

Age structure and age-related differences in molt status and fuel deposition of Dunlins during the nonbreeding season at Chongming Dongtan in east China

Chiyeung Choi,^{1,2} Ning Hua,¹ Xiaojing Gan,¹ Christer Persson,³ Qiang Ma,⁴
Hongxi Zang,⁴ and Zhijun Ma^{1,5}

¹Coastal Ecosystems Research Station of the Yangtze River Estuary, Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, Institute of Biodiversity Science, Fudan University, Shanghai, 200433, P. R. China

²Ecology Group, Massey University, Palmerston North, 4442, New Zealand

³Ljungsättersvagen 43, S-236 41 Höllviken, Sweden

⁴Chongming Dongtan National Nature Reserve, Chongming, 202183, P. R. China

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ABSTRACT. Although most shorebirds exhibit deferred migration and deferred breeding during their first summer, Dunlins (*Calidris alpina*) migrate to breeding areas and breed during their first summer. First-year and adult Dunlins should, therefore, have similar fueling and molt patterns if energetic and physiological constraints are responsible for deferred migration. From 2006 to 2008, we examined the age structure of Dunlins during the nonbreeding season at Chongming Dongtan, an estuarine wetland in the Yangtze River estuary in east China, and examined the effects of date, age, and molt status on fuel deposition during migration and during the winter. The Dunlin population at Chongming Dongtan was composed primarily of first-year birds. Most adults and first-year birds arrived together in late August. Regression analyses indicated that age, date, and molt status affected fuel deposition (as indicated by body mass) of Dunlins. Adults had significantly greater fuel deposits than first-year Dunlins near the end of northward migration (May: adults 70.8 ± 6.4 g, first-year 63.8 ± 8.0 g) and at the start of southward migration (September: adults 50.2 ± 6.1 g, first-year 47.2 ± 4.9 g). Adults also had significantly higher fuel deposition rates than first-year Dunlins during northward migration. Nonetheless, first-year Dunlins migrate and breed in their first summer. Thus, other factors, such as migration distance and body size, may be more important in determining if first-year shorebirds defer migration during their first spring and summer. During boreal spring and autumn, first-year Dunlins in active body molt had greater body mass than those that had not initiated body molt or those in suspended molt, and migratory fuel deposits for northward migration were greatest after prealternate molt was completed. These results suggest that body molt requires additional fuel deposits and imposes a constraint on fuel deposition for migratory flights.

RESUMEN. La estructura de edad y las diferencias relacionadas a la edad en la muda y el abastecimiento de reservas energéticas de *Calidris alpina* durante la época no-reproductiva en Chongming Dongtan en el este de China

Aunque la mayoría de las aves playeras demuestran un ritmo de migración y reproducción atrasada durante su primer verano, la especie *Calidris alpina* migra a sitios reproductivos donde se reproducen durante su primer verano. Entonces, si las restricciones energéticas y fisiológicas son responsables para una migración atrasada, los individuos de *C. alpina* en su primer año, y los adultos, deberían demostrar patrones similares en su abastecimiento de reservas energéticas, y en su muda. Desde el 2006 al 2008, examinamos la estructura de edades de *C. alpina* durante la época no-reproductiva en Chongming Dongtan, cual es un humedal en el estuario del Río Yangtze en el este de China. Examinamos los efectos de la fecha, edad y estado de muda sobre la acumulación de reservas durante la migración y el invierno. La población de *C. alpina* en Chongming Dongtan fue compuesto principalmente por individuos de primer año. La mayoría de los adultos e individuos de primer año llegaron juntos a finales de Agosto. Los análisis de regresión indicaron que la edad, fecha y el estado de muda afectaron la acumulación de reservas energéticas (indicado por la masa corporal) de *C. alpina*. Los adultos tenían significativamente mayores depósitos de reservas que los *C. alpina* en su primer año, al comienzo de la migración con dirección hacia el norte (Mayo: adultos 70.8 ± 6.4 g, primer año 63.8 ± 8.0 g), y cerca del final de la migración hacia el sur (Septiembre: adultos 50.2 ± 6.1 g, primer año 47.2 ± 4.9 g). Los adultos también tenían tasas de acumulo de reservas significativamente mas altas que los individuos de primer año al comienzo de la migración hacia el norte. Sin embargo, los individuos de primer año migran y se reproducen en su primer verano. Entonces, otros factores, como la distancia de la migración y el tamaño corporal podrían ser mas importantes en determinar si las aves playeras posponen la migración durante su primera primavera y verano. Durante la primavera y otoño boreal, los *C. alpina* de primer año con una muda corporal activa

⁵Corresponding author. Email: zhijunm@fudan.edu.cn

tuvieron una masa corporal mayor a los que no habían iniciado la muda corporal, o a los que habían suspendido da muda, y los depósitos de reservas energéticas premigratorias para la migración hacia el norte fueron mayores después de que la muda prealterna estaba completada. Estos resultados sugieren que la muda corporal requiere de reservas adicionales, y que impone una restricción sobre la deposición de reservas para realizar vuelos migratorios.

