Effect of fuel deposition rate on departure fuel load of migratory songbirds during spring stopover along the northern coast of the Gulf of Mexico

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(Abstract)

Migrants are generally assumed to minimize their overall migration time by adjusting their departure fuel loads (DFL) in relation to anticipated and experienced fuel deposition rates (FDRs). We utilized a 21-yr long migration banding station dataset to examine the relationship between FDR and DFL during spring migration in six Nearctic-Neotropical migratory songbird species during stopover along the northern coast of the Gulf of Mexico (GOM) following trans-gulf flight. Estimates of fuel stores, stopover durations, and FDRs from our long term migration data set were combined to determine DFL. We expected and found that migrants across all six species adjust their DFL to the rate at which they deposit fuel reserves. This robust finding suggests that songbird migrants are sensitive to time constraints during spring passage presumably to fine-tune their stopover schedule in relation to experienced and anticipated habitat quality. Two of the species studied showed an effect of age on the FDR–DFL relationship: one was consistent with the expectation that older birds would be less sensitive to changes in FDR, while the second was contrary to our expectations and likely suggesting an age-dependent response to habitat quality. We found sex-dependent differences consistent with male DFL being more sensitive to FDR in only two of six species studied, and argue that both males and females are time constrained during spring passage in relation to arrival at breeding destinations. The positive relationship between FDR and DFL among all species and for age and sex groups in some species reflects a migration strategy sensitive to time.

(Introduction)

Migration is thought to be time-constrained within the annual cycle (Alerstam and Lindström 1990, Hedenstr m et al. 2007, Hedenstr m 2008, Newton 2011), especially during spring passage (McNamara et al. 1998), which places migratory birds under strong selective pressure to make judicious departure decisions during stopover (Smolinsky et al. 2013, Deppe et al. 2015). Migrants are generally assumed (Hedenstr m and Alerstam 1997) to minimize the overall time of migration by adjusting their departure fuel loads (DFLs) to the experienced fuel deposition rates (FDRs; Alerstam and Lindström 1990, Hedenström and Alerstam 1997). We utilized a long-term (21 yr) migration banding station dataset to examine the relationship between FDR and DFL during spring migration in six intercontinental migratory songbird species when they stopover to rest and refuel along the northern coast of the Gulf of Mexico (GOM). The GOM is a conspicuous feature of the Nearctic-Neotropical bird migration system, and a very high volume of migratory songbirds pass through the northern coast of the GOM on their way to breeding destinations in North America (Simons et al. 2000, Buler and Moore 2011, Lafleur et al. 2016). This study is the first to examine the relationship between DFL and FDR in this migration system.

Context is important in understanding the relationship between DFL and FDR. Habitats along the northern coast of the GOM provide the last possible stopover before migrants make a nonstop flight of greater than at least 1000 km in fall, and the first possible landfall for birds returning north in spring (Moore and Kerlinger 1987, Moore et al. 1990, Deppe et al. 2015). Our study was conducted in southwestern Louisiana, which is dominated by open grassy marsh and wet prairie with forest occurring on narrow and elongated coastal ridges called Cheniers (Moore 1999, Barrow et al. 2000). Although trans-gulf migrants generally fly over the coastal plain in southwestern Louisiana during spring passage and make landfall in the bottomland forests 50 km inland (Gauthreaux 1972, 1999), coastal woodlands often concentrate migrants because they are essentially islands of suitable forested habitat, especially attractive to migrants during weather conditions unfavorable for northward movement (Gauthreaux 1971, 1999) or when energetically stressed (Moore and Kerlinger 1987, Yong and Moore 1997).

We expected that 1) birds would adjust their DFL and stopover duration to their FDR if constrained by time; 2) older, after-second-year (ASY) birds would differ from younger, second-year (SY) birds in the relationship between FDR and DFL during spring passage (Fig. 1A); and 3) males and females would differ in the relationship between FDR and DFL (Fig. 1B). The exact nature of the relationship between DFL and FDR depends on current stopover conditions and future expected conditions (Lindstr m and Alerstam 1992). Migrants may view their future speed of migration to be higher than that currently experienced at a coastal stopover site because coastal areas appear to be poor-quality stopover habitat for the majority of songbirds

(Kuenzi et al. 1991, Buler and Moore 2011), especially when migrants with similar food requirements and heightened energy demand are locally concentrated in an unfamiliar area (Moore and Yong 1991). Moreover, there is reason to believe that adjustment in the rate of migration among Nearctic-Neotropical migratory birds takes place within North America after negotiating the GOM (Cohen et al. 2015; see also Marra et al. 2005, Horton et al. 2016).

Specifically, we predicted that experienced ASY birds would be more expectant of higher refueling possibilities in the future, and so would be relatively insensitive to changes in FDR compared to inexperienced SY birds (Fig. 1A). These older migrants are likely to be socially dominant to younger birds (Moore et al. 2003) and possibly more efficient foragers (Heise and Moore 2003), which might translate to higher FDRs and DFLs. Older males may also be under greater pressure to migrate at a faster pace to arrive earlier on the breeding grounds than younger males (Smith and Moore 2005), and therefore adjust FDR and DFL accordingly. Although we did not necessarily expect the sexes to differ in their expected refueling capabilities (Moore et al. 2003), males are likely more time constrained during spring migration than females (Morbey and Ydenberg 2001) and the pace of migration may differ between males and females (but see Schmaljohann et al. 2015). If so, males would be more sensitive to changes in FDR at stopover sites, and the slope of the relationship between DFL and FDR would be steeper in males than in females (Fig. 1B).

