

Research Article

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Does predation danger on southward migration curtail parental investment by female western sandpipers?

Abstract: Theory predicts that if extending parental care delays migratory departure, and if later migration is more dangerous, then parental care should be curtailed to make an earlier departure. Adult western sandpipers (*Calidris mauri*) depart Alaska in July, and the presence of peregrine falcons (*Falco peregrinus*) along their route rises steeply during the migratory period. Pacific dunlins (*C. alpina pacifica*) are ecologically similar, but do not depart Alaska until October, after peregrine passage has peaked. Because peregrine migration begins earlier in years with early snowmelt, we predicted that the curtailment of parental investment by western sandpiper, but not of Pacific dunlins, should be more pronounced in these more dangerous years. We measured breeding phenology of these species on the Yukon Delta National Wildlife Refuge during three seasons with strongly differing snowmelt timing. We found that they initiated breeding simultaneously, and that western sandpipers, but not Pacific dunlins, ceased laying increasingly earlier, provided increasingly less parental care and departed increasingly sooner as snowmelt was earlier. Advancing departure date by the overall average of 5.2d relative to dunlin reduces migratory exposure to peregrines by an estimated 18%. Our results support the hypothesis that natural selection has favored curtailment of parental investment by western sandpipers to advance migratory departure.

Keywords: maternal care, migration danger hypothesis, predation risk, seasonal variation, shorebirds, trade-offs, waders

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1 Introduction

The life cycle of most migratory animals involves alternating periods of breeding, migration and wintering, and the timing of these periods has implications for the success of each. During the breeding season for example, the fundamental principle underlying parental care theory is that the time, energy, and risk-taking invested in parental care by an individual should reduce the expected number or success of future breeding attempts [1-3]. The fitness-maximizing level of parental investment is set by the trade-off between these opposing fitness components [4]. Here we apply this line of reasoning to one aspect of the diverse patterns of parental care shown by shorebirds, and ask how the timing of breeding activities are influenced by the inherent dangers of migration, namely predation.

Myers [5] identified a relationship between migration distance and parental care in shorebirds, noting that species with longer migrations show more asymmetrical parental investment between the sexes (see also [6]). He proposed that "... these [parental care] patterns are consistent with a hypothesis that through early departure an individual can decrease the risks of long-distance migration..." Myers [5] evidently associated the cost of migration with the challenges of accumulating large fuel reserves, especially for females. Ydenberg and colleagues [7, see also 8] explicitly consider the danger posed by predators as an important force selecting for the timing and routing of migration, and molt. They assume that birds are particularly vulnerable to predators during these times [9-11], and propose that migratory species schedule these stages of their annual cycles to lessen exposure to predators. We consider this concept in relation to the breeding and parental care of two shorebird species, the western sandpiper (*Calidris mauri*) and the Pacific dunlin (*C. alpina pacifica*).

Species in the genus *Falco* are the primary predators of shorebirds, and are themselves migratory [7]. In North America, the southward passage of peregrine falcons

(*Falco peregrinus*) progresses with a characteristic timing and geographical orientation [12], creating a zone of high danger that migrant shorebirds seek to avoid [13,14]. Migratory and nonbreeding falcons begin to appear along the migratory path of western sandpipers and Pacific dunlins in mid-July or August. Their numbers rise to a peak in October, and decline steadily in the course of the subsequent winter [8]. To minimize migratory overlap with these predators, shorebirds could either leave northern breeding areas early, completing migration ahead of falcons; or they could remain on (or nearby) breeding areas, migrating after falcon migration is completed [7].

Western sandpipers breed in Alaska and begin their southward migration in late June [8]. Nonbreeding areas range from California to Peru, and upon arrival after southward migration, adults undergo rapid molt. The Pacific dunlin is ecologically similar, and breeds sympatrically, but undertakes much later and shorter southward migration. Following breeding, adults depart the breeding grounds, but remain in Alaska until October to stage and molt along the coast before migrating to nonbreeding areas along the Pacific Coast, from Canada to Mexico [15-17].

