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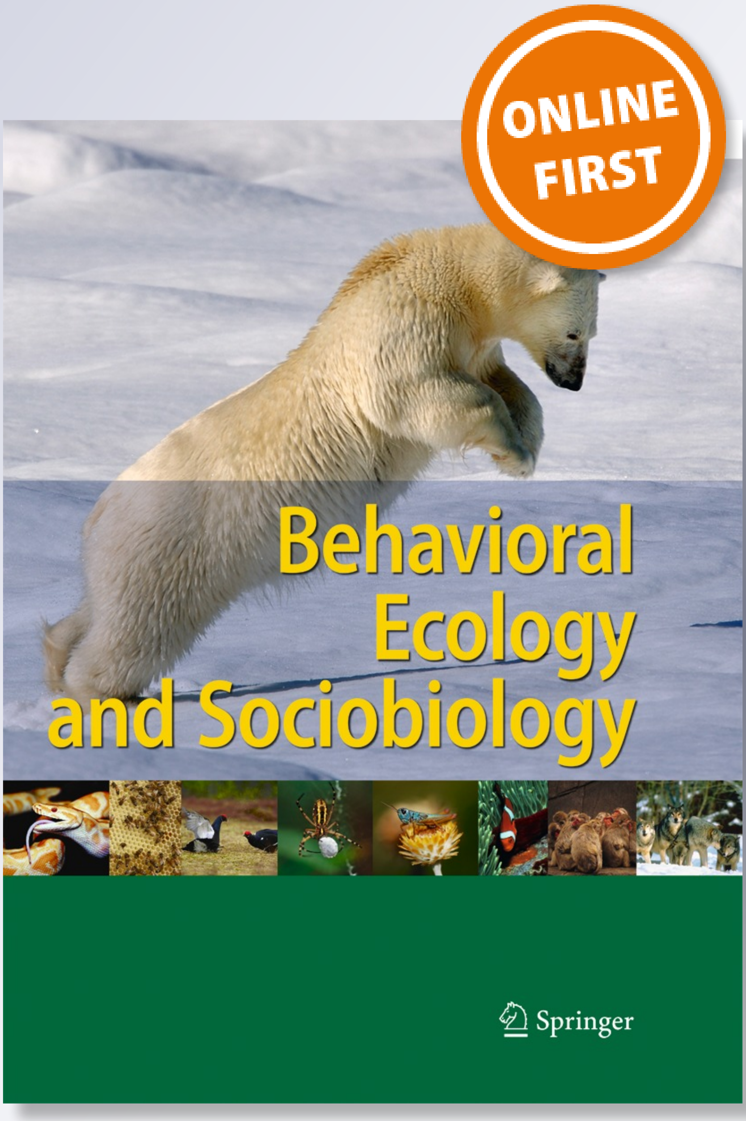

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ORIGINAL PAPER

Mortality-minimizing sandpipers vary stopover behavior dependent on age and geographic proximity to migrating predators

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Abstract Ecological theory for long-distance avian migration considers time-, energy-, and mortality-minimizing tactics, but predictions about the latter have proven elusive. Migrants must make behavioral decisions that can favor either migratory speed or safety from predators, but often not both. We compare the behavior of adult and juvenile western sandpipers *Calidris mauri* during the course of their temporally segregated passages at a major stopover site. Here, the passage and winter arrival of an important predator, the peregrine falcon *Falco peregrinus* begins near the end of the adult sandpiper passage (July) and increases rapidly through the juvenile passage (August). The mortality-minimizing hypothesis predicts that as the falcon front is distant but approaching, sandpipers should initially increase the fuel-loading rate (lowered vigilance and predator apprehension) to increase migration speed and so maintain their head start. As the falcon front gains proximity to and passes over the stopover site, sandpipers should become increasingly cautious. Our measurements show that adults decreased vigilance during the period prior to falcon arrival, and had lower vigilance overall than juveniles. Juveniles were more apprehensive, flying further and longer in response to disturbance by a falcon silhouette. This trend was reversed in response to a human approach. Both groups were more vigilant and more apprehensive in a study year with earlier falcon arrival. These results suggest that late (juvenile) and early (adult) migrants minimize mortality on migration in different ways, adults by increased migratory speed at the expense of caution on stopover sites, and juveniles by increased caution at the expense of speed.

Keywords Predation danger · Flight initiation distance · Vigilance · Predator model · Western sandpiper · Peregrine falcon

Long-distance migratory birds travel in a series of flights between stopover sites, at which fuel is acquired by foraging. While at stopovers, migrants make decisions about the amount of fuel to be loaded and the risks they are willing to take to load that fuel quickly. These decisions affect the stopover duration, migratory speed, and the exposure to danger, and hence determine the total time, energy, and danger of the migration (Alerstam and Lindström 1990). These basic attributes of migration cannot all be minimized simultaneously, and differing circumstances, life-history priorities, and the body condition of individuals can shift the strategic emphasis given to each factor (Fransson and Weber 1997; Farmer and Wiens 1999; Ydenberg et al. 2002; Pomeroy 2006; Duijns et al. 2009; Alerstam 2011). Hope et al. (2011, see their Fig. 2) portrayed stopover tactics as ranging between those favoring a slow/cautious versus a fast/risky migration. They defined a "mortality-minimizing" strategy as one that minimized the cumulative probability of mortality from all sources, and showed how the stopover tactics best serving that goal changed with circumstance, sometimes favoring speed and at other times favoring caution.

Western sandpipers *Calidris mauri* on southward migration travel from breeding grounds in Alaska to coastal nonbreeding sites that stretch from California to North Carolina to Peru

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(Franks et al. 2012, 2014). Adults depart from breeding grounds as early as midsummer, and complete a primary molt upon arrival at nonbreeding areas. Juveniles follow about a month later, with only the earliest migrants briefly overlapping on stopover areas with the latest adults. Juveniles do not molt flight feathers in their first autumn (O'Hara et al. 2002). The southward migration of western sandpipers interacts with that of the peregrine falcon *Falco peregrinus* to create spatial and temporal variation in predation danger (Lank et al. 2003; Ydenberg et al. 2007). Peregrines move southward from their northern breeding grounds in a wave (hereafter "falcon front"), resulting in a seasonal increase in danger at western sandpiper stopover sites as this wave approaches and passes over. Peregrine abundance remains higher following the arrival of the falcon front as individuals settle to spend their nonbreeding season at sites along the flyway.

