:

$$P_{pro} = \left(\frac{C_{pro}}{R_a} \right) \cdot \frac{(1.05 \cdot k^{\frac{3}{4}} \cdot m^{\frac{3}{2}} \cdot g^{\frac{3}{2}} \cdot S_b^{\frac{1}{4}} \cdot C_{Db}^{\frac{1}{4}})}{(\rho^{\frac{1}{2}} \cdot B^{\frac{3}{2}})}$$

Chemical power is inferred from the mechanical power by factoring in the conversion efficiency (the proportion of the fuel energy consumed that is converted into mechanical work by the muscles) and adding in basal metabolism and maintenance costs. The formula is:

$$P_{chem} = \frac{R(P_{mec} + \eta \cdot P_{bmr})}{\eta}$$

Predicted wingbeat frequency (f_{ref}) was calculated based on the equation:

$$f_{ref} = m^{\frac{3}{8}} \cdot g^{\frac{1}{2}} \cdot B^{-\frac{23}{24}} \cdot S_{wing}^{\frac{-1}{3}} \cdot \rho^{-\frac{3}{8}}$$

3.2.8. Daily Energy Expenditure Requirements

Detailed activity budgets were not made during this study, but based on previous work (Shepherd 2001) it was assumed that the only extended periods of flight were for OOF. An estimate of daily energy expenditure (DEE) was determined based on published studies of basal metabolic rate (BMR) and DEE for dunlin and a similarly-sized congener, the sanderling (*Calidris alba*) (Castro et al. 1992; Kelly et al. 2002; Piersma et al. 2003; Tulp et al. 2009; Gutiérrez et al. 2011).

The BMR for dunlins in saltwater environments was 49.1 kJ/d and 51 kJ/d for a 50 g dunlin based on respective equations in Gutiérrez et al. 2011 and Kelly et al. 2002. The BMR of sanderlings of same average mass (50.4 ± 4.6 (SD) g) was 48.1 kJ/d (Castro 1987). Sanderling DEE at four different wintering latitudes ranged from 100 to 200 kJ/d (Castro et al. 1992). The closest matching location in latitude to my study area was New Jersey ($\sim 40^\circ$ N), where wintering DEE for sanderlings was 200 kJ/d. Dividing sanderling DEE (at New Jersey) by sanderling BMR yielded a ratio of energy expenditure to metabolic rate that was then multiplied by the predicted dunlin BMR (50 kJ/d) to obtain an estimate of dunlin DEE for a temperate wintering latitude. As a contrast, a separate calculation was done using a lower DEE value of 142.5 kJ/d based on captive dunlins (50 g) in California (Kelly et al. 2002). Together these represent a lower and upper limit of OOF flight costs. This followed a similar method outlined by Kuwae et al. (2008), but without inclusion of fattening rates as I assumed that these dunlins were not adding fat mass during the study period. As none of the previous studies included birds that were over-ocean flocking, or otherwise noted extended flight events, I considered the flight costs of OOF to represent energy expenditure above the estimated DEE.

Chemical power (the rate of consumption of fuel energy) was calculated for four flight speeds (V_{mp} , V_{oof} , V_{mr} , and $V_{Transit}$), and for gliding flight. Total power is estimated twice at V_{oof} . The first case is for a bird that needs to recover losses of either speed or height in a glide, and the second is for when these losses are either negligible or do not need to be reclaimed. The power cost at V_{oof} where gliding losses do not need to be reclaimed is calculated by multiplying the gliding costs (0.72 W) by the proportion of time spent in glides (0.14) and adding in the predicted flight costs at V_{oof} for non-gliding flight

(3 W) multiplied by the proportion of time spent flapping (0.86). For the other flight speeds, the costs were simply the values predicted by aerodynamic theory (see results). These costs were determined for three time periods corresponding to minimum, mean, and maximum OOF durations. The result was a rate of energy use that was added to the DEE estimate to determine a refined DEE value for OOF dunlins.

A resting metabolic rate (BMR + thermoregulation) was calculated for each time period based on a value of 1.69 kJ/g/d (Kelly et al. 2002), and was assumed to be the background energy usage rate for both flying and roosting birds. The difference between the flight cost and this resting rate was used to determine the percent increase to basal (non-OOF) DEE that OOF entails, and hence the energetic cost of flight at these speeds.

3.2.9. Statistical Methods

Differences in mean values for OOF and transit flight airspeeds and wingbeat frequencies were assessed. First, a Shapiro-Wilk test was utilized to assess normality, followed by an F-test to compare two variances. Where variances were statistically equal, a student's t-test was performed, while Welch's t-tests were used where variances were unequal. Low to moderate deviations from normality were accepted, as the t-test is known to be robust to such deviations (Sawilowsky and Blair 1992). All statistics were run in program R version 2.15.0.

3.3. Results

3.3.1. Mass and Morphometrics

The all-up mass of the 44 dunlins with a fat score of 0 or 1 was 56.08 ± 4.92 (SD) g. Mass of all dunlins measured (n=53) was 56.26 ± 4.79 (SD) g. Payload mass of 1.5 g was subtracted from the all-up mass to calculate a body mass of 54.6 g that was input into the Flight program.

Wing morphometrics were measured from 30 dunlins. Wing area averaged 0.0144 ± 0.0014 (SD) m^2 (range = $0.0118 m^2$ to $0.0177 m^2$). The area of the wing proper (i.e. excluding root area) comprised 87% of the total measured area. Wingspan

averaged 0.334 ± 0.017 (SD) m (range = .300 m to 0.392 m). These mean values yielded a wing chord (Eqn. 1) of 0.043 m and aspect ratio of 7.75 (Eqn. 2).

3.3.2. Flight Kinematics

Video-recording analysis revealed similar flight kinematics between OOF and transit flights. The main difference between OOF and transit flight was in the amount of gliding. Individuals in over-ocean flocks ($n=50$) spent $14.3 \pm 2.3\%$ (range = 0 to 51.7%) of their flight time in glides while those undertaking transit flights ($n=50$) glided only $0.8 \pm 0.4\%$ (range = 0 to 13.7%) of the time, a significant difference ($W=1923$, $p<0.001$). Thirty of the 50 individuals in OOF had gliding bouts versus 5 of 50 birds in transit flight. Of those individuals that glided at all, the mean percentage of time spent gliding was $23.8 \pm 2.7\%$ and $7.7 \pm 2.3\%$ for OOF and transit flights respectively, which is a significantly greater amount of gliding for birds in OOF ($t = 2.34$, $df = 33$, $p\text{-value} = 0.03$).

Over-ocean flocking birds had a slightly but significantly lower wingbeat frequency of 9.16 ± 0.79 (SD) Hz (range = 6.82 – 12.19 Hz), compared to 9.45 ± 0.33 (SD) Hz (range = 8.5 – 10.0 Hz) for commuting birds (Welch's t-test: $t = -2.336$, $df = 66.4$, $p = 0.02$).

