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ASSESSING MIGRATORY STOPOVER SITE QUALITY FOR BIRDS DURING FALL MIGRATION ALONG TWO CALIFORNIA RIVERS

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ABSTRACT.—Measuring site quality for birds at migration stopover grounds and identifying critical stopover habitats are both important components of gauging the full life cycle conservation of migratory birds. We evaluated riparian stopover habitat quality on the San Joaquin and Mokelumne rivers in California's Central Valley for migrant Willow Flycatchers (*Empidonax traillii*), Orange-crowned Warblers (*Oreothlypis celata*), Yellow Warblers (*Setophaga petechia*), and Wilson's Warblers (*Cardellina pusilla*). For each species, we used 3 approaches to assess habitat quality: (1) we examined change in mass of individuals that were recaptured at least once; (2) we tracked body condition over the time of day and over the course of the migratory season; and (3) we compared the rates of hourly mass change for Wilson's Warbler to similar studies in Canada and the United States. On average, individuals of all species recaptured at stopover sites increased mass from initial capture to final capture (0.49 g to 0.88 g). Over the course of the day, the average condition of individuals of all study species either showed increases or remained stable, although most increases were driven by after-hatch-year birds in the population. Only Yellow and Wilson's warblers at the San Joaquin sites showed a positive relationship between capture date and condition. For Wilson's Warblers, rate of mass change was higher at California riparian sites than at other stopover sites in Canada and the United States. Our results demonstrate the importance of riparian floodplain forests in California as a stopover for migrating landbirds.

RESUMEN.—La medición de la calidad de los sitios para las escalas de las aves durante su migración y el identificar los hábitats críticos para hacer dichas escalas son componentes importantes para conservar el ciclo de vida completo de las aves migratorias. Evaluamos la calidad del hábitat de las escalas ribereñas en los ríos San Joaquin y Mokelumne en el valle central de California, para las siguientes aves migratorias: los mosqueros sauceros (*Empidonax traillii*), las birijitas de coronilla anaranjada (*Oreothlypis celata*), las birijitas amarillas (*Setophaga petechia*) y las birijitas de Wilson (*Cardellina pusilla*). Para cada especie utilizamos tres enfoques diferentes para evaluar la calidad del hábitat: examinamos (1) los cambios en la masa corporal de los individuos que se recapturaron por lo menos una vez, (2) la condición corporal según la hora del día y a lo largo de la temporada migratoria, y (3) comparamos las tasas de cambio en la masa corporal por hora de las birijitas de Wilson con estudios similares realizados en Canadá y los Estados Unidos. Todas las especies aumentaron su masa corporal (de 0.49 g a 0.88 g), desde el momento de la captura inicial hasta la captura final de los individuos recapturados en los sitios de escala. La condición de todas las especies estudiadas aumentó o se mantuvo estable en el transcurso del día, aunque la mayor parte de los incrementos se produjo en las aves de un año en la población. Sólo las birijitas amarillas y de Wilson en los sitios de San Joaquin mostraron una relación positiva entre la fecha de captura y su condición. En el caso de las birijitas de Wilson, la tasa de cambio en la masa corporal fue superior en los sitios ribereños de California al que se registró en otros sitios de escalas de Canadá y los Estados Unidos. Nuestros resultados demuestran la importancia de los bosques riparios inundables en California que sirven como escala de las aves terrestres migratorias.

The conservation of migratory birds is challenging because any successful strategy must address the birds' full life cycle of breeding, wintering, and migration (Sherry and Holmes 1996, Faaborg et al. 2010). As a result, there has been an increasing emphasis on identifying high-quality stopover habitat for migratory birds (Petit 2000, Seewagen and Slayton 2008, Carlisle et al. 2009). Because one of the largest constraints for migrating birds is the ability to consume enough food to build fat stores (Woodrey and Moore 1997, Dunn 2002), many assessments of stopover habitat quality have been based on the rate at which migrants are able to gain body mass (Dunn 2002, Flannery et al. 2004, Carlisle et al. 2005, Bonter et al. 2007). Furthermore, physical condition during migration can influence an individual's performance during other aspects of the annual cycle (Marra et al. 1998, Moore et al. 2005, Bauchinger et al. 2009).