These migration patterns interact with that of migratory falcons in different ways. Based on a study of breeding, staging, and stopover timing, Niehaus [18] showed that in western sandpipers the onset of migration closely follows the termination of breeding. Western sandpipers that extend breeding activities therefore delay migratory departure. Later migration brings greater exposure to peregrines due to their rising presence along the Pacific Coast from July to October. This rising danger penalizes extended breeding activity. Pacific dunlin parents do not face this cost because they migrate southward to nonbreeding areas after falcons have already settled there [8].

Breeding seasons of birds are generally assumed to have evolved to match the local availability of food for offspring. In many shorebirds, females cease laying eggs despite plentiful food [19-21], apparently because chick growth rate and survivorship from late nests falls as the availability of food for chicks declines seasonally [20,22-24]. We argue that this is true for Pacific dunlins, whose extended Arctic residence allows them to utilize the full period during which local habitat productivity makes breeding worthwhile. However, we suggest that in order to make an earlier migratory departure, western sandpipers cease laying earlier in the season, abbreviate parental care, and leave the breeding grounds before local conditions make continued breeding unprofitable. In essence, our hypothesis is that western sandpipers

sacrifice breeding opportunity for earlier, and hence safer, migration.

To test this ‘migratory danger’ hypothesis, we take advantage of fact that the timing of falcon migration varies greatly between years, and so affects the relationship between migratory danger and date. Assessed over 14 years, at the first major stopover site, in southeastern British Columbia, Niehaus and Ydenberg [25] showed that peregrine migratory timing advances linearly with snowmelt (by 1.09d for each day of snowmelt advance; $r = 0.81$, $p < 0.001$), but western sandpiper migration timing does not change at all ($p > 0.05$). This means that for western sandpipers, southward migration is more dangerous in an early snowmelt year, because on any date the number of peregrines at any location along the route is higher than in a later snowmelt year. The key prediction of our migratory predation danger hypothesis therefore is that western sandpipers should terminate their parental investment sooner in years with early snowmelt.

We measured the breeding phenology of western sandpipers and Pacific dunlins at the same location. If the initiation and termination of breeding are set by local breeding habitat phenology, we expect these ecologically-similar species to behave similarly each year. Breeding activity (e.g., timing of first, replacement, and last clutches) should progress simultaneously, in step with habitat phenology. But if migratory predation danger operates as we hypothesize, western sandpipers will cease laying earlier in the season, abbreviate parental care (see [26]), and depart earlier. Western sandpipers are smaller than Pacific dunlins, and incubation and fledging periods are slightly shorter (by one day for each), and on this basis one might expect two-day difference in parental care duration, but there is no reason on the basis of phenology alone to expect the initiation and cessation of breeding to differ. The key prediction of the migratory danger hypothesis is that the magnitude of the difference in breeding season termination between the two species will be greater in early snowmelt years. Such an effect is not predicted on the basis of size differences or on the well-known breeding biology of these species.

2 Methods

2.1 Study Species

We studied western sandpiper and Pacific dunlin breeding along the Kuyungsik River near the Kanaryarmiut Field Station, Yukon Delta National Wildlife Refuge, Alaska (61°22′N, 165°07′W) from 2004–2006. Western sandpipers

nested on dry upland tundra while Pacific dunlins nested on neighboring lowland wet meadows. In both species, males defended nesting territories unless they were caring for young. Western sandpipers and Pacific dunlins show biparental incubation with male-biased brood care [27]. Both species may renest if a nest fails (*i.e.*, females lay replacement clutches; [26,28]), but only Pacific dunlins are known to double brood (*i.e.*, females lay a second clutch with a new mate after deserting a brood to the care of its original mate; [28]). Renesting and double brooding males remained on their territory, whereas females often moved between the territories of different males. In western sandpipers at our study site, the egg-laying period is 4d, incubation lasts 21d, and the chicks fledge at 13–15d of age (total 38–40d; [23,26]). The Pacific dunlin schedule is similar, with 4d for laying, 22d for incubation, and 16–19d until fledging (total 42–45d; [17]; unpub. data of author). In both species the period of parental care is variable, and one (usually the female) or both parents may abandon chicks well before fledging [26,28].

