Wader

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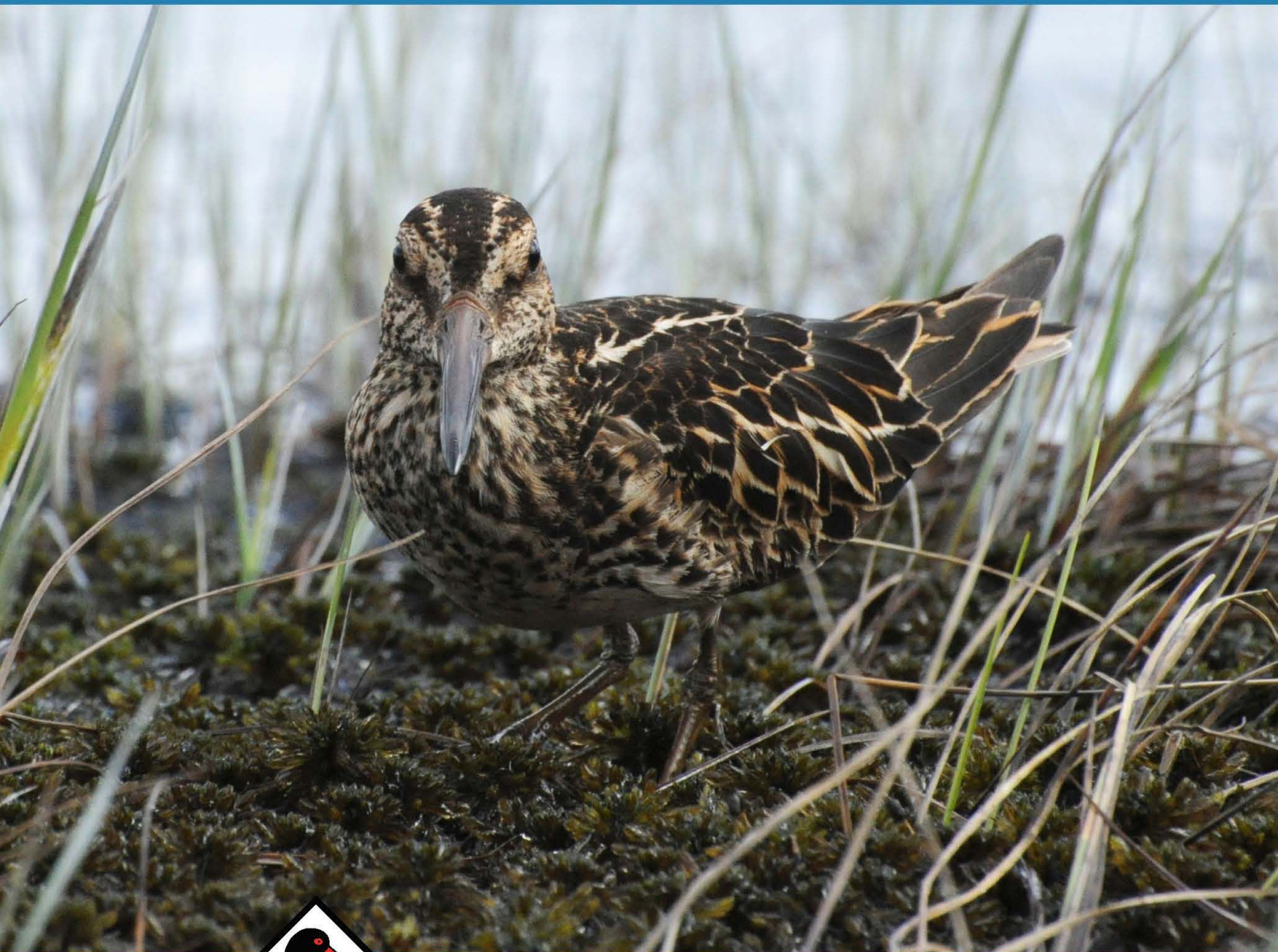
Sexual size dimorphism, disassortative pairing, and annual survival of Broad-billed Sandpipers in northern Norway

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The Broad-billed Sandpiper *Calidris falcinellus* is an elusive and seldom studied species of wader that breeds in wet fen habitats in the Palearctic taiga. In a 25-year population study from 1995–2019 near Kautokeino, Norway, we investigated the use of biometrics for sexing, tested for patterns of sexual size dimorphism, compared seasonal variation in biometrics, and calculated the first estimates of annual survival for the species. Most birds could be sexed using bill length: ≤29.9 mm = male, 30.0–31.5 mm = either sex, and ≥31.6 mm = female. Sexual size dimorphism was female biased with the greatest dimorphism in bill length (F/M = 1.12), with disassortative pairing for bill length between birds in mated pairs. Body mass and wing length of Broad-billed Sandpipers varied among different stages of the annual cycle and in a pattern consistent with the energetic demands of migration and timing of feather moult. Annual survival was estimated with Cormack-Jolly-Seber models based on time-since-marking to control for losses after first capture and imperfect detection, and to test for sex and age effects. Apparent survival was 0.736 ± 0.060 SE among previously marked birds that returned at least once to the study area, with a mean life expectancy of 5.3 ± 0.9 SE years and a new longevity record of 13+ years. Apparent survival was within the range of expected values based on published estimates for other small-bodied sandpipers. Population declines of –5.4% per year have been reported in Fennoscandia, and a better understanding of the factors affecting demographic performance during the migratory and overwintering stages of the annual cycle will aid future conservation of the Broad-billed Sandpiper.

Keywords

apparent survival

biometrics

Calidris falcinellus

Finnmark

life expectancy

mark-recapture

INTRODUCTION

Information on avian morphology and demography are central to questions in evolutionary ecology and conservation biology. Comparative analyses of shorebird traits have been used to investigate the evolution of migration strategies and habitat use (Elner & Seaman 2003, Piersma 2007), mating systems and parental care (Jönsson & Alerstam 1990, Székely & Reynolds 1995), and drivers of sexual size dimorphism (Jehl & Murray 1986, Figuerola 1999, Sandercock 2001). Similarly, estimates of biometrics and demographic rates have been useful for the applied goals of delineation of population structure (Nicoll *et al.* 1991, Gates *et al.* 2013) and investigating threats to population viability (Sandercock 2003, Piersma *et al.* 2016,

Kubelka *et al.* 2018). However, much of the available data for waders comes from a subset of well-studied species. Major knowledge gaps remain for many taxa, including some common species in Europe and North America (Piersma *et al.* 1997). For example, estimates of annual survival are not yet available for a majority of species in most families, including two-thirds of the species in the family Scolopacidae (Méndez *et al.* 2018).

