



RESEARCH ARTICLE

Dunlin subspecies exhibit regional segregation and high site fidelity along the East Asian–Australasian Flyway

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ABSTRACT

The degree to which individuals migrate among particular breeding, migration, and wintering sites can have important implications for prioritizing conservation efforts. Four subspecies of Dunlin (*Calidris alpina*) migrate along the East Asian–Australasian Flyway. Each subspecies has a distinct and well-defined breeding range, but their migration and winter ranges are poorly defined or unknown. We assessed the migratory connectivity of 3 of these subspecies by evaluating a dataset that encompasses 57 yr (1960–2017), and comprises more than 28,000 Dunlin banding records and 818 observations (71 recaptures and 747 band resightings). We present some of the first evidence that subspecific segregation likely occurs, with *arctica* Dunlin wintering in areas of Japan, and other *arctica*, *actites*, and *sakhalina* Dunlin wintering in areas of the Yellow and China seas. Observations indicate that whether an *arctica* Dunlin winters in Japan or the Yellow and China seas is independent of their breeding location, sex, or age. Furthermore, observations indicate that ≥83% of *arctica* Dunlin exhibit interannual site fidelity to specific wintering sites. This suggests that the degradation of specific wetland areas may negatively affect particular individuals of a particular subspecies (or combination of subspecies), and, if widespread, could result in population declines. Given the possible biases inherent in analyzing band recovery data, we recommend additional flyway-wide collaboration and the use of lightweight tracking devices and morphological and genetic assignment techniques to better quantify subspecies' migratory movements and nonbreeding distributions. This information, when combined, will enable effective conservation efforts for this species across the East Asian–Australasian Flyway.

Keywords: *Calidris alpina*, flyway conservation, migration ecology, migratory connectivity

LAY SUMMARY

- The East Asian–Australasian Flyway has more threatened and near-threatened migratory waterbird species than any other flyway in the world; however, developing flyway conservation plans has been challenging, in part due to limited information regarding population-specific migration patterns.
- Four subspecies of Dunlin migrate and winter along the East Asian–Australasian Flyway. Each has a well-defined breeding range; their migration and winter ranges are poorly defined or unknown.
- We assessed the migratory connectivity of 3 subspecies using data from 57 yr (1960–2017), which comprises more than 28,000 Dunlin banding records, 71 recaptures, and 747 band resightings.
- Subspecific segregation likely occurs, with *articolica* Dunlin wintering in Japan, and other *articolica*, *actites*, and *sakhalina* Dunlin wintering in the Yellow and China seas. It is likely that $\geq 83\%$ of *articolica* Dunlin exhibit interannual site fidelity to specific wintering sites.
- Our findings suggest that degradation of specific wetland areas may negatively affect particular individuals of a particular subspecies (or combination of subspecies) and could result in population declines.

东亚–澳大利西亚迁飞区内黑腹滨鹬亚种的区域隔离及高栖息地忠诚度现象

ABSTRACT

候鸟对其繁殖地、迁徙停歇地和越冬地的利用程度的差异对决定保护工作的优先次序安排有重要意义。目前黑腹滨鹬 (*Calidris alpina*) 有 4 个亚种在东亚–澳大利西亚迁飞区 (EAAF) 内迁徙, 这些亚种的繁殖区域分布有明显的区别, 但它们的迁徙停歇以及越冬分布情况则尚不明确或未知。我们从一个横跨了 57 年的数据库 (1960–2017 年) 中获取了超过 28,000 笔黑腹滨鹬环志记录和 818 笔回收记录 (71 笔环志回收和 747 笔野外目击), 从这些资料分析评估了其中 3 个黑腹滨鹬亚种的迁徙连接情况, 其中部分 *articolica* 亚种在日本越冬, 其余的 *articolica* 个体会跟亚种 *actites* 和 *sakhalina* 在黄海、东海及南海越冬, 这些黑腹滨鹬亚种间迁徙和越冬分布范围的分隔, 提供了首批证实其非繁殖地区域分隔现象的可能证据。观察记录表明黑腹滨鹬 *articolica* 亚种的越冬地与该个体的繁殖地点、性别和年龄没有关联。此外, 观察记录表明超过 83% 的黑腹滨鹬 *articolica* 亚种对个别越冬地点有跨年度的忠诚度, 这也说明个别湿地的退化会对某个亚种 (或多个亚种) 的个别个体造成负面影响, 如果湿地退化的情况在整个迁飞区普遍发生, 更将可能导致种群数量下降。鉴于分析环志回收数据时可能存在固有的偏差, 我们建议开展更多迁飞区域尺度上的合作、透过利用轻型的追踪器、个体的形态信息和遗传赋值技术去更好的量化各个亚种的迁徙活动和非繁殖期分布。把这些信息结合起来后, 将能更有效地在整个迁飞区内保护这个物种。

Keywords: *Calidris alpina*, 迁徙连接, 迁飞区保护, 迁徙生态学

INTRODUCTION

Determining the degree to which individuals migrate among particular breeding, migration, and wintering sites (i.e. population “migratory connectivity”; Webster et al. 2002) is an important and necessary step in prioritizing the protection of critical sites for populations of conservation concern (Martin et al. 2007, Taylor and Norris 2010, Iwamura et al. 2014). Within the East Asian–Australasian Flyway (EAAF) there are ~8 million migratory shorebirds belonging to 54 species, and more threatened and near-threatened migratory waterbird species than in any other flyway in the world (Bamford et al. 2008, Kirby 2011). Among the threatened and near-threatened migratory shorebirds, those showing the fastest population declines are ones that rely on the intertidal mudflats of the Yellow Sea region during their annual migrations (Amano et al. 2010, 2012, Studds et al. 2017). An ~2% annual decline of intertidal extent (1950s–2000s; Murray et al. 2014) has led to a substantial loss of critical habitats along the Yellow Sea coast, indicating the importance of protecting remaining intertidal habitats to slow future shorebird population

declines (Moores et al. 2016, Piersma et al. 2016, Murray et al. 2018). However, developing comprehensive flyway conservation plans for shorebirds on the EAAF has been a challenge, in part due to limited information regarding population-specific migration patterns (Kirby et al. 2008, Hua et al. 2015, Xia et al. 2017).