Key words: arrival phenology, body mass, *Calidris alpina*, deferred migration, East Asian-Australasian Flyway

Most shorebirds travel tens of thousands of kilometers in annual migratory flights. Both these migratory flights and breeding require adequate fuel deposition. Previous studies indicate that fuel deposition by migrants is age-dependent (Helseth et al. 2005, Verkuil et al. 2006, Choi et al. 2009). Young shorebirds, being less efficient foragers than adults, could have difficulty storing enough fuel for migration and arriving at breeding sites synchronously with adults in their first summer, thus facing a higher risk of breeding failure (Hockey et al. 1998). Such risk increases with migratory distance and, therefore, deferred migration may be more likely for first-year birds in species that are long-distance migrants (Summers et al. 1995, Hockey et al. 1998). Moreover, young shorebirds may face a higher risk of muscle damage than adults during migration (Guglielmo et al. 2001), and might therefore increase their chances of survival by spending their first summer in wintering areas instead of migrating north to breed (Marks and Redmond 1996). For these reasons, deferred migration and breeding are common among Holarctic-nesting shorebirds (Hockey et al. 1998).

Dunlins (*Calidris alpina*) are one of the most abundant shorebirds in the Northern Hemisphere (Bamford et al. 2008, Fernández et al. 2008) and up to 13 subspecies have been recognized (Piersma et al. 1996). These subspecies vary in timing of molt (Holmes 1971, Cramp and Simmons 1983, Greenwood 1986, Engelmoer and Roselaar 1998, Tomkovich 1998), with European Dunlins initiating primary molt during migration or on their wintering grounds and those along the East Asian-Australasian Flyway (hereafter EAAF) and in North America initiating primary molt on or near breeding areas (Holmes 1971, Cramp and Simmons 1983, Greenwood 1986, Engelmoer and Roselaar 1998, Tomkovich 1998, Holmgren et al. 2001). Unlike many shorebirds, Dunlins seldom winter south of the equator and thus the distance between wintering and

breeding grounds is relatively short (Piersma 1996). Moreover, first-year Dunlins migrate to their breeding grounds and breed during their first summer (Holmes 1966a, Soikkeli 1967, Pienkowski et al. 1976, Pienkowski et al. 1979), suggesting that the energetic constraints of migration and breeding by first-year birds may be reduced in Dunlins compared to other shorebirds that defer migration and breeding. However, few investigators have examined possible differences in fuel deposition patterns by adults and first-year birds in those species, like Dunlins, that migrate and breed during their first summer (Newton 2008).

Despite being well documented in North America (Page 1974, Kaiser and Gillingham 1981), Europe (Pienkowski et al. 1979, Johnson 1985, Persson 2003), the Middle East (Yosef and Meissner 2006), and northwest Africa (Dick and Pienkowski 1979), little is known about the migratory and wintering ecology of Dunlins along the EAAF. We examined the age structure of Dunlins during stopover and winter at Chongming Dongtan (hereafter CMDT) in east China, as well as the effects of date, age, and molt status on fuel deposition. We expected first-year and adult Dunlins to have similar fuel deposits and molt patterns if energetic and physiological constraints are responsible for deferred migration by shorebirds. We also examined the arrival phenology of Dunlins at CMDT to understand the linkage between the timing of southward migration and the timing of primary molt.

METHODS

Chongming Dongtan (31°30'N, 122°05'E) is an estuarine wetland in the Yangtze River estuary along the EAAF with both nonvegetated and vegetated tidal flats (Fig. 1). The main plants on the vegetated tidal area were native bulrush (*Scirpus mariqueter*) in the middle tidal zone, common reed (*Phragmites australis*) in the high tidal zone, and exotic smooth cordgrass (*Spartina alterniflora*) in both the middle and

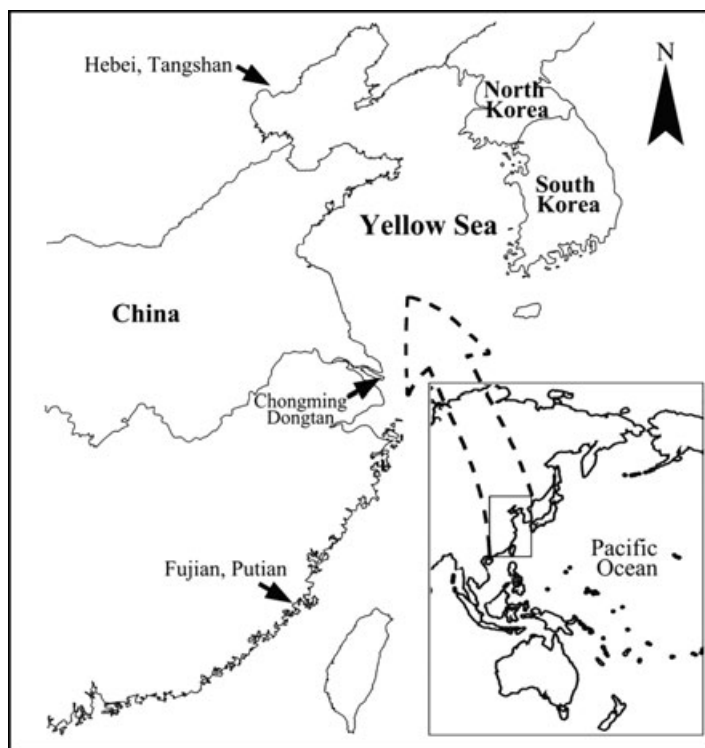


Fig. 1. Map of Chongming Dongtan National Nature Reserve in the Yellow Sea region. The inset shows the location of Yellow Sea region (square) within the East Asian-Australasian Flyway.

high tidal zones. Over the past two decades, large areas of intertidal flats at CMDT have been enclosed by dikes, and most of the enclosed land has been developed into farmland and aquacultural ponds. CMDT was listed as a Ramsar Site in 2002 (Ramsar 2010) because of its importance in providing habitat for waterbirds, especially shorebirds, during migration as well as during the winter. The total tidal area available for shorebirds was about 100 km² in 2005 (Xu and Zhao 2005).

