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Original Article

Site-specific flight speeds of nonbreeding Pacific dunlins as a measure of the quality of a foraging habitat

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Many studies have investigated how foraging behavior such as prey choice varies with factors such as prey size or density. Models of such relationships can be applied "in reverse" to translate easily observed foraging behaviors into assays of habitat attributes that cannot (easily) be measured directly. One such model analyzes the speed of a forager flying between patches, where it captures prey. Faster flight shortens the travel time and hence elevates the intake rate, but is increasingly expensive. The model shows that the net intake rate is maximized at the point at which the energetic cost of flight is equivalent to the net rate of intake. Easy-to-measure flight speeds can thus be translated into hard-to-measure foraging intake rates using established flight power relationships. We studied nonbreeding Pacific dunlins (*Calidris alpina pacifica*) at 4 intertidal sites on the Fraser River estuary, British Columbia, Canada. These sites differed sufficiently that we expected food availability and hence the attainable foraging rate to differ. We measured interpatch flight speeds of dunlins foraging along the tideline within each site. The measured ground speed, calculated airspeed, and the statistically derived zero-wind effect airspeed all differed significantly between sites, matching in rank order our expectation of habitat quality based on their physical differences. Intake rate estimates ranged from 4.10 W (best mudflat) to 3.48 W (poorest). We think it unlikely that we would have been able to find such small differences using direct measures of foraging intake.

Key words: **dunlin, foraging theory, optimal flight speed, shorebird habitat quality.**

INTRODUCTION

Many studies show that foraging behaviors are flexible and adjusted to the situation currently prevailing in a habitat. Ydenberg (2007) gives a list of examples. Many of these situations (see Stephens et al. 2007) have been modeled as behavioral decisions (i.e., choices between alternatives; see Ydenberg 2010) made to maximize the rate of energy gain or some related currency. If detailed enough, models of these situations could in principle be applied "in reverse," translating easily obtained measures of behavior to make inferences about conditions that cannot be measured (or at least not easily) directly (e.g., Houston 2000). For example, Kay (2002) used the response of worker ants to experimentally offered sucrose and protein solutions to estimate the availability of these nutrients in various habitats in Arizona. Brown and Kotler (2007) (and references therein) measured "giving up densities" of foragers in various situations to infer their estimate of the habitat level of danger. Here, we use the flight speed (easily measured) of a forager to estimate its intake rate (hard-to-measure).

The ecology of avian flight has been extensively investigated (Pennycuick 1989; Hedenström 1995) with special attention paid to the "power curve"—the quantitative relationship between flight speed and the required power. This relationship is U-shaped, with power requirements increasing steeply as flight speed increases above the minimum power speed. Flight speed should thus be sensitive to energetic costs and benefits, and as such is "a behavioral attribute rich with ecological implications" (Hedenström 1995). Basic flight speed optima include the minimum power speed (V_{mp}; that with the lowest power expenditure per unit time) and the maximum range speed (V_{mr}; that with the lowest power expenditure per unit distance). These have proven useful in understanding avian flight speeds in contexts such as migration (Welham 1994), song flight (Hedenström and Alerstam 1996), and over-ocean flocking (OOF; Hentze 2012).

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Norberg (1981) (see also Houston 1986; Hedenström 1995) was the first to investigate theoretically how a forager should adjust flight speed. In the version of his model shown in Figure 1, a forager flies between patches in a habitat. Increasing the flight speed reduces travel time and therefore raises the long-term gross rate of intake. (Here, "long term" refers to that attained over many patch visits. "Gross" refers to the total metabolizable energy intake. "Net" subtracts from this the energetic expenditure required to obtain it.) Above the minimum power speed V_{mp}, faster flight is increasingly expensive, so that the extra cost eventually lowers the net rate of energy gain. As shown in Figure 1, the flight speed maximizing the long-term net rate of intake is that at which *flight power expenditure matches the long-term net rate of intake in the habitat*.