The Dunlin (*Calidris alpina*) is one of the most abundant and widely distributed migratory shorebirds throughout the EAAF with a flyway-wide population estimate of 950,000 (Bamford et al. 2008). Four recognized subspecies use the flyway, each breeding in a geographically distinct region of eastern Russia or northern Alaska (Browning 1991, Engelmoer and Roselaar 1998, Lappo and Tomkovich 1998, Lappo et al. 2012; Figure 1A). Collectively these 4 subspecies migrate and winter inland and along the coasts of mainland China, Taiwan, the Korean Peninsula, and Japan (Bamford et al. 2008, Cao et al. 2009). Recent work suggests that Dunlin populations on the EAAF are in decline, mostly due to deteriorating conditions on their nonbreeding grounds (Amano et al. 2010, 2012, Weiser et al. 2018, Weiser et al. 2020). For example, Weiser et al. (2018) found that among the

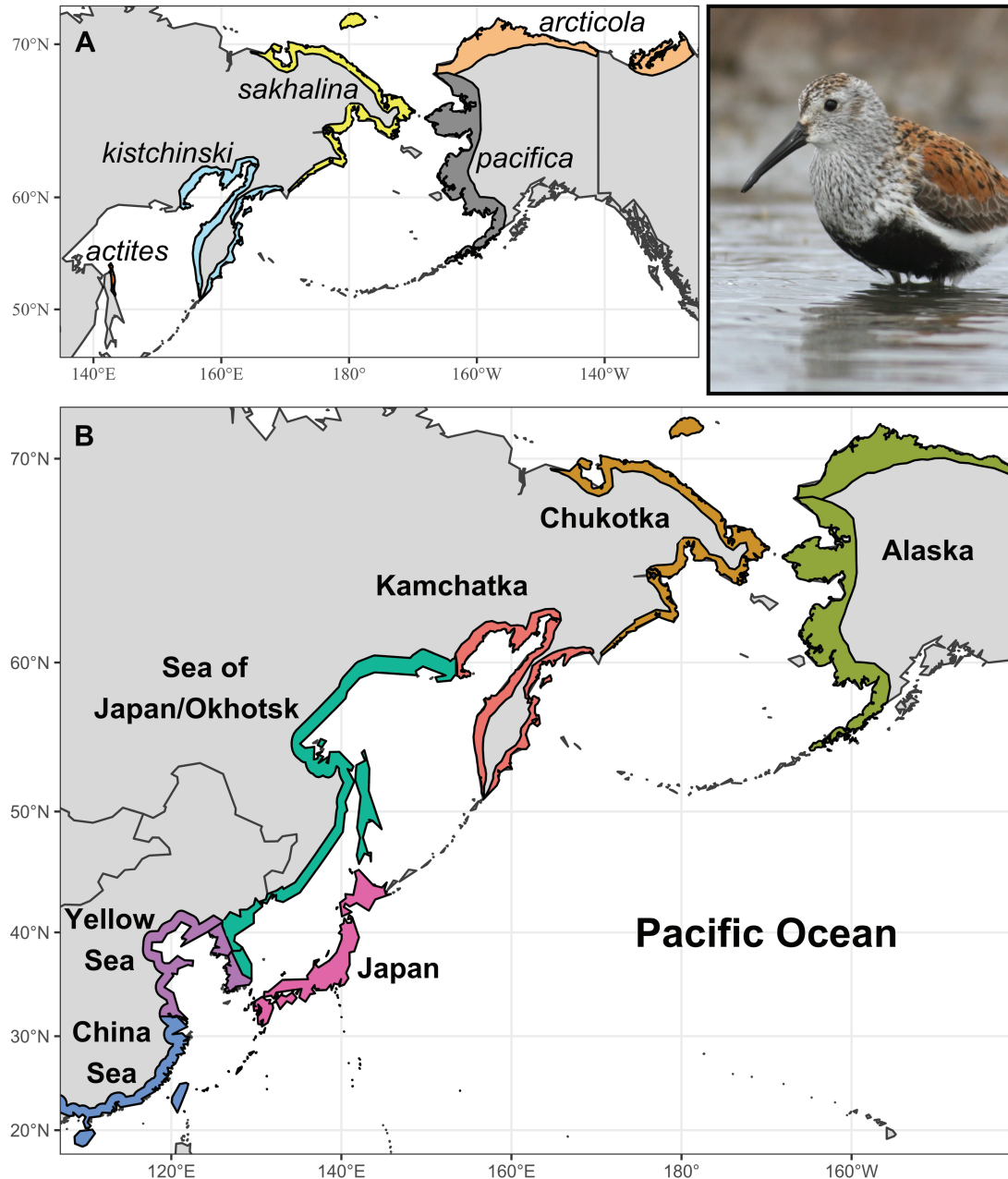


FIGURE 1. (A) Breeding ranges of the 4 subspecies of Dunlin (*Calidris alpina*) that migrate and winter along the East Asian–Australasian Flyway (EAAF). A fifth subspecies (*C. a. pacifica*) breeds in western Alaska and winters along the East Pacific Flyway of North America. (B) Regions used for summarizing geographic recovery patterns of marked Dunlin along the EAAF.

3 subspecies of Dunlin breeding in the North American Arctic (*arcticola*, *hudsonia*, and *pacifica*), *arcticola* Dunlin were the only birds to migrate to Asia, the authors attributed the lower adult survival to deteriorating conditions on their nonbreeding grounds along the EAAF. Furthermore, information from surveys in Japan indicates that the number of Dunlin there declined by 55–80% between 1975 and 2008 (Amano et al. 2010, 2012) and has

continued to decline through 2017 (T. Moriya personal communication). Diversification of Japanese rice fields and degradation of intertidal areas in the Yellow Sea have likely contributed to population declines (Amano et al. 2010, 2012). However, because population-specific migration patterns are poorly defined or unknown, actions to effectively improve adult survival rates in *arcticola* Dunlin and reverse population declines in Japan remain unclear (Norton 1971, Barter 2004, Lanctot et al. 2009, Choi et al.

2010b, Gill et al. 2013, Conklin et al. 2014, Bentzen et al. 2016, Valchuk et al. 2019).

Determining the degree to which Dunlin subspecies migrate among particular regions of the EAAF and whether their distributions are non-random and regionally structured is necessary to implement effective conservation actions (Barter 2004, Bamford et al. 2008, Conklin et al. 2014). Similar information is also needed to determine whether Dunlin of different sexes and ages segregate across nonbreeding areas and to ascertain the population-level effects of regional habitat degradation (Webster et al. 2002, Nebel 2007, Briedis and Bauer 2018). Indeed, sex- and age-specific segregation is common among migratory shorebirds with female and first-year birds typically wintering farther from their breeding grounds (Myers 1981, Cristol et al. 1999, Nebel et al. 2002). For EAAF Dunlin, females have been found more commonly than males in Changhua County, Taiwan, a southern wintering area (59–68% female; Yang et al. 2012), and first-year birds have been found more commonly than adults at Chongming Dongtan in eastern China (60–90% first-year; Choi et al. 2011). It is unclear, however, whether such sex- and age-specific segregation is consistent across the flyway's nonbreeding grounds. Similarly, determining the degree to which individual Dunlin exhibit nonbreeding site fidelity may have important conservation implications. It has been hypothesized, for instance, that returning to a site with prior knowledge of local predators and local food resources may be important for increasing adult survival and lifetime reproductive success in some species (Robertson and Cooke 1999). Interannual site fidelity to migration and wintering areas occurs commonly across shorebird taxa (e.g., Gill et al. 1983, 2010, Marks and Redmond 1996, Rehfisch et al. 1996, Buchanan et al. 2012, Lourenço et al. 2016, Ruthrauff et al. 2019), including Dunlin on the East Pacific and East Atlantic flyways (Rehfisch et al. 1996, N. Drumheller personal communication). However, the degree of interannual site fidelity among Dunlin on the EAAF is currently unknown.