Because of their early migratory departure, the first southbound adult western sandpipers are hypothesized to be sufficiently far ahead of the falcon front that they are able to migrate slowly and cautiously (see Fig. 2 in Hope et al. 2011). Later-departing migrants have a diminishing head start on the falcon front, and are predicted to shift stopover tactics toward increased migratory speed in order to remain ahead of or gain distance from the falcon front. But as the head start further diminishes and predation danger increases, stopover tactics should shift back to cautious behavior to reduce the proximate risk of predation. Hope et al. (2011) demonstrated that seasonal changes in the migratory stopover duration of both western sandpipers and semipalmated sandpipers *Calidris pusilla* are consistent with these predictions.

Here, we focus on seasonal changes in the stopover behavior of western sandpipers at their first major southbound stopover site, the Fraser River Delta in British Columbia. During the course of southward passage, we measured the proportion of time spent vigilant, and the response and flight initiation distance to two types of disturbance (peregrine silhouette and human). Each of these behaviors can be interpreted as indicating the emphasis placed on safety versus feeding (Ydenberg and Dill 1986; Elgar 1989; Alerstam and Lindström 1990). Vigilance increases predator detection (Sansom et al. 2009), but typically lowers the refueling rate (Elgar 1989). The Fraser River Delta has previously been well studied with respect to predation danger for sandpipers. Peregrine falcons and merlin use vegetation and the dyke system along the shoreline as cover for predation attempts on foraging shorebirds, leading to a strongly increasing gradient in predation danger towards the shore (Dekker and Ydenberg 2004; Pomeroy 2006; Pomeroy et al. 2006). Long reaction distances to approaching predators (Ydenberg and Dill 1986) and long escape flights after take-off (Nebel and Ydenberg 2005) increase safety, but at the expense of feeding opportunity. False-positive antipredator reactions result in lost foraging opportunities, but may increase the likelihood of survival for true attacks (Haftorn 2000). Each of these measures reflects a component of the emphasis placed by migrants on a fast versus a safe migration. Migrants prioritizing higher migratory speed should have lower levels of vigilance, choose higher food abundance, but possibly more dangerous feeding sites, and reduce flight initiation distances to an approaching predator.

Since adult western sandpipers migrate under safer circumstances (ahead of the peregrine front) than do juveniles (under the falcon front), they should favor tactics for speed, and increasingly so as the season progresses. In contrast, juveniles should favor tactics for caution. When the age groups overlap on stopover sites, adults should exhibit behavior that is more speed-oriented than that of juveniles because only adults must complete a molt following migration (Hedenström and Sunada 1999; Lank et al. 2003; Sansom et al. 2009). Since molting compromises their escape ability, adults should place an extra premium on speed in order to complete migration and molt prior to arrival of migrant falcons at their molting areas. While age-specific behavior and decisions can be driven by experience or physiological differences (Marchetti and Price 1989; Caro 2005; Stein and Williams 2006), we also make specific predictions for trends in behaviors within age groups and between years based on changing predation danger regimes.

Finally, we take advantage of phenological differences between years to test additional predictions about the relationships between predation danger and behavior at a stopover. The timing of peregrine arrival at the Fraser estuary stopover sites is advanced much more by weather conditions (snowmelt) on breeding grounds than is that of western sandpiper arrival (Niehaus and Ydenberg 2006). Therefore, years with early snowmelt have higher peregrine abundance by a given date, making migration overall more dangerous for sandpipers. We predict that the balance of tactics will shift toward greater caution in earlier snowmelt years.

Methods

Data were collected between 1 July and 10 September in 2007 and 2008 at Boundary Bay on the Fraser River Delta, British Columbia (49°4′N 122°58′W). Boundary Bay consists of a large sandy tidal flat, approximately 60 km^2 at low tide (Pomeroy 2006), which is relatively safe for migrating sandpipers (Ydenberg et al. 2002). The Fraser River delta and other estuarine sites in the Pacific Northwest are the first major stopover points for southbound western sandpipers, following a ~2,400 km direct flight over the Gulf of Alaska. Adult passage is predominantly in July and juveniles pass through in August and early September (Butler et al. 1987). Each individual migrant spends only a few days at the site before moving onwards; however, the stopover length can vary throughout the migratory period (Hope et al. 2011). Peregrine falcon numbers in the region increase sharply from late July (Lank et al. 2003), with some variation in the timing of their arrival between years, which is predictable from the timing of arctic snowmelt (Niehaus and Ydenberg 2006).

Vigilance

The proportion of time spent vigilant by individual migrants was measured. A flock was initially approached to approximately 50 m, and environmental- and flock-specific parameters were recorded. After waiting a minimum of 5 min to lessen potential influences of the initial approach, a focal individual was chosen haphazardly from the flock and identified as "juvenile" or "adult", based on plumage (Franks et al. 2014). Each bird was observed until it departed or for up to 2 min using a 45×60 spotting scope, during which time the total amount of time the bird spent vigilant was measured with a stopwatch. Vigilance was scored when the individual's beak was parallel to the ground (Pomeroy 2006). An observation was included in the final analysis if it lasted 30 s or longer. The procedure was repeated up to twice more on other individuals in the flock, taking care that the same individuals were not sampled twice.

Flight initiation distance to human approach

Upon completion of vigilance observations, flight initiation distance (FID) was measured on a bird in each flock. The FID test was started no less than 10 min after the observer's arrival. A bird was haphazardly selected with a scope and then located visually, and approached on foot at a constant rate of 0.5 m/s, a rate used in previous FID studies (Frid and Dill 2002; Blumstein 2003; Cooper 2005). Visual contact was maintained with the focal bird until escape flight was initiated. The time from the initiation of approach until the bird flew was recorded using a stopwatch. The observer's location and the bird's site of escape flight were marked using a GPS unit, and the initial distance to the bird (starting distance) and FID later calculated. FID was measured only once per day on a given flock unless at least 1 h had passed since the flock was last disturbed, and the flock size was large enough (>500) to eliminate the possibility of testing the same individual twice.