Directly measuring the intake rate of foragers in the field can be laborious, time-consuming, and subject to large errors. Diets are often varied, with food abundance and quality variable in time and space relative to the sampling scale. Furthermore, not all the food present is available to foragers, and even if availability can be taken into account, foragers may select only a portion of that on offer. Excellent and detailed examples of the effort required to measure the energy intake rates of free-living birds are provided by Blomert et al. (1996) and Zwarts (1996). Norberg's flight speed model potentially provides a way to use flight speed to assess the rate of food intake and could in many circumstances be faster, easier, cheaper, and more accurate than estimates based on observations of intake in the field. The aim of this study is to investigate this possibility by measuring the flight speed of wintering Pacific dunlins (*Calidris alpina pacifica*) at 4 intertidal foraging sites. These sites differ sufficiently that we expected food availability and hence the attainable foraging rate to differ between them. Consequently, the flight speeds of dunlins foraging on these sites are predicted to differ, specifically being higher on sites on which a higher intake rate is attainable.

METHODS

We measured flight speeds of Pacific dunlins at 4 intertidal mudflats on the Fraser River estuary in south-western British Columbia, Canada (49°10′N, 123°00′W): Boundary Bay, the "Inter-causeway" area, Roberts Bank, and Sturgeon Bank (see inset in Figure 3). These sites differ in tidal elevation, degree of enclosure by shorelines and causeways, exposure, particle grain size, organic content, and in the extent of freshwater influence from and sediment deposition by the Fraser River. Substrates consist of mud (sediment grain size < 2 μm), silt (sediment grain size 2–50 μm), and sand (>50 μm) mixtures.

The grain size distribution at these sites is strongly influenced by proximity to the Fraser River (Thomas and Bendell-Young 1999; Butler et al. 2002), the ultimate source of most of the sediment deposited on the estuary. Boundary Bay is exposed directly to the main winter storm direction and is shielded from direct Fraser River inflow by a large headland (Point Roberts). Its sediments therefore consist primarily of sand (Lovvorn and Baldwin 1996). The Inter-causeway area lies between 2 large causeways (Coal Port Jetty and Ferry Jetty), is shielded from direct river inflow, and therefore consists of sand and silty-sand substrates. This area also contains an extensive eelgrass bed (*Zostera* spp.; Lovvorn and Baldwin 1996). Roberts Bank is directly exposed to the main discharge of the Fraser River (the South Arm). Fine sediment settles along the northern side of the Coal Port Jetty, and Roberts Bank sediments consist of mud, silt, and sandy-silt (Sutherland et al. 2013). Sturgeon Bank is shielded from the South Arm outflow by the Steveston Jetty and receives outflow from the smaller North Arm of the Fraser River. Its sediments consist of silt and silty-sand.

Grain size and total organic carbon measures were derived from surface sediment samples collected at randomly selected points within 1 km of the high tide line in the area of each mudflat in which our flight speed measurements (see below) were made. Samples were collected between April 2012 and September 2013. Sample locations were generated using ArcGIS and located in the field using a handheld GPS unit. Three samples were collected within a 1 m^2 quadrat to a depth of 10 cm using a clean, stainless steel trowel, combined and thoroughly homogenized within a Ziplock bag. Samples were placed in a chest freezer and kept frozen until analyzed. All analyses were conducted by