Addressing questions of population connectivity and regional structuring for Dunlin populations along the EAAF nonbreeding grounds has been difficult because individual birds cannot be reliably assigned to subspecies or sex based on visual observation alone (Gates et al. 2013). In this study we used recaptures and resightings (hereafter “observations”) of birds marked at known breeding sites to identify regional connectivity patterns within and among subspecies of Dunlin migrating and wintering along the EAAF. We also examined the regional connectivity patterns of Dunlin of unknown subspecies captured and marked at sites on the nonbreeding grounds. Further, the large number of observations of *arcticola* Dunlin allowed us to investigate this subspecies in more detail, particularly the recovery patterns of birds initially captured on

the northwest (NW) and northeast (NE) portions of their Alaska breeding range, males and females, and Dunlin of different age classes. Finally, we assessed the propensity for individuals of the *arcticola* subspecies to exhibit nonbreeding site fidelity.

We predicted that each subspecies would show a distinct pattern of migratory connectivity among regions of the EAAF, but that there would be some level of subspecific overlap within flyway regions, as has been observed for other subspecies of Dunlin breeding in Alaska and the western Palearctic (Wennerberg 2001, Lopes et al. 2008, Gill et al. 2013). Limited information from the EAAF also indicates subspecific connectivity is likely. For example, geolocator-derived migration tracks of *sakhalina* Dunlin originating from NW and NE Chukotka, Russia, indicated that Dunlin from these 2 breeding sites used similar areas along the mainland of East Asia and avoided Japan altogether (Bentzen et al. 2016). Thus, we predicted that *arcticola* Dunlin from NW and NE portions of their Alaska breeding range would show connectivity patterns comparable with each other, and because they breed much farther east, we expected they might use areas in Japan. We also predicted that *arcticola* Dunlin would show sex- and age-specific segregation consistent with prior studies (Choi et al. 2011, Yang et al. 2012), and a high degree of interannual site fidelity to the same migration and winter sites as suggested by observations of Dunlin populations in other flyways (Rehfisch et al. 1996, Bentzen et al. 2016, Pakanen et al. 2018, N. Drumheller personal communication).

METHODS

Capture, Marking, and Resighting

Dunlin from each subspecies were captured on their breeding grounds (Figure 1A). Adults and newly hatched young were caught by hand with a bow net during incubation (Priklonsky 1960), or with mist nets during brood-rearing. On the nonbreeding grounds, Dunlin of unknown subspecies were captured with mist nets, rocket nets, cannon nets, walk-in traps, clap traps, or modified whoosh nets (Lanctot et al. 2009). Upon capture, biologists took morphological measurements, occasionally collected blood and feathers for sex determination (Gates et al. 2013), equipped birds with a uniquely numbered metal band, and applied a variety of markers to allow visual identification away from the capture site (Brown et al. 2014). These markers included dyeing body feathers with picric acid (mostly prior to the 1990s; Watkins 1997, Gill et al. 2013) and attaching combinations of color bands to create cohorts of similarly marked birds. Generally, birds were marked with the same combination at a given site; however, sometimes the cohort-marking scheme changed across years. This provided a unique cohort for

each year at some sites. Beginning in the early 2000s, adult Dunlin were each marked with unique color band combinations and/or engraved leg-flags at their breeding sites and at some nonbreeding locations, allowing each individual to be visually identified. Chicks were marked using a cohort-marking scheme in all years.

After migrating from a capture site, Dunlin were recaptured or resighted in Alaska and throughout East Asia by bird-watchers or during studies by professional researchers. Sightings of marked birds were reported to an organization or regional resighting database (i.e. Australasian Wader Studies Group, Global Flyway Network, Bird Ringing Center of Russia, Taiwan Wader Study Group, U.S. Fish and Wildlife Service, U.S. Geological Survey, Yamashina Institute for Ornithology, Facebook group: “Shorebird leg-flag sightings in the EAAF”). We collated observations from these databases and by corresponding directly with observers across the flyway. Although we do not know the level of effort that was spent observing birds at any particular site, the collated observations indicated that many areas were visited by observers multiple times both within and across years.

To allow a balanced analysis of connectivity patterns among populations that had individuals that were and were not uniquely marked, we used a 2-step process to convert observations of marked individuals into “recoveries”. First, we converted all uniquely marked individuals from the same capture location and year into a single cohort combination. This approach was necessary because the probability of resighting a bird from a cohort of marked birds is different to that of resighting a uniquely marked individual, thus potentially biasing connectivity patterns within a population that contains cohort-marked and uniquely marked birds (Clark et al. 2009, Thorup et al. 2014). By treating uniquely marked birds from the same capture location and year as a single cohort we effectively reduced the resighting resolution to the lowest common denominator. Second, to eliminate any site fidelity effects on population connectivity patterns, we discarded observations of birds of the same cohort that were seen <20 km apart (within and across years; after Gill et al. 2013). We did allow, however, a nonbreeding site to have multiple recoveries of the same cohort combination in cases where >1 bird with the same cohort combination were observed during a single visit (after Gill et al. 2013).

Migratory Connectivity

We attributed observations of birds initially marked on the breeding grounds, or birds marked on the nonbreeding grounds and later observed on the breeding grounds, to one of 3 subspecies (*C. a. actites*, *C. a. arcticola*, and *C. a. sakhalina*) according to their geographically distinct breeding ranges (Figure 1A); no individuals known to be from the *C. a. kistchinski* subspecies were observed. Birds

marked and observed only on the nonbreeding grounds could not be assigned to a subspecies but provided information on connections within and between nonbreeding regions. We divided the EAAF into the following nonbreeding regions: China Sea (including the East China Sea and South China Sea), Yellow Sea (including the Yellow Sea and Bohai Sea), Japan, Sea of Japan/Okhotsk (including the Sea of Japan and Sea of Okhotsk), Kamchatka, Chukotka, and Alaska (Figure 1B). These boundaries were based on prior knowledge of the distribution of Dunlin on the nonbreeding areas, and on locations where observers were actively banding and observing birds (Watkins 1997, Tomkovich 2003, Chiang and Liu 2004, Bamford et al. 2008, Cao et al. 2009, Gill et al. 2013, Tiunov et al. 2018, Valchuk et al. 2019). Finally, we considered Dunlin marked during southward migration at a shared staging area in western Alaska to belong to the *arcticola* subspecies if they were later observed along the EAAF (Gill et al. 2013). Although both *C. a. pacifica* and *C. a. arcticola* use western Alaska to stage during southbound migration, morphological analysis of Dunlin from nonbreeding areas (Maclean and Holmes 1971) and observations of Dunlin known to be *C. a. pacifica* (i.e. birds caught on nests in the *pacifica* breeding range) indicate that *pacifica* Dunlin migrate exclusively along the East Pacific Flyway of North America (R. Gill, B. Lagassé, and R. Lanctot personal observation).