The Broad-billed Sandpiper *Calidris falcinellus* is a poorly known species of Palearctic wader. Most of the available information on the natural history of the species is summarized in species accounts in regional volumes (Cramp & Simmons 1983, Bangjord 1994, Shimmings & Øien 2015, van Gils *et al.* 2020). A western subspecies

C. f. falcinellus breeds in northern Fennoscandia and northwest Russia, and an eastern subspecies *C. f. sibirica* breeds on the Taimyr Peninsula and northeast Siberia (van Gils *et al.* 2020). In Fennoscandia, Broad-billed Sandpipers breed in wet mire habitats in the taiga biome (Svensson 1987, Rae *et al.* 1998, 2022), use stopover sites in eastern Europe (Chernichko *et al.* 1991, Verkuil *et al.* 2006a,b, Pehlak 2008, Franks *et al.* 2022), and winter at coastal sites in the Middle East (Green *et al.* 1994, de Fouw *et al.* 2017, van Gils *et al.* 2020). Broad-billed Sandpipers are estimated to have a breeding population of *ca.* 33,000–44,000 pairs in Europe (Staneva & Burfield 2017), including *ca.* 1,650–1,800 pairs in Norway (Shimmings & Øien 2015). Population trends have indicated population declines of –5.4% per year in Fennoscandia during 2006–2018, primarily to losses during 2011–2012 and in the core breeding range in Finland (Lindström *et al.* 2019).

The objectives of our project were four-fold. First, we examined variation in biometrics among birds in mated pairs, and tested whether morphological traits could be used for sexing. The mating system is socially monogamous with songs and flight displays by both sexes, biparental incubation, and mainly male care of young (Cramp & Simmons 1983, Svensson 1987, R. Rae pers. obs.). Thus, we predicted sexual size dimorphism to be female-biased as described in other *Calidris* sandpipers (Jehl & Murray 1986, Jönsson & Alerstam 1990, Sandercock 1998), and possibly related to fecundity advantages of larger body size among females (Székely *et al.* 2007). Second, if aerial agility plays a role in mate choice, we predicted that dimorphism might be greater in wing length and body mass than culmen length (Mueller 1989), and that larger-bodied females might preferentially pair with smaller-bodied males (Jehl 1970, Jönsson 1987, Blomqvist *et al.* 1997). If intersexual competition or resource partitioning are important ecological processes, we predicted that dimorphism might be greatest in culmen length as a trophic structure (Sandercock 2001, Nebel 2005, Székely *et al.* 2007). Third, we compared the biometrics of Broad-billed Sandpipers captured on the breeding grounds in Finnmark with published data for birds captured at stopover (Waldenström & Lindström 2001, Meissner 2005, Verkuil *et al.* 2006a) and nonbreeding sites (Fry 1989, Gavrilov *et al.* 1995, Balachandran & Natarajan 1997). We tested for seasonal changes among different stages of the annual cycle and for potential differences between the two subspecies (Nicoll *et al.* 1991, Gates *et al.* 2013). Comparisons based on museum skins have suggested that the western *falcinellus* subspecies might be smaller than the eastern *sibirica* subspecies (Prater *et al.* 1977, Cramp & Simmons 1983). Last, we estimated apparent survival using mark-recapture models based on live encounter data. Based on their average body size (*ca.* 38 g) and medium-distance migration (*ca.* 6,000 km), we predicted that the annual survival of Broad-billed Sandpipers might be in the range of estimates for other small-bodied sandpipers (*ca.* 0.6–0.8; Sandercock 2003, Méndez *et al.* 2018).

METHODS

Spatial and temporal sampling

The breeding range of Broad-billed Sandpipers includes fens and wetlands across a large area of northern Fennoscandia and Russia (van Gils *et al.* 2020). The study area included wetland complexes near Kautokeino, Finnmark in northern Norway (68°55'N, 23°10'E; altitude 350–400 m asl). Our core study sites consisted of three mires in adjacent valleys within 2 km and a second mire site 30 km to the south, and the surrounding region was also suitable habitat (Borge *et al.* 2017). The total area of each mire varied from *ca.* 10–100 ha, and nesting areas were restricted to two types of wet fen habitats (Rae *et al.* 1998, 2022). Broad-billed Sandpipers arrive in late May and early June at the breeding grounds in northern Scandinavia (Cramp & Simmons 1983, Svensson 1987), following peak passage at stopover sites in eastern Europe (Verkuil *et al.* 2006a, Pehlak 2008). The study area was surveyed for 10–14 days each year in the 3-week period between 15 June and 8 July over a 25-year period from 1995 to 2019. Nest sites were initially located by searching suitable habitats and by looking for birds performing aerial courtship displays over the mire complexes during the pre-laying period. From 2000, effort was focused on individually marking and resighting of breeding birds and monitoring of breeding behaviour in our core study area. All sites were searched two or more times by experienced observers during the incubation period when parents were attending nests.

Field methods

Broad-billed Sandpipers are secretive during nesting, and active nests were located by flushing incubating birds at short distances, watching parents return to the nest site after alarm calls were heard, and rechecking nest scrapes used in previous years (Rae *et al.* 2022). Some nests were located at sites in the mires with difficult access. We did not trap at nests in treacherous locations that could not be reached safely for both the nest contents and the observers. Birds were captured at accessible nests by laying a mist net over them when incubating eggs or brooding chicks. To minimize disturbance, we did not conduct trapping or surveys during days with rain or high winds, and all trapping was conducted during the last stages of the incubation period. We observed no cases of nest desertion due to trapping of birds at nest sites. All captured birds were uniquely marked with a metal ring and a combination of colour rings at first capture (Fig. 1). Each year, we also surveyed the same mire complexes and adjacent areas to resight colour-ringed birds. Resightings allowed us to collect detection data on birds that returned to the study site while reducing unnecessary disturbance to active nests.