Dunlins are among the most abundant shorebirds at CMDT during migration and the winter. About 9000 Dunlins were recorded at CMDT during northward migration in 1996 (Barter et al. 1997), and almost 5000 were counted during the winter of 2008 (Q. Ma, unpubl. data). Dunlins forage on areas of the intertidal flats that are sparsely vegetated or nonvegetated and often roost on exposed tidal flats or in aquacultural ponds during high tide.

Some Dunlins also forage in aquaculture ponds when water is drained for harvesting in late winter.

Capture and measurement. Dunlins were captured during each month (except February and June) from August 2006 to May 2008. Capture efforts during each migration period were similar, but we only attempted to capture Dunlins two to three times per month during one winter (November 2006–early March 2007). All birds were captured using clap nets (2.5 m × 12 m) with the assistance of local hunters. Sampling bias could affect determination of age structure if the probability of being captured differs between age groups (Page 1974). We minimized such bias by trying to capture foraging Dunlins during low tide when individuals of different ages may be more likely to mix (Conklin and Colwell 2008).

Each captured Dunlin received a numbered metal band (issued by the National Bird Banding

Center of China) as well as colored and, sometimes, engraved leg flags attached to the tibia or tarsus. Wing length was measured (± 1 mm) as the maximum length of flattened and straightened wings (Svensson 1992) with a stopped ruler. Bill length (exposed culmen) and tarsus length were measured with calipers (± 0.1 mm). Body mass was determined using digital balances (± 0.1 g). Most captured birds were processed and released within 3 h.

The molt status and breeding plumage score of captured Dunlins were recorded when possible. As described by Holmes (1966b), the molt status of five body parts (crown, nape, back, flank, and belly) was categorized as old plumage, new plumage, or active molt. Any sign of a growing feather, ranging from a pin feather to a feather completely grown, but still with a basal sheath, indicated active molt status. Molt status of birds not in active molt was categorized as either old or new plumage depending on the dominant type. Primaries were ranked with an integral score between 0 for an old feather and 5 for fully grown new feathers (Ashmole 1962). The sum of the scores for the 10 primaries on the right wing was used as the primary molt score indicating the progress of the primary molt in adult Dunlins.

Aging. We followed the enhanced nomenclatural system of Humphrey-Parkes (Humphrey and Parkes 1959, Howell et al. 2003) and defined the formative plumage as “any nonbasic plumage present in the first plumage cycle but not in subsequent cycles” (Howell et al. 2003). Therefore, young Dunlins fledge with juvenile plumage then attain formative plumage after preformative molt (postjuvenile) of body feathers during southward migration or shortly after arrival on the nonbreeding grounds. First-year Dunlins undergo a prealternate molt either shortly before or during northward migration, and adult plumage is first attained in a complete second prebasic molt at about 12 mo of age. Dunlins were aged as either first-year birds (birds in juvenile, formative, and first-alternate plumages) or adults (birds in their second basic plumage, second-alternate plumage, or definitive plumages) by a set of criteria (see Choi et al. 2010 for details) including: (1) presence of remaining breeding or juvenile plumage on the belly (Prater et al. 1977), (2) color of the tip of the carpal covert and sometimes the carpal remex (1st primary

covert; Persson 2008), (3) pattern of white edges on the innermost (2nd–3rd) primary coverts (Choi et al. 2010), (4) presence of a dark subterminal band on the tertial or tertial coverts (Gromadzka 1986), and (5) color of the inner median wing coverts (Prater et al. 1977, Meissner and Skakuj 2009). Most ageing was done in the field by C. Y. Choi and, occasionally, using photos that were always checked by C. Y. Choi and C. Persson.

Data analysis. Data collected from August 2006 to May 2008 were used for analysis. We used body mass to reflect fuel deposition status because body mass and fuel deposition are positively related (Mascher and Marcstrom 1976, Alerstam 1990). Regression analyses (generalized least squares methods) were conducted to examine the effects of date, age, and molt status on the body mass of Dunlins during boreal spring, autumn, and winter, respectively. We defined the period from March to May as boreal spring, late July to October as autumn, and November to February as winter based on shorebird migration phenology at CMDT. We conducted principal component analysis (PCA) with three measurements (head and bill, tarsus, and wing length), and the first principle component (that explained 70.9% of the total variances) was then included in regression models as a body-size variable. Candidate models were ranked according to Akaike’s information criterion (AIC; Burnham and Anderson 2002). We calculated delta AIC and AIC weights (w_i) based on the candidate models. The model with the smallest AIC and the largest w_i was considered the best explanatory model. However, other models with delta AIC < 2 were considered equally plausible (Burnham and Anderson 2002).