When migratory songbirds must cross large arid regions, riparian areas often provide important stopover habitat (Flannery et al. 2004).

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Many migrants pass through the seasonally arid Central Valley of California where they occur in large numbers in riparian habitat (Humple and Geupel 2002). Historically, there was extensive riparian habitat in California's Central Valley, but today only about 5% of this historical habitat remains (Katibah 1984). This loss and degradation of habitat has been attributed to many factors, including water diversion, urbanization, livestock grazing, timber harvest, water pollution, gravel and gold mining, and clearing for agriculture (RHJV 2004). Such a dramatic habitat loss can contribute to population declines in many species (Gardali et al. 2006). This loss may also mean that remaining migrants are concentrated into relatively small areas of habitat. Consequently, the quality of these important stopover sites may decline as increased competition reduces availability of resources (Moore and Yong 1991).

In the San Joaquin Valley, the southern region of the Central Valley, few studies have investigated the use of riparian areas by migrating landbirds (Humple and Geupel 2002). Despite the importance of Central Valley riparian areas to birds, we know of no studies that investigate the habitat quality for migrating songbirds. Our goal was to evaluate stopover habitat for migratory birds along the San Joaquin and Mokelumne rivers (Fig. 1). Specifically, our objectives were to evaluate stopover habitat quality by (1) comparing change in mass of individuals that were recaptured at least once, (2) assessing body condition over the time of day and over the course of the migratory season, and (3) calculating rate of hourly mass change for migrant species such that our results are comparable to other studies; specifically, we wanted to compare the rate of change of Wilson's Warbler mass at our sites to that reported in other studies in Canada and the United States.

METHODS

Study Area and Survey Period

We gathered data at 2 sites on the San Joaquin River, California, and 3 sites on the Mokelumne River, California (Fig. 1). The San Joaquin River sites were Lost Lake Island (36°59′N, 119°43′W) and Willow Unit (36°56′N, 119°45′W), both owned by the California Department of Fish and Game. These sites were separated by approximately 7 km. Vegetation at San Joaquin River sites was dominated by black willow (*Salix gooddingii*), Fremont's cottonwood (*Populus fremontii*), Valley oak (*Quercus lobata*), white alder (*Alnus rhombifolia*), sandbar willow (*Salix exigua*), blackberry species (*Rubus ursinus* and *Rubus discolor*), and annual grasses. Data were collected at the San Joaquin sites in the fall seasons (mid-August to end of October) of 2003–2005.

The Mokelumne River sites were Woodbridge Regional Park (38°10′N, 121°19′W) and 2 private properties (Fig. 1). The 2 private property sites and the Woodbridge site were all within 11 km of each other. The vegetation at Mokelumne River sites consisted primarily of Fremont's cottonwood, mixed willows (*Salix* spp.), California grape (*Vitis californica*), California rose (*Rosa californica*), poison oak (*Toxicodendron diversilobum),* blue elderberry (*Sambucus mexicana*), blackberry (*Rubus* sp.), mugwort (*Artemisia douglasiana*), and giant reed (*Arundo donax*). Data were collected at the Mokelumne sites during the same time period as at the San Joaquin sites. However, in the first 2 years of the study, we sampled only at Woodbridge and one of the private properties, and in the third year of the study, we were unable to sample at the Woodbridge site, so we instead sampled at the 2 private property sites.

In all analyses, we pooled individual site data for each river such that we compare variation between the 2 rivers, rather than among all 5 sites. For simplicity, we will refer to each group of banding stations along each river as one site: the San Joaquin site and the Mokelumne site. Additionally, results are pooled over the 3 years of the study because Dunn (2000) found annual variation in the rate of mass change and recommended that estimates be based on several years of data to better reflect typical conditions.