Five biometrics were recorded for each bird and all measurements were taken by one observer (R. Rae) to reduce inter-observer variability. Bill length and total head were measured using dial vernier callipers (±0.1 mm). Wing

Fig. 1. Colour-ringed Broad-billed Sandpiper foraging in breeding habitat near Kautokeino, Norway, 2017 (photo: S. Rae).

length was recorded as flattened wing chord on a stopped wing rule (±1 mm; Evans 1993). Total length of tarsus and toe was measured using a stopped wing rule (±0.5 mm). Body mass was measured with a digital balance (±0.01 g). Breeding birds were aged by partial post-juvenile wing moult as either second years (hatched in the previous year) or as older birds (*ca.* 2+-year olds; Fig. 2). Second years had moult limits in the wing with greater contrast between worn inner and fresh outer primaries, whereas older birds had primary feathers that were uniform in coloration and wear (Prater *et al.* 1977, Gratto & Morrison 1981).

Morphometrics, assortative mating, and sexing

Statistical analyses of biometric data were conducted in an R environment (R Core Team 2020). Females were known to be larger than males based on sexing from gonads and measurements of museum skins for Broad-billed Sandpipers (Cramp & Simmons 1983). We sexed Broad-billed Sandpipers by comparing birds in mated pairs and by their behaviour during incubation. Biometric data were compared between individuals in 33 unique mated pairs where females were assumed to be the larger partner. In two cases where individuals had switched partners between years, we also compared birds to their different partners. The sexes differed in incubation rhythms where males were usually captured during the day whereas females were captured during evening visits to the nests. We calculated an index of sexual size dimorphism (SDI) as the ratio of female/male traits. Descriptive statistics and two-sample *t*-tests were conducted with functions of base R and Hedge's *g* was calculated as a standardized mean
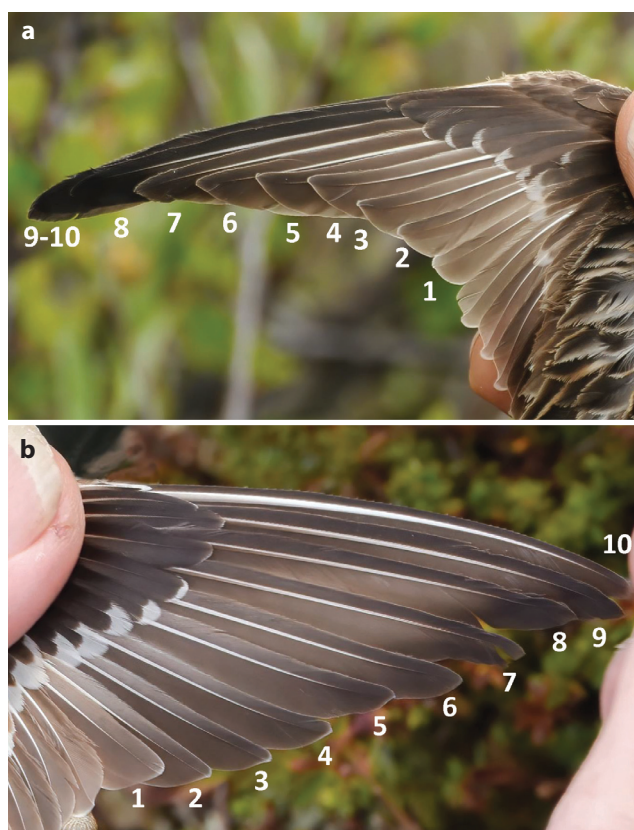
Fig. 2. Broad-billed Sandpipers were aged as **(a)** second calendar year or **(b)** older birds by patterns of coloration, shape and wear in the primary wing feathers (photos: S. Rae). In second-year birds, the inner primaries (P1–P6) were light brown, had sharp tips and more wear than the outer primaries (P7–P10). In contrast, the primaries of older birds were black and more uniform in shape and wear.

difference with functions of the 'esc' package. Values of $g \geq 0.8$ were considered large effect sizes for sexual dimorphism. Correlation charts were created with functions of the 'PerformanceAnalytics' package. We tested for assortative mating with pairwise comparisons of traits between birds in mated pairs.

Our survival analyses were based on all birds, including individuals where pairing information was not available. To sex birds from morphological data, we first compiled the information from known-sex birds in pairs and conducted a linear discriminant function analysis with functions of the 'MASS' package. The sign and the magnitude of the coefficients indicate the relative importance of each variable to the discriminant function. The error rate of the discriminant function was calculated using a jackknife procedure based on leave-one-out cross validation. We then used the function to determine the sex of all birds captured at the nests. Birds were classified as female or male if the posterior distributions for sex assignment from the discriminant function gave a high probability of assignment (>0.7). Sexes were coded as unknown if the posterior distributions indicated uncertainty or if complete morphometric data were not available. We did not have adequate data to consider second years and older birds separately. To investigate population differences in morphology, we compared measurements from older birds to published estimates of biometrics for the two subspecies of Broad-billed Sandpipers (*falcinellus* and *sibirica*). We conducted pairwise comparisons of biometrics between birds in Norway and other sites with a function based on a two-sample *t*-test.

Mark-recapture analyses of annual survival

Recaptures and resightings of birds from the breeding seasons were combined to create encounter histories for each individual bird. Each year within the encounter history was coded as 1 = captured or resighted on the study area, or 0 = not detected during the breeding season. A subset of 34 birds marked as pulli were not included in the survival analysis because none returned to the study area. All birds included in the encounter histories were first captured and ringed as either second years or older birds, and we excluded 22 birds where their sex was uncertain. Similarly, eight birds captured and marked in the last year of the study (2019) were not included in the analysis because they could not be reencountered. We analysed the encounter histories with Cormack-Jolly-Seber (CJS) models to estimate annual probabilities of apparent survival (ϕ) corrected for the probability of encounter (*p*).

Mark-recapture analyses were conducted in Program Mark in an information theory framework (White & Burnham 1999). First, we selected factors to include in the global model for the probabilities of apparent survival (ϕ) and encounter (*p*). We modeled both parameters as a function of sex because males and females can differ in reproductive roles and behavior during the breeding season (Sandercock & Gratto-Trevor 1997, Sandercock *et al.* 2000), and in timing of migration and habitat use during the nonbreeding season (Shepherd *et al.* 2001, Nebel *et al.* 2002). We used time-since-marking models (tsm) that separated apparent survival in the interval after first capture for newly marked individual (ϕ^1) from later intervals for previously marked individuals (ϕ^{2+}) because initial inspection of the encounter histories indicated that many birds were not encountered after the first year of capture (Sandercock 2003). We also modeled the interval after first capture as an effect of age-class (age) to test for potential differences between birds first marked as second years or older age-classes (Summers *et al.* 2001). The average number of individuals detected per year was relatively low (mean = 6.7, range = 1–15) and we opted not to test models with effects of time-dependence. Our global model was a CJS model with the effects of age-class, time-since-marking, and sex in apparent survival, and sex in the probability of encounter: ϕ^1(sex×age), ϕ^{2+}(sex), p(sex). We used the median c-hat procedure to evaluate the goodness-of-fit of the global model to the encounter histories and to calculate a variance inflation factor ($\hat{c}$). The procedure simulates encounter histories and we bounded $\hat{c}$ from 1 to 5 with 10 steps and 100 replicates per step for a total of 1,200 simulations. Moderate amounts of overdispersion are common in mark-recapture data and values of $\hat{c} < 3$ indicate that the global model is an acceptable fit to the data.