We examined possible effects of age on body mass during different seasons and differences in rate of body mass change between age groups using ANCOVA, with date as a covariate. We also investigated the possible effects of molt status on body mass using ANCOVA, with date as a covariate. Possible differences in body mass between age groups and among months were also analyzed separately using one-factor ANOVA. When significant differences were found, we used post hoc Bonferroni tests that adjust the significance level according to the number of multiple comparisons made to identify significant differences among means. Contingency

table analysis was used to examine possible deviation from random in the advance of body molt and attainment of alternate plumage between different age groups during different months (Zar 1999). Chi-square tests were used primarily to estimate significance, whereas Fisher's exact tests with Monte Carlo simulation were used when cells with expected frequencies <5 exceeded 20%. This allows interpretation despite low expected frequencies (Zar 1999).

Data were log-transformed if the assumption of normality and homogeneity of variances was violated. Nonparametric Kruskal-Wallis H -tests were used if the assumptions still could not be met after data transformation, significant results were followed by nonparametric post hoc comparison (Mann-Whitney) with corrected level of significance using Bonferroni correction. All analyses were performed using SPSS 12.0 for Windows (SPSS Inc. 2003). All tests were two-tailed with significance level (α) set at 0.05, and results are presented as means \pm 1 SD.

RESULTS

Age structure. From August 2006 to May 2008, 1495 Dunlins were captured and 1184 (79.2%) were aged at CMDT. Most unaged individuals were not aged either because a skilled person was not present in the field or because high-quality photographs were not available. Few Dunlins were captured before late August, and peak arrivals in the southward migration did not begin until September. Most early arrivals during southward migration were adults (seven of nine Dunlins captured between 29 July and 25 August), but the percentage of adults at CMDT dropped rapidly in late August and remained at about 10% or less until early December (Fig. 2). Adults increased to about 40% of the Dunlin population by mid-January, with a similar proportion of adults present in March. From late March to mid-May, the proportion of adults dropped to about 15–20% (Fig. 2). Overall, the Dunlin population at CMDT was dominated by first-year birds.

Molt status. During boreal autumn, primary molt was recorded only for early-arriving adults. Of seven adults that arrived at CMDT before 24 August, four were in active primary molt (with molt scores of 2, 3, 5, and 21, respectively), one had suspended primary molt (molt score 30), and two birds had not initiated

primary molt (molt score 0), indicating that most were still in the early stage of primary molt.

Analysis of body molt by age group from September to October indicated that the percentages of adults with different body molt status were not significantly different than expected (Fisher's exact test = 1.6, $P = 0.49$, $N = 35$), but the proportion of first-year Dunlins that had either not initiated or had suspended preformative molt (20.8%, Std. Residual = -2.8) was lower than expected in October (Fisher's exact test = 26.2, $P < 0.01$, $N = 284$). Thus, there was a gradual progression in body molt status of first-year Dunlins from September to October (Fig. 3). Our sample size of adult Dunlins was too small to compare the molt strategies of adult and first-year Dunlins during southward migration. The same analysis between age groups in March indicated that the percentage of adult Dunlins in full basic plumage (41.4%, Std. Residual = 2.9) was higher than expected, whereas the percentage of first-year Dunlins in full formative plumage (8.3%, Std. Residual = -2.6) was lower than expected ($\chi^2 = 19.8$, $P < 0.01$, $N = 130$). Thus, first-year Dunlins initiated prealternate molt earlier than adults during northward migration at CMDT.

Fuel deposition. Regression analyses indicated that body mass of Dunlins during winter was best explained by the model containing the variables body size, date, age, and molt status. However, five other models had delta AIC <2 and were competitive in explaining variation in body mass. These six competitive models that included date, body size, age, and molt status explained 70% of the variation among the 15 models considered (Table 1). During northward and southward migration, the best models to explain variation in body mass of Dunlins again included body size, date, age, and molt status. Models with delta AIC <2 explained 87% and 100% variation, respectively, among the 15 models considered.

Body mass of first-year and adult Dunlins increased with date (Julian) during southward (July–October; first-year: $F_{1,394} = 44.3$, $R^2 = 0.10$, $P < 0.001$; adult: $F_{1,50} = 11.3$, $R^2 = 0.18$, $P = 0.001$) and northward (March–May; first-year: $F_{1,240} = 107.9$, $R^2 = 0.31$, $P < 0.001$; adult: $F_{1,56} = 9.3$, $R^2 = 0.14$, $P < 0.01$) migration, but not during the winter (November–February; first-year: $F_{1,160} = 0.2$, $R^2 = 0.001$,