Data Collection

We captured birds in mist nets and followed methods for data collection as described in Ralph et al. (1993, 2004). We operated 10 nets at each site twice per week during each fall period. Nets were opened 15 min after local sunrise, checked every 30–40 min (more often in hot weather), and were kept open for 5 h. All birds received a standard aluminum U.S. Geological Survey Biological Resource Division band for permanent identification and were

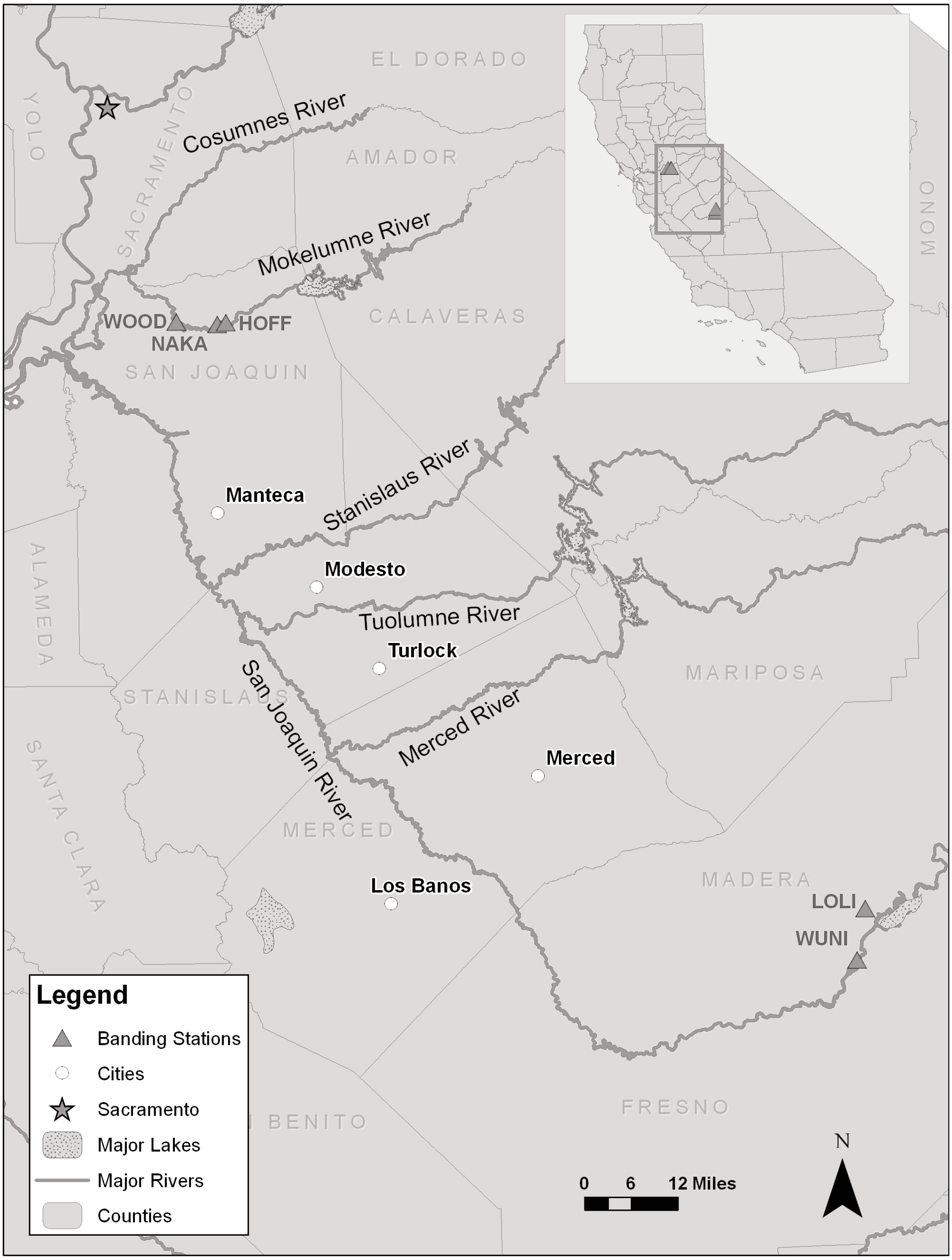

Fig. 1. Locations of study sites (banding stations) along the Mokelumne and San Joaquin rivers, California. Sites include Lost Lake Island (LOLI), Willow Unit (WUNI), Woodbridge Regional Park (WOOD), and 2 private properties (NAKA and HOFF).