To examine these expectations, it is necessary to obtain the following data on individual migrants: 1) when and in what fuel load they arrive and leave the stopover site and 2) their refueling rate. Other than a study of songbird migrants by Schaub et al. (2008) and an analysis of rufous hummingbird *Selasphorus rufus* stopover data by Lindstr m and Alerstam (1992), the relationship between FDR and DFL has not been studied without the use of artificial feeding stations (Dänhardt and Lindstr m 2001, Dierschke et al. 2005), due to difficulties in determining departure time and, even more problematic, DFL in a field setting. We refined an approach developed by Schaub and colleagues (2008) and combined estimates of fuel stores and FDRs of recaptured birds from our long term data set with estimation of daily probabilities of persistence at our study site to determine stopover duration and DFL.

Material and methods

Study site and data collection

The study site, located near Johnson's Bayou (29°45'N, 93°37'W), Louisiana, USA is about 1.5 km inland from the Gulf of Mexico within a narrow, isolated coastal woodland (Chenier). Birds were captured using 20–30 mist nets (12 and 6 m length × 2.6 m with 30 mm mesh) that were

operated daily 07:00–17:00 CST, weather permitting, throughout spring migration, mid-March to early May, in 1993–1996 and 1998–2014 (see Cohen et al. 2015 for more information). After capture, birds were transported to a central processing area where they received a United States Geological Survey leg band, and mass (nearest 0.01 g) as well as wing length (unflattened wing chord; nearest 0.5 mm) were recorded. Sex and age were determined based on Pyle et al. (1987) or Pyle (1997). If we were unable to confidently determine whether a bird belonged to a specific age class (SY or ASY), it was recorded as the less specific after-hatch-year (AHY) age class. The amount of subcutaneous fat in the furcular and abdominal areas was categorized based on the six-point scale in Helms and Drury (1960). We used data from species that met the following criteria: 1) they are true passage migrants at our site (do not breed or winter there), 2) we had > 1 d recapture data from at least 100 individuals, and 3) we had > 1 d recapture data from at least 20 individuals of each sex and at least 20 individuals of each of the more specific SY and ASY age categories. Of the 51 regularly captured migratory songbird species at the study site, six species met all three of these criteria (Table 1).

Stopover duration modeling

The crucial parameters to estimate in our study are fuel deposition rate (FDR) and departure fuel load (DFL). To gain the best possible estimates, we need to know, for each individual bird, stopover duration, rate of mass increase and mass at departure. Initially, regressions were performed between FDR and the fuel load at last capture, adjusted to 1900 (see section below for calculation of FDR and time adjustment methods). All species showed a significant positive relationship between FDR and day of last capture fuel load, but the R^2 values were very low (average: 0.17, SD: 0.08). It is likely that many birds departed subsequent to the day of last capture (Schaub et al. 2001), and so a mark–recapture modelling approach was used to estimate the stopover duration of migrants and determine DFLs that more accurately represent fuel loads on the day of departure.

We used Cormack–Jolly–Seber models in Program MARK (White and Burnham 1999) to estimate stopover duration, which enabled us to correct the DFL of individuals to reflect the amount of time they spent on the site. Data for this modeling were confined to our six focal species but included all captures and recaptures of each bird. The 'survival' estimates generated from these models corresponded to daily probabilities of persistence at the site (Table 2), corrected for imperfect capture probability of individuals even when they are still present at the site, and were transformed into stopover duration estimates using the formula for life expectancy (Schaub et al. 2001, Efford 2005). Across our six focal species, the majority of individuals that were captured on more than one day had days in which they were known to be present but were not captured. The daily recapture probability of individuals known to be

present at the site averaged 0.23 (range: 0.11–0.41). Overall, estimates of stopover duration based simply on first and last capture would be biased low, further supporting the need to account for imperfect recapture probability to estimate stopover duration and DFL.

We examined candidate models that incorporated effects of sex, age, mass at first capture, and ordinal date of first capture on daily persistence and recapture probability using Akaike's Information Criterion adjusted for small sample size (AIC_c; Burnham and Anderson 2002). After first determining the best-fitting structure for recapture probability, we evaluated candidate models that incorporated single, additive, and interactive effects of sex, age, and mass at first capture on daily persistence; all candidate models for persistence incorporated an additive effect of ordinal date of first capture (declining persistence with increasing date; Table 3).

To generate confidence intervals for our stopover-duration estimates, we first refit our best-ranked model using a Bayesian Markov Chain Monte Carlo approach (White et al. 2009). We fit models using 5000 tuning samples, 5000 burn-in samples, and 100 000 samples retained for the posterior distribution. We then resampled from the posterior distribution 10 000 times, on each iteration randomly selecting one of the 100 000 sets of simultaneously produced parameter estimates. During each iteration, we used the parameter estimates to generate the linear prediction (on the logit scale) given the covariate values of interest, exponentiated this logit-scale value, and used the resulting estimate of daily persistence probability to generate the expected lifespan (i.e. stopover duration).