We proceeded with model testing by fitting reduced models with fewer parameters. All models were constructed with parameter index matrices and the logit-link function. Starting with our global model, we applied constraints to the parameters in the following order: encounter rates (*p*) and then apparent survival (ϕ). Parameters were modeled as factorial models (sex×age), single factor (sex or age) and constant models (con). The parameter count (*K*) and the deviance were combined to calculate Akaike's Information Criterion (QAICc) and models were ranked by the difference from the minimum AICc model (ΔQAICc). Akaike weights (w_i) were used to determine the relative likelihood of a model within the set of candidate models, and sums of weights for candidate models with or without explanatory factors were used to quantify the relative support for different factors.

Our analyses of annual survival were based on birds first captured as second years or older age-classes and we found strong support for time-since-marking models. Accordingly, we calculated the average life expectancy ($\hat{E}$) of sandpipers from hatching as

$$\hat{E} = 2 + \frac{-1}{\ln(\hat{\phi}^{2+})}$$

where 2 years is the minimum age of previously marked birds that returned to the study area, and $\hat{\phi}^{2+}$ was the apparent survival of the 2+-year-old age-class. We used the delta method to derive an expression for calculating the variance for our extrapolated estimates of life expectancy (Powell 2007):

$$SE(\hat{E}) = \sqrt{\left[\,SE(\hat{\phi}^{2+})\,\right]^2 \times \left[\,\frac{1}{\hat{\phi}^{2+}\ln(\hat{\phi}^{2+})}\,\right]^4}$$
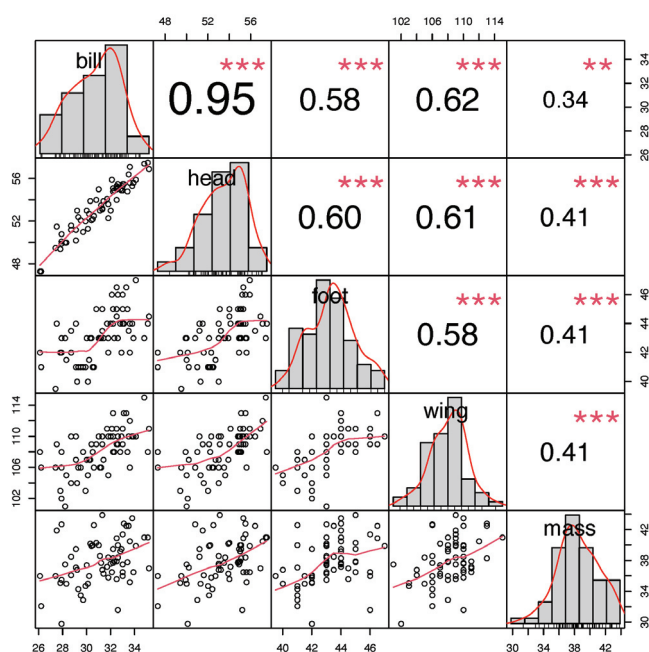
RESULTS

Sexing from biometrics

Broad-billed Sandpipers of known sex exhibited female-biased sexual size dimorphism where females were significantly larger than males in the four linear measurements of body size, and also in body mass (Table 1). The greatest degrees of sexual size dimorphism were in the length of the bill (SDI = 1.12) and total head (SDI = 1.07) where females were up to 12% larger than males with effect sizes of g = 2.45–2.77. Dimorphism was less pronounced in foot, wing and body mass (SDI < 1.05) where females were up to 5% larger with smaller effect sizes of g < 1.72. The five biometrics were positively correlated with a strong correlation between bill and total head length (r_p = 0.95) and weaker correlations among other pairs of variables ($r_p \approx 0.34$ to 0.61; Fig. 3).

The coefficients of the linear discriminant function for the five biometrics were bill: –0.603, total head: –0.026, foot: –0.353, wing: –0.125, and mass: +0.082. The jackknife procedure correctly classified 95.7% of the sample (67/70) where three males were misclassified as females. When a linear discriminant function was fitted with bill length alone, the classification rate was reduced to 91.4% (64/70) with six errors: five males misclassified as females and one male misclassified as a female. Therefore, we used the linear discriminant function based on five traits to sex all sandpipers included in the analyses of apparent survival. Based on the sex assignments from the multivariate analysis, a rule of thumb for sexing of Broad-billed Sandpipers by bill length alone would be: ≤29.9 mm = male, 30.0–31.5 mm = either sex, and ≥31.6 mm = female.
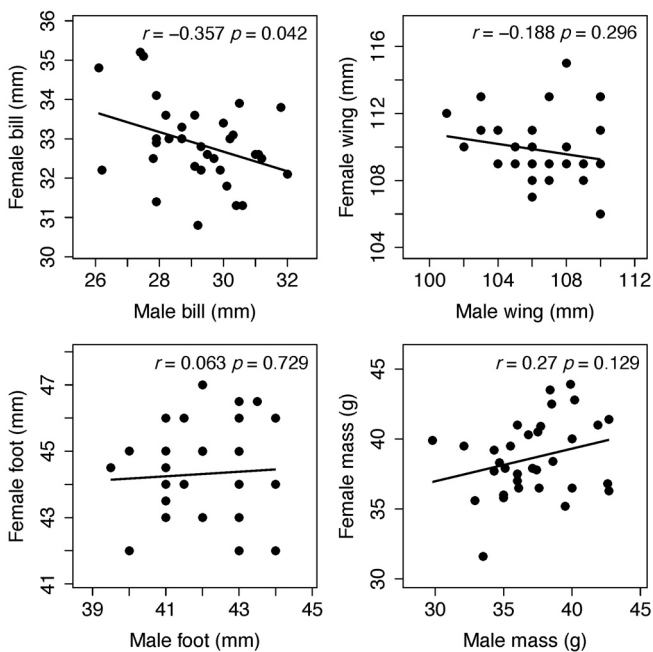
Disassortative pairing

We found evidence for disassortative pairing with a negative correlation in bill length between females and males in mated pairs (r_p = –0.357, P = 0.042; Fig. 4). The average within-pair dimorphism was much greater for small-billed males (26.0 vs. 33.6 mm, SDI = 1.30) than large-billed males (32.0 vs. 32.2 mm, SDI = 1.01). Given the strong correlation between bill and total head length, we dropped head from our tests of assortative mating. We found no significant correlations between paired birds for any of the morphological traits that might be associated with body size or aerial agility in flight displays: wing length, tarsus length, and body mass ($|r_p|$ < 0.27, P > 0.12; Fig. 4).