identified to species. When possible, age was determined by the degree of skull pneumaticization and plumage criteria following Pyle (1997). We classified age as hatch-year (HY; hatched in the current calendar year), after hatch-year (AHY; hatched prior to the current calendar year), or unknown. We measured wing chord (unflattened) to the nearest millimeter and mass to the nearest 0.1 g. Subcutaneous fat was scored (0 = no visible fat; 1 = trace of fat visible in furculum; 2 = furculum 5%–33% filled with fat; 3 = furculum 34%–67% filled; 4 = 68%– 100% filled; 5 = furculum bulging slightly, abdomen well-mounded; 6 = furculum bulging greatly, abdomen with greatly distended mound).

Statistical Analysis

RECAPTURE METHOD.—We calculated change in mass as the difference between mass at first capture and mass at last capture. We averaged values for all recaptured individuals by species and calculated the standard error (SE). Willow Flycatcher (WIFL), Wilson's Warbler (WIWA), and Yellow Warbler (YEWA) do not overwinter at our sites, and therefore, all recaptures were included. Because a few Orange-crowned Warblers (OCWA) overwinter in the Central Valley of California (Gilbert et al. 2010), we omitted recaptured Orange-crowned Warblers with stopover lengths of >14 days, assuming that birds with such long stopovers were most likely winter residents. The longest stopovers amongst the migrant species were 2 Wilson's Warblers that stayed 14 days each, and we used this period to determine our cutoff for Orange-crowned Warblers.

TIME OF DAY AND DATE OF CAPTURE METHOD.—Because various factors may play a role in how long an individual remains at a stopover location (Moore and Yong 1991, Russell et al. 1994, Schaub et al. 2008), and because the probability of recapture is biased toward individuals that remain at a site longer, we assessed mass changes at stopover sites by looking at a species' mass change, where data for all birds captured can be used, regardless of whether the birds were recaptured (Winker et al. 1992). For species with a sample size of at least 50 captures (Orange-crowned, Wilson's and Yellow warblers, and Willow Flycatcher), we conducted analyses on the relationships between mass change and time of day by age class, and between mass change and date of capture. We did not have sufficient sample sizes for Willow Flycatcher and Yellow Warbler at the Mokelumne sites. We used linear regression to describe the relationships. We converted time of day to decimal values as hours after local sunrise to account for progressive change in timing of sunrise during each season (Dunn 2002). We converted capture date to Julian date. We adjusted mass for body size by calculating a condition index (CI = mass × 100/wing length, where multiplication by 100 reduces rounding error) as described by Winker (1995). Linear regression of condition on capture time was calculated for each species as $CI = b_0 + b_1H$, where H is the hour of capture past sunrise. The intercept, b_0, is the estimate of the average condition of each species at hour zero (sunrise before foraging). The slope of the regression line, b_1, is the estimate of hourly change in condition. The same method was used to evaluate date of capture on condition, but hour (H) was replaced with Julian date. Though use of condition indices may not always be the best measure of physical condition (Schamber et al. 2009), for the purpose of comparison with other studies, we felt it was appropriate here.

RATE OF HOURLY MASS CHANGE.—To compare our results to other studies (Dunn 2002, Bonter et al. 2007), we converted the estimate of hourly change in condition to hourly change in mass with the following formula: hourly mass change = b_1(wing length)/100. We calculated the average wing length for each species at each site to account for variation in wing length between sites. Next, we calculated the percent change in lean mass for each species and site using the following expression: (hourly mass change/average lean mass)*100. We calculated average mean mass for each species and site and used only birds with a fat score of 0 or 1 (see above). Wilson's Warbler was the only migrant species with sufficient sample size to compare to Dunn (2002) and Bonter et al. (2007).

All regression analyses were carried out using the program STATA (STATA Corp. 2003). Significance was assumed when $P < 0.05$. Values presented are means and standard errors (SE).

TABLE 1. Average change in mass from initial capture to final capture for recaptured individuals along the San Joaquin and Mokelumne rivers during fall seasons of 2003 to 2005.