Fuel deposition rate, estimated departure mass, and departure fuel load calculations

We estimated the FDRs (g d^{-1}) of migrants stopping over at our study site using methods detailed by Cherry (1982) that is, the rate of mass change was standardized by computing the percent change/hour (Moore and Kerlinger 1987, Loria and Moore 1990, Morris et al. 1994, Nemeth and Moore 2012, Zenzal and Moore 2016). We did this by subtracting the final capture mass from the initial capture mass for birds recaptured the same day of initial capture, and then dividing by the number of hours between captures (Table 4). For birds that were captured on more than one day (stopover duration ≥ 1 d; sensu Schaub et al. 2008), we used the species-specific hourly FDR to correct initial and final capture masses to 19:00 h since we expect nocturnal migrants to depart shortly after civil twilight (Smolinsky et al. 2013, Deppe et al. 2015). After masses were corrected for birds captured on more than one day, we calculated daily FDR (g d^{-1}) by subtracting the final time-corrected capture mass from the initial time-corrected capture mass and dividing by the number of days between captures (Table 5).

We estimated the departure mass (EDM; g) of each individual based on the individual's stopover duration as determined by banding data or mark–recapture model estimates (described above), which ever was longer. For example, if an individual had a minimum stopover duration (based on banding data; Cherry 1982) shorter than that estimated by our mark–recapture stopover models (Table 2), we used the estimate provided by the model as the bird's stopover duration (47% of individuals). In these cases, we calculated the EDM by first multiplying the FDR (g d^{-1}; described above) with the model estimated stopover duration and then adding that value to the individual's time corrected initial mass. However, if the bird's minimum stopover duration (based on banding data) was longer than the model estimated stopover duration, we then used the time corrected final capture mass as the bird's EDM (53% of individuals). Although this latter situation may, at first, seem counterintuitive, our estimates of stopover duration are population-level estimates with inherent variability. Thus, even after adjusting for imperfect recapture probability, some naïve (i.e. unadjusted) estimates of stopover duration for individuals will exceed the adjusted population average.

The EDM of migrants was size-corrected as in Ellegren (1992) and Owen and Moore (2006). For each species, birds captured at the study site with similar (unflattened) wing chord measurements (rounded up to the nearest mm) were grouped together. For each wing chord increment, mass at first capture was regressed against fat scores and the y-intercept was taken as the estimated fat-free mass for that wing chord increment. In a second regression, the estimated fat-free masses were regressed on their corresponding wing chords. If the second regression explained less than two-thirds of the variation in the data, then Cook's distances were calculated and any wing chord increment with a value higher than 4/n was removed. This process was repeated until either the resulting $R^2 \geq 0.65$ or all Cook's distances were < 4/n (Bollen and Jackman 1990). The resulting equation was then applied to all individuals of each species used in the present study to calculate its expected fat-free mass. This value was then subtracted from the bird's EDM to determine the bird's DFL.

Regression analyses

Departure fuel loads were regressed against fuel deposition rates. For each species, 3 separate regressions were performed: 1) all individuals, 2) only individuals of known sex regardless of age (sex was a factor), and 3) only individuals of the more specific age classes regardless of sex (age was a factor). All analyses, including the resampling process, were performed in R 3.1.2 (R Core Team).

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.XXXXX> (Moore et al. 2016).

Results

We found a significant positive relationship between FDR and DFL for all six species examined (p < 0.001; Table 6; Fig. 2); fuel loads upon departure are dependent on FDR for stopover migrants stopping over. This consistent positive relationship between FDR and DFL appears to be biologically meaningful and not simply an artifact of the modeling effort to correct DFL, as all species showed a significant relationship even before modeling was undertaken to estimate stopover duration. However, the R^2 values were very low (average: 0.17, SD: 0.08) when we regressed uncorrected DFL (simply based on day of last capture) against FDR, not to mention the problem inherent in simply using capture data to estimate timing of departure. It is quite likely that birds have been on the site for one or more days after last capture, and we simply did not catch them, which would lead to an erroneous calculation of DFL and low degree of fit observed in the uncorrected regression. The MARK analysis enables us to more accurately estimate true stopover duration, which we believe provides a more accurate estimate of DFL than simply using day of last capture.

The strength of the relationship between FDR and DFL did vary among species (R^2 range: 0.17–0.52; Table 6). For example, the fit between FDR and DFL is rather weak in Tennessee warblers *Oreothlypis peregrina*, and especially so among ASY birds (Figure 3A). We found a significant interaction (p ≤ 0.01) between FDR and age for Tennessee warblers and indigo buntings *Passerina cyanea* (Table 6). The strength of the relationship was greater ($R^2 = 0.35$) and DFL more sensitive to changes in FDR (i.e. steeper slope) in SY Tennessee warblers compared to older individuals of that species ($R^2 = 0.16$; Fig. 3A), whose DFL was less dependent on changes in FDR. On the other hand, older, ASY indigo buntings ($R^2 = 0.55$) displayed a stronger relationship between FDR and DFL than did SY birds ($R^2 = 0.29$; Fig. 3B), and the slope was somewhat steeper for ASY indigo buntings.

We also found a significant interaction (p ≤ 0.04) between FDR and sex in three of our focal species. However, one male black-and-white warbler *Mniotilta varia* was a statistical outlier (Cook's distance > 1); it had the lowest FDR of any black-and-white warbler (-2.2 g d^{-1}), yet a very high DFL (1.6 3g). This individual had the highest fuel load of any black-and-white warbler upon first capture, and even though it had lost 2.2 g when recaptured 18 h later, it still departed with a relatively high fuel load. When this individual was removed from our analyses, there was no significant difference between sexes in this species (Fig. 4A). In both Kentucky warblers *Geothlypis formosa* (Fig. 4B) and hooded warblers *Setophaga citrina* (Fig. 4C) there was a sex-dependent relationship between FDR and DFL (Table 6). The relationship between FDR and DFL was stronger in males (Kentucky warbler $R^2 = 0.44$, hooded warbler $R^2 = 0.39$) than

females (Kentucky warbler R^2 = 0.25, hooded warbler R^2 = 0.23) for both species, and incremental changes in FDR resulted in a greater change in DFL in males of both species.