Calculated mean air speed values (\pm SD) were significantly lower for OOF versus transit flights (Welch's $t = -6.2915$, $df = 16$, $p < 0.01$), being 11.9 ± 2.5 m/s (range = 5.3-17.0 m/s) and 28.3 ± 10.2 m/s (range = 11.5-49.3 m/s) respectively (Fig. 3-1). Ground speed measurements ranged from 1.58-15.27 m/s for OOF flight and from 4.9-55.66 m/s for transit flights (Fig. 3-2, Appendix B).

Some of the speed values I obtained for transit flight (up to 49 m/s or 177 km/h) were unrealistically high. Individuals were followed for as long as possible, but the intra-track points used to calculate groundspeeds were only 1 to 9 seconds long. The five highest transit flight groundspeeds were all measured on a 1 or 2 second time interval, and the highest value was based on a 1 second period. If I exclude all measurements based on time differences of 1 or 2 seconds, the resulting mean transit airspeed is 22.6 ± 7.3 m/s. This revised airspeed is still significantly higher than OOF flight speed (Welch's t-test: $t = -6.73$, $df = 35$, $p < 0.001$), though not statistically different than the uncorrected airspeed ($t = 1.3975$, $df = 22$, $p\text{-value} = 0.18$). As it is a more realistic flight

value, I use this lower transit airspeed for energy calculations (below). Three of the top five highest measured OOF groundspeeds were also based on 2-second intervals, but excluding OOF speeds based on 2-second intervals (there were no 1-second intervals for this flight) had little to no effect ($t = 0.69$, $df = 48$, $p\text{-value} = 0.50$) on the mean OOF airspeed (which became 11.4 ± 2.3 m/s).

3.3.3. Theoretical Flight Model

Flight speeds increased from V_{mp} to OOF flight to V_{mr} to transit flight. The power to fly over a given period of time increased with flight speed. When gliding periods are factored into the V_{oof} speed, and assuming that losses to speed and/or height during glides do not need to be recovered, then total power required to fly at V_{oof} including glides results in the lowest power output. V_{mp} was 9.2 m/s while V_{mr} was 15.6 m/s (Figs. 3-3, 3-5, 3-6, 3-7, and 3-8). The power required to fly a given distance increased from V_{mr} to $V_{transit}$ to V_{mp} to V_{oof} . Here again though, the cost of flight per unit distance was lowest at V_{oof} when gliding losses of speed or height are considered non-influential. Flight power required for flapping flight is 2.86 W, 3.00 W, 3.60 W, and 6.08 W for V_{mp} , V_{oof} , V_{mr} , and $V_{transit}$ respectively (Figs. 3-3, 3-5, 3-6, 3-7, and 3-8). Glide polar analysis indicated that there is substantial energy savings to gliding. Chemical power during a glide was estimated at 0.72 W. The minimum sink speed (the speed at which a bird will lose the least altitude) was estimated to be 6 m/s and the maximum glide speed (the speed at which the bird will cover the greatest distance) was estimated at 9.1 m/s (Fig. 3-4). This latter speed is very close to the predicted minimum power speed. The wingbeat frequency predicted by the aerodynamic model was substantially higher than that observed; being 11.5 Hz and 11.4 Hz for OOF and transit flights respectively. The lower observed frequency had the main result of increasing mass-specific work, which is the amount of work done per unit mass of muscle per wingbeat (Pennycuick 2008).

3.3.4. Daily Energy Expenditure Requirements

My resulting DEE estimate for locally wintering dunlins, based on previously published BMR and DEE values (see above) was 207.9 kJ/d. The resting metabolic rate was calculated as 84.5 kJ/d for a 50 g dunlin. The cost of flight (excluding BMR and thermoregulation costs) was calculated as between a 3.7% increase to DEE for the

minimum OOF duration at $V_{\text{oof glide}}$ to a 57.4% increase to DEE at the maximum OOF duration at V_{transit} , for the higher basal DEE estimate (Table 3-2). These numbers increase to 5.4% and 83.8% respectively for the lower basal DEE estimate of 142.5 kJ/d (see methods; Table 3-2). The increase to DEE that OOF entails at average OOF airspeed and duration is 9.2-13.4%. Transit flights are 3.0 times more expensive than OOF flights incorporating glide savings, and 1.9 times more expensive than flight at V_{mr} . In contrast, flight at V_{mr} is only 1.4 times more expensive than V_{mp} , which in turn is 1.1 times more expensive than OOF flight with glide savings. At a 10% increase to DEE, birds in OOF incorporating glide savings will have an additional flight distance potential of 145 km, while birds in transit could fly an extra 92 km.

Table 3-2 *Percent increase to daily energy expenditure of flying costs at four flight speeds plus the over-ocean flocking speed that incorporates gliding cost savings. Percent increases are shown for three flight durations corresponding to minimum, mean, and maximum over-ocean flocking durations, for upper (207.9 kJ/d) and lower (142.5 kJ/d) estimates of daily energy expenditure.*

Flight Speed	Percent Increase to Daily Energy Expenditure					
	75 min		187 min		390 min	
	Upper	Lower	Upper	Lower	Upper	Lower
$V_{\text{oof glide}}$	3.7	5.4	9.2	13.4	19.2	28.0
V_{mp}	4.1	5.9	10.2	14.8	21.2	30.9
V_{oof}	4.4	6.4	10.9	15.9	22.8	33.2
V_{mr}	5.7	8.3	14.2	20.6	29.5	43.1
V_{transit}	11.0	16.1	27.5	40.2	57.4	83.8

3.4. Discussion

Dunlins must fly to migrate, move amongst foraging patches (transit flights), escape attacking predators, and to provide safety from perceived predation danger (over-ocean flocking). Over-ocean flocking dunlins are temporally segregated from

foraging opportunities by the tide. While roosting options in saltmarsh, shoreline edge, or fields exist, these are inherently more dangerous due to lower response times from attacking predators and sometimes fewer escape options. Flocking off-shore provides relative safety, but is also energetically costly. Over-ocean flocks incorporated flight characteristics that minimized energy expenditure relative to transit flights, such as incorporating more gliding bouts, flying at lower speeds, and lowering wingbeat frequencies. Individuals in OOF flew close to, but faster than, their theoretical minimum-power speed. The characteristics of this long-duration, endurance flight, which is made without respect to time-minimization or destination, allows dunlins to maximize safety from predators by staying airborne at the lowest flight-cost possible.