We assigned each observation to the winter period if it occurred during December–February or to the migration period if it occurred during July–November or March–June (after Gill et al. 2013). If repeat observations of a cohort combination occurred both within and outside a winter period, we considered them to represent a single winter recovery. In these cases, we assumed a bird had arrived at the winter site earlier than December or had departed the winter site later than February. Because we could not differentiate whether repeat observations of a cohort combination were of the same individual, this approach could bias recovery classifications towards the winter period. For example, if a site had been used by 2 Dunlin with the same cohort combination, the first Dunlin only observed during migration and the second only during the winter, then after discarding repeat observations of that cohort combination, the recovery would have been assigned as a single winter recovery. Therefore, by assigning recoveries in this way, we differentiated areas used during migration and/or winter vs. those used only during migration.

To determine the degree to which Dunlin subspecies were independently distributed among the primary nonbreeding regions, we compared the proportion of recoveries for each subspecies that occurred in the Japan, Yellow Sea, and China Sea regions using pair-wise Fisher’s exact tests. Migration and winter recoveries were analyzed separately. We restricted our comparisons to these 3 regions because the other 4 regions were mostly outside of where

we expected *actites* Dunlin to occur. Therefore, by restricting the regions, we were able to make comparatively balanced comparisons between the Dunlin subspecies. We used this same approach to compare recovery patterns between nonbreeding Dunlin of unknown subspecies that were captured at sites in the Japan, Yellow Sea, and China Sea regions and later recovered in the 3 regions during migration or winter.

For the *arcticola* subspecies, we used pair-wise Fisher's exact tests to compute probabilities that observed winter recoveries in the Japan, Yellow Sea, and China Sea regions were distributed independent of an individual's breeding location (NW vs. NE Alaska), sex (male vs. female), or age (adult: ≥ 1 -yr-old vs. first-year: < 1 -yr-old). We used 152°W as the geographic dividing line between NW and NE portions of the Alaska breeding grounds because it separated the Alaska breeding grounds into the 2 primary areas where banding occurred. We used Wilcoxon rank-sum tests to assess whether the medians of minimum geographic distances between breeding and wintering sites differed by breeding location, sex, or age. Recoveries of male and female Dunlin were based on observations of uniquely banded birds that had been sexed using genetic markers or morphology (Gates et al. 2013). Recoveries of adult and first-year Dunlin were limited to observations of birds with a year- and age-specific cohort combination and a known date of recovery.

To determine the effect of creating cohorts from uniquely marked birds on our results, we used a Fisher's exact test to compare the regional recovery patterns derived from a dataset comprising only uniquely marked *arcticola* Dunlin (not combined into site/year cohorts as described above; $n = 139$ recoveries) with a dataset comprising observations of cohort-marked and uniquely marked *arcticola* Dunlin ($n = 202$ recoveries). The results of this comparison do not rule out that the 2 datasets derived from a single (identical) distribution (Fisher's exact test for migration and winter periods: $P = 0.37$ and 0.80 , respectively; Lagassé et al. 2020), and that our cohort approach therefore did not result in any loss of information, but rather allowed us to make equitable comparisons among populations with and without uniquely marked birds.

Nonbreeding Site Fidelity

As a first estimate of nonbreeding site fidelity (F) for Dunlin along the EAAF, we calculated the proportion of uniquely marked Dunlin observed returning to a site for ≥ 2 yr. To do this, we first determined the number of years each uniquely marked *arcticola* Dunlin was observed at the same site. A site included all observations within 20 km of each other, and a year included the migration and winter periods that followed a breeding season (July–June, see dates above). We then divided the total number of

individuals that returned to a site in at least one subsequent year (X) by the total number of individuals observed across all years and all sites (Y). However, because birds may not be observed returning to a site due to mortality, we partially corrected Y by multiplying the number of individuals observed across all years and all sites (Y) by the mean annual survival rate for *arcticola* Dunlin of 0.54 (Weiser et al. 2018). This allowed us to estimate the maximum number of birds available to return ($Y \times 0.54$) to a site before estimating the proportion with observed site fidelity ($F = X / (Y \times 0.54)$). This calculation was performed for migration and winter periods separately to assess potential differences between the seasons. We could not control for the effect of inconsistent observer effort or emigration. Finally, we calculated the proportions of *arcticola* Dunlin with site fidelity that were observed returning to a site 1–7 yr later. All statistical analyses were performed in program R 3.5.2 (R Core Team 2018).

RESULTS

Capture, Marking, and Resighting

From July 1960 to July 2017, $\sim 11,375$ Dunlin were captured and marked on or near the breeding grounds in Alaska and eastern Russia, and $\sim 17,225$ Dunlin were captured and marked at nonbreeding locations in the Japan, Yellow Sea, and China Sea regions (Table 1). Of the $\sim 9,325$ possible *arcticola* Dunlin, 1,700 adults and 2,350 chicks were banded on their breeding grounds in northern Alaska, and 5,275 were either *C. a. arcticola* or *C. a. pacifica* banded during southward migration at a shared staging site in western Alaska; the ratio of each subspecies is unknown although a large number likely belonged to the *pacifica* subspecies that migrates along the East Pacific Flyway of North America (Gill et al. 2013). Data on age composition were not available for all $\sim 2,050$ Dunlin banded on Russian breeding grounds. Subspecific assignments were not possible for the $\sim 17,225$ Dunlin that were captured at nonbreeding locations in the Japan, Yellow Sea, and China Sea regions.

We collated a total of 818 Dunlin recaptures (71; 9%) and resightings (747; 91%) from across the EAAF. Among these observations, 96% occurred from 2000 to 2017, and 69% after the last analysis of Dunlin observations was completed in 2007 (Lanctot et al. 2009). After converting uniquely banded individuals into cohorts according to the site and year that they were banded, we identified 132 total cohort combinations, of which between 2 and 67 were attributable to each marked population (Table 1). After discarding repeat observations of the same cohort combination at a site, we analyzed 377 recoveries, of which 223 (59%) could be assigned to a subspecies (Table 1).