Response to falcon silhouette

We created a fiberglass silhouette of a falcon mounted on an arrow. The design mimicked the shape and size of a small peregrine falcon or large merlin in flight (see Online resource Fig. S1). This silhouette was shot from a bow, and sandpiper responses recorded. We experimented with the design until the arrow consistently flew ~10 m before flipping and falling in a manner resembling a diving falcon. Reactions to the arrow ranged from escape flights resembling those made in response to live peregrines to apparent indifference. We intended the silhouette to be similar but not identical to an actual falcon, thereby eliciting a "false alarm" response by some, but not all sandpipers. Some flocks scrutinized the flying silhouette before determining that it should be ignored while others started and fled in a manner resembling that of flocks pursued by a real falcon. The exposure to the falcon silhouette is not intended to mimic a falcon attack or elicit a full antipredator reaction from the sandpipers, but it is likely that anything slightly related to the shape and movement of a peregrine attack should create a stronger response than that from a human approach.

Flocks were chosen opportunistically and approached to within approximately 50–100 m. The experimenter's location was marked on a GPS unit, and the silhouette fired towards the flock. The flight duration of the flock was recorded. Once the flock landed, the original and landing locations were marked using the GPS instrument. The distance from the birds at firing and the straight-line distance flown were later calculated from these data. The procedure was not repeated on a day unless it could be determined that a later flock had not been previously been exposed to the falcon silhouette.

Spatial usage

Food abundance and predation danger at the study site have previously been shown to be highest close to shore and decrease with distance from the shoreline and cover (Dekker and Ydenberg 2004; Pomeroy 2006). Spatial usage of the tidal flat was quantified by counting sandpiper droppings, following the methodology of Pomeroy (2006). A permanently situated 1,000-m transect was run perpendicular to the salt marsh and shoreline, starting at the edge of the salt marsh. Points to 600 m were marked at 50 m intervals and at 100 m intervals beyond this. The transect was walked daily at low tide to record dropping density. At each marker, fifteen 1 m^2 quadrats were randomly laid down, and the number of western sandpiper droppings with at least part of their area inside each was counted.

Data analysis

The analyses focused on testing for differences within seasons, and between age groups and years as patterns of interest with respect to differences in their responses to predation danger. Additional environmental or other covariates were included where relevant. For all analyses except vigilance, only dates known to be within exclusively the adult or juvenile migration period were included (Butler et al. 1987). The short period of time where the age groups overlapped was excluded.

Vigilance

We used an information-theoretic approach to examine the importance of age and predation danger on the proportion of time vigilant (Burnham and Anderson 2002). We generated 30 candidate models from a set of variables relevant to the hypothesis (age, day of year, and year), plus those shown previously to influence vigilance, but which were not part of the hypotheses being tested ("BASE" variables). The BASE variables included distance to cover from the bird, estimated flock size, position of the focal bird in the flock, distance from the observer to the bird, and a measure of the density of the flock (see Online resource Table S1 for details; Elgar 1989; Pomeroy 2006; Fernández and Lank 2010; Beauchamp 2013). Interactions between BASE variables were examined post hoc to the initial analysis and were only added to the previously top model due its overwhelming support from the data (see Online resource Table S4 for these initial model weights). Variables were examined for covariance before inclusion in the analyzed models (Pearson's $r<0.40$ for all variables when compared). A multicollinearity analysis was also run on the global model for the vigilance, FID and falcon silhouette analyses, and all variables other than age, date, and their interaction term had variance inflation factors of less than 10.

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

Flight initiation distance to human approach

For the FID analysis, 27 candidate models were constructed to test the influence of age, day of year, and year and control for starting distance and the BASE variables, which include the tidal state, wind strength, distance to cover, flock size, and flock density (see Online resource Table S2 for details; Elgar 1989; McGowan et al. 2002; Blumstein 2003; Pomeroy 2006).

Generalized linear models were run in SAS© 9.1 using the "proc genmod" procedure (SAS© Institute 2005). FID models were run using a normal distribution with a log link function. Model selection, averaging, and parameter estimation followed similar procedures as the vigilance data.

Response to falcon silhouette

Nine flight time and 16 landing distance candidate models were constructed to test the influence of age, day of year, and the interactions between them on time in flight and distance flown. We also included the distance to the bird at firing and a measure of the cloud cover in the models. Parameters used to generate flight response models are described in Online resource Table S3. Firing distance was included in all models except the null. Both flight time and distance flown were normalized using $\log_{10}(x+1)$ transformations. Linear models were run in R (version 2.10.1, The R Foundation for Statistical Computing 2008) using the "linear model" procedure. Flight distance and time were analyzed separately, and model selection and parameter estimation followed similar procedures as the vigilance data. However, AICc values were used instead of QAIC_c values.

Spatial usage

To control for variation in duration of tidal exposure across the mudflat, raw dropping counts were divided by the number of 1-m^2 quadrats and the number of minutes that that the flat area had been exposed using tidal data (Fisheries and Oceans Canada, Tsawwassen). The resulting droppings/m^2/min of exposure gives a measure of the intensity of usage for that day. This allows us to separate decisions made by migrants from areas where they are forced to feed because of tidal height. In addition, some areas close to shore are not flooded by up to 72 h during the summer, and this method removes that bias from our counts. We controlled for the total intensity of foraging across the mudflat for each day by calculating the proportional intensity of droppings at each distance from cover. This gave a value between 0 and 1 for each distance for each date. The means of these daily proportions were calculated for each age and year group. R (version 2.10.1, The R Foundation for Statistical Computing 2008) was used to run a two-sample Kolmogorov-Smirnov goodness-of-fit test (Zar 1999) to compare adult versus juvenile distributions of proportions of droppings with distance from cover. Time periods when both age groups were present were not included in this analysis. All means are presented±standard error (SE) unless otherwise noted.

Results

Vigilance

The proportion of time spent vigilant by sandpipers varied between 0.00 and 0.93 with a mean of 0.049±0.002 (n= 781). The model that initially received nearly all of the support from the data included all of the BASE variables, age, day of year, day of year squared, year, and the interactions of age with both day of year and day of year^2 (ω_i=0.996). Little support was shown for any of the other models (see Online resource Table S4). When the interaction terms with age, distance to cover, and tide were included in the model set, the top model included the age and distance to cover term (ω_i=0.392), with support for the model that included the interaction with tide as well (ω_i=0.365). Support for the previously top model fell, but there was still substantial support for it (ω_i=0.217; see Table 1).