Fig. 3. Correlation chart for biometrics of known sex birds in mated pairs (n = 33) of Broad-billed Sandpipers breeding at Kautokeino, Norway. Pairwise comparisons at lower left, distribution of values on the diagonal, and significant Pearson correlation coefficients (r_p) are marked with 1–3 asterisks at upper right (* P < 0.05, ** P < 0.01, *** P < 0.001).

Table 1. Biometrics, body mass, and sexual dimorphism of known sex birds in mated pairs of Broad-billed Sandpipers (n = 36 females and 34 males) breeding at Kautokeino, Norway. Sexual dimorphism index (SDI) was calculated as the ratio of mean traits for female/male. Hedge's g was calculated as the standardized mean difference, where $g \geq 0.8$ is a large effect size for sexual dimorphism.

Trait	Females (mean ± SD)	Males (mean ± SD)	SDI	Hedge's g (± SE)	t-test	$P \leq$
Bill (mm)	32.81 ± 1.05	29.25 ± 1.47	1.12	2.77 ± 0.34	11.6	0.001
Total head (mm)	55.12 ± 1.16	51.49 ± 1.71	1.07	2.45 ± 0.32	10.2	0.001
Foot (mm)	44.25 ± 1.32	42.03 ± 1.23	1.05	1.72 ± 0.28	7.3	0.001
Wing (mm)	109.78 ± 1.87	106.41 ± 2.27	1.03	1.61 ± 0.28	6.7	0.001
Mass (g)	38.64 ± 2.71	37.01 ± 3.17	1.04	0.55 ± 0.24	2.3	0.024

Seasonal and population differences in biometrics

We compiled biometrics for Broad-billed Sandpipers captured as second years or older birds, and tested for differences in biometrics between breeding birds in Norway versus published reports from live captures of birds in other populations in Eurasia (Table 2). Foreign captures of three birds caught at our study site (DFH 81512594, DFH 81528204, and NOS 8643719) confirmed migratory connectivity between our breeding population at Kautokeino, Norway and migratory stopover sites at Sivash Bay on the Crimean Peninsula (*ca.* 2,700 km apart). We expected that all study sites in Europe were likely to be the same migratory population of *falcinellus*, and that populations of *sibirica* should be separate. Bill and total head length of birds in Norway did not differ from *falcinellus* captured during migration, and the significant differences from *sibirica* were inconsistent (bill in India: +4.4% longer, head in Australia: –1.1% smaller). Wing length of birds from our study site in Norway were significantly different from four other sites, although all of the mean differences were relatively small (range = –1.4% in Australia to +3.1% in Kazakhstan). With the exception of birds captured during late summer in Sweden (+0.6%), wing length tended to be shorter during southward migration (–1.4%) and longer during the nonbreeding period and northward migration (+1.8 to +3.1%). The largest differences among sites for *falcinellus* were in body mass. Breeding birds captured during incubation in Norway had an average body mass of 37.9 g. In contrast, birds captured during northward migration at Sivash averaged 41.9 g (+10.0% heavier) whereas birds captured on southward migration in Poland averaged 33.7 g (–11.7% lighter).

Return rates and longevity

Encounter histories were constructed for 119 Broad-billed Sandpipers which were ringed and resighted during the breeding seasons of 1995–2019. Return rates were low because few birds were resighted or recaptured after their first year of capture (21%, 25 of 119). Return rates were low among second-year females (14%, 3 of 22), older females (27%, 9 of 33), second-year males (25%, 6 of 24), and older males (18%, 7 of 40), and were not significantly different among the four demographic classes (logistic regression, sex: $\chi^2_1 = 0.04$, $P = 0.84$, age-class: $\chi^2_1 = 0.10$, $P = 0.75$, interaction: $\chi^2_1 = 1.92$, $P = 0.17$). The longevity record from our 25-year field study was a male Broad-billed Sandpiper (NOS 8627946) that was captured on a nest and ringed as a 2+-year old bird on 2 Jul 1996 and then recovered dead in the same mire

Fig. 4. Assortative mating for four morphometric traits in mated pairs (*n* = 33) of Broad-billed Sandpipers breeding at Kautokeino, Norway.

Table 2. Biometrics and body mass (mean ± SD, *n*) for Broad-billed Sandpipers captured at field sites in the western (*C. f. falcinellus*) and eastern Palearctic (*C. f. sibirica*). Pairwise comparisons between breeding sandpipers in Norway versus other sites (two-sample *t*-test: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

Seasonal stage	Location	Subsp.	Bill length (mm)	Total head (mm)	Wing (mm)	Body mass (g)	Source[1]
Breeding	Norway	*fal*	30.9 ± 2.1 (133)	53.0 ± 2.2 (130)	108.3 ± 3.3 (134)	37.9 ± 3.1 (128)	1
Northward migration	Crimea	*fal*	31.2 ± 0.2 (879)	53.0 ± 0.2 (502)	109.0 ± 0.3 (898)*	41.9 ± 0.8 (943)***	2
Southward migration	Sweden	*fal*	—-	53.1 ± 2.0 (48)	110.3 ± 4.3 (47)**	38.6 ± 5.1 (48)	3
Southward migration	Poland	*fal*	30.6 ± 1.8 (16)	52.6 ± 2.0 (16)	108.1 ± 4.0 (20)	33.7 ± 4.6 (27)***	4
Southward migration	Kazakhstan	*sib*	-	-	106.8 ± 2.4 (80)***	37.6 ± 5.8 (201)	5
Nonbreeding	Australia	*sib*	31.1 ± 2.1 (505)	52.4 ± 2.1 (464)**	111.7 ± 3.4 (556)***	37.1 ± 3.4 (69)	6
Nonbreeding	India	*sib*	32.3 ± 3.0 (101)***	-	107.4 ± 3.8 (68)	-	7

[1] Sources: 1. This study, 2. Verkuil *et al.* 2006a, 3. Waldenström & Lindström 2001, 4. Meissner 2005, 5. Gavrilov *et al.* 1995, 6. Fry 1989, and 7. Balachandran & Natarajan 1997.