Species	Location	*n*	% Recaptured of total	Average change in mass (g)	SE
WIFL	San Joaquin	2	2%	0.75	0.25
OCWA	Mokelumne	3	3%	0.5	0.61
	San Joaquin	12	9%	0.52	0.18
YEWA	San Joaquin	26	12%	0.88	0.11
WIWA	Mokelumne	6	6%	0.83	0.45
	San Joaquin	11	10%	0.49	0.18

TABLE 2. Relationship between condition and time of capture, by age class (AHY = after hatch-year, HY = hatch-year). Significant changes in condition are indicated in bold.

Species	Location	Age	*n*	Slope	SE	*P*
WIFL	San Joaquin	**AHY**	**23**	**0.51**	**0.21**	**0.03**
		HY	65	–0.05	0.18	0.80
OCWA	Mokelumne	AHY	23	–0.168	0.162	0.313
		HY	63	0.207	0.161	0.202
	San Joaquin	**AHY**	**16**	**0.85**	**0.40**	**0.05**
		HY	82	0.10	0.15	0.52
YEWA	San Joaquin	**AHY**	**79**	**0.31**	**0.13**	**0.02**
		HY	126	0.05	0.09	0.63
WIWA	Mokelumne	**AHY**	**21**	**0.44**	**0.12**	**0.003**
		HY	82	0.07	0.10	0.50
	San Joaquin	AHY	49	0.04	0.11	0.72
		HY	**53**	**0.30**	**0.15**	**0.05**

TABLE 3. Regression estimates of daily changes in mass during fall migration.

Species	Location	*n*	Mean hourly mass change (SE)	95% CI Lower	95% CI Upper
WIFL	San Joaquin	89	0.63% (0.81)	–0.98	2.25
OCWA	Mokelumne	95	0.87% (0.78)	–0.66	2.42
	San Joaquin	132	1.84% (0.92)	0.02	3.67
YEWA	San Joaquin	221	1.01% (0.50)	0.03	1.99
WIWA	Mokelumne	108	1.41% (0.67)	0.09	2.73
	San Joaquin	115	1.33% (0.63)	0.08	2.58

RESULTS

For individuals that were recaptured, all species increased in mass (from 0.49 g to 0.88 g) during their stopovers along both rivers (Table 1), although recaptured individuals represented a small proportion of birds captured (2%–12% of all birds captured were recaptured, depending on species).

Yellow Warbler (b_1 = 0.017, SE = 0.0073, P = 0.021) and Wilson's Warbler (b_1 = 0.022, SE = 0.0088, P = 0.012) exhibited a positive relationship between body condition index and date of capture at the San Joaquin River sites, but not at Mokelumne River sites, while Willow Flycatchers and Orange-crowned Warblers showed no such relationship. After-hatch-year Willow Flycatcher, Orange-crowned (San Joaquin only), Yellow, and Wilson's (Mokelumne only) warblers all exhibited a positive relationship between time of capture and condition (Table 2). Of the hatch- year birds examined, only Wilson's Warblers along the Mokelumne River exhibited a significant positive relationship between time of capture and condition (Table 2).

Mean hourly mass change ranged from 0.63% to 1.84% at San Joaquin and Mokelumne river sites (Table 3).

DISCUSSION

Based on recapture data, all species showed an increase in mass during stopover at San

Joaquin and Mokelumne river sites. However, there are some limitations to using only birds that are recaptured, such as small sample sizes and potential biases associated with recapturing birds in poorer condition (Morris 1996). Also, though understanding mass change at the individual level can be helpful in interpreting results from a stopover site, mass changes may not illuminate stopover patterns at the population level and can produce results that differ from those that consider all capture data (Winker et al. 1992, Woodrey and Moore 1997, Bonter et al. 2007).