Weighted parameter estimates and unconditional standard errors show higher vigilance in 2007 than 2008, with onshore than with offshore wind in smaller flock sizes, closer to shore, on the edge rather central position in flocks and for juveniles over adults (Table 2). The influences of tidal position, cloud cover, distance to bird, and nearest neighbor were minimal because the unconditional SE of the effect size crossed 0, though the interaction between tidal position and distance to shore showed a stronger effect.

In adults, vigilance was highest early in migration and declined quadratically with date (Fig. 1). In juveniles, vigilance was higher than in adults, even during the short period when the two age classes overlapped in time and varied less throughout the migratory period.

The pattern of vigilance with distance to cover varied depending on the tidal state. On outgoing tides, vigilance declined with distance from cover. On incoming tides, vigilance remained consistently high. There was not a strong difference in these patterns between age groups (Fig. 1).

FID to human approach

FID to human approach varied between 5 and 89 m with a mean (±SE) of 19.59±0.97 m (n=180). The top-supported model included the BASE variables plus age and year with moderately strong support for models including date, and age and date as well as the BASE variables and year (Table 3). The top model received over three times the support of the next model (Δ_i=3.17). The sum of all Akaike weights of models containing the BASE, year, and age variables were 0.98, 0.85, and 0.87, respectively, suggesting these variables influenced FID. Weighted parameter estimates and unconditional standard errors are described in Table 2. FID was greater in adults, in 2007, when approached from a farther starting distance, on an outgoing tide, when wind was low, in large flocks, further from shore, and in less dense flocks. The influence of day of year, wind strength, and all interactions of age, date, and year was minimal. Figure 2 shows the model average predictions for age, date, and year with the daily means of the data and associated SEs.

Response to falcon silhouette

The time in flight after a disturbance from exposure to a falcon silhouette varied between 0 and 134 s, with an average (±SE) of 26±3 (n=63). The model with the most support from the data included the variables firing distance, cloud cover, and age (ω_i=0.46; r^2=0.32). Substantial support was also found for models that included the date term (ω_i=0.16; r^2=0.30) and age and date terms (ω_i=0.13; r^2=0.32). The null model had no support from the data (ω_i=0.00) (Table 4). Flight time decreased with greater firing distance, was higher in juveniles (Fig. 3), and with greater cloud cover. Age, date, date^2, and their interaction may not have strong effects as the unconditional standard error of their effect sizes crossed 0 (Table 2).

Table 1 Support for models predicting proportion of time spent vigilant by migrating western sandpipers at Boundary Bay. BASE parameters are those listed in Table 2 that are not related to mortality-minimizing predictions (not age, date, or year). Global model includes all parameters and interactions included in other models. See Online resource Table S1 for a description of analysis parameters. The number of parameters (K) included three extra values as Akaike's information criterion adjusted for small sample size and overdispersion (QAIC$_c$) values were used. A $\hat{c}$ of 1.0303 was used in calculating QAIC$_c$ values to correct for overdispersion. log(L) is the log-likelihood value, Δ_i is the difference in QAIC$_c$ value from that of the top model (i.e., lowest QAIC$_c$), and w_i is the Akaike weight; n=781 observations. McFadden's R^2 are listed to show improvement of model fit between null and fitted model; n=781 observations. Except for the null model, only models with Δ_i<10 are shown (see Online resource Table S4 for complete list)

Model	Log(L)	K	Δ_i	w_i	R^2
BASE age date date^2 year age×date age×date^2 D2C×age	−509.17	21	0.00	0.39	0.20
BASE age date date^2 year age×date age ×date^2 D2C×age×tide	−508.16	22	0.14	0.37	0.20
BASE age date date^2 year age×date age×date^2	−510.87	20	1.19	0.22	0.19
Global	−507.64	25	5.54	0.02	0.20
Null	−633.98	3	205.09	0.00	0.00

[a] Top model; QAIC$_c$=1,031.62

Table 2 Parameter likelihoods, model-averaged parameter estimates and associated unconditional standard errors (SE) "estimate±SE (parameter likelihood)" for proportion of time spent vigilant, flight initiation distance in response to human approach, and flight time and landing distance in response to falcon silhouette by migrating western sandpipers at Boundary Bay. Nominal parameters listed are additive above those included in the intercept. Parameter values of "age" for vigilance and flight initiation distance show the effect size for adults, while for the falcon silhouette responses it shows the juvenile effect size. Parameter estimates for vigilance and FID are in $\log_{10}$ scale. Day of year is the day number after day number 180

Parameter	Vigilance[a]	Flight initiation distance[b]	Flight time[c]	Landing distance[c]
Intercept	−0.3307±0.5904 (1.00)	2.5040±0.2830 (1.00)	1.4389±0.2651 (1.00)	1.4450±0.7328 (1.00)
Age	−0.6054±0.5961 (1.00)	0.2920±0.1920 (0.87)	0.3083±0.3607 (0.71)	1.0860±1.7815 (0.83)
Day of year	−0.049±0.0232 (1.00)	0.0000±0.0034 (0.50)	0.0134±0.0354 (0.49)	0.1127±0.1907 (0.76)
Year 2007	0.1472±0.046 (1.00)	0.1782±0.1260 (0.85)		
Day of year by age	−0.0482±0.028 (1.00)	−0.0009±0.0023 (0.09)	−0.0107±0.1571 (0.08)	−0.1204±0.2635 (0.46)
Day of year^2	0.0005±0.0002 (1.00)		−0.0005±0.0035 (0.16)	−0.0070±0.0117 (0.48)
Day of year^2 by age	0.0015±0.0004 (1.00)		0.0005±0.0105 (0.05)	0.0069±0.0126 (0.39)
Adult in 2007	0.0072±0.0172 (0.02)	0.0162±0.0374 (0.06)		
Day of year in 2007	0.0001±0.0003 (0.02)	−0.0003±0.0009 (0.07)		
Day of year for adult in 2007	−0.0002±0.0004 (0.02)	−0.0002±0.0005 (0.01)		
Incoming tide	−0.0318±0.0537 (1.00)	−0.1921±0.0948 (0.98)		
Onshore/offshore wind	−0.0034±0.0021 (1.00)	−0.0045±0.0053 (0.98)		
CC—mainly clear	0.0535±0.0449 (1.00)		−0.0483±0.1389 (1.00)	−0.0094±0.2178 (0.42)
CC—partially cloudy	0.0126±0.0469 (1.00)			
CC—mostly cloudy			−0.0388±0.1122 (1.00)	0.0129±0.1766 (0.42)
CC—cloudy or rain			−0.6419±0.1710 (1.00)	−0.2983±0.5022 (0.42)
Flock size <20 birds	0.2543±0.1038 (1.00)	−0.1776±0.2770 (0.98)		
Flock size 20–200 birds	−0.0215±0.0383 (1.00)	−0.2520±0.0918 (0.98)		
Nearest neighbor	0.0085±0.0166 (1.00)	−0.0598±0.0391 (0.98)		
Distance to bird/starting distance	0.0004±0.0007 (1.00)	0.0063±0.0009 (1.00)	−0.0077±0.0031 (1.00)	−0.0037±0.0071 (0.42)
Position of bird—edge	0.0761±0.0363 (1.00)			
Distance from cover	−0.0005±0.0001 (1.00)	0.0002±0.0001 (0.98)		
Distance from cover—incoming tide	0.0005±0.0002 (1.00)			
Distance from cover—adult	0.0002±0.0002 (0.78)			
Distance from cover—adult—incoming tide	−0.0001±0.0002 (0.39)			
Scale	0.4644±0.0118 (1.00)	10.2000±0.0548 (1.00)		