Discussion

We expected that Nearctic-Neotropical migratory songbirds would adjust their DFL to the rate at which they deposit fuel reserves during spring passage, and we found a positive relationship between DFL and FDR in all six focal species. The faster a migrant deposits fuel during stopover, the larger the fuel load upon departure. This robust finding suggests that these intercontinental migratory songbirds are sensitive to time constraints during spring passage (Alerstam and Lindström 1990), presumably to fine-tune their stopover schedule in relation to experienced and anticipated habitat quality (Hedenstr m 2008). A higher FDR favors a larger fuel load upon departure, which means that a migrant could fly farther with fewer stopovers, faster between stopover sites, or simply depart with a greater margin of safety in relation to adverse circumstances that might arise along the route to the breeding destination. If a migrant arrives late at a stopover site or stays longer than usual and does not make up lost time, a penalty may be attached to late arrival at the next stopover site if, for example, resource levels have been depressed by earlier migrants (cf. Moore and Wang 1991). If a migratory bird expects to 'catch-up' with the overall time-schedule and maintain a margin of safety in the face of anticipated energetic demands, she must refuel faster than average (Paxton and Moore 2015). Birds that experience en route delays in their migration schedules may arrive late and experience negative reproductive consequences (Smith and Moore 2003, 2005, Moore et al. 2005). Moreover, migrants that arrive on the breeding grounds with surplus fuel loads have some insurance against predictably variable environmental conditions upon early arrive (Widmer and Biebach 2001), are able to devote more time to territory or mate assessment upon arrival, and ultimately enjoy enhanced reproductive performance (Sandberg and Moore 1996).

The strength of the relationship between DFL and FDR varied among the six species, with the weakest for Tennessee warbler and to a lesser extent black-and-white warbler. Although we do not know the precise destination of birds that were sampled following trans-gulf migration, Tennessee warblers breed exclusively across the boreal forest, while breeding populations of black-and-white warblers are distributed across eastern North America as well as the boreal forest (Paxton and Moore 2015, Covino et al. 2016). The breeding distributions of the other four species, which display a stronger relationship between DFL and FDR than either of the boreal-breeding species, are essentially confined to temperate forests within the eastern United States, and it is likely that some individuals are engaged in a sprint to nearby breeding grounds (Alerstam 2006, Karlsson et al. 2012). The pressure to minimize time during passage

may increase with proximity to the breeding destination, and might explain the inter-specific variation in strength of the FDR–DFL relationship. The initial onset of migration is known to be under the control of an endogenous rhythm (Gwinner 1996, Maggini and Bairlein 2010), and if the endogenous program also controls resumption of migration from stopover, it may reflect proximity to destination. There is some evidence that rate of passage increases over the course of spring migration (Dierschke and Delingat 2001, Cohen et al. 2014), and reason to believe that adjustment in the rate of migration among Nearctic-Neotropical migratory birds takes place within North America. If migrants are arriving on temperate breeding grounds earlier in North America (Root et al. 2003, Ellwood et al. 2010), but are not arriving any earlier across the Gulf of Mexico (Cohen et al. 2015), they must speed up the rate of migration within North America. In fact, migrants are known to adjust the speed of migration from the northern coast of the Gulf of Mexico to temperate breeding areas in the northeast US (Marra et al. 2005) not to mention move at a faster pace and with more precision in spring (Horton et al. 2016).

We predicted older, ASY birds would be less sensitive to changes in FDR at our study site after crossing the Gulf of Mexico because they would anticipate higher fuel deposit rates at better quality sites further along the migratory route. Interestingly, two species showed an effect of age on the FDR–DFL relationship: in Tennessee warblers the DFL of SY birds was more sensitive to changes in FDR, consistent with our expectation, while the interaction with age in indigo buntings was counter to our expectations (Fig. 1A), but consistent with age-related sensitivity to en route time constraints and a more 'hurried' age-dependent migration strategy (see also Schaub et al. 2008).

Species-specific en route habitat suitability (Cohen et al. 2014) may have been a confound contributing to observed variation in the relationship between DFL and FDR especially in relation to age in Tennessee warblers. Although songbirds are plastic in their foraging behavior during passage (Loria and Moore 1990, Martin and Karr 1990), Tennessee warblers are generally associated with the canopy during stopover in habitat that characterizes our Chenier study area (Barrow et al. 2000), and birds may have found the habitat progressively less suitable over the course of the study period as the canopy has deteriorated after hurricane impacts in 2005 and 2008 (Lain 2012). Whereas we might have expected the fuel loads of older, more experienced individuals upon departure to be more sensitive to changes in FDR, older birds may view the coastal stopover habitat as less suitable than sites further along the migratory route and simply leave regardless of their fuel load. Less experienced SY birds, on the other hand, may be making the best of the situation. The fact that SY Tennessee warblers displayed a FDR–DFL relation comparable to that of other species makes the 'response to habitat' argument appealing as both SY and ASY Tennessee warblers are traveling to distant boreal breeding grounds.