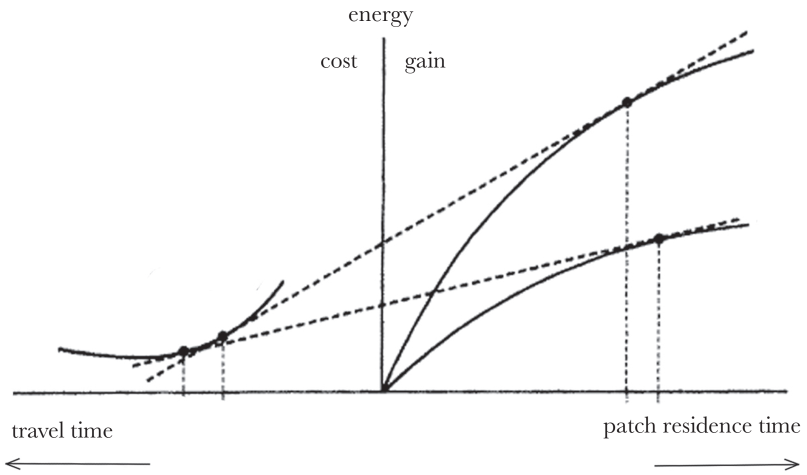

Figure 1
The predicted effect of habitat quality on the flight speed of foragers. Patch residence time increases to the right from the origin on the *x* axis, whereas the travel time between patches increases to the left (i.e., flight speed slows). The patch residence time maximizing the long-term rate of intake is defined by the well-known marginal value theorem (Charnov 1976). The long-term intake rate is higher (upper dashed diagonal) in habitats with better-quality patches (upper gain curve). Higher flight speed reduces travel time, but the energy expended is higher, as given by the height of the concave-up cost curve. The net intake rate-maximizing flight speed is attained at the point that the rate of flight power expenditure is equal to the long-term rate of gain. Flight speed should therefore be higher when habitat quality is higher. The graphical illustration is based on Hedenström and Alerstam (1995).

ALS Environmental Laboratory (http://www.alsglobal.com/en/Our-Services/Life-Sciences/Environmental/Capabilities/North-America-Capabilities/Canada/Canada-Laboratories/Vancouver-Laboratory) using standard procedures. Table 1 summarizes these data.

The physical differences between the tidal flats create differences in their infaunal compositions and densities. In general, food density for dunlins is correlated positively with sediment organic content (Yates et al. 1993), the proportion of fine sediment (Yates et al. 1993; Sewell 1996), and proximity to freshwater input (see Thomas and Bendell-Young 1999; Zharikov et al. 2009; Sutherland et al. 2013). Levings and Rafi (1978), for example, show that on the Fraser estuary, the density of tanaids (Crustacea) varies inversely with sediment grain size. Based on these considerations, we expect the quality of these 4 tidal flats for feeding dunlins to be rank ordered (high to low) as follows: Roberts Bank, Sturgeon Bank, Inter-causeway, and Boundary Bay. The data in Table 1 further indicate that Roberts Bank and Sturgeon Bank are more similar to each other than to the other 2 sites. The same is true of Boundary Bay and the Inter-causeway site. An additional feature of the latter is a large eelgrass bed, which according to Green et al. (2015) reduces its quality as a feeding site for shorebirds.

Approximately 40000 Pacific dunlins winter on the Fraser estuary and forage at these sites during the November–April nonbreeding period. The feeding habits and behavior of nonbreeding dunlins are described in Shepherd and Lank (2004), Evans Ogden et al. (2005), Ydenberg et al. (2010), and St. Clair et al. (2015). During high tide, dunlins roost or engage in OOF, and begin to feed actively as the tide begins to fall. Small flocks of dunlins (tens to hundreds) fly low (1–2 m) along the falling tide line (Jiménez et al. 2015), landing and feeding for short intervals (seconds to minutes) before flying to another patch (tens to hundreds of meters). The orientation of these interpatch flights parallels the tide line and provides a convenient opportunity to measure flight speeds. Interpatch flights are easy to distinguish from other flight modes such as OOF (Ydenberg et al. 2010; Hentze 2012), escape flights from predators, and transit flights to other sites. The latter generally occur on the rising tide (because some sites are immersed before others) and involve distances of several kilometers. Flocks in transit to other sites fly higher, gaining altitude to cross headlands and jettys.

To measure flight speeds, four 2-m-high poles were placed in a 50-m square on the mudflat, with the base parallel to and the sides perpendicular to the tide line. By sighting from shore along one pair of poles and using a video camera (Panasonic DMC-FT3, 1080p HD video; 30 frames/s) with a timer synchronized to the observer's smartphone to sight along the second pair, the travel time of a flock of dunlins flying between the 2 sets of poles could be measured from the video record. These measurements were made during the 2-h period following high tide on 44 days between 16 November 2012 and 8 January 2013. Tidal elevations of the sites differ, which in combination with short winter days and the semidiurnal tidal rhythm meant that the measurements could not always be made at each site on every high tide. The travel distance between sites permitted work at just one site on any given day, whereas the required set-up time made it more efficient to work at a site for several successive days. Accordingly, we measured sites in an irregular sequence dictated by tidal and weather conditions. Each site was visited on multiple occasions, with an observation day yielding 0–10 estimates.