Moore and Yong (1991) found that rates of mass gain may vary within a season, and our results support this for 2 species. Yellow Warblers and Wilson's Warblers that arrived later in the season at San Joaquin River sites had higher body condition index values than birds arriving earlier, suggesting that for Yellow and Wilson's warblers, resource availability may improve over the season, or perhaps site conditions improved at stopover sites prior to ours. While index of body condition may be driven by the food resources available, the changes we observed could also have been affected by weather conditions, a decrease in competition over the course of the season, or changing predator pressures. We did not find this relationship with Willow Flycatcher or Orange-crowned Warbler. Flannery et al. (2004) also found that condition indices were influenced by capture date, but only for spring migrants, and the direction of the effect varied among species.

All species at San Joaquin and Mokelumne river sites had at least one age class with significant increases in condition over time of day, and no species decreased in condition during fall migration. Compared to a similar study at the Salton Sea, birds in our study areas increased condition at a faster or comparable rate: Wilson's Warblers at the Salton Sea showed no significant increase in condition during fall migration, but Yellow Warblers exhibited increased condition in all age classes (Flannery et al. 2004).

There was only one case, Wilson's Warblers along the Mokelumne River, where hatch-year birds showed a significant increase in condition, while after-hatch-year birds of all species showed significant increases in condition over the course of the day at one or both sites. This difference may be because adults have more foraging experience and are generally more efficient at acquiring food (Richardson and Verbeek 1987, Sullivan 1988, Jones et al. 2002, Heise and Moore 2003). A study of Wilson's Warblers in riparian habitat along the Rio Grande River found that adults arrived with more fat than young birds (Yong et al. 1998), and this extra fat may result in higher foraging efficiency if the adults are in better condition initially. Other studies have shown that less dominant birds (often including young individuals) tend to be pushed to suboptimal habitat or territories on breeding and wintering grounds (Holmes et al. 1996, Marra et al. 1998), and these patterns may also be true at migratory stopover sites. Therefore, researchers should consider the proportion of young to adults in their population when assessing mass changes and combining age classes (Ralph 1971, 1981). Furthermore, the ability of migrants to find enough food may also be related to the number of individuals using a site because of competition for food (Moore and Yong 1991, Kelly et al. 2002).

When compared to results from other stopover studies, Wilson's Warblers at our study sites showed higher rates of hourly mass increase, suggesting high resource availability. Thus, migrants appeared to have sufficient resources to replenish reserves and continue their migration. Dunn (2002) found that the rate of hourly mass change for Wilson's Warblers at sites across Canada ranged from 0.37% to 0.99% ($\bar{x}$ = 0.79%) and Wilson's Warblers at a site near Lake Ontario had a rate of change of 0.98% (Bonter et al. 2007). In our comparisons of species-specific results, we were limited to species in common with Dunn (2002) and Bonter et al. (2007); however, when we considered other warbler species, our results of hourly mass change (range 0.87%–1.84%) were very comparable to the warbler species examined in the Bonter et al. (2007) study (range 0.80%–1.58%), but rates of change for species at our sites tended to be higher than most warblers at most sites examined by Dunn (2002; range –0.14% to 1.2%). Delingat et al. (2009) found that the sample sizes necessary to detect a significant relationship when using the first-trap-by-time-of-day method should be increased as rate of mass change decreases and as individual variation in body mass of birds in the sample increases. While Bonter et al. (2007) and Dunn (2002) usually had far greater sample sizes than we had, it is possible that individuals at their sites were more variable in size than individuals at our sites.

The loss and degradation of the riparian habitat in California's Central Valley has been immense, and pressures on the natural resources will likely continue. However, efforts are being made to restore habitat and water flows in many areas throughout the Central Valley that have been beneficial to bird populations (Gardali et al. 2006, Golet et al. 2008, Howell et al. 2010). The overall positive change in body mass of landbirds and the magnitude of that change both suggest that, although the riparian habitat in California's Central Valley has been highly modified, it remains important to migrant species as fall stopover habitat. For Wilson's Warbler, the one species we had in common with other studies, change in body mass was higher at our sites in the Central Valley. Comparing rates of mass change in migrants in different geographic areas and habitat types and at varying distances from geographic barriers can help identify patterns of mass change and inform conservation efforts (Bonter et al. 2007). Additionally, studies of mass change at stopover sites by use of the same methods can help us to identify high-quality important stopover sites and put results from a local study into a larger-scale context.

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