TABLE 1. Number of birds banded, observations, recoveries, and cohorts of Dunlin (*Calidris alpina*) along the East Asian–Australasian Flyway (EAAF) from July 1960 to July 2017.^a

(A) Known subspecies				
	<i>C. a. actites</i>	<i>C. a. sakhalina</i>	<i>C. a. kistchinski</i>	<i>C. a. arctica</i>
Birds banded ^b	~800	~1,200	~50	~4,050 ^c
Observations	18	13	0	523
Recoveries	9	12	0	202
Cohorts	2	10	0	67
(B) <i>C. a. arctica</i> by Alaska breeding region and age				
	NW Alaska	NE Alaska	Adult	First-year
Birds banded ^b	~3,525	~525	~1,700	~2,350
Observations ^d	137	11	138	10
Recoveries ^d	70	8	73	6
Cohorts	32	7	36	5
(C) Unknown subspecies				
	China Sea	Yellow Sea	Japan	
Birds banded ^b	~4,250	~5,700	~7,275	
Observations	93	116	55	
Recoveries	50	58	46	
Cohorts	15	19	19	

^a See text for definition of observations, recoveries, cohorts, NW and NE Alaska breeding regions, and adult and first-year age classes. See Figure 1 for the boundaries of subspecies' breeding ranges and flyway regions.

^b Number of birds banded is approximated due to incomplete records. Data come from Gill et al. (2013), Valchuk et al. (2019), Bird Ringing Center of Russia, China National Bird Banding Center, Taiwan Wader Study Group, USGS Bird Banding Laboratory, Yamashina Institute for Ornithology, and email correspondence with individual banders.

^c An additional ~5,275 Dunlin were marked on a staging area of the Yukon-Kuskokwim Delta in western Alaska where *C. a. pacifica* also occur during southbound migration (Gill et al. 2013). Individuals of these subsequently observed along the EAAF were considered to be the *arctica* subspecies.

^d Totals only include observations and recoveries that occurred during the winter (December–February).

Migratory Connectivity and Nonbreeding Site Fidelity

Known subspecies. *C. a. sakhalina* ($n = 12$) were recovered only during migration and occurred across the EAAF, including 2 in Chukotka, 2 in the Sea of Japan/Okhotsk, 1 in Kamchatka, 1 in Japan, 4 in the Yellow Sea, and 2 in the China Sea regions (Figure 2A). Recoveries of *C. a. arctica* during migration ($n = 110$) primarily occurred in Japan (56%), the Yellow Sea (21%), and the China Sea (13%) regions although a few occurred in the Sea of Japan/Okhotsk (7%), Chukotka (1%), and Alaska (2%) regions (Figure 2B). During the winter, recoveries of *C. a. arctica* ($n = 92$) were from Japan (62%), the Yellow Sea (6.5%), and the China Sea (31.5%) regions (Figure 2B). *C. a. actites* were recovered during migration ($n = 6$) in Japan ($n = 1$), the Yellow Sea ($n = 3$), and the China Sea ($n = 2$) regions and entirely within the China Sea region during the winter ($n = 3$; Figure 2C). There were no migration or winter recoveries of *C. a. kistchinski*.

During migration, *sakhalina* ($n = 7$), *arctica* ($n = 99$), and *actites* ($n = 6$) Dunlin were recovered in similar proportions in the Yellow Sea (pair-wise Fisher's exact tests: $P = 0.07$ – 1.00) and China Sea regions ($P = 0.23$ – 1.00), but the odds of recovering *arctica* Dunlin in Japan were

8.22 (95% confidence interval [CI]: 0.87–401.63, $P = 0.04$) times greater than those for *actites* Dunlin and 9.85 (95% CI: 1.13–468.56, $P = 0.02$) times greater than those for *sakhalina* Dunlin (Figure 2). During the winter, *arctica* ($n = 92$) and *actites* ($n = 3$) Dunlin were recovered at a similarly low rate in the Yellow Sea region ($P = 1.00$), *actites* Dunlin were recovered more often in the China Sea region ($P = 0.04$), and *arctica* Dunlin were recovered more often in Japan ($P = 0.06$; Figure 2). Collectively, our analyses indicate *arctica*, *actites*, and *sakhalina* Dunlin occurred in similar proportions across the Yellow Sea and China Sea regions but higher proportions of *arctica* Dunlin consistently occurred in Japan (Figure 2).

***C. a. arctica* regional segregation.** Dunlin from the NW ($n = 70$) and NE ($n = 8$) Alaska breeding grounds showed no clear regional segregation (pair-wise Fisher's exact tests: $P = 0.49$ – 1.00) during the winter. Indeed, *arctica* Dunlin from NW Alaska were recovered in proportions similar to *arctica* Dunlin from NE Alaska in the Japan (60% NW and 50% NE; odds ratio [OR] = 1.49, 95% CI: 0.26–8.72, $P = 0.71$), Yellow Sea (7% NW and 12.5% NE; OR = 0.54, 95% CI: 0.05–29.06, $P = 0.49$), and China Sea regions (33% NW and 37.5% NE; OR = 0.82, 95% CI: 0.14–5.72, $P = 1.00$).