2.2 Data Collection

Study plots for Pacific dunlins and western sandpipers totalled 0.64 km² and 0.16 km², respectively. Each was surveyed every 1–3d and the presence of all known individuals noted. Nests were found through behavioral observations and territory plotting. If a clutch was complete when found (*i.e.*, four eggs), it was aged using the flotation method [29]. Once a nest was complete, both parents were trapped and banded. Each adult received a metal band and a unique combination of color bands. Sex was assigned according to culmen length and breeding behavior [30,31]. In some cases, individuals could not be marked because the nest failed prior to trapping. Nests were checked every 1–4d for incubation activity and daily as the estimated hatch date approached. If a nest was

depredated, the predation event was assumed to have occurred at the midpoint between the date the nest was found depredated and the prior visit. If a nest hatched, the brood was located at least once daily and the identity of the attending parent(s) recorded. A parent was considered to have deserted if it was not seen accompanying its brood for three consecutive days. The desertion date was assumed to be the day following the last date it was observed. We define female departure date as the last observation date of females that were the last known partner of territorial males nesting on the study plots. Animal ethics approvals were provided by Simon Fraser University's Animal Care Committee (755B-05).

Temperature data are from the Alaska Climate Research Center website (<http://climate.gi.alaska.edu/Climate/Location/TimeSeries/Data/betT> accessed 18 May 2009).

2.3 Data Analysis

We tested the predictions using data collected from females because they determine the timing of egg-laying, typically desert broods earlier than their mates, and show more variability in the timing of their desertions [26,28]. We examined the timing of termination of breeding effort for western sandpipers and Pacific dunlins by comparing renesting probability (*i.e.*, whether or not a nest was replaced following failure) using logistic regression analysis (dependent: renesting or not; fixed main effects: failure date, species, year, all interactions; random effect: female; modelling a binomial distribution and logit link). We compared the rates at which brood care changed with hatching date for the two species using a linear mixed model (dependent: brood care duration; fixed: hatching date, species, year, all interactions; random: female). Up to a third of female Pacific dunlins double brood in any year, and searching for a new mate can result

Table 1: Sample sizes of data collected from western sandpipers and Pacific dunlins nesting on the Yukon Delta National Wildlife Refuge, Alaska.

		2004	2005	2006
Nesting events with total parental care duration measured	western sandpipers	28	24	26
	Pacific dunlins	26	33	39
Failed nesting events from which renesting behaviours were followed	western sandpipers	47	32	8
	Pacific dunlins	21	34	18
Broods with known female brood care duration	western sandpipers	4	10	15
	Pacific dunlins	10	10	22
Departure dates of females	western sandpipers	37	28	29
	Pacific dunlins	23	34	37

in these females providing relatively little brood care (2.6 ± 1.0 d, [28]). Consequently, parental care decisions during the earliest part of the season would often be influenced by additional within-season breeding opportunities rather than migration considerations alone. For both species, we therefore considered the duration of care only for females attending nests hatched after 17 June, which was the latest hatch date of any first nest laid by a double brooding female. We compared breeding ground departure dates of the species using a linear mixed model (dependent: departure date; fixed: species, year, all interactions; random: female). For these three analyses, we first tested models including all interactions, and sequentially removed non-significant terms, using $p > 0.10$ for interactions. When year effects were significant, pairwise comparisons among specific years were made with Tukey's honestly significant difference tests (Tukey's HSD). Statistical analyses were carried out with SAS 9.3 (2011). Graphs were produced with SigmaPlot 12.3 (SPSS Inc. 2011). We report means and 95% confidence intervals.