Over-ocean flocking is a relatively inexpensive flight compared to transit flight, but it is still an energetically demanding behaviour. Over-ocean flocking incorporates more glides, which may have energetic savings. In level, powered flight, the overall power output for a flap-gliding bird will equal that of a bird solely flapping, but the power will be delivered over a shorter time period (the flap), to offset losses to flight speed or height during the glide. Individuals in OOF glide on average 14% of the time, but this equates to single gliding bouts of only about 0.9 seconds between flapping periods. It is possible that the losses to speed or height are negligible over this short time period, and that this period of coasting offers flight savings. When OOF flight costs disregard maintaining speed or height, the resulting flight minimizes energy both per unit time, and per unit distance, making it the most economical flight of the types investigated. When compared to a traditional roosting strategy, over-ocean flocking requires a 3.7% to 28.0% increase to daily energy expenditure, depending on duration of flight and DEE estimate used. Two values are presented here reflecting a theoretical upper and lower bound to DEE. The upper bound of 207.9 kJ/d is closer to observed values 200 kJ/d for wintering sanderlings in New Jersey (Castro et al. 1992), and for DEE estimates of 192.7 and 231.4 kJ/d for dunlins on their arctic breeding grounds (Piersma et al. 2003; Tulp et al. 2009), so I feel that this most likely reflects the local DEE before incorporating OOF. The lower DEE estimate is from a study on captive, *ad libitum* fed dunlins from California (Kelly et al. 2002). If heat produced during activity substitutes all or partially for thermoregulatory costs, then my values will be overestimates to some extent. Various studies have reported zero to complete substitution of thermoregulatory costs (see

Bruinzeel and Piersma 1998). In addition, Poot and Piersma report that heat substitution in walking knots was cancelled out by increased thermal conductance (1994). As it is not clear to what extent, if any, substitution occurs in dunlins, and due to other confounding factors (e.g. thermal conductance) that may affect substitution, my calculations assume that energetic costs are additive.

Over-ocean flocking dunlins are essentially “running in place”, since their departure point is also their destination. As no distance technically needs to be traveled, dunlins should fly at V_{mp} for the period of time that they are in the air, regardless of wind strength. Counter to my prediction, V_{oof} was slightly higher than V_{mp} . Several factors could account for this. Wind drift is one of these factors. While wind drift will not need to be corrected for on a fine-scale, dunlins should remain out over the water, where distances to the nearest predator-concealing cover or obstructions are farther, to maximize safety. I found that dunlins do remain in one general area over an OOF event (Chapter 1), and so will experience both positive and negative forces associated with tailwinds, headwinds and sidewinds, if present. Hedenström and Ålerstam (1996) found that sky larks (*Alauda parvensis*) in song flight flew at V_{mp} when wind speed was lower than V_{mp} , but matched windspeed at windspeeds $\geq V_{mp}$, to prevent being blown off territory. This is analogous to the situation with dunlins if “territory” is considered as the region of the bay that minimizes danger. Larks can, however, return to the ground at any time to forage, a scenario not possible for mudflat feeding dunlins. The common swift (*Apus apus*), like the dunlin, also becomes temporally separated from foraging opportunities, as they remain in flight at night, but do not feed (Cramp 1985). Swifts were found to fly near V_{mp} (though slightly faster) while in nocturnal flight, as predicted (Bäckman and Ålerstam 2001). The combined results from Chapter 1 and calculated flight speeds are consistent with the prediction that dunlins are minimizing energy costs in OOF, and reactions to local conditions, such as wind drift, may help explain deviations in measured vs. predicted velocities.

Glide optimization may also account for a higher than expected V_{oof} . The periods of gliding that OOF individuals incorporate use considerably less energy than an equivalent period of flapping flight. However, at any given speed, the energy output for flapping flight will equal that of flap-gliding flight, though the distribution of that energy will differ in timing (Pennycuik 2008). Energy savings can be found where glides are

conducted at the expense of speed or height. The predicted best glide speed in my study is essentially equivalent to V_{mp} . The minimum sink speed may be a more desirable target for staying aloft, but is lower than V_{mp} . Speeds below V_{mp} are inherently unstable for powered flight (Pennycuick 2008), and even in OOF, dunlin predominantly flap. Flapping flight at the minimum sink speed is more costly than flight at V_{mp} , and thus would require acceleration to a more stable, lower-cost flight. For this reason the maximum glide speed is likely the optimum dunlin gliding speed. Glide speeds (*sensu stricto*) were not measured in this study, but the result of OOF airspeeds greater than V_{mp} could be due to birds flying slightly faster such that when they begin to decelerate they reach the speed that actually maximizes glide efficiency, and hence energy savings, so long as height losses do not need to be reclaimed.

In contrast, birds in transit fly faster than V_{mr} and much faster than V_{oof} . This result is counter to my prediction based on energy savings per unit distance flown; however, it is not unexpected if dunlin are optimizing some other currency. It is not known whether transit flights were made to move birds between foraging patches, or to traditional roost sites (e.g. fields), but it has been shown by others that optimal inter-patch movements will exceed V_{mr} if net energy intake rate is being maximized (Pyke 1981; Hedenström and Ålerstam 1995). Furthermore, optimal flight speeds between foraging patches should increase with increasing patch quality (Houston 1986; Hedenström and Ålerstam 1995). Transport flight exceeding V_{mr} has been noted among multiple bird families (e.g. hummingbirds: Gill 1985; swallows: Blake et al. 1990; alcids: Elliott et al. 2004). Gill found flight speeds of 1.6 times the predicted V_{mr} for trap-lining hermits (*Phaethornis superciliosus*), rather close to my dunlin transit speeds of 1.4 times V_{mr} . However, constant refinements of mechanical flight theory make comparisons between studies somewhat dubious. The parasite drag coefficient, for example, is now thought to be lower than historically assumed (Pennycuick 1995, 1997; Rayner 1999, 2001). Reanalysis of field studies with this revised coefficient has shown that most birds fly below V_{mr} (Pennycuick 1997, 2008). Unlike V_{mp} , the maximum range speed is not independent of wind speed. V_{mr} is expected to increase in a headwind, and decrease in a tailwind. Dunlins selected for ground speed measurements were flying approximately into a headwind, and V_{mr} will therefore be somewhat higher than predictions made for

still-air conditions. Regardless of V_{mr} , dunlins in transit flight are clearly flying much faster than those in OOF flight, and do not appear to be minimizing flight costs.

Hedenström and Ålerstam (1995) caution that field studies investigating flight speed cannot directly test aerodynamic theory, or errors in it, unless there is sound knowledge of the ecological context (optimization strategies) in which different flight is occurring. Elliott et al. (2004) tested predictions of flight theory for marbled murrelets (*Brachyramphus marmoratus*) in light of behavioural hypotheses and aerodynamic theory. They found that murrelets flew significantly faster than V_{mr} , and also had significantly lower wingbeat frequencies than predicted. They concluded that current aerodynamic theory is insufficient for predicting values for very fast-flying birds. Dunlin airspeeds were measured using tracking radar in Sweden at 18.6 m/s, 18.9 m/s, and 20.7 m/s on three separate tracks (Green 2003). Though slower than my birds in transit flight, these migrating birds were likely optimizing a different currency, such as V_{mr} . Nonetheless, these speeds confirm that dunlins are capable of fast flight, within range of other fast fliers such as alcids. While there is uncertainty around my transit speed measurements (see below), the general conclusions of Elliott et al. (2004) that current aerodynamic theory is inadequate when it comes to fast-flying seabirds may be applicable to shorebirds as well.