[a] Reference groupings for vigilance include:juveniles, outgoing tidal position, cloudy, birds in the middle of a flock, flocks larger than 200 birds, and 2008

[b] Reference groupings for FID include for juveniles, outgoing tidal position, flocks larger than 200 birds and 2008

[c] Reference groups for response to falcon silhouette include adults and zero cloud cover

The landing distance of the flock of sandpipers after a disturbance trial varied between 0 and 800 m with an average (±SE) of 135 m±20 (n=91). The best supported model included age, date^2, and the interaction between the two (ω_i= 0.36; r^2=0.26). Substantial support was found for a model that included firing distance, cloud cover, and age (ω_i=0.18; r^2= 0.24). Some support also found many of the other models (Table 5), but not the null (ω_i=0.01). Weighted parameter estimates showed that flight distance was farther in juveniles than adults and decreased with firing distance. The distance flown decreased throughout the migratory period for both groups (Fig. 4). However, the unconditional standard errors of the effect size of all variables crossed 0 (Table 2).

Spatial usage

Dropping counts varied between 0 and 69 droppings per 15 quadrats with an average (±SE) of 3.3±0.2 (n=1075). The daily relative dropping intensity at a particular distance to cover varied between 0 and 1 with a mean (±SE) of 0.078± 0.005. There was a trend for adults to have slightly higher dropping intensity closer to shore, but the distribution of proportion of droppings/m^2/min did not differ significantly between adults and juveniles in either year (Fig. 5; Kolmogorov–Smirnov test (KS); 2007: D=0.31, N=13, P>0.10; 2008: D=0.23, N=13, P>0.20). The peaks of usage were slightly further from cover for both adults and juveniles in

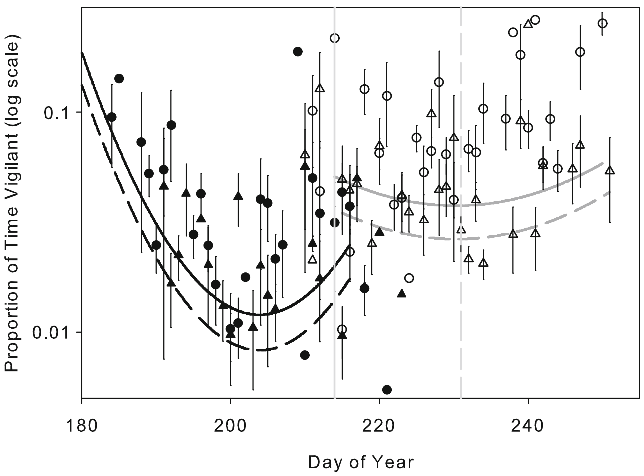

Fig. 1 Weighted model outputs for proportion of time vigilant with day of year, n=781. The *points* represent averages with SE for each day for adults (*solid*) and juvenile (*open*) in 2007 (*circles*) and 2008 (*triangles*). The *lines* are adult (*black*) and juvenile (*gray*) vigilance levels in 2008 (*dashed*) or 2007 (*solid*) as predicted by the weighted parameter estimates from an AIC analysis. *Gray vertical lines* indicate predicted 50 % falcon arrival dates for 2007 (*solid*) and 2008 (*dashed*) (Niehaus and Ydenberg 2006)

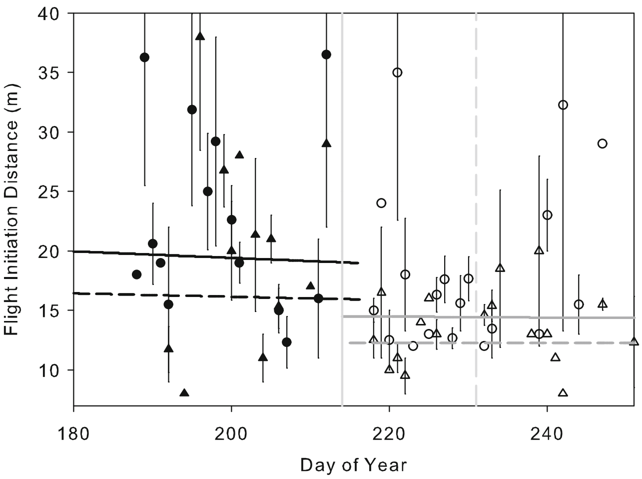

Fig. 2 Weighted model outputs for flight initiation distance with day of year. The *points* represent averages with SE for each day for adults (*solid*) and juvenile (*open*) in 2007 (*circles*) and 2008 (*triangles*). The *lines* are adult (*black*) and juvenile (*gray*) vigilance levels in 2008 (*dashed*) or 2007 (*solid*) as predicted by the weighted parameter estimates from an AIC analysis. *Vertical lines* indicate predicted 50 % falcon arrival dates for 2007 (*solid*) and 2008 (*dashed*) calculated based on values from Neihaus and Ydenberg (2006)

2007 than in 2008 (250 m compared with 200 m). There was no difference between years within adults (KS test: D=0.31, N=13, P>0.10) or juveniles (KS test: D=0.31, N=13, P>0.10). Pooling the years does not make a difference in the result between age groups (KS test: D=0.23, N=13, P>0.20).