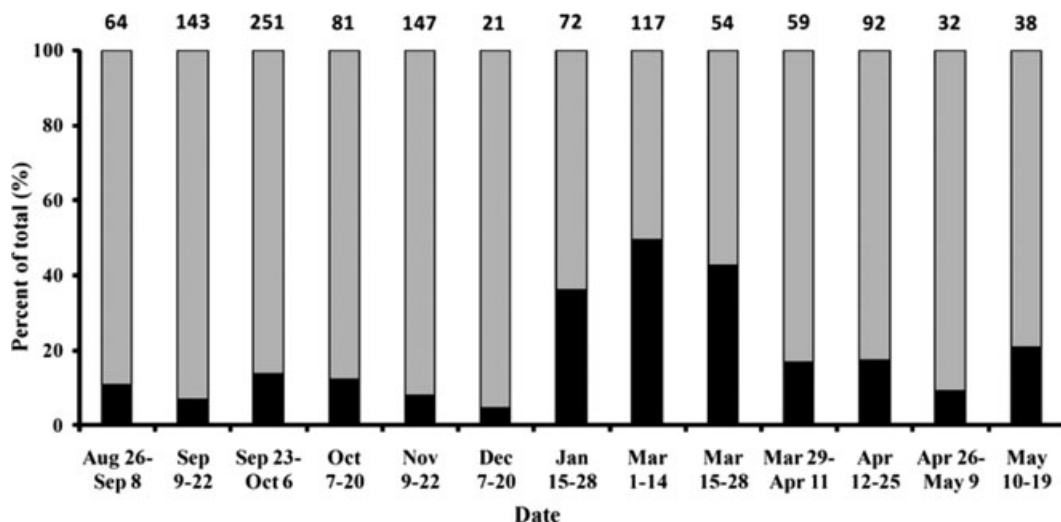


Fig. 2. Biweekly age structure of Dunlins at Chongming Dongtan from August 2006 to May 2008. First-year Dunlins are indicated by gray bars and adults by black bars. Numbers above bars indicate sample sizes. Few Dunlins were captured from 29 July to 11 August (five adults), 12 to 25 August (two adults and two first-year), and none were captured during six periods (21 October–8 November, 23 November–6 December, 21–31 December, 1–14 January, 29 January–11 February, and 11–25 February).

$P > 0.05$; adult: $F_{1,28} = 0.02$, $R^2 = 0.001$, $P > 0.05$; Fig. 4). The rate of body mass increase was higher for adults than first-year Dunlins during northward migration ($F_{1,336} = 4.1$, $P = 0.04$; Fig. 4), but we found no difference between age groups during southward migration ($F_{1,450} = 0.3$, $P = 0.62$; Fig. 4). Increases in body mass were greatest during April and May when at least 10 g increases in mean body mass were found for both age groups (Fig. 4).

After controlling for date, body mass of adult Dunlins was greater than that of first-year birds

during southward migration (adults: 49.7 ± 5.6 g, first-year birds: 48.0 ± 4.9 g; $F_{1,452} = 10.7$, $P = 0.001$). However, we found no difference between age groups either during northward migration (adults: 52.7 ± 8.4 g, first-year: 54.4 ± 7.2 g; $F_{1,337} = 1.6$, $P = 0.2$) or during the winter (adults: 50.9 ± 3.9 g, first-year: 51.7 ± 5.2 g; $F_{1,188} = 0.9$, $P = 0.34$).

Overall, mean body mass of first-year ($F_{8,791} = 47.6$, $P < 0.001$) and adult ($F_{7,176} = 11.3$, $P < 0.001$) Dunlins differed significantly among months. Post hoc tests revealed that mean

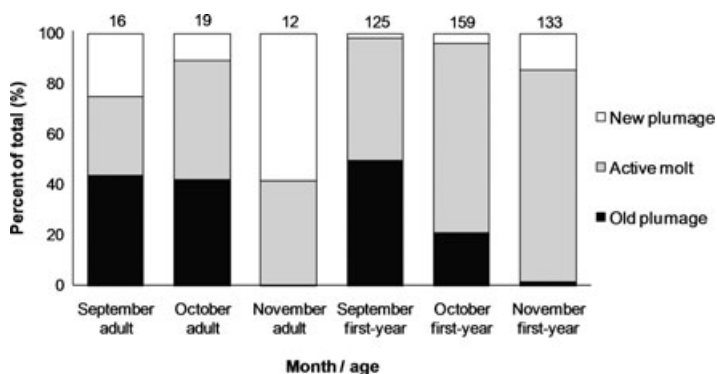


Fig. 3. Percentage of adult and first-year Dunlins in different stages of molt in September, October, and November at Chongming Dongtan. Numbers above bars indicate sample sizes.

Table 1. Regression models considered for predicting body mass of Dunlins captured at Chongming Dongtan during the nonbreeding season. Models were compared with the second-order collected Akaike Information Criterion (AIC; Burnham and Anderson 2002).