The higher mean transit flight being faster than OOF flight is unmistakable. However, some of the speed values I obtained for transit flight are likely erroneous. Transit flocks were relatively close to shore, and fast-moving, thereby reducing accuracy compared to the slower, farther OOF birds. Additionally, some values may inadvertently refer to accelerating flight (though the same could be true for measurements on OOF individuals). The potential bias in the groundspeed measurements (and resulting airspeed calculations) may lend doubt to the true airspeed of transit flight, but the relation of $V_{transit}$ to V_{oof} appears unequivocal.

Over-ocean flocking requires considerable energy expenditure, but this is true of powered bird flight in general. Over-ocean flocking can be considered analogous to long-distance flights between foraging and roosting locations, but provides the added advantage of allowing individuals to monitor patches continuously for any opening foraging opportunities. Rogers (2003) found cumulative commuting flights of up to 60

km per day, and one-way flights of up to 18 km, for great knots (*Calidris tenuirostris*) in Australia. Furthermore, Rogers et al. (2006b) predicted that short flights were 3.6 times as energetically costly as commuting flights. Thus, flying to further, safe roost sites may simultaneously decrease predation risk and decrease net energetic expenditure if there are no nearby safe roost sites. It has been suggested that extra energy expenditure may affect shorebird survival, especially in the winter (Rehfisch et al. 1996; Drake et al. 2001; Durrell et al. 2005), but considering that the alternative to OOF is to fly long distances to safe sites (which may not be present in my study region) or to roost in nearby unsafe sites where predator attack rates and success are likely high, OOF is a good strategy balancing energy expenditure with safety from predators.

Over-ocean flocking is a relatively inexpensive flight strategy that provides safety from predators throughout the winter. The Fraser Estuary is a productive ecosystem, and dunlins can probably easily make up the ~10% average increase to daily energy expenditure that this flight costs. This cost may be less trivial at sites where food energy is more limited. This behaviour might not be expected as often on less productive estuaries, but as this behaviour prioritizes maximizing survival over minimizing energy expenditure, it should still occur. Similarly, it might not be expected to occur, or occur for as long a duration, during migration, when there is increased pressure to gain fat mass for migratory flights. The observation of mixed-species flocks performing OOF during migration (pers. obs.) indicates that it is a viable strategy, even during periods of heightened energetic demand. This further strengthens my prediction that over-ocean flocking will continue to be seen at an increasing number of estuaries throughout the wintering range of the Pacific dunlin.

3.5. References

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3.6. Appendix. Figures

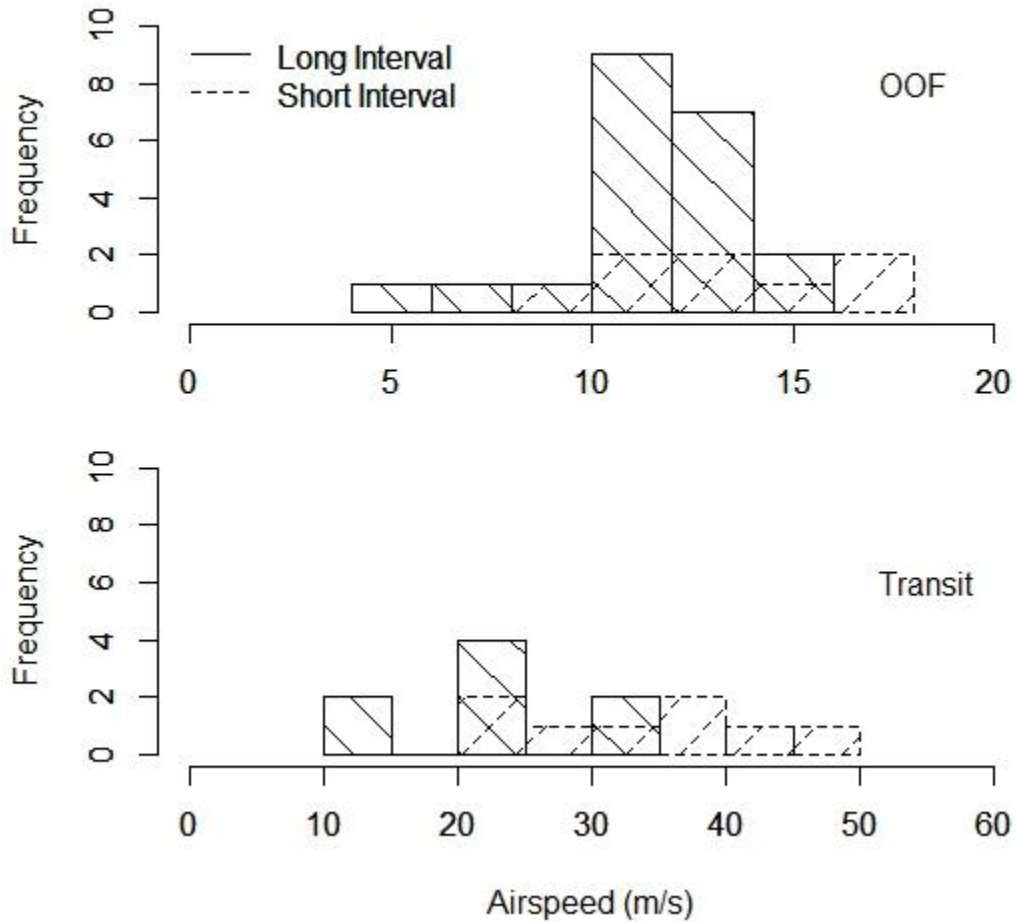


Figure 3-1 Histogram of calculated airspeeds for over-ocean flocking (top) and transit (bottom) flights. Long interval bars refer to airspeed measurements calculated from inter-point time intervals of greater than two seconds (see text). Short interval bars are for airspeeds calculated from inter-point intervals of one to two seconds.