We expected to see sex-dependent differences in the relationship between FDR and DFL, and found that the DFL of male Kentucky warblers and hooded warblers were more sensitive to changes in FDR than the DFL of females of either species. This pattern is consistent with greater sensitivity to time constraints among males during passage in these two species. The lack of a sex-dependent difference in four species and only a subtle difference in two species suggests that both males and females are time constrained during spring passage, especially after entering North America (Marra et al. 2005, Cohen et al. 2015). For example, male–male competition for breeding territories and mates is well documented in songbirds, which would lead to increased pressure on males to arrive in a timely fashion on the breeding grounds. Arrival time of females also influences reproductive performance (Smith and Moore 2005) as female–female competition for mate choice and nest sites is likely strong. Despite pressures for timely arrival, females do experience at least two constraints that may affect the relationship between FDR and DFL during stopover: 1) given that females do not advertise for territories, settling prior to males may result in failure to find a mate and 2) a female's nutritional condition and health limit her ability to produce eggs. Moreover, the time schedule of female passage may be adjusted to reduce overlap with male passage if socially subordinate to males (Moore et al. 2003), which may affect sensitivity to time constraints.

Conclusions

Our study is the first to examine the relationship between DFL and FDR among Nearctic-Neotropical songbird migrants. All species examined and both age and sex groups showed a significant positive relationship between FDR and DFL, implying a migration strategy sensitive to time (Alerstam and Lindström 1990). That said, variation among individuals within species, age and sex groups as well as among species was striking and points to the complexity inherent in understanding the stopover biology of migratory birds. A migrant's decision to depart or remain at a stopover site is likely governed by the bird's actual behavioral and physiological states as well as its temporal and spatial position within its endogenously programmed migration schedule (Jenni and Schaub 2003, Hedenstr m 2008). Yet, the spatio-temporal program provides only a framework within which other factors influence stopover decisions (Gwinner 1996, Deppe et al. 2015). A mix of intrinsic and extrinsic factors, including species-, age- and sex-specific use of habitat (Cohen et al. 2012) as well as day-to-day variation in the threat of predation (Cimprich et al. 2005), competitor density (Moore and Wang 1991), and weather (Dänhardt and Lindstr m 2001, Deppe et al. 2015) will influence the relationship between FDR and DFL and likelihood of departure. Moreover, migrating birds gather information, integrate environmental and internal state data, and make decisions about when to depart a stopover site presumably in relation to anticipated conditions. Some of the variation in FDL–DFL

relationship observed in our study reflects the fact that we had little, if any information about future conditions of the migrants studied much less how they calculate or gauge future conditions. That aside, some of the observed variation surely reflects the capacity for individual 'strategic' variation in decision making (sensu Winker et al. 2014).

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Table Legends

Table 1. Sample sizes for the species used in analyses of fuel deposition rate and departure fuel load by age and sex. Common name and abbreviated species code are provided. It was not always possible to determine the more specific age classes of captured individuals thus the 'All' column under each sex reflects individuals belonging to each of the more specific age classes (SY and ASY) as well as those for which we were unable to determine specific age.

Common name	Scientific name	Species code	Total	Male			Female		
				SY	ASY	All males	SY	ASY	All females
Black-and-white warbler	*Mniotilta varia*	BAWW	220	55	38	122	40	32	97
Prothonontary warbler	*Protonotaria citrea*	PROW	103	4	30	56	17	15	47
Tennessee warbler	*Oreothlypis peregrina*	TEWA	124	19	20	68	24	19	55
Kentucky warbler	*Geothlypis formosa*	KEWA	355	36	118	203	38	51	111
Hooded warbler	*Setophaga citrina*	HOWA	416	70	76	218	83	45	193
Indigo bunting	*Passerina cyanea*	INBU	377	93	100	217	56	58	148

Table 2. Stopover duration is provided for each species as well as age and/or sex groups. Mean modeled stopover was based on model selection results (see text; Table 3) and sample sizes used to generate estimates are provided. Mean minimum stopover is based on the number of days between first capture and last capture (for individuals captured more than once) and sample sizes of birds that were captured across multiple days are provided. Refer to Table 1 for full species names.

Species code	Sex	Age	Mean modeled stopover duration [days ± SD (sample size)]	Mean minimum stopover duration [days ± SD (sample size)]
BAWW	All	All	1.74 ± 0.10 (1016)	2.63 ± 2.25 (220)
	Male	All	1.52 ± 0.11 (579)	2.31 ± 1.73 (122)
	Female	All	2.02 ± 0.18 (437)	3.03 ± 2.72 (98)
PROW	All	All	2.30 ± 0.27 (495)	3.11 ± 2.29 (103)
	Male	SY	2.26 ± 0.64 (29)	4 ± 3.46 (4)
	Male	ASY	2.39 ± 0.39 (91)	2.87 ± 2.03 (30)
	Female	SY	3.36 ± 0.70 (50)	3.59 ± 3.04 (17)
	Female	ASY	1.70 ± 0.33 (76)	3.07 ± 2.63 (15)
TEWA	All	All	1.40 ± 0.13 (1497)	2.03 ± 1.70 (124)
	Male	All	1.38 ± 0.14 (848)	1.93 ± 1.63 (68)
	Female	All	1.42 ± 0.16 (649)	2.02 ± 1.63 (55)
KEWA	All	All	1.86 ± 0.08 (911)	2.63 ± 2.02 (355)
HOWA	All	All	1.56 ± 0.06 (1841)	2.47 ± 2.33 (416)
	Male	All	1.69 ± 0.09 (950)	2.43 ± 2.13 (219)
	Female	All	1.44 ± 0.08 (891)	2.34 ± 1.96 (194)
INBU	All	All	1.65 ± 0.11 (3367)	2.89 ± 2.47 (377)
	All	SY	1.41 ± 0.15 (1292)	3.05 ± 2.42 (153)
	All	ASY	1.95 ± 0.15 (1385)	2.52 ± 1.97 (162)