Model no.	Independent variables	K	AIC	Δi	ω_i
Winter					
1	BodySize + Date + Age + Molt	5	1065.76	0.00	0.19
2	BodySize + Date + Molt	4	1066.27	0.52	0.15
3	BodySize	1	1067.00	1.24	0.10
4	BodySize + Date + Age + Molt + Age*Molt	7	1067.27	1.51	0.09
5	BodySize + Age	2	1067.36	1.60	0.09
6	BodySize + Date + Age + Age*Molt	5	1067.50	1.75	0.08
7	BodySize + Age + Age*Molt	4	1068.27	2.51	0.05
8	BodySize + Date + Age	3	1068.49	2.73	0.05
9	BodySize + Date	2	1068.80	3.04	0.04
10	BodySize + Age*Molt	3	1068.92	3.16	0.04
11	BodySize + Molt	3	1069.30	3.54	0.03
12	BodySize + Date + Molt + Age*Molt	6	1069.87	4.11	0.02
13	BodySize + Age + Molt	4	1070.08	4.32	0.02
14	BodySize + Date + Age*Molt	4	1070.17	4.42	0.02
15	BodySize + Age + Molt + Age*Molt	6	1071.38	5.62	0.01
Spring					
1	BodySize + Date + Age + Molt	5	1459.32	0.00	0.56
2	BodySize + Date + Age + Molt + Age*Molt	7	1460.52	1.19	0.31
3	BodySize + Date + Molt	4	1462.89	3.57	0.09
4	BodySize + Date + Molt + Age*Molt	6	1465.24	5.92	0.03
5	BodySize + Date + Age*Molt	4	1481.92	22.6	0.00
6	BodySize + Date + Age + Age*Molt	5	1483.69	24.4	0.00
7	BodySize + Date + Age	3	1484.37	25.1	0.00
8	BodySize + Date	2	1486.89	27.6	0.00
9	Date + Age + Molt	4	1516.18	56.9	0.00
10	Date + Molt	3	1516.91	57.6	0.00
11	Date + Age + Molt + Age*Molt	6	1517.67	58.4	0.00
12	Date + Molt + Age*Molt	5	1519.37	60.1	0.00
13	BodySize + Molt	3	1522.37	63.1	0.00
14	BodySize + Age + Molt + Age*Molt	6	1522.72	63.4	0.00
15	BodySize + Molt + Age*Molt	5	1523.43	64.1	0.00
Autumn					
1	BodySize + Date + Age + Molt	5	1556.27	0.00	0.70
2	BodySize + Date + Age + Molt + Age*Molt	7	1557.94	1.67	0.30
3	BodySize + Date + Age + Age*Molt	5	1568.89	12.6	0.00
4	BodySize + Date + Molt	4	1585.07	28.8	0.00
5	BodySize + Date + Molt + Age*Molt	6	1585.44	29.2	0.00
6	BodySize + Date + Age	3	1587.09	30.8	0.00
7	BodySize + Age + Molt + Age*Molt	6	1588.03	31.8	0.00
8	BodySize + Age + Molt	4	1588.32	32.1	0.00
9	BodySize + Date + Age*Molt	4	1592.24	36.0	0.00
10	BodySize + Date	2	1610.89	54.6	0.00
11	BodySize + Age + Age*Molt	4	1611.30	55.0	0.00
12	BodySize + Molt	3	1612.96	56.7	0.00
13	BodySize + Molt + Age*Molt	5	1615.68	59.4	0.00
14	BodySize + Age*Molt	3	1632.45	76.2	0.00
15	BodySize + Age	2	1636.54	80.3	0.00

K = number of estimable parameters; Δi = delta AIC; ω_i = model weights.

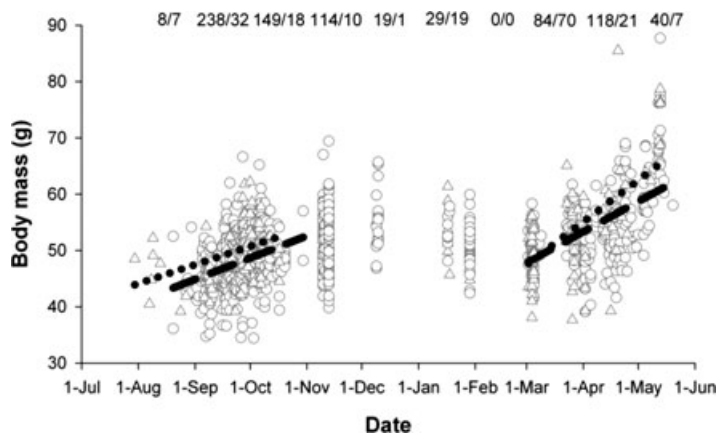


Fig. 4. Body mass of adult (triangles) and first-year (circles) Dunlins during southward migration (July–October), winter (November–February), and northward migration (March–May) at Chongming Dongtan. The dotted lines indicate the linear regression of body mass on date in adult Dunlins and the dashed lines of first-year Dunlins. The slopes of these two lines indicate the rate of body mass change for the corresponding age group. Numbers at the top indicate the sample sizes for first-year birds/adults.

body mass of first-year Dunlins was significantly higher in May (63.8 ± 8.0 g) than other months ($P < 0.001$) and significantly lower in September (47.2 ± 4.9 g) than other months except August ($P < 0.001$, except August when $P = 1.0$). Post hoc tests revealed that body mass was higher for adults in May (70.8 ± 6.4 g) than during the other months ($P < 0.001$; Fig. 4). In addition, mean body mass was significantly greater for adult than first-year Dunlins in September ($F_{1,269} = 9.9$, $P = 0.002$) and May ($F_{1,45} = 4.8$, $P = 0.03$; Fig. 4), but did not differ between age groups during the other months ($P \geq 0.13$).