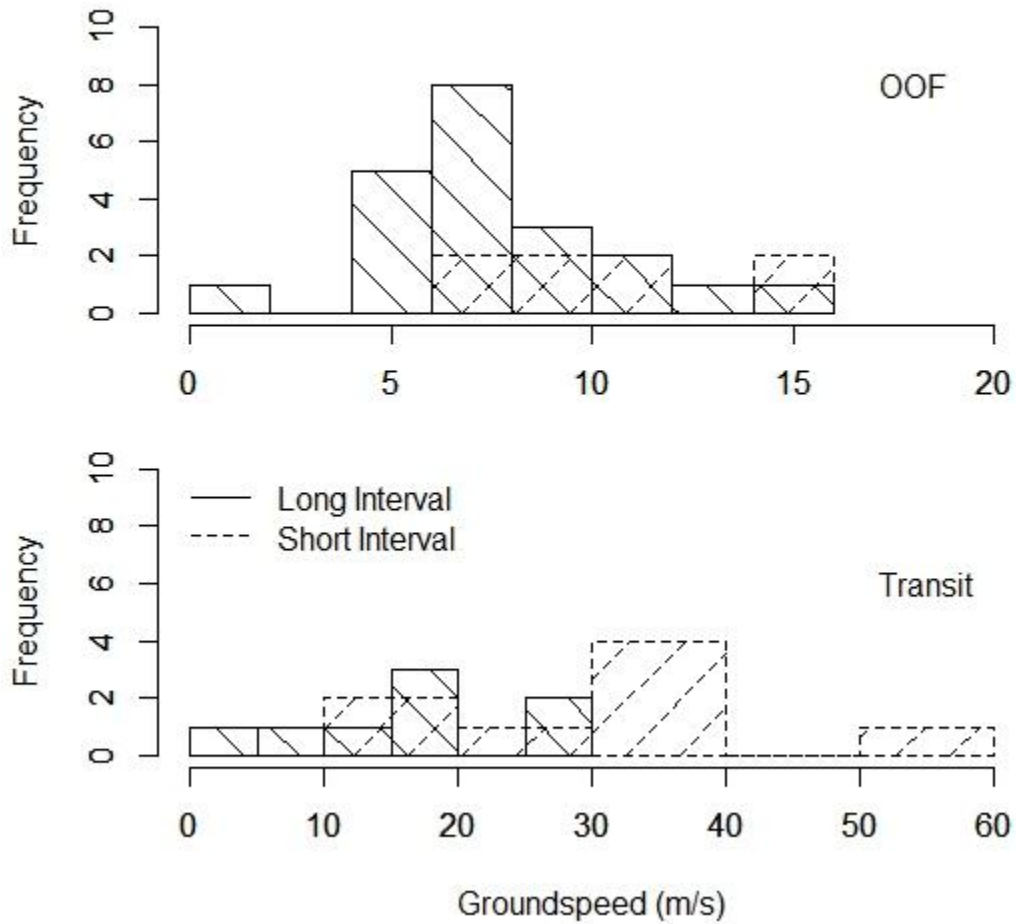


Figure 3-2 *Histogram of measured groundspeeds for over-ocean flocking (top) and transit (bottom) flights. Long interval bars refer to groundspeeds measured from inter-point time intervals of greater than two seconds (see text). Short interval bars are for groundspeeds calculated from inter-point intervals of one to two seconds.*

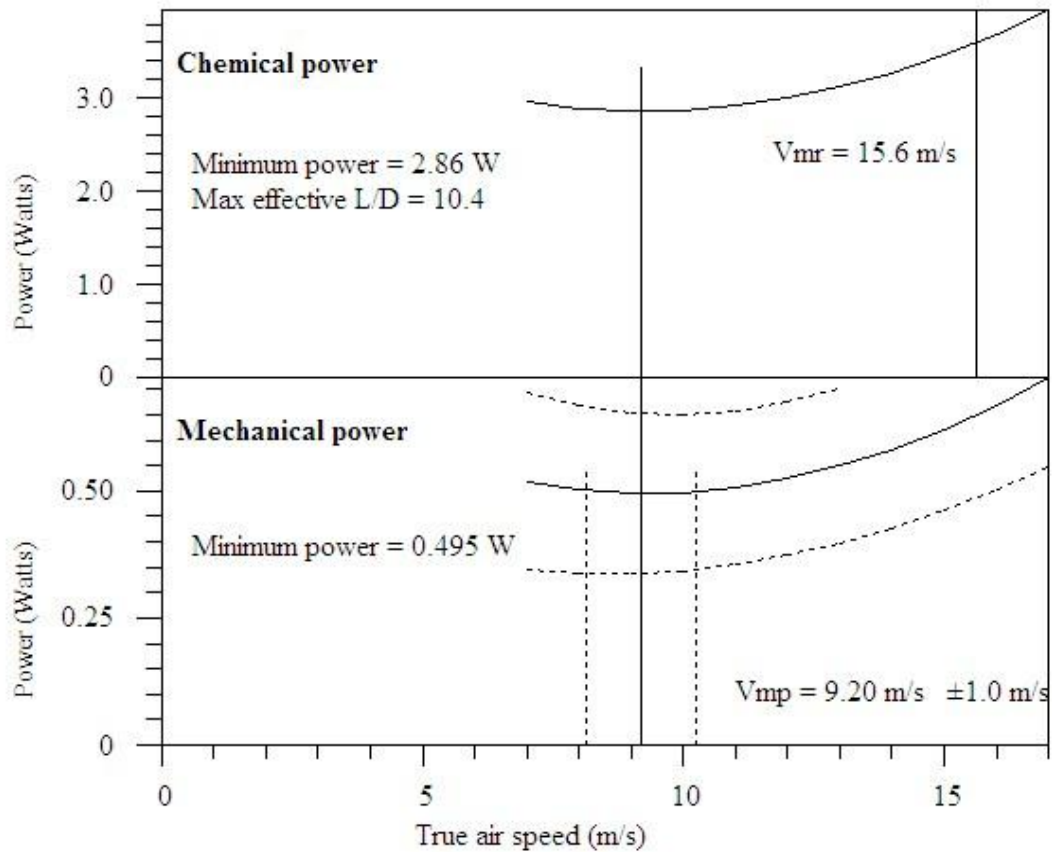


Figure 3-3 Chemical and mechanical power curves and associated minimum power (V_{mp}) and maximum range (V_{mr}) speeds. The dashed lines in the mechanical power graph indicate uncertainty bands around the estimates.

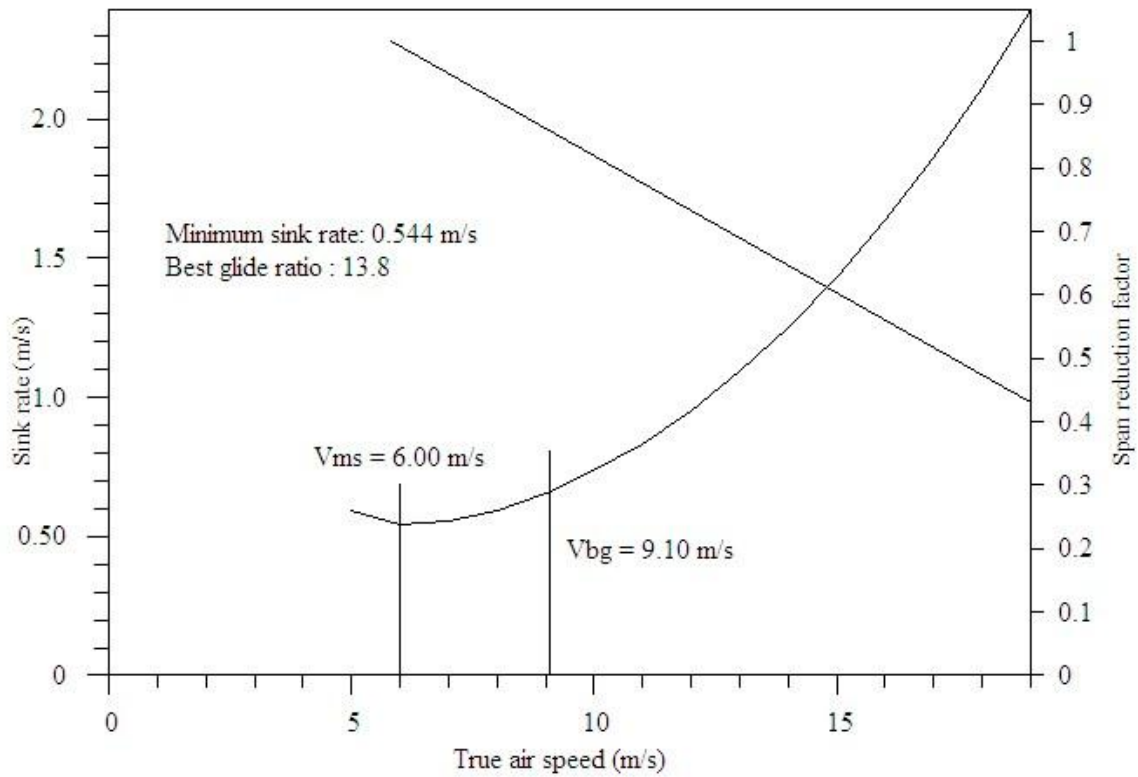


Figure 3-4 *The sink rate of a gliding dunlin at various airspeeds. Rate of sink increases with increasing speed above the minimum sink speed. The speed at which glide distance is maximized is indicated as the best glide speed (V_{bg}).*