3 Results

Over the three field seasons we measured the total parental care duration of 78 western sandpiper and 98 Pacific dunlin nesting events, and renesting data for an additional 87 failed western sandpiper nests and 73 failed Pacific dunlin nests. Further, we collected female brood care duration for 29 western sandpiper broods and 42 Pacific dunlin broods. We assessed departure dates for 94 female western sandpipers and 94 female Pacific dunlins. Sampling details are described in Table 1.

Environmental conditions varied substantially among the three years (Table 2). 2004 was an extraordinarily

early year (Kuyungsik River ice break-up 6 May) and temperatures were high throughout the season (mean daily temperature April to July = 9.7°C). 2005 was an intermediate year, both in terms of ice break-up (24 May) and mean temperature (7.4°C), and 2006 was a late and cold year (ice break-up June 2, 5.6°C). Thus our three breeding seasons provide an excellent contrast in terms of estimated migratory danger, with 2004 the earliest and hence most dangerous year, and 2006 the latest and hence least dangerous year.

For both species, the onset of breeding activity varied with environmental conditions, being early in 2004, late in 2006, and intermediate in 2005 (Table 2). As expected if breeding habitat requirements are similar, Pacific dunlins and western sandpipers began nesting almost simultaneously in each year, with the very first dunlin clutch completed one day earlier than the very first western nest (2004: 13 vs. 14 May; 2005: 18 vs. 19 May; 2006: 29 vs. 30 May; dunlin date given first). The mean completion dates of first clutches on each nesting territory are also just slightly earlier for dunlins (presented are mean dates \pm SD in days, 2004: 22 May \pm 7.2 vs. 23 May \pm 5.0; 2005: 22 May \pm 3.6 vs. 28 May \pm 5.2; 2006: 1 June \pm 2.5 vs. 2 June \pm 4.8). In contrast, the likelihood of renesting decreased with date although this effect was earlier for female western sandpipers than female Pacific dunlins (Fig. 1), and western sandpipers breeding season concluded earlier (last clutch dates, 2004: 26 vs. 23 June; 2005: 1 July vs. 21 June; 2006: 1 July vs. 22 June).

Our key prediction is that the cessation of western sandpiper breeding activities should be differentially earlier relative to those of Pacific dunlins in years with earlier snowmelt. The probability of replacement laying after nest failure varied as predicted among years. We fitted logistic regressions separately to each year and

Table 2: Summary of annual environmental conditions and breeding phenology western sandpipers relative to Pacific dunlins, on the Yukon Delta National Wildlife Refuge, Alaska. Italicized rows are differences between species, with negative numbers indicating that western sandpiper values are earlier or less. The overall column is based on pooled data. 'Replacement date' refers to the difference between species in the date that clutches had a 50% probability of being replaced. Statistics are reported in Table 3.

Parameter	2004	2005	2006	Overall
Ice out	May 6	May 24	June 2	May 21
Mean temperature ($^\circ\text{C}$)	9.7	7.4	5.6	7.4
First dunlin clutch	May 13	May 18	May 29	May 20
Last dunlin clutch	June 26	July 1	July 1	June 29
First clutch (d)	1	1	1	1.0
Mean first clutch (d)	1.1	6.3	1.1	2.1
Last clutch (d)	-3	-10	-11	-6
Replacement date (d)	-7.2	-5.8	-2.3	-6.6
Parental care duration (d)	-7.8	-13.0	-1.1	-7.3
Departure (d)	-8.8	-5.9	-1.0	-5.2