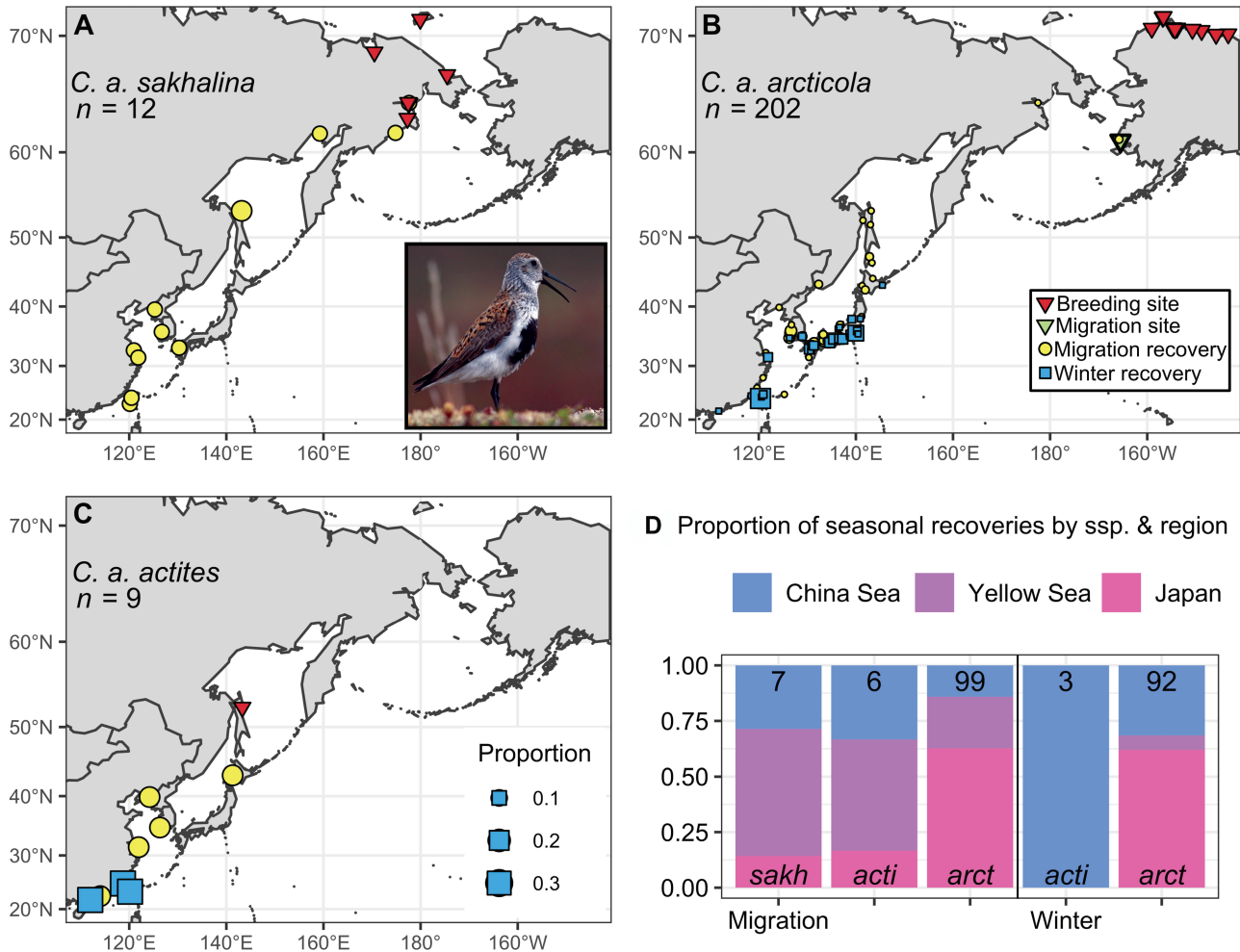


FIGURE 2. (A–C) Sites where subspecies of Dunlin (*Calidris alpina*) were marked and later recovered along the East Asian–Australasian Flyway. Symbol size represents the proportion of migration or winter recoveries that occurred at each site. Proportions are calculated separately for migration (July–November and March–June, combined) and winter (December–February). (D) Proportion of each subspecies recovered in the China Sea, Yellow Sea, and Japan regions during migration or winter. No *sakhalina* Dunlin were recovered during winter. Sample sizes indicate the number of recoveries for each subspecies during each season.

Distributions of minimum distances between breeding and wintering sites were broadly overlapping for *arctica* Dunlin from NE Alaska (median: 6,347 km; range: 5,731–7,765 km) and *arctica* Dunlin from NW Alaska (median: 5,875 km; range: 4,385–7,798 km; Wilcoxon rank-sum test: $W = 396$, $P = 0.06$).

Winter recoveries of uniquely marked male ($n = 30$) and female ($n = 27$) *arctica* Dunlin showed no clear regional segregation (pair-wise Fisher's exact tests: $P = 0.17$ – 0.42); males and females were recovered in similar proportions in the Japan (50% male and 63% female; OR = 0.59, 95% CI: 0.18–1.92, $P = 0.42$), Yellow Sea (3% male and 11% female; OR = 0.28, 95% CI: 0.01–3.77, $P = 0.34$), and China Sea regions (47% male and 26% female; OR = 2.46, 95% CI: 0.72–9.08, $P = 0.17$). Distributions of minimum distances between breeding and wintering sites were also similar for male (median: 6,929 km; range: 5,141–7,798 km) and

female (median: 5,931 km; range: 5,219–7,733 km) *arctica* Dunlin (Wilcoxon rank-sum test: $W = 352$, $P = 0.40$).

Finally, winter recoveries of adult ($n = 73$) and first-year ($n = 6$) *arctica* Dunlin showed no clear regional segregation (pair-wise Fisher's exact tests: $P = 1.00$); adults were recovered in similar proportions to first-years in the Japan (58% adult and 67% first-year; OR = 0.68, 95% CI: 0.06–5.10, $P = 1.00$), Yellow Sea (8% adult and 0% first-year; $P = 1.00$), and China Sea regions (34% adult and 33% first-year; OR = 1.04, 95% CI: 0.14–12.26, $P = 1.00$). Minimum distances between breeding and wintering sites were also similar for adult (median: 5,910 km; range: 5,045–7,798 km) and first-year (median: 5,587 km; range: 4,385–7,355 km) *arctica* Dunlin (Wilcoxon rank-sum test: $W = 263$, $P = 0.42$).

***C. a. arctica* nonbreeding site fidelity.** Uniquely marked *arctica* Dunlin had a high degree of interannual site fidelity (F) to migration and winter sites (37 of 131

observed individuals; $F = 52\%$ of birds after correcting for mortality; see Methods). Twelve of 78 individuals showed interannual site fidelity to a migration site ($F = 29\%$; 1 site in Republic of Korea, 1 site in Taiwan, 6 sites in Japan), and 25 of 56 individuals showed interannual site fidelity to a winter site ($F = 83\%$; 1 site in mainland China, 2 sites in Taiwan, 10 sites in Japan; site details available in Lagassé et al. 2020). Most individuals were observed returning to a site during the migration or winter period for 1 to 2 subsequent years (81% of returning individuals), while the remaining were observed returning to the same site for up to 7 yr.

Unknown subspecies. During migration, the odds of recovering a Dunlin in the China Sea region that was originally marked in the Yellow Sea region ($n = 40$) was 4.12 (95% CI: 1.11–19.33, $P = 0.03$; pair-wise Fisher's exact tests) times greater than the odds of recovering a Dunlin originally marked in Japan ($n = 32$); and the odds of recovering a Dunlin in the Yellow Sea region that was originally marked in the China Sea region ($n = 37$) was 19.08 (95% CI: 4.60–117.75, $P < 0.001$) times greater than the odds of recovering a Dunlin originally marked in Japan. Dunlin originally marked in the Yellow Sea and China Sea regions were recovered in Japan at similarly low rates (OR = 0.66, 95% CI: 0.18–2.30, $P = 0.58$).

During the winter, Dunlin originally marked in Japan ($n = 6$) and the China Sea region ($n = 3$) were recovered in the Yellow Sea region at similarly low rates ($P = 0.33$); the odds of recovering a Dunlin in the China Sea region that was originally marked in the Yellow Sea region ($n = 13$) was 18.53 (95% CI: 1.17–1,261.02, $P = 0.02$) times greater than the odds of recovering a Dunlin originally marked in Japan, and Dunlin originally marked in the Yellow Sea and China Sea regions were recovered in Japan at similarly low rates (OR = 0.20, 95% CI: 0.002–19.58, $P = 0.35$). Collectively, these recovery patterns indicate Dunlin frequently moved between the Yellow Sea and China Sea regions but a limited proportion moved between those 2 regions and Japan (Figure 3).