Table 1

Indicators of food abundance on the 4 study mudflats

Mudflat	TOC (%)	Mud (%)	Silt (%)	Sand (%)	Salinity (‰)	N
Boundary Bay	0.28	1.3	3.2	70.1	31.9	38
Inter-causeway	0.32	2.4	11.7	41.2	31.6	62
Sturgeon Bank	0.75	9.2	55.7	9.9	15.7	33
Roberts Bank	0.95	10.1	62.9	7.6	17.9	101

TOC, total organic carbon.

We made a total of 231 flight speed measurements (Sturgeon Bank, $n = 67$; Roberts Bank, $n = 70$; Inter-causeway, $n = 23$; Boundary Bay, $n = 71$). Among these are 8 that we classed as outliers. All come from just 2 days at Sturgeon Bank and share the same flight direction. No flight speeds in the other direction were outliers. All 8 fall into a single clear group with a mean speed double that of all other measurements, separated from the others by almost 3 standard deviation. With outliers excluded, both ground and airspeeds at each site are normally distributed. The analysis reported here excludes these 8 points, but for completeness, we also report the main results if they are included.

Wind speed was recorded just prior to the start of each set of measurements using a Kestrel 2000 anemometer handheld at 1.5-m height, averaging conditions over a 2-min period. A wind vane and compass were used to measure wind direction. Track direction of a flock was estimated as the compass direction of the tide line. The ground speed (m/s) of each flock was measured by dividing the flight distance (50 m) by the travel time. Airspeed was estimated by the vector addition of ground and wind speed following the procedure described by Pennycuick (1978) (see also Alerstam et al. 1993; Hedenström 1998; Bruderer and Boldt 2001). We calculated interpatch flight (chemical) power expenditure using Pennycuick's (1978) flight program Flight 1.24. Parameter values are given in Table 2.

We estimated the accuracy of our method as follows. The video camera ran at 30 frames/s, so the time at which a dunlin flock (judged by the beak position of the lead bird) passed poles could be timed to within 1 frame or 0.033 s. We judged that the observer had about the same accuracy. With an overall average interpatch time of about 3.3 s, this is a relative measurement error of 2%. Dunlin flocks generally flew parallel to the tide line, and we excluded from analysis any that did not fly directly across our measurement field. We judged that we were unable to detect deviations smaller than 15°, which could have increased the transect length by 1.6 m, and hence introduced a further relative measurement error of up to 3.2%. We conclude that we are able to measure the ground speed of dunlin flocks to within about 5%.

Wind has contrasting effects on air and ground speeds, as birds alter speed and heading to compensate (Liechti et al. 1994): A headwind decreases ground speed but increases airspeed. We followed the procedure outlined by Hedenström (1995), plotting the airspeed against the speed increment (ground speed minus airspeed) due to wind. Airspeeds are higher with head winds (negative speed increment), producing a negatively sloped graph. We took the intercept (i.e., airspeed at zero speed increment) of a linear regression fitted to the data as an estimate of the wind-free airspeed at each site.

We used the "within subject centering" procedure described by van de Pol and Wright (2009) in a general linear model with speed increment as a covariate to compare the effects of measurement date and mudflat on ground speed and on airspeed. As chemical power expenditure was not measured directly, but calculated from the estimated airspeed, we did not test location differences in metabolic power statistically.

RESULTS

Dunlins adjusted flight speeds with wind conditions as predicted by Pennycuick (1978). Headwinds decreased ground speed and increased airspeed, whereas tailwinds had the reverse effects (see Figure 2). The reduction in ground speed due to a headwind is not completely compensated for by the increase in airspeed; ground speed diminished by 0.65 m/s (standard error [SE] = 0.148; $F_{1,221} = 35.81$, $P < 0.0001$) for each meter/second increase in heading wind speed, whereas airspeed increased by 0.35 m/s (SE = 0.148; $F_{1,221} = 10.46$, $P < 0.001$). Incomplete compensation is expected due to the steep increase in power expenditure with airspeed.