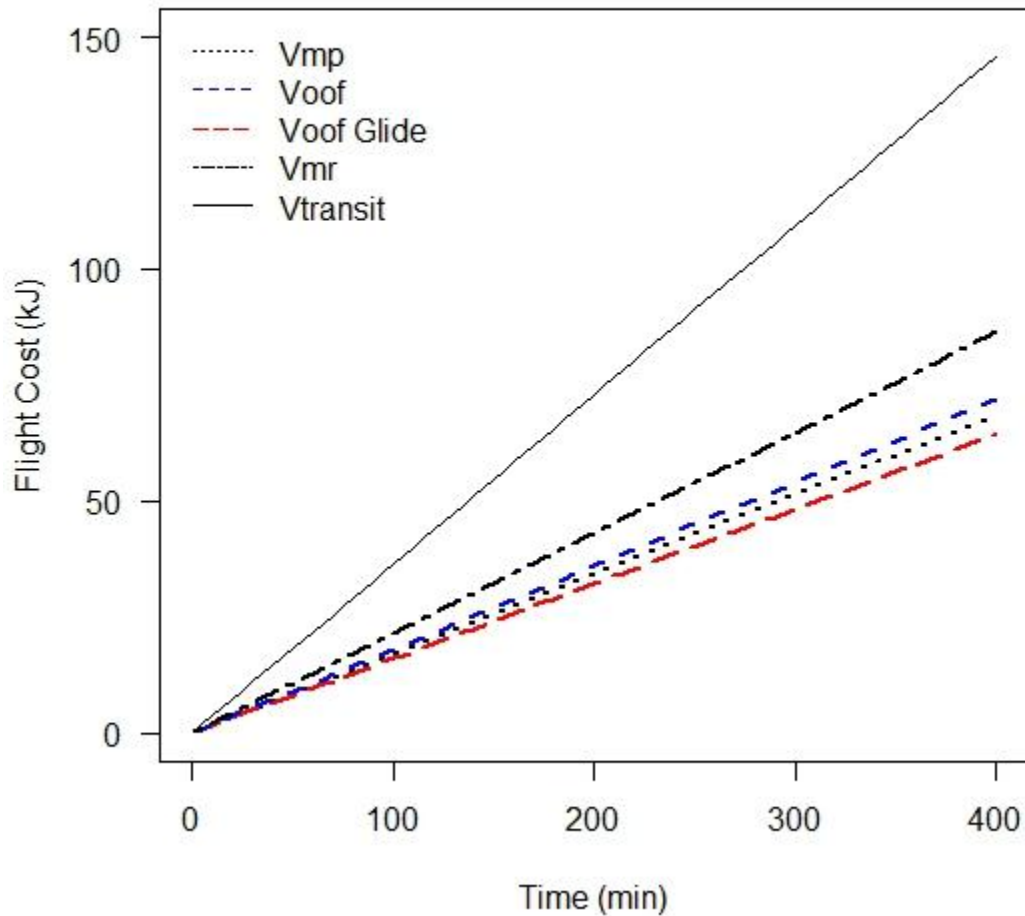


Figure 3-5 *The cost of flight as a function of time for the four different flight speeds plus over-ocean flocking flight where there is no requirement to maintain speed or height in a glide. The minimum-power speed and the speed of over-ocean flocking are similar, and represent the most energetically inexpensive flight speeds per unit time. Transit flight speed is noticeably more expensive than all other flight speeds.*

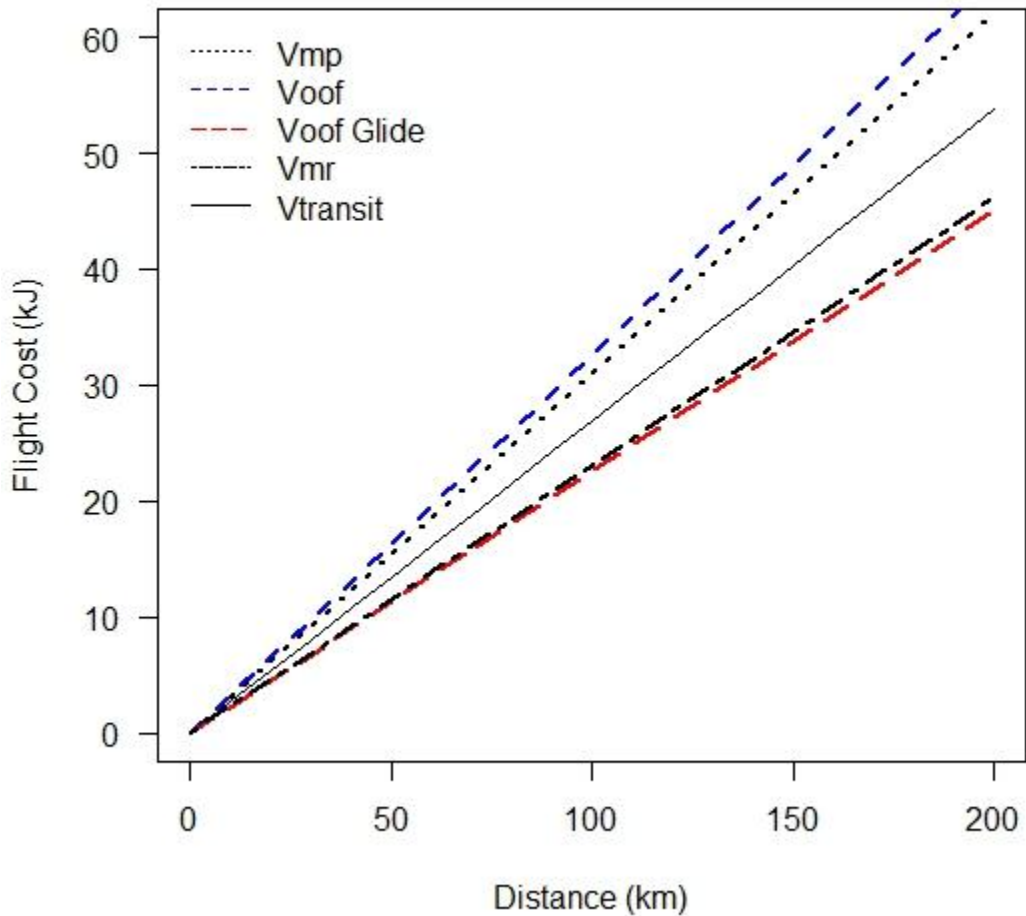


Figure 3-6 *The cost of flight as a function of time for the four different flight speeds plus over-ocean flocking flight when there is no requirement to maintain speed or height in a glide. The maximum-range speed and the speed of over-ocean flocking with negligible glide losses are similar, and represent the most energetically inexpensive flight speeds per unit distance. The minimum power speed and over-ocean flocking flight that incorporates the need to maintain compensate for glide losses are the most expensive modes of flight.*