DISCUSSION

Migratory Connectivity and Nonbreeding Site Fidelity

The recoveries summarized here provide the first subspecies-level comparison of Dunlin migration and wintering geographies within the EAAF. We found that 56–62% of *arctica* Dunlin used areas in Japan during both migration and winter, with the remainder primarily recorded in the Yellow Sea and China Sea regions. Although there were fewer recoveries of the other subspecies, there was only a single recovery of *actites* (11%) and of *sakhalina* (8%) Dunlin in Japan; all of the remaining recoveries of *actites* Dunlin (during migration and winter) and 50% of

sakhalina recoveries (all during migration) occurred in the Yellow Sea and China Sea regions (Figure 2). Together, these findings suggest that subspecies' use of the EAAF is regionally structured. However, the percentage of the *arctica* Dunlin population that occurs in Japan is likely less than our band recoveries suggest. For example, surveys in Japan indicate that ~40,000 Dunlin occur there (Barter 2004). This estimate, if entirely *arctica* Dunlin, would only comprise ~8% of the subspecies' estimated population of 500,000 (95% CI: 304,000–696,000) birds (Andres et al. 2012, Bart et al. 2012). This disparity in numbers highlights the continued need to determine the proportion of each subspecies that occur in each region of the EAAF (Barter 2004, Fernández et al. 2010).

C. a. arctica. We found that the odds of recovering an *arctica* Dunlin in Japan was 8.22 times greater than that for *actites* Dunlin and 9.85 times greater than for *sakhalina* Dunlin. This suggests that Dunlin population declines in Japan from 1975 to 2017 (Amano et al. 2010, 2012, T. Moriya personal communication) were primarily due to a loss in the number of *arctica* Dunlin. It is also possible, however, that a portion of the population decline was due to a loss in the *kistchinski* subspecies because their migration patterns are unknown (Barter 2004) and could not be determined in this study (Table 1). Furthermore, recovery patterns of Dunlin marked on the nonbreeding grounds indicate that a limited proportion of Dunlin moved between Japan and the Yellow Sea or China Sea regions. These results suggest that previous Dunlin population declines in Japan were more likely due to a loss in intertidal habitats or flooded fallow rice fields (from more efficient drainage systems, crop diversion programs, and vegetation succession) within Japan, than to a loss of Dunlin migrating through Japan to/from the Yellow Sea (Amano et al. 2010, 2012). If so, the seasonal flooding of fallow rice fields in select areas of Japan may be an effective approach to create needed habitats to reverse declines in local populations of Dunlin, and in the *arctica* subspecies in particular (Elphick and Oring 1998, Amano 2009, Amano et al. 2010, 2012, Weiser et al. 2018, 2020, Jackson et al. 2020).

The large number of observations of *arctica* Dunlin provided other key insights into their migration ecology. First, recoveries suggest that an individual's breeding location, sex, or age has little effect on its eventual wintering sites. Second, repeat among-year observations of individuals indicate that $\geq 29\%$ and $\geq 83\%$ of *arctica* Dunlin have interannual site fidelity to specific migration and wintering sites, respectively. This behavior is similar to that found in other subspecies of Dunlin in Europe, Asia, and North America (Rehfish et al. 1996, Bentzen et al. 2016, Pakanen et al. 2018, N. Drumheller personal communication), and suggests that by returning to specific sites individual Dunlin may improve their annual

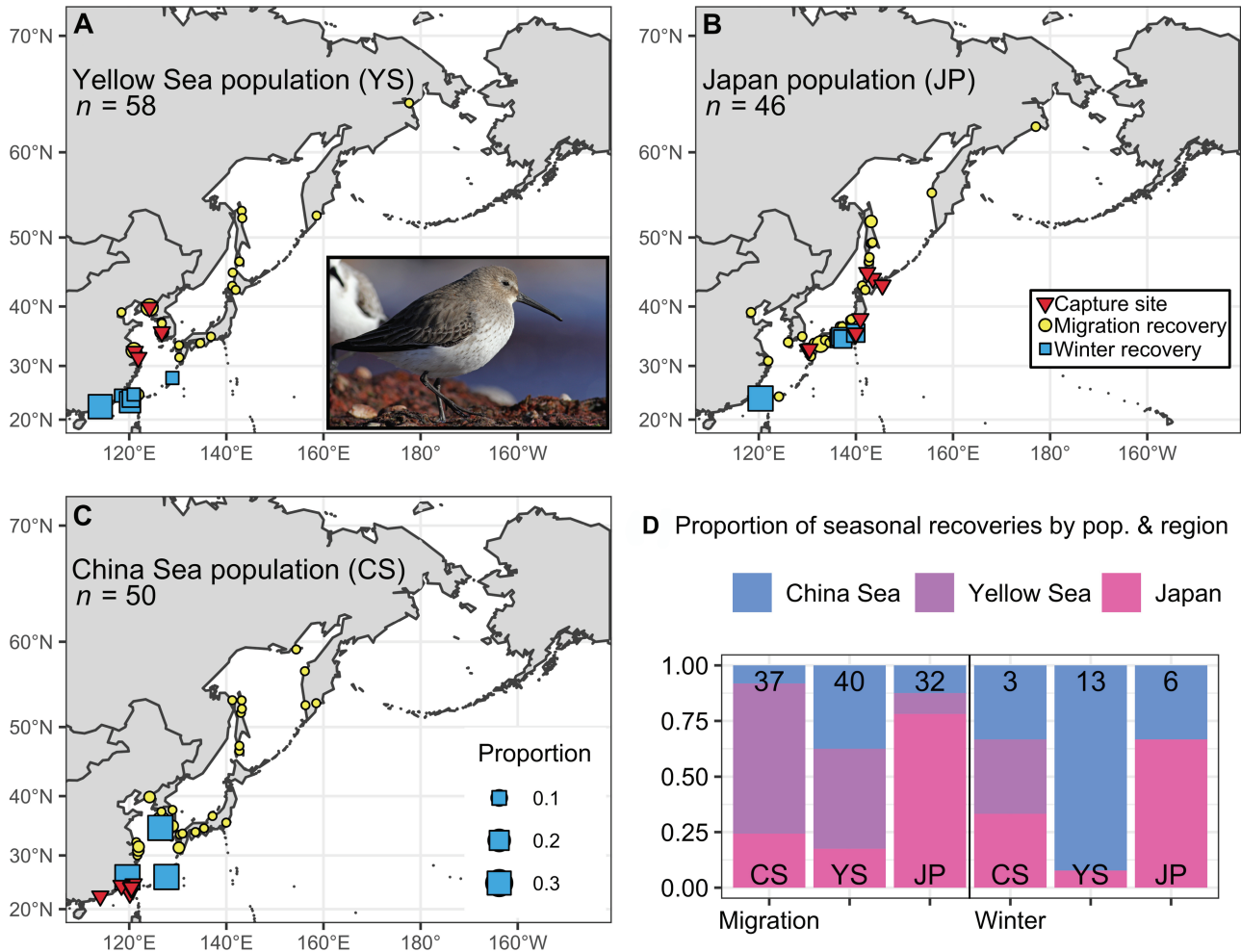


FIGURE 3. (A–C) Sites where Dunlin (*Calidris alpina*) of unknown subspecies were marked and later recovered along the East Asian–Australasian Flyway. Symbol size represents the proportion of migration or winter recoveries that occurred at each site. Proportions are calculated separately for migration (July–November and March–June, combined) and winter (December–February). (D) Proportion of each population of unknown subspecies recovered in the China Sea, Yellow Sea, and Japan regions during migration or winter. CS, YS, and JP at the bottom of each bar indicate where individuals were initially captured. Sample sizes indicate the number of recoveries for each population during each season.