Table 3. Summary of the top models used to predict daily persistence probability (ф) of each focal species captured at Johnson's Bayou, LA during spring migration from 1993–2014. Candidate models were fit using the best-fitting structure for recapture probability. For each species we provide the top model, K, and AIC$_c$ weight (w). The ΔAIC$_c$ for each species model equals zero.

Species code	Model	K	w_i
BAWW	ф(sex + mass + dayofyear)p(sex)	6	0.38
PROW	ф([sex × mass × age] + dayofyear)p(dayofyear)	15	0.84
TEWA	ф([sex × mass] + dayofyear)p(dayofyear)	7	0.46
KEWA	ф(mass + dayofyear)p(dayofyear)	5	0.57
HOWA	ф(sex + mass + dayofyear)p(.)	5	0.51
INBU	ф(mass + age + dayofyear)p(age)	8	0.60

Table 4. The stopover duration (hours) and hourly FDR (g h^{-1}) of each focal species based on same day recaptures.

Species code	Stopover duration (hours)	FDR (g h^{-1})	Sample size
BAWW	4.53 ± 2.53	0.0006 ± 0.10	39
PROW	4.24 ± 1.83	−0.01 ± 0.12	28
TEWA	4.67 ± 1.95	−0.04 ± 0.42	45
KEWA	4.26 ± 2.59	−0.12 ± 0.69	127
HOWA	3.96 ± 2.12	−0.03 ± 0.30	137
INBU	3.91 ± 2.10	−0.04 ± 0.15	122

Table 5. Arrival fuel load (g), estimated fuel deposition rate (g d^{-1}), and estimated departure fuel load (g) for each focal species. Arrival and departure fuel loads are defined as mass exceeding fat-free body mass based on wing chord regressions (see methods for details). For arrival fuel load we present data on all captures, birds only captured once, and birds recaptured ≥ 1 d later. For recaptured birds, we also provide fuel deposition rate and estimated departure fuel load.

| Species code | Arrival fuel load | | | Fuel deposition rate | | Departure fuel load | |
	All birds [mean ± SD (sample size)]	Single captured birds [mean ± SD (sample size)]	Recaptured birds [mean ± SD (sample size)]	Mean [± SD]	Range	Mean [± SD]	Range
BAWW	0.86 ± 0.99 (1023)	0.93 ± 0.99 (801)	0.62 ± 0.92 (220)	0.15 ± 0.45	−2.20–2.60	1.12 ± 0.96	−1.65–4.86
HOWA	0.54 ± 0.92 (1882)	0.63 ± 0.92 (1462)	0.18 ± 0.78 (416)	0.22 ± 0.40	−1.75–1.85	0.57 ± 0.87	−2.13–3.69
INBU	1.55 ± 2.13 (3439)	1.66 ± 2.17 (3059)	0.54 ± 1.09 (377)	0.13 ± 0.47	−1.61–1.67	0.85 ± 1.54	−6.65–7.29
KEWA	0.79 ± 1.20 (1048)	0.94 ± 1.24 (693)	0.50 ± 1.05 (355)	0.27 ± 0.70	−1.81–4.95	0.52 ± 1.52	−3.72–9.69
PROW	0.91 ± 1.23 (537)	0.95 ± 1.24 (429)	0.81 ± 0.96 (103)	0.33 ± 0.48	−0.98–1.55	1.93 ± 1.60	−2.20–6.01
TEWA	1.02 ± 1.01 (1879)	1.06 ± 1.01 (1707)	0.57 ± 0.89 (124)	0.25 ± 0.48	−1.13–1.76	0.82 ± 0.91	−1.84–2.94

Table 6. Results of regression analyses for each focal species captured at Johnson's Bayou, LA during spring migration. Fuel deposition rate (FDR) was used as the independent variable and departure fuel load (DFL) as the dependent variable. For each species, three models were run: 1) all birds (1st row), 2) only birds of known sex (males/females, 2nd row) with sex as a factor, and 3) only birds where a more specific age was known (SY/ASY, 3rd row) with age as a factor. The t and p values are provided for the entire model ('Model' column), the effect of age (for the age factor model) or sex (for the sex factor model) on DFL ('Age or sex' column), and the effect of the FDR × age (for the age factor model) or FDR × sex (for the sex factor model) interaction on DFL ('FDR × age/sex interaction' column). The degrees of freedom (DF) and R^2 are provided for each model.