Table 3 Support for models predicting flight initiation distance by migrating western sandpipers at Boundary Bay; n=180. BASE parameters are those described in Table 2 that are not related to mortality-minimizing predictions (not age, date, or year). Global model includes all parameters and interactions included in other models. See Online resource Table S2 for a description of analysis parameters. A $\hat{c}$ of 1.0909 was used in calculating QAIC$_c$ values to correct for overdispersion. McFadden's R^2 are listed to show improvement of model fit between null and fitted model. Except for the null model, only models with Δ_i<10 are shown (see Online resource Table S5 for complete list)

Model	Log(L)	K	Δ_i	w_i	R^2
SD BASE age year[a]	−672.69	12	0.00	0.41	0.06
SD BASE age date year	−672.68	13	2.31	0.13	0.06
SD BASE date year	−674.25	12	2.87	0.10	0.06
SD BASE age	−675.71	11	3.24	0.08	0.06
SD BASE age date year age×date	−672.10	14	3.61	0.07	0.06
SD BASE age date year date×year	−672.13	14	3.66	0.07	0.06
SD BASE age date year age×year	−672.30	14	3.97	0.06	0.06
SD BASE age date	−675.71	12	5.53	0.03	0.06
SD BASE date	−677.13	11	5.85	0.02	0.06
SD BASE age date age×date	−674.94	13	6.45	0.02	0.06
SD year age	−684.45	6	8.19	0.01	0.05
SD BASE year	−678.47	11	8.30	0.01	0.05
Global with BASE	−670.76	17	8.38	0.01	0.06
Null	−716.87	3	61.27	0.00	0.00

[a] Top model, QAIC$_c$=1,259.14

Discussion

Under the mortality minimizing hypothesis, migrants that face a seasonal increase in predation danger should vary their tactics based on their proximity to the falcon front. We looked

Table 4 Support for models predicting flight time by migrating western sandpipers in response to exposure to falcon silhouette at Boundary Bay; n=63 observations. See Table 3 for an explanation of parameters used. All models except the null include cloud cover (CC) and firing distance (FD) parameters. Global model includes all parameters and interactions included in other models. SSE is the sum of squared error of each model, and R^2 is the multiple regression correlation coefficient. See Online resource Table S3 for a description of other parameters

Model	SSE	K	Δ_i	w_i	R^2
Age[a]	12.594	7	0.00	0.46	0.32
Date	13.013	7	2.06	0.17	0.30
Age date	12.575	8	2.54	0.13	0.32
Date date^2	12.789	8	3.60	0.08	0.31
Global	11.319	11	4.42	0.05	0.39
CC+FD	14.125	6	4.69	0.04	0.24
Age date date^2	12.560	9	5.19	0.03	0.32
Age date age×date	12.574	9	5.26	0.03	0.32
Null	18.521	2	12.46	0.00	

[a] Top model, AICc=−87.42

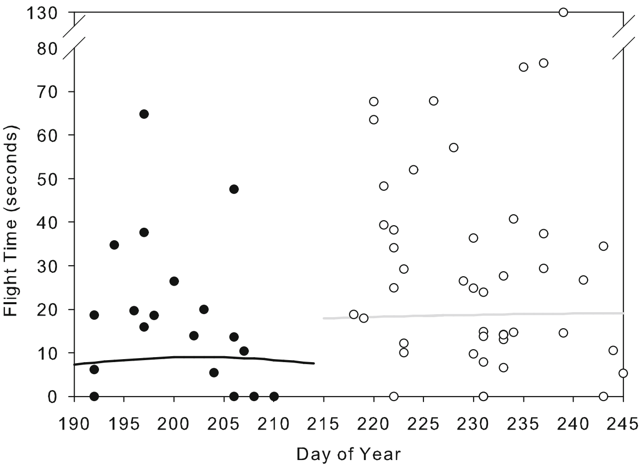

Fig. 3 Weighted model outputs for flight time in response to disturbance by a falcon silhouette, $n=63$. The *points* represent the data for adults (*solid*) and juvenile (*open*). The *lines* are adult (*black*) and juvenile (*gray*) flight times as predicted by the weighted parameter estimates from an AIC analysis

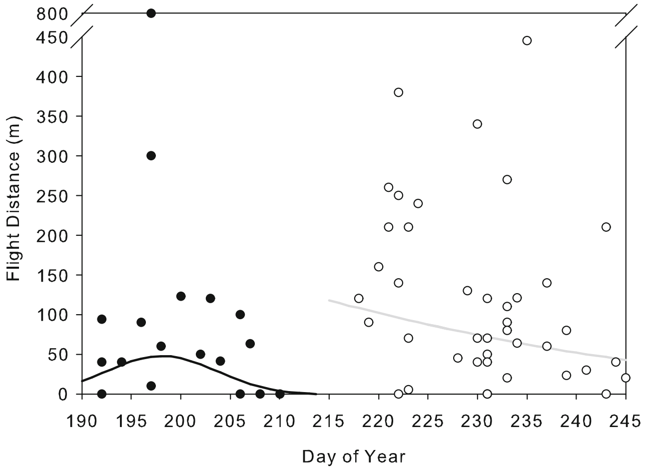

Fig. 4 Weighted model outputs for flight distance in response to disturbance by a falcon silhouette, $n=62$. The *points* represent the data for adults (*solid*) and juvenile (*open*). The *lines* are adult (*black*) and juvenile (*gray*) flight distances as predicted by the weighted parameter estimates from an AIC analysis

at a large stopover site with an annual seasonal pattern of relatively low predator abundance during the adult migration and a rapid increase in peregrine falcon abundance during the juvenile migratory period. We predicted that throughout the adult migration, migrants would increasingly choose behaviors that increased migration speed to stay ahead of their predators, while juveniles would make decisions that increased their safety at a cost to migration speed. Patterns of vigilance and the response to a visual stimulus suggest

Table 5 Support for models predicting landing distance by migrating western sandpipers in response to disturbance by a falcon silhouette at Boundary Bay; $n=62$ observations. BASE variables include the cloud cover (CC) and firing distance (FD) parameters. See Table 3 for an explanation of all parameters used. See Online resource Table S3 for a description of other parameters