Table 3. Model selection for estimation of apparent survival (ϕ) and the probability of encounter (p) with Cormack-Jolly-Seber (CJS) models for Broad-billed Sandpipers breeding at Kautokeino, Norway, 1995–2019. Alternative models included time-since-marking effects to separate apparent survival after first capture (ϕ^1) from later transitions (ϕ^{2+}), sex and age-classes, and constant (con). Model statistics include the number of parameters (K), quasi-deviance (QDev), quasi-Akaike's Information Criterion corrected for small sample sizes (QAICc), rankings based on differences from the best fit model (ΔQAICc), and model weights (w_i). Models were adjusted for overdispersion ($\hat{c} = 1.357 \pm 0.116$SE).

| Model structure | | | | Model statistics | | | |
ϕ^1	ϕ^{2+}	p	K	QDev	QAICc	ΔQAICc	w_i
con	con	con	3	177.9	234.3	0.0	0.498
sex	con	con	4	177.7	236.2	1.9	0.197
age	con	con	4	177.9	236.3	2.0	0.180
sex	sex	con	5	177.8	238.4	4.1	0.066
	con	con	2	185.9	240.2	5.9	0.026
sex×age	sex	con	7	175.4	240.3	6.0	0.025
sex×age	sex	sex	8	175.3	242.4	8.1	0.009

complex on 20 Jun 2007. The elapsed time gave a minimum age of 10 years, 11 months, 19 days (4,006 days), but since the bird was 2+-years old at first capture, the extrapolated longevity was *ca.* 13+ years. Based on the fresh bird remains with plucked feathers found at the mortality site, we concluded that the bird was recently killed by a Merlin *Falco columbarius*.

Estimation of apparent survival and probability of encounter

Goodness-of-fit tests based on the median c-hat procedure showed that our starting global model ϕ^1(sex×age), ϕ^{2+}(sex), p(sex) was a good fit to the encounter histories with low levels of overdispersion ($\hat{c} = 1.357 \pm 0.116$SE). We used the variance inflation factor to adjust for overdispersion and used QAICc for model ranking and selection (Table 3). Models with time-since-marking effects in apparent survival were strongly supported in the candidate set (ratio of model weights: 0.97/0.03 = 32.3×). Models with constant rates had greater support than models with sex or age effects for apparent survival after first capture (ϕ^1, ratio: 0.52/0.48 = 1.1×) and later intervals (ϕ^{2+}, ratio: 0.88/0.12 = 7.7×), and also the probability of encounter (p, ratio: 0.99/0.01 = 99×).

Parameter estimates from our unconstrained global model ϕ^1(sex×age), ϕ^{2+}(sex), p(sex) showed a strong effect of time-since marking with low apparent survival among newly marked birds in the year after first capture ($\hat{\phi}^1$ = 0.219–0.498), and higher apparent survival among previously marked sandpipers that returned to the study area at least once ($\hat{\phi}^{2+}$ = 0.706–0.756; Table 4). Apparent survival in the interval after first capture (ϕ^1) showed different patterns between the sexes: apparent survival was higher among older than second-year females whereas males had the opposite pattern. Sex differences in the apparent survival of returning birds were small, males tended to have higher apparent survival ($\hat{\phi}^{2+}$ = 0.756) than females ($\hat{\phi}^{2+}$ = 0.706). Parameter estimates from the best fit model ϕ^1(con), ϕ^{2+}(con), p(con) indicated that apparent survival was low in the transition after the year of first capture ($\hat{\phi}^1$ = 0.353) and higher among subsequent transitions for birds that returned to the study area ($\hat{\phi}^{2+}$ = 0.736), with intermediate estimates for the probability of encounter ($\hat{p}$ = 0.381). Overall parameter estimates from a standard CJS model ϕ(con), p(con) that did not control for time-since-marking were negatively biased for both apparent survival ($\hat{\phi}$ = 0.628) and the probability of encounter ($\hat{p}$ = 0.280). Based on our best overall estimate of apparent survival for returning sandpipers ($\hat{\phi}^{2+}$ = 0.736 $\pm$ 0.060), the average life expectancy of Broad-billed Sandpipers from hatching was $\hat{E}$ = 5.3 $\pm$ 0.9 SE years (95% CI = 4.0–7.6 years).

DISCUSSION

Our 25-year field study of Broad-billed Sandpipers in northern Norway provides some of the first estimates for biometric measurements, sexual size dimorphism, disassortative pairing and annual survival for a poorly studied species of Palearctic wader. First, we compared patterns of dimorphism in the measures of structural size and body mass to test the predictions from alternative hypotheses for evolution of body size in waders. Second, we compared the biometrics of breeding birds in Norway to published estimates to test for seasonal variations in body mass and wing length and possible differences between the two subspecies of Broad-billed Sandpipers. Last, survival was highest among previously marked birds that returned to the study area due to strong effects of time-since-marking, and weaker effects of sex and age-class. We evaluated the ecological explanations for time-since-marking effects in apparent survival and intermediate estimates for the probability of encounter.