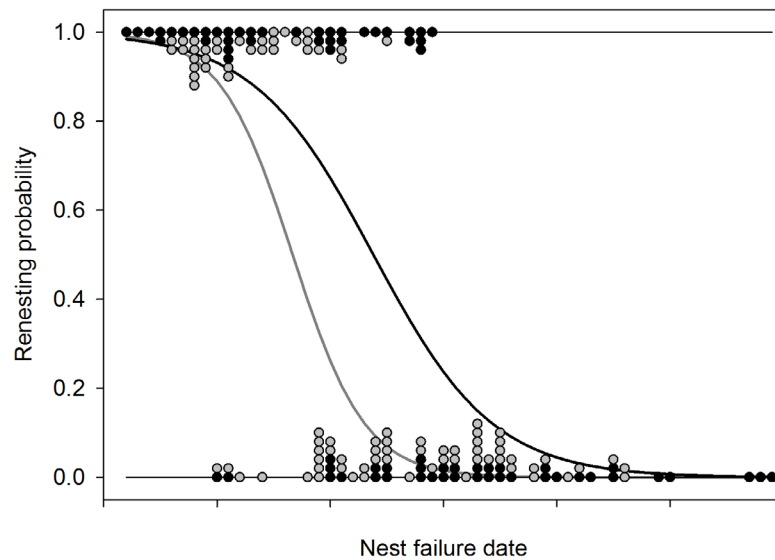


Figure 1: Over all years combined, female western sandpipers (grey) ceased replacing failed nests earlier in the season than Pacific dunlin females (black; $p = 0.02$). Each circle represents an individual nest and the curved lines represent fitted logistic regressions.

species to estimate the date at which the probability that a failed nest was replaced fell to 50%. Statistically, failure date was an overwhelming predictor of replacement probability ($p < 0.0001$), and the failure date-species interaction was the only interaction approaching significance ($F_{1,29} = 2.87$, $p = 0.10$). A model run with main effects only (failure date, species, year, female as random effect) showed a significant species difference ($F_{1,30} = 6.25$, $p = 0.02$) and marginal year effect ($F_{1,30} = 2.88$, $p = 0.07$). Table 3 provides a summary of the significance levels in these comparisons.

Female western sandpipers invested an average of 24.9 ± 1.7 d in parental care, while female Pacific Dunlins invested 32.1 ± 1.7 d, a difference 3.6 times greater than the 2 day difference in the total egg–fledging period, and 7.2 times greater than the 1 day difference in the fledging period. The duration of parental care provided by females during the latter part of the season declined in both species, and more steeply in western sandpipers than in Pacific dunlins (species*duration interaction:

$F_{2,16} = 10.43$, $p = 0.011$; Fig. 2). Over all years combined, female western sandpipers departed the breeding grounds 5.2 days earlier than female Pacific dunlins ($F_{1,37} = 11.02$, $p = 0.002$; Table 3).

The duration of parental care showed a significant species by year interaction in the predicted direction ($F_{2,33} = 8.196$, $p = 0.001$; Table 3; Fig. 3). Western sandpipers provided 7.8d less parental care than dunlins in 2004, 13.0d less in 2005, but only 1.1d less in 2006. The species differences are significant in 2004 and 2005, but not in 2006, the year with the latest spring (Tukey's HSD- 2004: $p = 0.014$, 2005: $p < 0.001$, 2006: $p = 0.991$; Fig. 3).

Patterns of departure dates also showed a significant interaction between species and year in the predicted manner ($F_{2,37} = 3.46$, $p = 0.042$; Table 3). There were no significant differences between years in the departure times of Pacific dunlins (Tukey's HSD- p values ranging from 0.341 to 1.00). In contrast, the departure dates of western sandpiper females were earlier in early snowmelt years (2004: 8.4d sooner than

Table 3: Statistical evaluation of predictions testing the migratory danger hypothesis. Procedures are described in the text. Table entries are the significance level of day-of-year, year, species and the year by species interaction effect. '/' indicates effect was not in the model.