The measured ground speed, estimated airspeed and hence calculated power expenditure differ between mudflats, and follow the predicted rank order (Table 3). All are highest at Roberts Bank, followed by Sturgeon Bank, with the Inter-causeway and Boundary Bay sites ranking lowest. The mean airspeed (mean and 95% confidence interval) at each location is shown in Figure 3 in relation to the calculated power expenditure.

Table 2

Parameter values used to calculate flight power expenditure with Pennycuick's (1978) flight program Flight 1.24

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 interpatch)
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)	1.2×10^{-6}
Respiration factor	1.1
Conversion efficiency	0.23
Fat energy density (J/kg)	3.9×10^7
Dry protein energy density (J/kg)	1.83×10^7
Protein hydration ratio	2.2
Minimum energy from protein	0.05
Maximum life coefficient	1.8
Planform slope	1
B-stop	5
Gravity (m/s^2)	9.81

Sources are described in Hentze (2012).

Ground (222 degrees of freedom [df], $t = 4.241$, $P < 0.0001$) and airspeeds (222 df, $t = 3.217$, $P < 0.002$) differ significantly between the sites, as do the zero-wind effect airspeeds ($t = 4.311$, $P < 0.0001$). In post hoc testing (t-tests on ground speed), no significant differences could be detected between Boundary Bay and the Inter-causeway sites, or between Roberts Bank and Sturgeon Bank, but all pairwise comparisons between members of these 2 groups were significant. The zero-wind effect airspeed also shows a location—speed increment interaction ($t = -2.869$, $P < 0.005$), with the relation between speed increment and airspeed differing between sites (Table 4). Note that Boundary Bay, the site differing most, is oriented almost E–W, whereas the other sites are oriented almost N–S. Neither ground speed (t value with 222 df = 0.644, $P = 0.52$) nor airspeed (t value with 222 df = 0.237, $P = 0.81$) changed significantly with date.

DISCUSSION

There are consistent and significant differences among 4 tidal flat foraging sites in the interpatch flight speed of flocks of wintering Pacific dunlins. The rank order of the flight speeds matches that of our estimates of the foraging quality of the tidal flats, based on their physical characteristics. The highest flight speeds were measured on Robert Bank, which has the finest sediments, greatest organic content in its sediments, and greatest riverine input, all factors known to increase the amount of invertebrate prey that dunlin feed on (Zharikov et al. 2009). The lowest flight speeds were observed on the Inter-causeway site. Dunlins used this site after their return on southward migration, but were never observed there after December 6. This site has coarser sediments and low riverine input, and in addition has a large eelgrass bed, that we anticipated would lower its quality as a foraging site for dunlins.

We estimate that our field measures of flight speed have an accuracy of about 5%. The data appear well behaved, and both ground and airspeeds were affected by sidewinds as predicted by flight theory and documented in other contexts. The measured airspeeds all exceed our estimate of V_{mp}. Also as predicted by flight theory, dunlins engaged in OOF (measured by Hentze (2012) at Boundary Bay—see Figure 3) fly at or near V_{mp} (Hedenström and Alerstam 1996). These considerations bolster our confidence that the estimates of flight speed are reliable, that the flight theory predicting

Table 3

Flight speed and power expenditure varies between mudflats

Mudflat	Ground speed (m/s)			Airspeed (m/s)			Power (W)		
	Mean	SD	CV	Mean	SD	CV	Mean	SD	CV
Boundary Bay	14.03	4.24	0.30	14.77	3.79	0.26	3.79	0.93	0.24
Inter-causeway	14.14	3.45	0.24	13.92	2.56	0.18	3.48	0.40	0.11
Sturgeon Bank[a]	17.54	5.73	0.33	17.60	5.73	0.33	4.98	3.01	0.60
Sturgeon Bank[b]	15.77	3.20	0.20	15.90	3.49	0.22	4.01	1.07	0.26
Roberts Bank	17.16	2.64	0.15	16.46	3.12	0.19	4.10	0.96	0.23

The means, SDs, and CVs in interpatch flight speed and chemical power expenditure of Pacific dunlins at 4 locations on the Fraser River estuary. CV, coefficients of variation; SD, standard deviation.