Species code	Sex	Age	Model		Age or sex		FDR × age/sex interaction		DF	R^2
			t	p	t	p	t	p		
BAWW	All	All	9.22	< 0.001	n/a	n/a	n/a	n/a	218	0.28
	Males/females	All	7.67	< 0.001	−0.50	0.62	−2.39	0.02	215	0.31
	All	SY/ASY	5.37	< 0.001	−0.75	0.46	1.19	0.24	162	0.31
PROW	All	All	10.51	< 0.001	n/a	n/a	n/a	n/a	101	0.52
	Males/females	All	7.00	< 0.001	−0.03	0.98	−0.02	0.98	99	0.52
	All	SY/ASY	6.57	< 0.001	0.12	0.91	0.99	0.33	62	0.51
TEWA	All	All	4.93	< 0.001	n/a	n/a	n/a	n/a	122	0.17
	Males/females	All	3.38	< 0.001	1.44	0.15	−0.78	0.44	119	0.18
	All	SY/ASY	2.62	0.01	−1.25	0.22	2.61	0.01	79	0.27

KEWA	All	All	17.97	< 0.001	n/a	n/a	n/a	n/a	353	0.48
	Males/females	All	6.61	< 0.001	−0.40	0.69	2.03	0.04	310	0.37
	All	SY/ASY	10.62	< 0.001	1.41	0.16	−0.88	0.38	251	0.39
HOWA	All	All	13.66	< 0.001	n/a	n/a	n/a	n/a	414	0.31
	Males/females	All	7.85	< 0.001	2.06	0.04	2.56	0.01	407	0.35
	All	SY/ASY	5.73	< 0.001	−0.12	0.9	0.84	0.40	270	0.25
INBU	All	All	15.88	< 0.001	n/a	n/a	n/a	n/a	375	0.40
	Males/females	All	10.30	< 0.001	1.48	0.14	−1.18	0.23	361	0.41
	All	SY/ASY	13.91	< 0.001	5.28	< 0.001	−3.44	< 0.001	308	0.47