Effect	Day-of-year	Year	Species	Year x species
Renesting probability	<0.0001	0.07	0.02	0.10
Parental care duration	0.01	0.07	0.06	0.001
Departure date	/	<0.0001	0.002	0.042

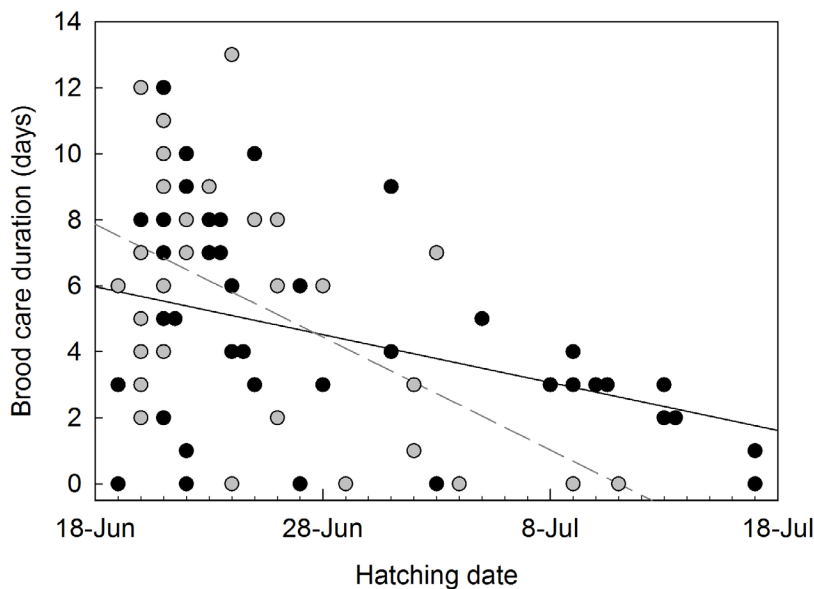


Figure 2: The duration of brood care provided by females declined at a significantly greater rate in western sandpipers (grey) than in Pacific dunlins (black; linear mixed model, species*hatching date: $p = 0.011$). The solid line depicts Pacific dunlin (brood care duration = $30.499 - 0.145$ hatching date, $R^2 = 0.148$) and the dashed line represent western sandpipers (brood care duration = $65.650 - 0.342$ hatching date, $R^2 = 0.286$).

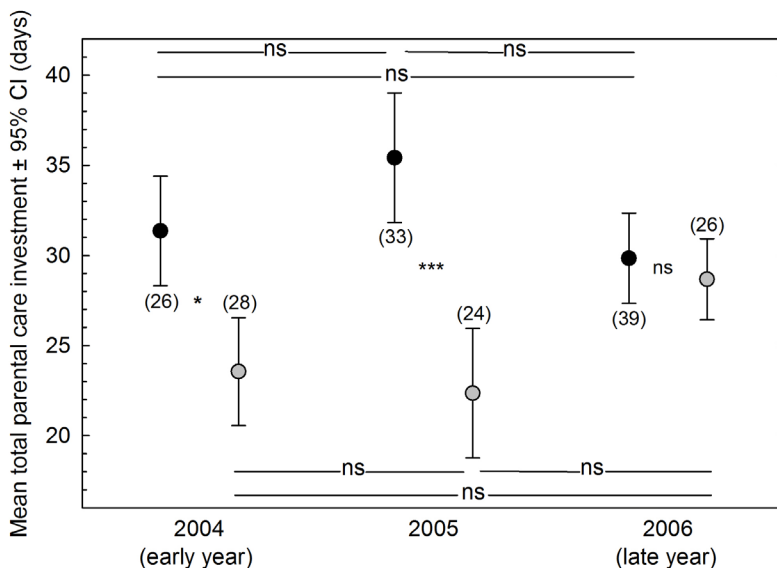


Figure 3: A comparison of total parental care investment for nests laid after June 17 by female Pacific dunlins (black) and western sandpipers (grey) nesting on the Yukon Kuskokwim Delta, Alaska. Numbers associated with the error bars are sample sizes. Comparisons were made using Tukey's honestly significant differences tests (ns = $p > 0.05$, * = $p < 0.050$, *** = $p < 0.001$). Symbols between means show comparisons between species and within years. Horizontal lines represent comparisons made within species and among years.