Molt status had similar effects on the body mass of first-year and adult Dunlins during northward migration. After controlling for date, first-year (Kruskal-Wallis $H_2 = 31.5$, $P < 0.001$, $N = 173$) and adult ($F_{2,62} = 4.3$, $P = 0.02$) Dunlins that had completed prealternate molt had significantly greater body mass (first-year: 64.3 ± 9.8 g; adults: 71.3 ± 6.1 g) than either those in active molt (first-year: 54.2 ± 5.7 g, $U = 638$, $N = 158$, $P < 0.001$; adults: 53.3 ± 6.9 g, post hoc Bonferroni tests, $P < 0.001$) or those that had not initiated molt (first-year: 50.7 ± 5.4 g, $U = 44$, $P < 0.001$; adults: 50.0 ± 5.7 g). In addition, first-year Dunlins in active molt tended to have greater body mass than those that had not initiated molt ($U = 639$, $N = 147$, $P = 0.025$, $\alpha = 0.017$ after Bonfer-

roni correction). During southward migration, first-year Dunlins in active body molt (49.5 ± 4.7 g) had greater body mass ($F_{2,255} = 11.4$, $P < 0.001$) than those that either had completed (45.3 ± 5.2 g; post hoc Bonferroni tests, $P = 0.023$) or had not initiated or suspended body molt (46.0 ± 4.2 g). No significant effect of molt status on body mass was found for adult Dunlins during southward migration ($F_{2,32} = 1.7$, $P = 0.2$).

DISCUSSION

Age structure. Most Dunlins at CMDT were first-year birds, especially during migration (90% during autumn and 80% during spring). Dunlin populations consisting of more than 75% first-year birds during migration have also been reported in Germany (Gromadzka 1989) and Sweden (Persson 2003). This might be the result of the different timing of migration between age groups and subspecies (Gromadzka 1989, Persson 2003), and this may also be the case for Dunlins in the EAAF because the timing of breeding and primary molt differs among subspecies of Dunlins along the EAAF (Holmes 1966a, Tomkovich 1998). Higher percentages of adult Dunlins are present in other areas of China than at CMDT. More than 80% of the 204 Dunlins captured at Putian, Fujian Province in January 2007 and 2008 were adults,

and almost 70% of the 81 Dunlins found at Tangshan, Hebei Province, in January 2008 were adults (Choi 2009; Fig. 1). Thus, there is age-specific segregation of Dunlins on the nonbreeding grounds in the EAAF.

Our results suggest that adults arrived at CMDT before first-year Dunlins during southward migration. However, numbers of early-arriving adults in early August were small and they were still in early stages of primary molt. Such a small number and late initiation of primary molt compared to their counterparts (Holmes 1971, Tomkovich 1998) indicated that they were likely second-year birds and were either failed breeders or nonbreeders that tend to migrate earlier than successful breeders (Holmes 1966a, Nechaev 1998, Meissner and Strzalkowska 2006, Newton 2008). This is because Dunlins along the EAAF initiate primary molt in or near the breeding grounds during late June and early July (Holmes 1971, Tomkovich 1998). Therefore, most adults (presumably successful breeders) and first-year birds arrived at CMDT at about the same time. Similarly, juvenile Dunlins arrive at about the same time as adults on the west coast of the United States (Holmes 1966a, Page 1974). This pattern differs from the general southward migration pattern of shorebirds, where failed breeders migrate first, successful breeders second, and first-year birds last (Newton 2008). In Europe, most adult Dunlins undergo primary molt after starting southward migration (Gromadzka 1989, Engelmoer and Roselaar 1998), and arrive at staging and wintering sites earlier than first-year birds (Meissner 1998, Serra et al. 1998, Persson 2003, Meissner and Strzalkowska 2006, Yosef and Meissner 2006). Because adult Dunlins in the EAAF and North America initiate primary molt on or near their breeding grounds, the time of southward migration for adults could be delayed (Holmes 1971, Tomkovich 1998). Consequently, comparison of different Dunlin subspecies provides evidence that the timing of the southward migration is linked with the timing of primary molt (Newton 2008).

The percentage of adults at CMDT increased from 10% in early December to about 40% in January and March. Similar increases in the percentage of adult Dunlins in wintering areas have been reported in northern Italy (Serra et al. 1998) and in western Washington and the Bolinas Lagoon in the United States (Page 1974,

Kus et al. 1984, Buchanan et al. 1986). Such increases may be due to higher mortality rates for first-year Dunlins during the winter because they may be more vulnerable to predators than adults (Kus et al. 1984, Whitfield 1985). In addition, first-year Dunlins that arrived at wintering grounds early in boreal autumn may have left CMDT if they were more likely to disperse and took longer to settle at wintering sites than adults (Baccetti et al. 1999). Moreover, additional adult Dunlins could have arrived from other adult-dominated sites (Choi 2009) due to deterioration of feeding conditions at those wintering sites (Warnock et al. 1995). The decrease in the percentage of adults in April in our study was probably caused by the earlier start of northward migration by adults than first-year Dunlins (Holmes 1966a). Early arrival of adults at the breeding grounds allows them to establish territories required for successful breeding (Soikkeli 1967, Newton 2008).