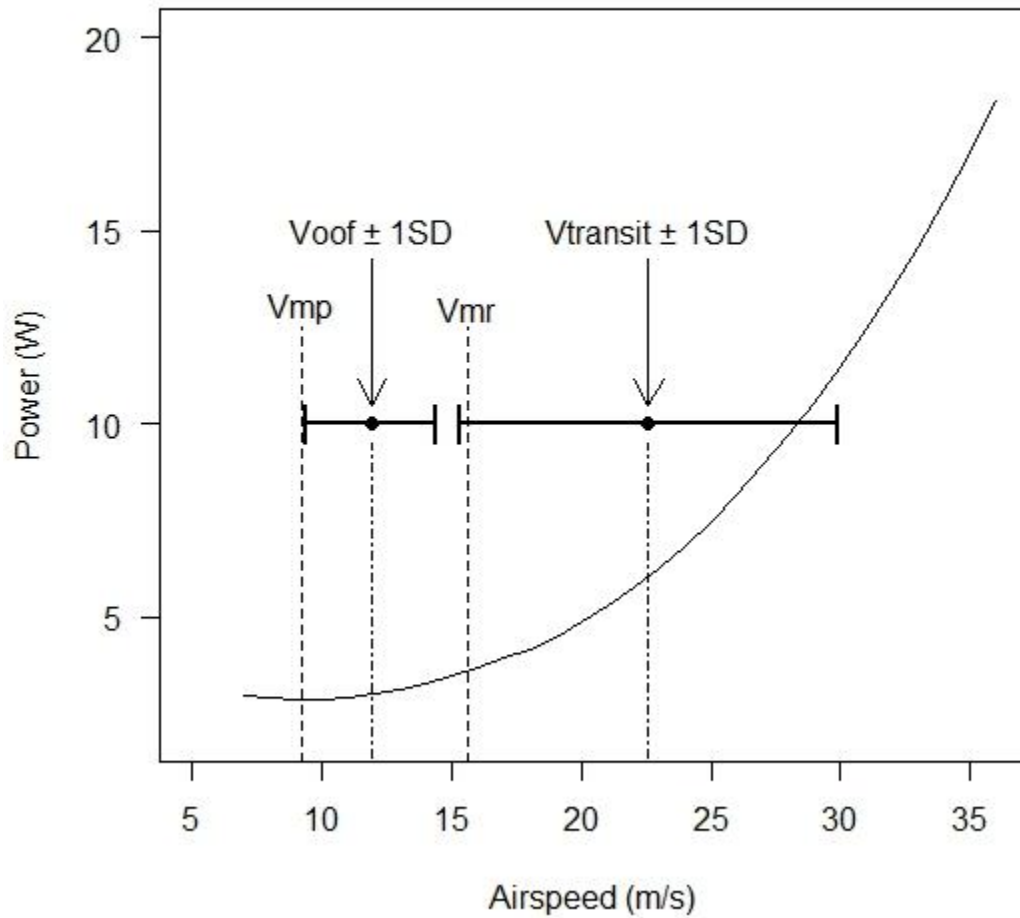


Figure 3-7 Power curve showing power output with airspeed flown. Predicted minimum-power (V_{mp}) and maximum range (V_{mr}) speeds are shown, along with measured OOF (V_{oof}) and transit flights ($V_{transit}$) ± 1 standard deviation.

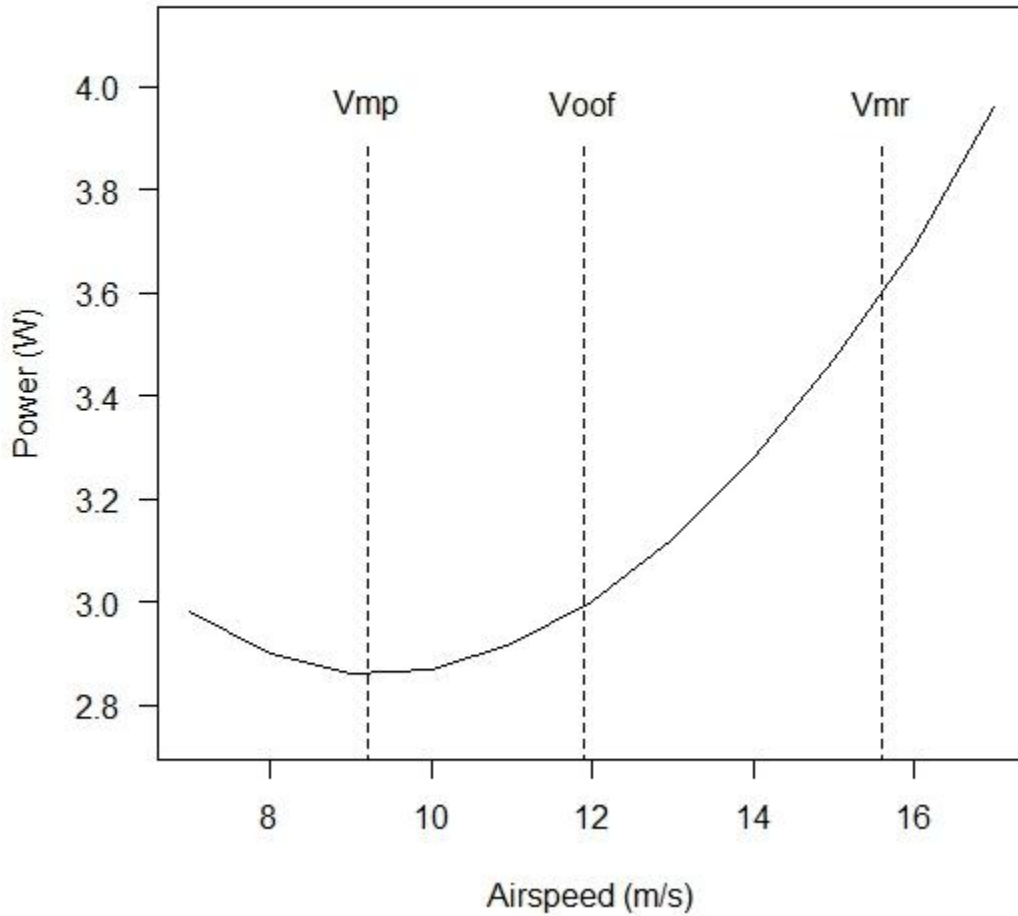


Figure 3-8 *Power curve showing power output with airspeed flown for speeds up to the maximum-range speed. Predicted minimum-power (V_{mp}) and maximum range (V_{mr}) speeds are shown, along with measured OOF speed (V_{oof}). This is the same curve as Fig. 3-7, but the airspeed is limited to lower speeds to better illustrate the characteristic U-shaped power curve predicted by aerodynamic theory.*