[a] Estimates including the 8 outliers.

[b] Estimates excluding the 8 outliers.

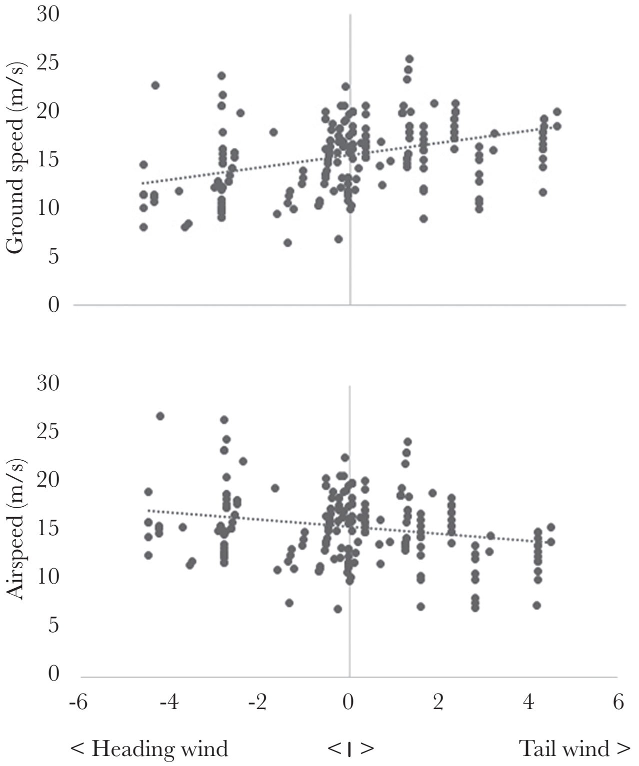

Figure 2
The effect of head and tail winds on ground (upper panel) and airspeed speed (lower panel). The effect on ground speed (slope −0.649 m/s) is larger than the effect on airspeed (0.351 m/s).

Table 4
Wind effect at each site

Mudflat	Slope	*R*	Intercept (m/s)
Boundary Bay	0.06	0.028	14.82
Inter-causeway	−0.21	0.254	13.97
Sturgeon Bank	−1.63	0.433	15.69
Robert Bank	−0.72	0.575	16.97
Overall	−0.35	0.213	15.51

The relationship between speed increment due to wind (groundspeed–airspeed) and airspeed of interpatch flights by Pacific dunlins at 4 locations on the Fraser River estuary. Given is the slope (predicted to be negative) and correlation coefficient, and the intercept (i.e., airspeed with no speed increment). Note that the intercepts closely match the mean airspeeds reported in Table 1.

the various effects is applicable, and hence that our interpretation of the flight speeds differences has a solid foundation.

As part of their study of flock structure, Major and Dill (1978) (see their Table 4) estimated dunlin flight speeds at Sturgeon Bank. Their estimate (19.8 m/s) is ~25% higher than ours (15.77 m/s; see Table 1). They used a different method (speed was determined from the positions of individual birds in successive 3D photographs), measured just 4 flocks, and did not correct for wind speed and direction. Furthermore, their measurements were made prior to the onset of foraging (Dill LM, personal communication; see their Figure 1).

Based on the estimated flight power, and applying the foraging model shown in Figure 1, our estimates of the net foraging rates on the 4 sites range from 3.48–4.10 W (Table 3). On the basis of the allometric equation reported by Bryant and Westerterp (1980), a bird species with body mass of 50 g is expected to have a foraging rate of about 8 W, with wide variation (range ~3–30 W) around the regression line at this value (see Figure 8.3 in Maurer 1996). Moreover, the estimate made here is the *net* intake rate, whereas Bryant and Westerterp's (1980) allometric equation refers to the *gross* intake rate. We conclude that our estimates of the field intake rate of Pacific dunlins are well within the range documented by Bryant and Westerterp (1980).