Molt. Among shorebird species where first-year birds defer migration or breeding in the first summer, fuel deposition or prealternate molt may be absent or delayed (Prater et al. 1977, Branson et al. 1979, Johnson et al. 1989, McNeil et al. 1994, O'Hara et al. 2005). However, most first-year Dunlins in the EAAF migrate north (Nechaev 1998) because Dunlins were rarely recorded in their wintering and staging grounds during summer (Hong Kong: shorebird monitoring at the Mai Po Inner Deep Bay Ramsar Site 1999–2009; CMDT: Q. Ma, pers. comm.; Yalujiang: Q. Q. Bai, pers. comm.) and one-third breed during their first summer (Holmes 1966a). Our results indicated that first-year Dunlins also initiated prealternate molt earlier than adults, whereas Holmes (1966b) reported that the timing of prealternate molt was similar for both age groups in California. This difference may have been due to the presence of more than one subspecies at our study site; only one subspecies likely occurs in California (Warnock and Gill 1996, Wenink and Baker 1996). During boreal autumn, we found a gradual progression in the preformative body molt in first-year Dunlins from September to November, with the percentage of first-year Dunlins with either juvenile plumage or suspended molt decreasing steadily during these months. However, the progression of prebasic molt in adults was rather abrupt. There was no decline in the proportion of adults with alternate feathers or suspended

molt from September to October, but a sudden increase in the proportion of birds with completed body molt from October to November. This might be the result of rapid turnover or further arrival of adult Dunlins with incomplete prebasic molt in October at CMDT. The high proportion of adults with completed body molt in November suggests a faster body molt by adults than by first-year Dunlins. However, the prebasic and preformative body molt of Dunlins is initiated at breeding areas (Holmes 1971), leaving adults and first-year Dunlins with different stages of body molt when they arrived at wintering areas and making comparison of the speed of body molt difficult. In addition, sample sizes for adults in our study were small so more data are needed before drawing any conclusions.

Fuel deposition. At CMDT, body mass of adult and first-year Dunlins was lowest in August, then increased from August to October and remained steady during winter. Fuel deposition by Dunlins started at the end of March and peaked in May, apparently in preparation for northward migration. The higher fuel deposition rates and greater fuel deposits of adult Dunlins at the start of northward migration might reflect greater foraging efficiency by adults than by first-year birds, as shown in studies of closely related Curlew Sandpipers (*Calidris ferruginea*; Hockey et al. 1998) and other shorebird species, including Ruddy Turnstones (*Arenaria interpres*; Groves 1978) and Eurasian Oystercatchers (*Haematopus ostralegus*; Goss-Custard and Durell 1987).

Despite lower fuel deposition rates and smaller fuel deposits than adults at the start of northward migration, almost all first-year Dunlins at CMDT migrate (Q. Ma, pers. comm.) and one-third breed during their first summer (Holmes 1966a). This suggests that energetic constraints alone may not have led to the evolution of deferred migration and breeding in shorebirds (Hockey et al. 1998), but may lead to delayed northward migration and lower reproductive success in first-year shorebirds (Lyons and Haig 1995, Ruthrauff 2002). Migratory distance and body size may be more important in determining whether first-year birds migrate and breed during their first summer because the physiological and energetic constraints of migration and, subsequently, of breeding may be greater for larger and longer-

distance migrants (Summers et al. 1995, Hockey et al. 1998, O'Hara et al. 2005). The relatively small body size and short migratory distances of Dunlins (<15,000 km per year along the EAAF) mean that physiological and energetic constraints might be lower than for other larger, Arctic-, deferred-breeding shorebirds (>20,000 km per year along the EAAF; Piersma et al. 1996, R. Lancot, pers. comm.). Moreover, the benefits of breeding and gaining experience about breeding locations in the first summer may outweigh the risks of migration for first-year Dunlins (Summers et al. 1995).

We found that the body mass of first-year Dunlins in active body molt was greater than that of those that had either not initiated, had suspended, or had completed body molt during the boreal autumn. Although the same trend was found for body mass of adult Dunlins with different molt status in boreal autumn, the result was not significant, probably due to the small sample size. During boreal spring, body mass was higher for first-year and adult Dunlins that had completed prealternate molt than for those that had not initiated prealternate molt or were in active molt. Moreover, body mass of first-year Dunlins in active prealternate molt was greater than that of those that had not initiated molt. Similar results have been reported for Dunlins, Red Knots (*Calidris canutus*), and Bar-tailed Godwits (*Limosa lapponica*) in Banc d'Arguin (Zwarts et al. 1990), suggesting that greater fuel deposits are required for growing new feathers. Together with similar results reported for Dunlins at Banc d'Arguin (Zwarts et al. 1990), the Wadden Sea (Boere 1976), and the central Mediterranean (Serra et al. 1998), where the greatest fuel loads were found as prealternate molt approached completion, it becomes clear that active body molt can conflict with fuel deposition for migratory flight not only in songbirds (Winker et al. 1992), but also shorebirds. This may be one of the reasons why body molt was often suspended before migration in some shorebirds (Zwarts et al. 1990).

Up to 13 subspecies of Dunlins have been recognized (Piersma et al. 1996). These subspecies differ in the timing of primary molt, with primary molt overlapping with migration in some subspecies and with breeding activities in others (Holmes 1971, Cramp and Simmons 1983, Engelmoer and Roselaar 1998, Tomkovich 1998, Holmgren et al. 2001). Such

overlap of primary molt with migration and breeding do not generally occur in migratory birds (Newton 2008). Further comparisons of the ecology and behavior of different Dunlin populations along different flyways will help us understand how environmental factors (such as migration distance, predation risks, and food availability) shape the life-history characteristics (such as the timing of primary molt) of different Dunlin populations.

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