Sexual size dimorphism

The breeding behavior of Broad-billed Sandpipers is typical of socially monogamous species with flight displays and songs during settlement, joint incubation by mated pairs and mainly male care of young (Cramp & Simmons 1983, Svensson 1987, Rae *et al.* 1998, R. Rae pers. obs.). Our findings of female-biased dimorphism in Broad-billed Sandpipers are consistent with patterns of sexual dimorphism found in other species of waders with a similar mating system. Female-biased dimorphism has also been reported in Dunlin *C. alpina* (Jönsson 1987, Gates *et al.* 2013), Least Sandpipers *C. minutilla* (Jiménez *et al.* 2015), Western *C. mauri* and Semipalmated Sandpipers *C. pusilla* (Sandercock 1998, 2001), and Purple Sandpipers *C. maritima* (Nicoll *et al.* 1991, Hallgrimsson *et al.* 2008). The pattern of female-biased dimorphism in monogamous shorebirds could be the result of sexual selection by females for small-bodied males that are agile in flight displays (Jehl & Murray 1986, Figuerola 1999). However, the magnitude of sexual size dimorphism in Broad-billed Sandpipers was ranked: bill length > foot, wing and body mass. The same general pattern has been reported for most *Calidris* sandpipers (Hallgrimsson *et al.* 2008, Niemc *et al.* 2018, Witkowska & Meissner 2020). We found evidence of disassortative pairing based on bill length among Broad-billed Sandpipers, but not for traits such as wing length or body mass that could affect wing-loading. Disassortative mating for bill length has been previously reported for Least Sandpipers and Stilt Sandpipers *C. himantopus* (Jehl 1970), as well as Dunlin (Jönsson 1987). Variation in bill morphology is unlikely to be associated with mate choice based on visual characteristics in waders (Mueller 1989), but does affect song quality and mate choice in songbirds (Demery *et al.* 2021). Both sexes sing in Broad-billed Sandpipers and some other *Calidris* species (Holmes 1973, Jehl 1973, R. Rae pers. obs.), but the potential role of vocalizations in mate choice remains unknown.

Bill length is a trophic structure which affects foraging behaviour via success in pecking, probing, and other feeding behaviors (Sandercock 2001, Elner & Seaman 2003). The magnitude of dimorphism in bill length of Broad-billed Sandpipers (SDI = 1.12) was comparable to other dimorphic species of *Calidris*, including Dunlin (SDI ≤ 1.15; Gates *et al.* 2013), Purple Sandpipers (SDI ≤ 1.18; Nicoll *et al.* 1991, Halgrimsson *et al.* 2008) and Western Sandpipers (SDI = 1.18; Sandercock 1998). Sexual differences in foraging behaviour and habitat use often persist during the nonbreeding season for wader species with strong bill dimorphism (Fernández & Lank 2008, Halgrimsson *et al.* 2008), sometime leading to latitudinal clines in age or sex distributions (Shepherd *et al.* 2001, Nebel *et al.* 2002, Nebel 2006, Mathot *et al.* 2007). In Broad-billed Sandpipers, the annual cycle includes a short 6-week breeding season and ~46 weeks migrating and residency at the nonbreeding grounds. Hence, most of their lives are spent in nonbreeding habitats. Tests of ecological hypotheses for sexual size dimorphism based on intersexual competition and resource partitioning will require new data on foraging ecology in nonbreeding habitats (Sandercock 2001, Nebel 2005). Observing individual birds is possible when Broad-billed Sandpipers are alone or in small groups (Verkuil *et al.* 2006b), but more difficult when they feed and roost in mixed species flocks (Green *et al.* 1994, de Fouw *et al.* 2017). Nevertheless, the observed patterns of sexual size dimorphism suggest that Broad-billed Sandpipers might have sexual differences in diet and habitat use, or possibly latitudinal gradients in sex distributions during the nonbreeding season.

Sexual size dimorphism was helpful for sexing Broad-billed Sandpipers from biometrics with high classification rates of 91.4% with bill length alone and 95.7% with a combination of five different traits (SDI ≤ 1.12). Classification rates based on discriminant functions covary with degree of dimorphism in *Calidris* sandpipers, ranging from a low of 82–83% in Curlew Sandpipers *C. ferruginea* (SDI ≤ 1.09; Witkowska & Meissner 2020) and Little Stints *C. minuta* (SDI ≤ 1.05; Niemc *et al.* 2018), 86% in Sanderling *C. alba* (SDI ≤ 1.09; Wood 1987) and Temminck's Stints *C. temminckii* (SDI ≤ 1.10; Lislevand *et al.* 2009), 87–98% for different subspecies of Dunlin (SDI

Table 4. Annual estimates of apparent survival and probability of encounter from selected CJS models for a breeding population of Broad-billed Sandpipers at Kautokeino, Norway, 1995–2019. The sample of 119 birds included 22 second-year females, 33 older females, 24 second-year males, and 40 older males.

| Model structure | | | Class | | Parameter estimates | | |
ϕ^1	ϕ^{2+}	p	Sex	Age	$\phi^1 \pm$ SE	$\phi^{2+} \pm$ SE	$p \pm$ SE
sex×age	sex	sex	F	Y	0.219 ± 0.137	0.706 ± 0.097	0.405 ± 0.116
			F	A	0.405 ± 0.151		
			M	Y	0.498 ± 0.183	0.756 ± 0.076	0.367 ± 0.091
			M	A	0.266 ± 0.113		
con	con	con	All	All	0.353 ± 0.078	0.736 ± 0.060	0.381 ± 0.071
	con		con	All	All	0.628 ± 0.053		0.280 ± 0.058

< 1.15; Gates *et al.* 2013), ≥88% for Buff-breasted Sandpipers *C. subruficollis* (1/SDI ≤ 1.10; Almeida *et al.* 2020), 91% for Least Sandpipers (SDI ≤ 1.08; Jiménez *et al.* 2015), and up to 97% for Purple Sandpipers (SDI ≤ 1.15; Halgrimsson *et al.* 2008) and Western Sandpipers (SDI ≤ 1.24; Jiménez *et al.* 2015). Our sexing was based on morphometric comparisons of birds in breeding pairs and incubation behavior. Our classification rate was high but confirmation of our findings awaits genetic sexing with blood or feather samples.

Population and seasonal variation in biometrics

Variation in biometrics has been previously described for different populations and subspecies of Purple Sandpipers and Dunlin (Nicoll *et al.* 1991, Gates *et al.* 2013). In the Broad-billed Sandpiper, comparisons based on museum skins have suggested that the nominate subspecies *falcinellus* is smaller than the eastern Palearctic subspecies *sibirica* (Prater *et al.* 1977, Cramp & Simmons 1983). Here, we compared measurements of live birds but found little evidence for differences in body size between the two subspecies. Variation in bill, head and wing length were inconsistent and the two subspecies did not differ in average body mass (Balachandran & Natarajan 1997, this study). Differences in biometrics could be due to intrinsic differences between the subpopulations, but also to variation in sex ratios within the samples or to differences in the measurement techniques used by independent observers.