The theory presented in Figure 1 assumes that dunlins have an expectation of the rate of foraging intake attainable at each site, presumably built up by experience. This seems reasonable: Pacific dunlins return to their nonbreeding range in the course of October, so by the time our measures were made they had spent 1–2 months in the area. Pacific dunlins are long lived, and many individuals must therefore have spent several winters foraging on the Fraser estuary. Individual birds are site-faithful in winter, spending much of their foraging time in home ranges that occupy only a portion of a mudflat (Shepherd 2001). We assume that their estimate of the food value of these sites, as revealed by their choice of flight speed, somehow integrates all this experience.

It seems unlikely that all the members of any dunlin flock had identical foraging experiences. These (slightly) different experiences would, according to the flight speed model in Figure 1, lead them to prefer (slightly) different flight speeds. However, to maintain sufficient airspace around itself (Major and Dill 1978), each individual in a flock must fly at the same speed as the others. The observed flight speed must somehow be the outcome of social interactions between the flock's members (Couzin et al. 2005). As it integrates the experience of all flock members, the flight speed of a flock may be a good representative measure of habitat foraging quality.

Our inference that the feeding rate differs between 4 tidal flats raises the question of why the dunlins present do not all feed at the best foraging site. All the sites lie within a few minutes' flight, so any individual could easily commute to any of these sites. There are 2 possible explanations. First, individuals may be constrained from moving freely between foraging areas by territoriality, the dominance of certain age or sex classes, or some other form of despotic behavior. For example, van den Hout et al. (2014) showed that interference competition from adults forced juvenile red knots (*Calidris canutus*) to poorer and more dangerous feeding areas. We are as yet unable to assess whether this applies to Pacific dunlins, though van der Have et al. (1984) showed that among dunlins in the Dutch Wadden Sea, juveniles were over-represented in areas with low dunlin density, suggesting that they were somehow excluded from better feeding areas. An alternative hypothesis is that some other site attribute is negatively correlated with foraging rate, so that sites better in foraging terms are poorer in some other respect. One possibility is predation danger (sensu Lank and Ydenberg 2003) as demonstrated by Ydenberg et al. (2002) and Pomeroy et al. (2008). Under this hypothesis, Pacific dunlins distribute across the sites in accord with an ideal free distribution, balancing intake rates and predation danger so that fitness (rather than just feeding rate) is equilibrated across sites (Abrahams and Dill 1989).

The potential usefulness of the procedure described here is that it makes possible easy-to-obtain, accurate estimates of the rate of intake of birds in field situations. Many of the prey items consumed by dunlins on the Fraser estuary are too small to see as they are ingested, and the diet even includes some biofilm (St. Clair et al. 2015). This makes direct field measures of their rate of intake impossible. Even when individual prey items are large, visible, and handled slowly, field estimates are subject to compounding errors. For example, Ens et al.