4. Conclusion

The main hypothesis put forth for over-ocean flocking is that it is an anti-predator behavioural response (Dekker and Ydenberg 2004; Ydenberg et al. 2010). My observations support this view, with OOF being performed by the majority of individuals, but only during the day when falcons were a threat. Over-ocean flocking is likely not implemented at night as less costly anti-predator strategies exist which allow for increased foraging opportunities in areas that are perceived as too dangerous during the day (i.e. agricultural fields). The flights lasted the two to four hour duration of the high-tide period, when dunlin would otherwise be concentrated close to shore, and therefore most at risk of predation. Birds moved offshore flying in a zone of relative safety, but remained in the general vicinity of their foraging grounds. However, the influence of temperature on OOF occurrence and duration indicated that there was a trade-off between predation and starvation risk that determined whether or not this behaviour was displayed. Increased basal metabolic rate and food consumption are both related to decreases in air temperature below thermoneutrality (Kersten and Piersma 1987). At low temperatures, dunlins may not be able to recover energetic costs incurred by prolonged OOF, or might be able to do so only by resorting to foraging in riskier situations. Alternatively, birds may refrain from OOF to increase body mass in preparation for winter storms.

Over-ocean flocks incorporated flight characteristics that minimized energy expenditure relative to other flight types. Birds in OOF incorporated more gliding bouts, had lower wingbeat frequencies, and flew at much lower speeds. These characteristics allowed wintering dunlins to participate in an energetically costly behaviour that simultaneously reduced predation risk. As no distance technically needs to be traveled, dunlins should fly at the minimum power speed for the period of time they are in the air. Over-ocean flocking dunlins flew at speeds greater than the minimum power speed, but still slower than both the maximum range speed and observed transit flights.

In contrast, birds in transit fly much faster than those in OOF. These birds also fly faster than the maximum range speed. This result is counter to what I predicted based on energy savings per unit distance flown; however, it is not unexpected if dunlins are minimizing some other currency. For example, it has been shown that optimal inter-patch movements will exceed the maximum range speed if net energy intake rate is being maximized (Pyke 1981; Hedenström and Ålerstam 1995). Regardless of maximum range speed predictions, dunlins in transit flight are clearly flying much faster than those in OOF flight, and do not appear to be minimizing flight energy costs.

I estimated that over-ocean flocking in place of traditional ground-based roosting adds about 10% to the daily energetic expenditure of dunlins in Boundary Bay. “Classical” shorebird biology predicts that this increased energy expenditure should increase mortality (Rehfishch et al. 1996; Drake et al. 2001; Durrell et al. 2005), but these authors did not consider predation danger. The trade-off hypothesis advanced here assumes that shorebirds adjust their wintering behavior to minimize the mortality from all sources. Aspects of winter behavior that improve protection from predators but increase vulnerability to starvation — including OOF duration and the amount of fat carried — vary as circumstances alter the balance of danger posed by predators and starvation. Pacific dunlins in my study area are able to meet the increased energy demand during normal circumstances, but as predicted, they reduce the duration of OOF in cold weather. If there is ice that allows them to roost far offshore, they adopt that option in place of OOF. Overall, it appears that the trade-off hypothesis is a good explanation for the occurrence of OOF.

Dunlins in this study area appear to perform OOF as an anti-predator behaviour developed in response to increased falcon predation danger. Over-ocean flocking allows dunlins to remain in close contact with their foraging grounds, providing access to high quality feeding opportunities as soon as mudflats are exposed, while greatly reducing predation risk. Though energetically costly relative to traditional roosting behaviours, dunlins utilize flight strategies that minimize energy expenditure relative to other modes of flight. I expect over-ocean flocking to be witnessed at an increasing number of sites globally, as raptor populations continue to increase and sites become unsafe for traditional roosting.

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Appendices

Appendix A.

Values used to calculate flight estimates in Program Flight

Field	Value
Body Mass (kg)	0.0546
Crop Mass (kg)	0.0015
Wing Span (m)	0.334
Wing Area (m ²)	0.0144
Air Density (kg/m ³)	1.26 OOF (1.27 Transit)
Flight Muscle Fraction	0.171
Fat Fraction	0.0356
Profile Power Constant	8.4
BMR Factor	1
Wingbeat Frequency Factor	1
Frontal Area Factor	1
Body Drag Coefficient	0.1
Wing Drag Coefficient	0
Induced Power Factor	1.2
Induced Drag Factor	1.1
Mitochondrial Inverse Power Density (m ³ /W)	1.2x10 ⁻⁶
Respiration Factor	1.1
Conversion Efficiency	0.23
Fat Energy Density (J/kg)	3.9x10 ⁷
Dry Protein Energy Density (J/kg)	1.83x10 ⁷
Protein Hydration Ratio	2.2

Minimum Energy from Protein	0.05
Maximum Life Coefficient	1.8
Planform Slope	1
B-stop	5
Gravity (m/s²)	9.81

Appendix B.

The measured groundspeed (based on theodolite values) and resultant calculated airspeeds for all recorded dunlins in OOF or transit flights.

Flight Type	Measured Groundspeed (V_g)	Calculated Airspeed (V_a)
OOF	1.58	9.22
OOF	5.76	13.31
OOF	10.19	15.33
OOF	9.58	14.72
OOF	15.81	10.68
OOF	10.42	5.31
OOF	6.60	11.73
OOF	6.59	11.73
OOF	6.86	11.99
OOF	11.90	17.02
OOF	7.60	12.72
OOF	4.90	10.02
OOF	14.69	9.56
OOF	12.38	7.27
OOF	15.27	10.18
OOF	7.07	12.19
OOF	11.62	16.73
OOF	8.55	13.68
OOF	5.32	10.45
OOF	6.15	11.28
OOF	7.05	12.19
OOF	5.98	11.12
OOF	5.37	10.51
OOF	8.02	13.16

Flight Type	Measured Groundspeed (V_g)	Calculated Airspeed (V_a)
OOF	6.06	11.20
OOF	9.18	14.32
OOF	7.17	12.31
OOF	8.25	13.27
OOF	7.43	12.46
Transit	17.29	24.01
Transit	27.83	34.21
Transit	17.01	23.33
Transit	15.95	22.01
Transit	4.90	11.49
Transit	19.54	22.93
Transit	18.49	22.12
Transit	33.50	37.03
Transit	8.49	14.62
Transit	14.55	20.97
Transit	55.66	49.28
Transit	32.78	26.48
Transit	26.79	31.93
Transit	30.07	35.19
Transit	39.60	44.69
Transit	27.37	32.42