Variation in biometrics among different stages of the annual cycle for *C. f. falcinellus* were consistent with seasonal timing of moult and migration. Wing length was longer during northward migration and usually shorter in post-breeding southward migration, consistent with patterns of feather wear, moult and replacement during the nonbreeding season (Pienkowski & Minton 1973, Prater *et al.* 1977, Fry 1989). The greatest seasonal changes were in body mass, where breeding birds in Norway were lighter than birds captured on spring migration at Sivash but heavier than birds captured on autumn migration in Poland. Variation in body mass could be due to dynamics of fat stores or to changes in body composition at different stages of the annual cycle (Guglielmo & Williams 2003). A heavier body mass during spring migration might include resources used for breeding activities such as the flight displays or egg formation. Estimating the relative importance of endogenous and exogenous resources for breeding would require additional sampling with stable isotopes or other methods (Hobson & Jehl 2010). Recaptures of birds at stopover sites have reported average rates of mass gain of 1.04 g/day during northward migration (Verkuil *et al.* 2006a) and 1.02–1.60 g/day on southward migration (Gavrilov *et al.* 1995, Waldenström & Lindström 2001, Meissner 2005). Based on their body size and fat stores, Broad-billed Sandpipers have been predicted to be a short-hop migrant with a theoretical flight range of up to 1,400 km (Meissner 2005).

Factors affecting probability of encounter and apparent survival

Return rates were low for Broad-billed Sandpipers breeding at our field site in Norway (21.0%), but higher than return rates to a stopover site in Kazakhstan (1.1%, 4 of 371 birds; Gavrilov *et al.* 1998). Use of Cormack-Jolly-Seber models with time-since-marking effects controlled for the effects of losses after first capture and imperfect detection when estimating annual survival (Sandercock 2020). Gaps in the encounter histories were common and the annual probability of encounter for a color-banded bird was $\hat{p}$ = 0.381 during a 2-week field season. The probability of encounter was likely affected by the challenges of resighting secretive birds that were feeding and nesting at difficult to access sites in the wet mire habitats. Encounter rates can also be affected by temporary emigration and we had some field seasons where few nests were discovered despite considerable effort in nest searching (Rae *et al.* 1998). Low encounter rates could indicate that Broad-billed Sandpipers skip nesting in years of unsuitable conditions, as has been reported elsewhere for arctic-breeding populations of Semipalmated Sandpipers (Gratto-Trevor 1991), Sanderling (Parmelee & Payne 1973), and other species of waders (Ganter & Boyd 2000).

Apparent survival rates after first capture were lower among second years than older birds, and highest among previously marked birds that had returned to the study site at least once. About a third of birds were first captured and ringed as second-year birds and some of the variation could be explained by the effects of age on true survival, with higher mortality rates among young or inexperienced birds nesting for the first time (Summers *et al.* 2001, Sandercock 2003). Some losses could also have been due to breeding dispersal if local habitat conditions changed between years due to changes in hydrology or permafrost dynamics in the mire habitats (Tahvanainen 2011, Hofgaard *et al.* 2020), or if birds moved after experiencing loss of a nest or mate (Flynn *et al.* 1999, Sandercock *et al.* 2000). Two cases of breeding dispersal were recorded, where birds moved 0.7 and 1.3 km to settle at adjacent sites in a different year (Rae *et al.* 1998). All other returning Broad-billed Sandpipers nested in the same mire complex, often reusing the same nest scrape (Rae *et al.* 2022). Apparent survival rates did not differ between the sexes, which could indicate that females and males have similar rates of survival and breeding site fidelity, or that sexing of birds by morphology was actually less reliable than the classification rates estimated in our discriminant function analysis.

The best estimate of annual survival for Broad-billed Sandpipers was based on the subset of previously marked birds that returned to the study area ($\hat{\phi}^{2+}$ = 0.736 ± 0.060). A growing number of estimates of apparent survival based on CJS models are available for other species of *Calidris* sandpipers. Our new estimate of apparent survival for Broad-billed Sandpipers was higher than annual survival

rates of small-bodied species like Western (ɸ = 0.57; Sandercock *et al.* 2000) and Semipalmated Sandpipers (ɸ = 0.59–0.66; Sandercock & Gratto-Trevor 1997, Sandercock *et al.* 2000), but comparable to estimates for Temminck's Stints (ɸ = 0.695; Koivula *et al.* 2008) and Dunlin (ɸ = 0.76; Warnock *et al.* 1997). Higher rates of annual survival have been reported for at least three other species of *Calidris* sandpipers: Sanderling (ɸ = 0.74–0.87; Reneerkens *et al.* 2020), Purple Sandpiper (ɸ = 0.795; Summers *et al.* 2001), and Red Knot *C. canutus* (ɸ = 0.78–0.87; Leyrer *et al.* 2013). Our estimates of average life expectancy of *ca.* five years were consistent with the standing age distribution of our study population where the median for minimum age at last sighting among returning birds was four years (range = 2–13+ years, *n* = 27 birds). A new longevity record from our field study was a male sandpiper found dead on the same mire where it was ringed after 10 years, 11 months, 19 days (4,006 days) and had a minimum age of *ca.* 13+ years. The previous longevity records for Broad-billed Sandpipers included 8 years, 10 months, 13 days (3,240 days) for a Norwegian bird that was recaptured at Sivash, Crimean Peninsula (Norwegian Bird Ringing Centre 2021), and 5 years, 10 months to 6 years, 10 months for two birds controlled by ringers in Sweden (*ca.* 2,130–2,495 days; EURING database, Fransson *et al.* 2017).

Implications

The new demographic estimates from our long-term field study of Broad-billed Sandpipers in northern Norway show that breeding numbers can be variable, nest success is high with low predation rates, and annual survival rates are typical of small-bodied waders (Rae *et al.* 2022, this study). Our new biometric data and a small number of foreign recaptures demonstrate migratory connectivity between the breeding population in Norway with recognized stopover sites at Sivash in eastern Europe. Changes in habitat conditions have contributed to shifts in the migratory routes and breeding distributions of other Palearctic waders, including Ruff *C. pugnax* (Verkuil *et al.* 2012). Thus, conservation of the key stopover habitats could reduce risk for breeding populations of Broad-billed Sandpipers in northern Fennoscandia. The overwintering range remains poorly known, although from knowledge of migration routes and available distributional data, most birds appear to winter in the Middle East (de Fouw *et al.* 2017, van Gils *et al.* 2020, Franks *et al.* 2022). Nonbreeding habitats are perhaps the most imminently threatened, due to expanding human development. In ongoing work, we are tracking birds with geolocators to obtain better information on migratory movements and to identify critical habitats used in the nonbreeding range.

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