Model	SSE	K	Δ_i	w_i	R^2
Age date date^2 age × date age × date^{2a}	30.205	7	0.00	0.36	0.26
BASE age	30.887	7	1.38	0.18	0.24
Age date	35.582	4	2.79	0.09	0.13
BASE age date	30.29	8	2.82	0.09	0.26
Age date age×date	34.811	5	3.80	0.05	0.15
Age date date^2	35.176	5	4.44	0.04	0.14
Age date date^2 age × date age × date^2	27.209	11	4.73	0.03	0.33
BASE date	32.622	7	4.77	0.03	0.20
Age	38.258	3	4.99	0.03	0.06
BASE age date age×date	30.238	9	5.46	0.02	0.26
BASE age date date^2	30.286	9	5.55	0.02	0.26
BASE	34.542	6	5.77	0.02	0.15
BASE date date^2	31.958	8	6.14	0.02	0.22
Null	40.739	2	6.68	0.01	
Date	40.287	3	8.20	0.01	0.01
Date date^2	39.933	4	9.94	0.00	0.02

[a] Top model, $AIC_c=-30.28$

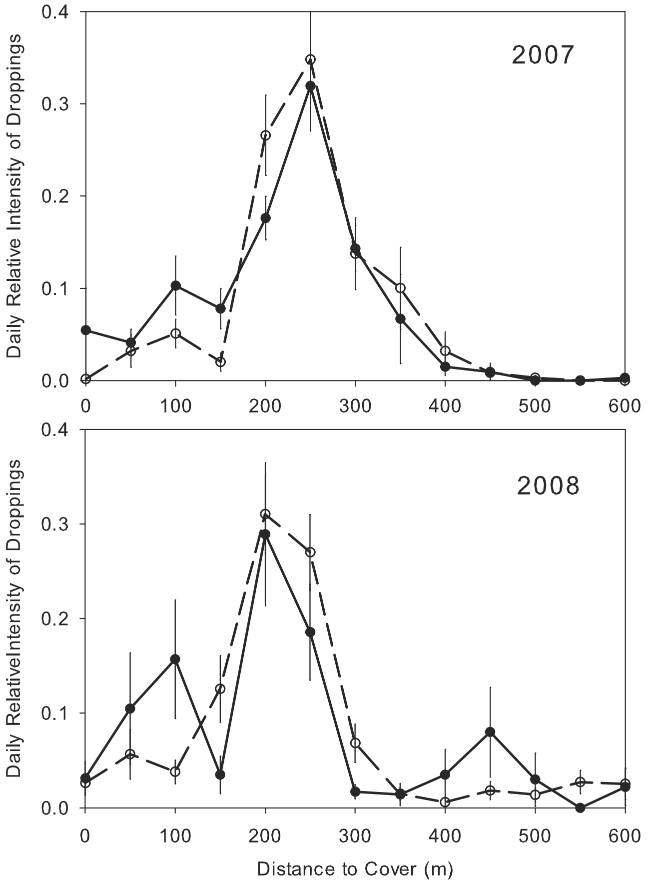

Fig. 5 Average values of relative dropping intensity with SE for each distance from cover in 2007 and 2008. Adults are *solid lines* and juveniles are dashed

juveniles are, as predicted, placing overall higher priority towards safety than the earlier migrating adult western sandpipers. Compared to adults, juveniles were more vigilant (Fig. 1), and made longer (Fig. 3) and farther (Fig. 4) escape flights in response to disturbance by a falcon model. For the brief period that the two age classes overlapped, which controls for variation in other environmental conditions, adults were less vigilant than juveniles, providing more time for foraging, which could increase migration speed.

The temporal pattern of vigilance within adult migration suggests a shift by adults toward increased migration speed at the expense of caution. Not only were adult sandpipers less vigilant overall than juveniles, their vigilance level generally dropped during the course of passage. Reduced vigilance could allow for higher refueling rate, which could increase migratory speed by shifting the optimal departure time earlier or increasing the optimal departure fuel load. Higher fuel load at departure allows for longer flights between stopovers and provides the potential to skip sites. Due to the acclimation period required upon arrival at a stopover period, making fewer stops increases the speed of migration (Alerstam and Lindström 1990). Hope et al. (2011) found that the duration of stopover increased in the course of adult passage, which could increase overall migration speed by decreasing the number of total stopovers along the migration route. Juveniles showed the opposite pattern with stopover length decreasing through juvenile passage, which could decrease the overall speed of migration due to having to make additional stopovers to reach their nonbreeding sites (Alerstam and Lindström 1990). Our results provide further support for use of this tactic.

We predicted that migrants would behave more cautiously in the more dangerous year of 2007 due to interannual variation in timing of peregrine migration. The timing of peregrine passage at Boundary Bay is earlier relative to sandpiper passage in years with early springs (Niehaus and Ydenberg 2006). The timing of snowmelt on breeding areas in Alaska was 2 weeks earlier in 2007 (day of year 115) than in 2008 (day 130; long-term average mean day of year is 125). Based on these dates, peregrine passage should have been about 16 days earlier in 2007, but sandpiper migration timing unchanged, making conditions overall more dangerous for earlier migrating sandpipers in 2007 than in 2008. Consistent with this, both adult and juvenile western sandpipers were more vigilant in 2007 than in 2008. Variation between years in flight initiation distance also was supported from the data, but the strength of the effect size was minimal. Our ability to predict the direction of differences between years of study using the same mortality-minimizing framework used to make other predictions provides further support for our general hypothesis. However, these interannual differences may have arisen from an unmeasured attribute of the system, and with only 2 years of study, our ability to make inferences about the year effect is limited.