Figure Legends

Figure 1. Predicted differences in the relationship between fuel deposition rate and departure fuel load based on age (A) and sex (B) during spring at a coastal stopover site. SY (second year); ASY (after second year). See text for explanation.
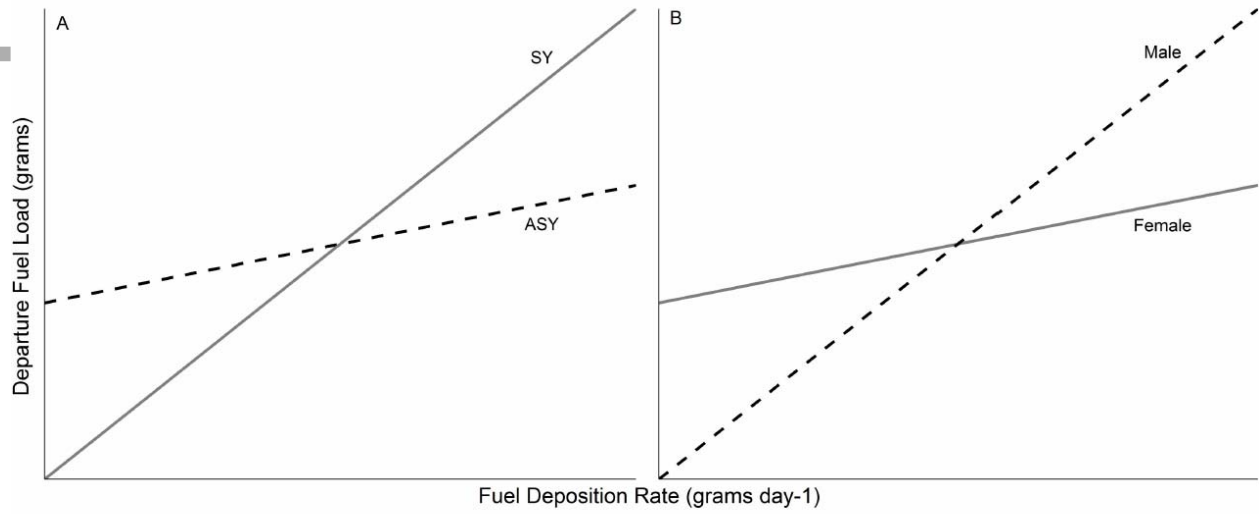
Figure 2. The relationship between departure fuel load (DFL; g) and fuel deposition rate (FDR; g d^{-1}) in six species of migratory songbirds captured near Johnson's Bayou, Louisiana, USA. Each dot represents an individual and dashed lines represent the relationship between DFL and FDR for each species. Refer to Table 1 for full species names.
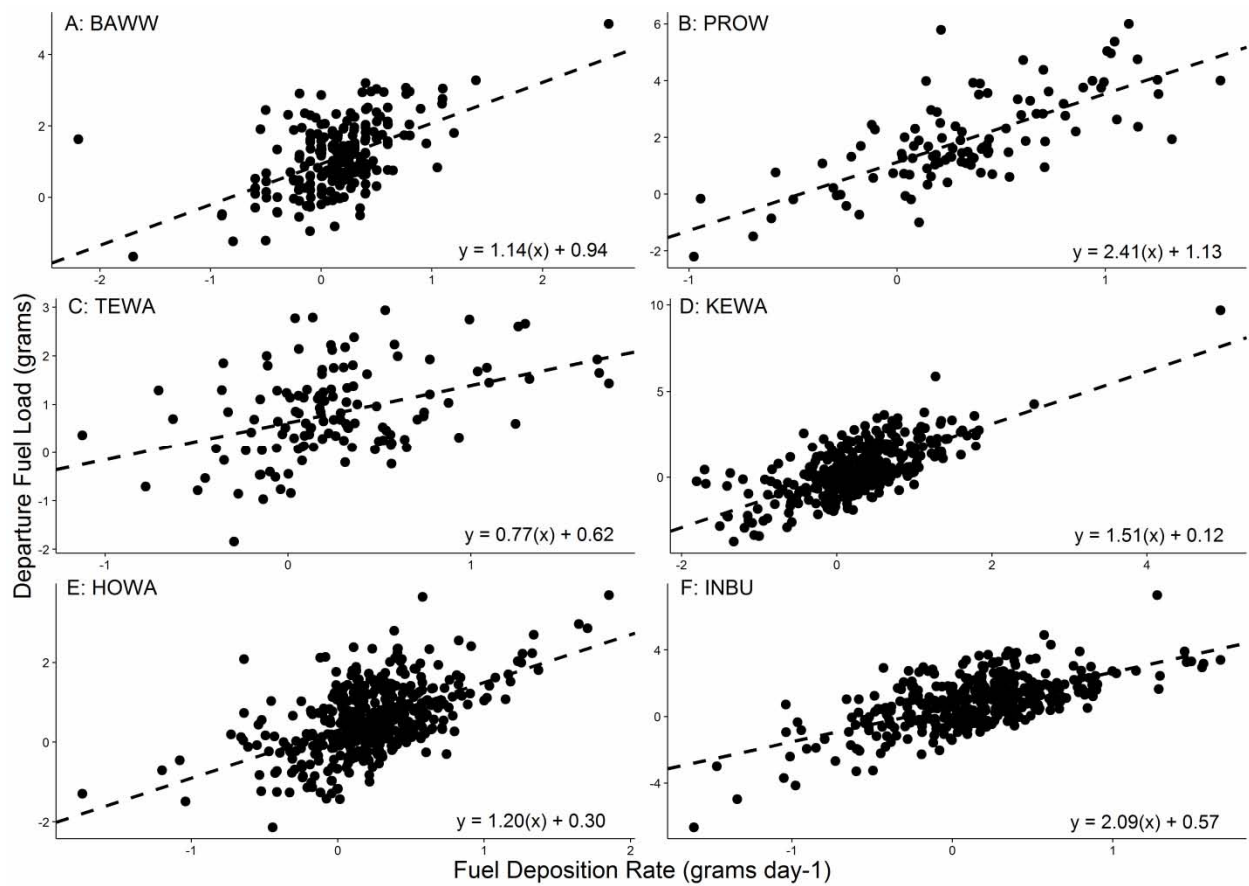
Figure 3. The relationship between departure fuel load (DFL; g) and fuel deposition rate (FDR; g d^{-1}) between second year (SY) and after second year (ASY) (A) Tennessee warblers and (B) indigo buntings captured near Johnson's Bayou, Louisiana, USA. Each dot represents an individual and dashed lines represent the relationship between DFL and FDR for each age class per species.
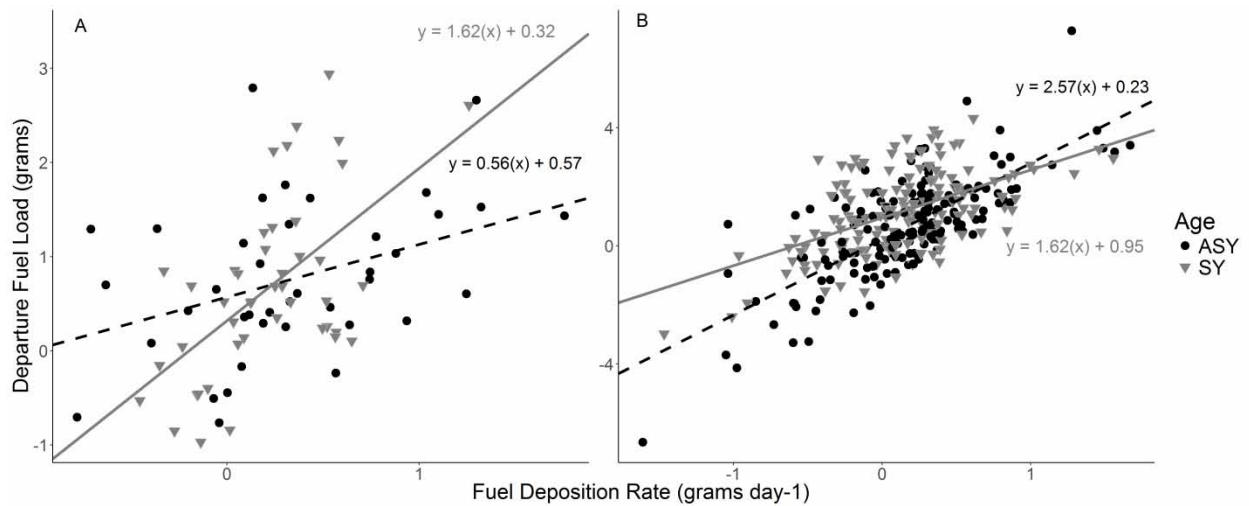
Figure 4. The relationship between departure fuel load (DFL; g) and fuel deposition rate (FDR; g d^{-1}) between sexes of (A) black-and-white warblers, (B) Kentucky warblers, and (C) hooded warblers captured near Johnson's Bayou, Louisiana, USA. Each dot represents an individual and dashed lines represent the relationship between DFL and FDR for each sex per species.