survival and lifetime reproductive success (Robertson and Cooke 1999). If the loss of important sites is widespread, it could lead to population-level declines. For example, a large-scale development of the Saemangeum tidal flats in the Republic of Korea led to a 29% reduction in the peak number of Dunlin that occurred there from 2006 (82,718 birds) to 2013 (58,730 birds). Surveys over a much broader area of the west coast of the Republic of Korea indicated that the missing birds had not relocated but had likely perished (Moore et al. 2016). Of the 20 sites that supported *arctica* Dunlin with some level of site fidelity, most were intertidal habitats and only 35% had any level of protected status (Lagassé et al. 2020). These findings highlight the immediate importance of identifying and protecting key migration and wintering sites for each subspecies to stem future declines. This is a particular priority for the *actites*

subspecies given their small population size (900–2,000 birds; Nechaev and Tomkovich 1987, Blokhin et al. 2004, Bamford et al. 2008, Conklin et al. 2014).

Possible Biases

Although our findings provide useful insights into how Dunlin might use the EAAF, it is important to note that the recovery of marked birds depends on observer effort and reporting mechanisms and so results are likely biased by variability in regional recovery and reporting probabilities (Clark et al. 2009, Thorup et al. 2014). For example, Lisovski et al. (2016) compared band recoveries and migration tracks of Sanderling (*Calidris alba*) on the EAAF and found band recoveries overestimated their use of Japan and underestimated their use of the central mainland China coast and Taiwan. Similarly,

we did not identify any band recoveries from the freshwater wetlands of the Yangtze River floodplain in central China, despite reports of >25,000 Dunlin occurring there in the winter (Lei et al. 2011). Indeed, recovery and reporting probabilities are likely higher for Dunlin at certain coastal sites where multi-year efforts have been made to locate, resight, and capture Dunlin (e.g., Choi et al. 2010a, Yang et al. 2012). However, if we assume each cohort of marked birds had a similar probability of being recovered within each region, observed differences in recovery rates between cohorts within a region suggest there are actual differences in how Dunlin subspecies are distributed across the EAAF.

Effects of the Degradation of the Yellow Sea on Dunlin

The extent to which shorebird populations depend upon the Yellow Sea during migration is believed to be a primary indicator of population-level declines with more dependence linked to greater declines (Amano et al. 2010, 2012, Piersma et al. 2016, Studds et al. 2017, Murray et al. 2018). The observations presented here provide an insight into which Dunlin subspecies may be affected by habitat loss in the Yellow Sea. Individuals of all subspecies frequented the Yellow Sea, with 21–50% of a subspecies' migration recoveries connected to the area. However, the relative importance of the Yellow Sea may be much greater considering the region is vast with few observers to locate marked birds (Lanctot et al. 2009). Indeed, a recent study indicated that 17 of 18 *sakhalina* Dunlin tracked from their breeding grounds in Russia migrated through the Yellow Sea and 10 spent the winter there (Bentzen et al. 2016). This is far greater than the 33% and 0%, respectively, of *sakhalina* Dunlin we observed to migrate or winter in the area (Figure 2A). Furthermore, surveys in the Yellow Sea indicate Dunlin are one of the most abundant shorebirds in the region with an estimated 70% of the flyway population using the intertidal areas during northward migration (Barter 2002). In fact, >1% of the flyway population of Dunlin occurs in at least 14 recognized sites in the Yellow Sea (Bamford et al. 2008, Cao et al. 2009). For these reasons, continued habitat degradation in the Yellow Sea would likely have a significant negative effect on at least 3, but maybe all 4, of the Dunlin subspecies. However, for none of the subspecies is this concern more immediate than for the *actites* subspecies, due to having 50% of migration recoveries in the region (Figure 2C) and a small population size (Conklin et al. 2014).

Prioritizing Conservation Efforts

Approaches to conserving Dunlin on the EAAF have often prioritized areas that support at least 0.25% of the species' flyway population during migration or 1% during the winter (Bamford et al. 2008). Our finding that

Dunlin subspecies on the EAAF exhibit non-random and regionally structured flyway use suggests that these criteria, when applied at the species level, could bias conservation efforts toward areas supporting large numbers of the more abundant subspecies. For example, an area that supports 100% of *actites* Dunlin, which number 900–2,000 individuals (Nechaev and Tomkovich 1987, Blokhin et al. 2004, Bamford et al. 2008), would never reach the 1% flyway population threshold of 9,500 unless it also supported many individuals from the other subspecies. A growing number of studies indicate that conservation efforts could be more effective by also prioritizing areas that maintain the interconnected nature of a population's migratory network (Taylor and Norris 2010, Iwamura et al. 2014, Dhanjal-Adams et al. 2017). This includes prioritizing sites that not only support the greatest number of birds, but those sites that function to facilitate the flow of individuals from principal wintering areas to breeding areas, and vice versa. However, taking more population-specific and connectivity-based approaches to conserving Dunlin on the EAAF would require a more detailed understanding of subspecific migration patterns and site use than is currently available. To address this knowledge gap we recommend a coordinated effort that combines deploying tracking devices at breeding sites to quantify subspecies' use of migration routes (e.g., Bridge et al. 2011, Kays et al. 2015, Brown et al. 2017) with the collection of morphological measurements, genetic samples (Gates et al. 2013, Miller et al. 2015), and flock counts at nonbreeding sites to quantify subspecies' use of nonbreeding areas (e.g., Lopes et al. 2006, Lisovski et al. 2016). Collectively these efforts would provide the greatest opportunity to scale our understanding of Dunlin space-time dynamics from dozens of individuals to entire populations, and ultimately enable more effective conservation efforts for Dunlin on the EAAF (Harrington et al. 2002, Barter 2004, Bowlin et al. 2010).

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Data depository: Analyses reported in this article can be reproduced using the data provided by [Lagassé et al. \(2020\)](#).

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