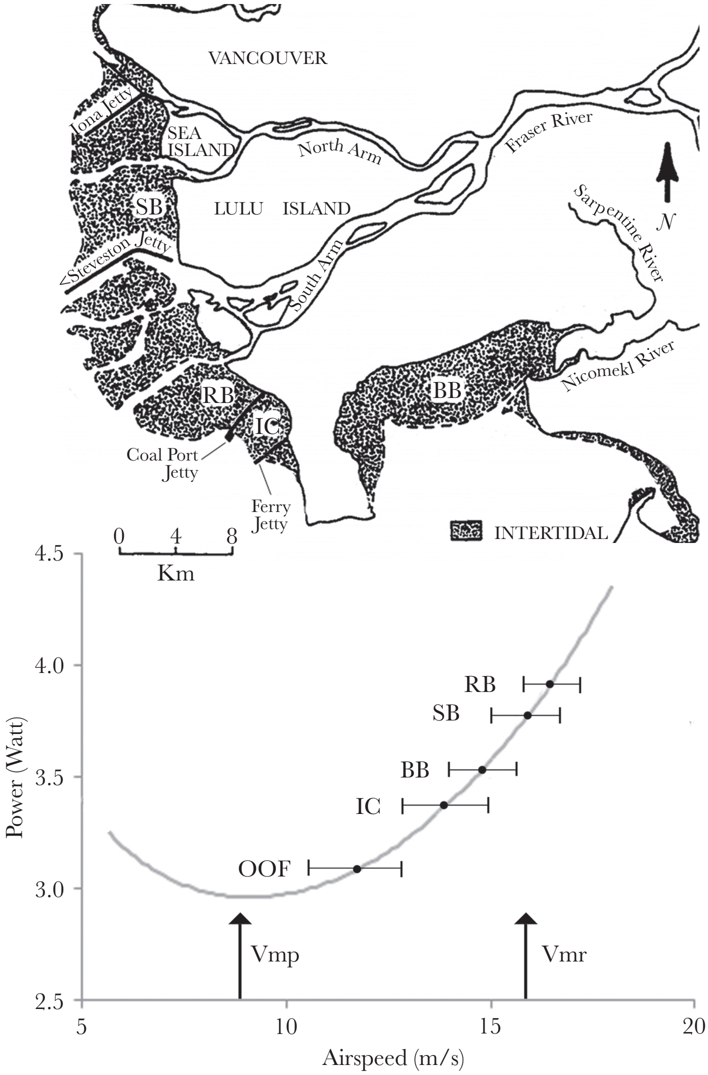

Figure 3

A comparison of the estimated power expenditure in interpatch flights at 4 foraging sites on the Fraser River estuary. The gray line is the flight power curve, calculated using Pennycuick's Flight 1.24 program (parameter values in Table 3). The minimum power (V_{mp} 9.1 m/s) and maximum range speeds (V_{mr} 15.8 m/s) are indicated below. Positioned on the power curve are the measured mean (with 95% confidence interval [CI]) airspeeds at Roberts Bank (RB), Sturgeon Bank (SB), Boundary Bay (BB), and the Inter-causeway area (IC). For comparison, we show the airspeed (mean and 95% CI) of dunlins in over-ocean flocking (OOF) at Boundary Bay (Hentze 2012), during which they are predicted to fly at V_{mp}. The inset map is modified from Lovvorn and Baldwin (1996).

(1996) estimated the intake rate of oystercatchers *Haematopus ostralegus* feeding on large bivalves (20–60 mm in length), which require handling times of 30–90 s. They measured the metabolizable energy content of prey items (varies between years and seasons) in relation to their length, estimated by eye through a telescope of the length of captured prey items, and observed the rate of prey capture (items per 10 min) in the field. Intake rate was estimated as a function of these variables, each of which has some measurement error. The total measurement error is the sum of the individual uncertainties (e.g., Baird 1995, p. 20), and is thus larger than that of each component part.

We relied here on general habitat characteristics to establish a predicted rank order of foraging quality on our 4 sites, but diel, seasonal, geographic, or weather contrasts could provide other opportunities. Further testing ideally requires a situation in which food availability can be experimentally controlled or one in which the intake rate can be directly measured. von Frisch and Lindauer (1955), for example, measured the flight speed of individually marked honey bees (*Apis mellifera*) between the hive and an experimental feeder. They adjusted the sucrose concentration and found that bees flew faster on the outbound flight when it was higher. Similarly, starling (*Sturnus vulgaris*) parents provisioning nestlings increased their flight speed between feeder and nest when food availability at the feeder collected was higher (see Table 1 in Ydenberg 1994).

Food and nutrient availability, the rate of intake, and predation danger are just a few examples of attributes of natural systems that are often difficult to measure in field situations. The idea behind this article is that basic behavioral models, if well founded, can be used to translate easily measured behavioral parameters into quantitative estimates of their value. Flight speed is useful in this regard because both its energetics and theoretical relationship with intake rate have been studied, but the basic idea is not specific to flight speed: Variation in any behavioral attribute of the journey between feeding patches that affects the rate of energetic expenditure could in principle reveal the forager's estimate of the intake rate.

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