dunlins, 2005: 5.9d, 2006: 1.0d; $F_{2,37} = 15.43$, $p < 0.0001$). In 2004, western sandpipers left the breeding grounds significantly earlier than they did in 2005 and 2006 (Tukey's HSD- 2005: $p = 0.012$, 2006: $p < 0.001$), but no difference could be detected in the departure dates of

western sandpipers between 2005 and 2006 (Tukey's HSD- $p = 0.276$). The difference between the departure dates of the species was significant only in 2004, the year with the earliest spring (Tukey's HSD- 2004: $p = 0.012$, 2005: $p = 0.203$, 2006: $p = 0.999$).

4 Discussion

The onset and early portions of the breeding season progressed in close synchrony for western sandpipers and Pacific dunlins, and as expected on the basis on their known phenology, female western sandpipers provided less parental care, had a steeper seasonal decline in the duration of brood care, and departed the breeding grounds earlier. But as predicted on the basis of the migratory danger hypothesis, breeding effort was increasingly truncated with earliness of the onset of spring by western sandpipers, but not by Pacific dunlins.

We interpret the near-simultaneous start of breeding activities in each year as the onset of suitable conditions for both species, and it is synchronous due to their similar breeding requirements. We interpret the termination of breeding by Pacific dunlins to reflect the end of the window of opportunity for breeding activities for small sandpipers, likely due to environmental conditions such as food availability for chicks [22,24]. In contrast, we propose that the earlier termination of breeding activity by western sandpipers is a life history adaptation selected for specifically by the inherent danger of migration to distant nonbreeding areas. By comparison with the phenology of the ecologically-similar Pacific dunlin, we estimate that western sandpipers could have remained on the breeding grounds and continued breeding activities for a further 8.8d (2004) to 1.0d (2006). We assume that this represents foregone opportunity by western sandpipers that could have been used to improve offspring survival [32,33], or for more renesting or perhaps double brooding, both of which are highly expressed by Pacific dunlins [28].

The summer arrival of migratory peregrines along their shared migration route places a premium on earlier migration for western sandpipers, and this premium is greater in years with earlier springs. Our three study seasons were very different from each other, but are typical of the inter-annual variability faced by breeding sandpipers in Alaska. Niehaus and Ydenberg [25] report that inter-annual variation in the timing of snowmelt in western Alaska (their sample 1978 – 2001) varies over 43d. Though we used a different measure to establish spring timing, the range of ice break-up dates encountered in our study (May 6 – June 2; 28d) represents an appreciable portion of the recorded snowmelt range. Based on the seasonal progression of the peregrine index presented in Lank *et al.* [8], we estimate that in an average snowmelt year, a five day advance in departure date from July 1 to June 26 would reduce the cumulative exposure to peregrines over a

20d, 5000 km migration (*i.e.*, to Sinaloa, Mexico) by 17.6%. The advantage over a 40d, 10,000 km migration (to Colombia) would be more than twice as large. The exact value depends on the departure date, the distance travelled, and on the relative migration speed of peregrines and sandpipers, but it is clear that even a few days advance has the potential to substantially reduce the exposure to falcons while on migration.

4.1 Alternative Hypotheses

Several alternative explanations might be proposed to account for the patterns reported here. The interspecies difference might be associated with the greater distance that western sandpipers travel to reach nonbreeding areas than do Pacific dunlins [5; *e.g.*, feather wear]. However, as migration distance does not change from year to year, such factors appear unable, at least on their own, to predict the year-to-year relationship with snowmelt date.