The general distribution of feeding time across the tidal flat was consistent with that found by Pomeroy (2006), but contrary to our prediction there was no significant difference in this apparent tradeoff between age groups or years. The peak of the feeding distribution was shifted slightly (~50 m) further away from shore in the relatively dangerous year 2007, but the overall distribution was not different from 2008. Taylor et al. (2007) previously showed that the distribution of feeding time across the flat is sensitive to the danger posed by peregrines, but we did not see similarly strong variation within or between years. Although Pomeroy (2006) found no difference in food abundance at this site between years, subtle changes in food distribution could also have affected or masked tradeoffs sandpipers made between years

A result we did not predict was that adults took flight from an approaching human at greater distances than did juveniles, apparently acting more rather than less cautiously. Lima and Bednekoff (1999; see also Relyea 2003; Lind and Cresswell 2006) considered how animals ought to allocate antipredator effort when the danger varies temporally, or if there are multiple predators. They reason that the effort and time put into lessening the danger from one risk, even if rare, necessarily reduces the effort available to manage other risks, and show that most effort should be allocated to the most dangerous predators or times, at the expense of increasing the chance of a successful attack from the less dangerous predator. Under the reasonable assumption that western sandpipers regard peregrines as much more dangerous than humans, this theory would predict that juveniles allowed closer encroachment by humans than adults because the higher late-season abundance of peregrines made an increased allocation of effort to antiperegrine behavior worthwhile. It should also be noted, however, that the strength of any inferences made from the flight initiation distance test is not strong, as there was little difference between the top model and the null model and the unconditional errors of age and year are large (Table 5). Varying the number of risk factors that individuals experience when approached by humans has been shown to influence flight initiation results (Cooper 2009). Sandpipers experiencing different peregrine predation danger levels could cause them to react to the approach of humans differently.

Proximate factors other than the season affected vigilance and flight initiation distance. As expected, vigilance decreased with increasing distance from cover (Pomeroy 2006). However, on incoming tides, this trend disappeared and vigilance remained consistently high as distance from cover increased. Vigilance was also higher for individuals at the edge of a flock and in flocks smaller than 20 individuals (Elgar 1989; Lima 1995). Additionally, wind direction and strength and cloud cover affected the level of vigilance. Flight initiation distance was lower on incoming tides and closer to cover. Some of these results are likely explicable by the effect of environmental variables on sandpiper vulnerability (e.g., predator detection diminished in bright sunlight), energy metabolism (e.g., thermoregulatory costs), or predator behavior (more attacks on falling tide; Dekker and Ydenberg 2004), but this reasoning is all post hoc and our model structure was not designed to isolate such effects. These conventionally expected patterns nonetheless provide evidence that the measurements were meaningful with respect to assessing the birds' responses to predation danger.

The seasonal change in predation danger created by the southward migration and winter settlement patterns of falcons and accipiters conceptualized here is basic, simple, and general. Overall, the results illustrate that migrants' behavior while on stopover varies with respect to their position within the migratory period, which we interpret as tactics to shift the balance between migrating quickly and migrating cautiously. The mortality-minimizing balance depends on the proximity of the falcon front and likely other factors. We conclude that though details remain unexplained, our data are in broad accord with the changes in the behavior we predicted. The influence of predator landscapes has largely been ignored in discussions of migratory strategies (Lank et al. 2003; Ydenberg et al. 2007).

Alternative hypotheses

Our mortality-minimizing approach does not obviate the need to consider effects of time, energy, or other influences in shaping migratory behavior. To predict the behavioral changes we observed, hypotheses based on time and energy minimization would require specific changes in environmental conditions related to energy gain (e.g., prey availability) or expenditure (e.g., favorable winds) throughout the passage period. Such factors have often been invoked. For example, adult semipalmated sandpiper adults are hypothesized to depart early in order to take advantage of high food abundance at a major stopover, while juveniles migrate quickly to avoid migrating under later and lower food conditions (Schneider and Harrington 1981). As discussed by Lank et al. (2003) and Hope et al. (2011), actual foraging circumstances along migratory pathways are likely to be far more varied, and even when foraging conditions change, migrants are able to make tradeoffs using a complex set of behaviors, so that there may be little change in the realized fuelling rate between groups or individuals (Lind and Cresswell 2006).

The mortality-minimizing hypothesis requires no particular assumptions about the interannual or seasonal patterns in the availability of food for migrating sandpipers. We make the simplifying assumption for our interpretations of behavior that food abundance does not vary significantly within or between years in such a way that would cause the observed patterns of behavior. We feel this is a safe assumption based on previous work that has looked at food abundance at the site (Pomeroy 2006). Predicting vigilance based on food abundance is not straightforward and varies on the state, foraging method, group size, and priorities of the individual (reviewed by Beauchamp 2009).

The behavioral differences between adult and juveniles, when both are present, indicates strategic differences of some kind. Metcalfe and Furness (1984) found that juvenile and adult ruddy turnstones did not differ in vigilance during the winter. As they prepared to migrate northward, adults decreased vigilance, whereas the nonmigratory juveniles did not adjust their vigilance levels. The variation between age classes suggests differences in priorities can influence the foraging strategies for both adults and juveniles.

Differences in the behavior of adult and juvenile migrant birds are often attributed to the inexperience, recklessness, or poorer competitive ability of juveniles (e.g., Marchetti and Price 1989; Rappole 1995; Summers et al. 1995; Dierschke 1998; Caro 2005; see discussion in Ydenberg et al. 2007). Could our results be simply predicted from a hypothesis that juvenile and western sandpipers differ in one or more of these attributes? “Lower competitive ability” is not a viable hypothesis here due to the disjunctive migratory timing of adults and juveniles. The recklessness hypothesis can also be eliminated because juveniles are more cautious in almost every regard. This leaves “inexperience” as a potential explanation.

It is of course true that juvenile western sandpipers must have had less experience than adults. But how much does this affect their migratory behavior? From our results, juveniles do not seem to be naïve about predation danger. For example, they show higher vigilance when foraging in more dangerous places (e.g., closer to shore), and based on the distribution of feeding time are as adept as adults at balancing the higher food availability close to shore against the higher danger there. Further, they, as with adults, increased their vigilance in the more dangerous year. Moreover, at least not without additional assumptions, it is not clear how a hypothesis based on inexperience could explain any of the observed intraseasonal changes in behavior, whereas the “speed—caution tradeoff” in our mortality-minimizing hypothesis can account for all these effects. We conclude that simple hypotheses based on the inferior abilities of juveniles are much less powerful as explanations for our results.

Our findings would not seem to be explained solely by inherent age-related differences or through attempts to minimize time or energy spent on migration. Instead, we found that cautious juveniles and adults with different levels of cautious behavior, based on their position within the migratory period, were well predicted by a hypothesis based on the idea of mortality minimizing. It seems likely, as hypothesized by Ydenberg et al. (2007), that the behavior of both adult and juvenile migrants is selected for by the ecological conditions under which they must migrate. Future studies of age-specific behavior should take these conditions into account when generating predictions of migratory behavior.

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Ethical standards All experiments in this manuscript comply with the current laws of Canada, the country in which the experiments were performed.

Conflict of interest The authors declare that they have no conflict of interest.

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