One could argue that a difference in the timing of food availability for chicks could not only account for the earlier truncation of breeding by western sandpipers, but might additionally be able to account for the annual differences. The species' nesting habitats do differ, but both dunlin and western sandpiper broods are highly mobile following hatch, have similar diets [34,35], and both overlap on the local habitat mosaic, especially along wetland margins [27, Ruthrauff cited in 36]). It seems unlikely that this mechanism could drive the observed patterns, though it remains a possibility. Many authors propose that the timing of shorebird migration relates to the seasonal abundance of food availability at stopover sites (*e.g.*, [37]). The data show that the food availability for small sandpipers remains high or increases through the summer period on stopover sites of the Pacific Northwest [8], so this does not seem a reasonable explanation for either the earlier migratory departure by western sandpipers or for the annual differences.

A further possibility is that environmental factors such as temperature and predator abundance affect hatching failure, which in turn affect parental care and departure date. To explain the differential departure timing we observed, this would have to vary between the species accordingly. We found that hatching failure varied between years in concert for the species (Mayfield hatching success (mean \pm 95% CI) for Pacific dunlins and western sandpipers, respectively: 2004: 0.41 \pm 0.02, 0.13 \pm 0.02; 2005: 0.43 \pm 0.01, 0.29 \pm 0.01; 2006: 0.59 \pm 0.01, 0.52 \pm 0.01) although the changes were more pronounced for western sandpipers.

4.2 General implications

Myers [5] developed the ‘migration distance’ hypothesis to explain a particular aspect of shorebird parental care diversity, namely the asymmetrical parental care patterns between sexes. He assumed that the cost of migration was related to the buildup of large fuel reserves, and that due to their large energetic investment in egg production females face a larger challenge in doing so. They therefore terminate parental care before males. Recent work does not support his ‘fuel buildup’ interpretation [38]. Reynolds and Székely [6] considered a variety of other potential costs, but neither they, nor Myers [5], identified predation danger as a potential cost of migration. The evidence presented here, as well as work on the behavior of western sandpipers on stopover sites [13,14,39] supports our contention that predation danger is a major cost of southward migration for western sandpipers.

As developed here, our migratory danger hypothesis does not address directly the male-female difference at which Myers [5] aimed his migration distance hypothesis. Like Myers, we assume that departure on southward migration is determined by fitness costs and benefits, and we explicitly consider that some of these are date-dependent. In standard optimality terms, the fitness-maximizing departure date occurs at the point at which the marginal fitness benefits and costs of continued breeding area residence are equal. In everyday terms, an extra day’s residence on the breeding area brings benefits (e.g., longer parental care and thus improved survival of offspring; the ‘marginal’ benefit is the extra survival thus attained), but also costs. The fitness-maximizing departure date occurs at the point that (declining) marginal benefit is equal to the (increasing) marginal cost.

The magnitude of these costs and benefits differs between species, and may also differ between individuals within species [40]. For example, it is commonly assumed [11,41-43] that an individual’s body size or mass is negatively related to flight agility. Assuming that agility affects the predator escape performance and hence migration mortality, predictions could be made about the relative departure timing of differently-sized individuals of the same sex. One might also surmise that females are larger and more vulnerable to falcons on migration, and facing these costs abbreviate parental care and depart on southward migration before their mates. However, analysing the parental investment of pair members requires an explicitly game theoretic approach because the best parental investment strategy of each pair member depends on that of the other. Myers did not state his [5] hypothesis in game theoretical terms, and it is unclear how well it applies.

McNamara *et al.* [44] present a framework to analyse this problem in game theoretical terms. They state explicitly that their analysis is suitable for cases in which a period of biparental care is followed by the desertion of one of the parents, as in many shorebirds. As in Myers’ hypothesis, asymmetries in the costs of parental care between males and females are important, but a novel feature is that details of the process whereby parents establish their respective levels of breeding investment are critical. Details that strongly affect the evolutionary stable strategy include the order in which decisions about parental effort are made and the degree of interaction between parents. More theoretical work, as well as detailed field observations, are needed to carry this analyses further.

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Conflict of interest: Dr. Jamieson has nothing to disclose.

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