

Research paper

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A high proportion of the world population of the Spoon-billed Sandpiper occurs at Tiaozini, China, during the post-breeding moult

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The Critically Endangered Spoon-billed Sandpiper *Calidris pygmaea* breeds in arctic and subarctic Russia and migrates to winter on coastal mudflats in south-east Asia. Its world population is probably about 700 individuals. We report Lincoln-Petersen closed-population estimates of the number of Spoon-billed Sandpipers at Tiaozini, a coastal site in Jiangsu Province, China, based upon resightings and scan surveys of individually-marked leg-flagged birds. Surveys were conducted in September–October, when adult Spoon-billed Sandpipers are moulting their primary feathers and long-distance movements are unlikely. We estimated that 220 birds were present at Tiaozini in 2017 and 224 in 2018. Nearly all of them were adults (one-year old or older), so about 40% of the world population of this age class was estimated to be present. Hence, protection of the mudflats and roost sites at Tiaozini is of global importance for the conservation of the Spoon-billed Sandpiper.

Keywords: mark-resighting, Lincoln-Petersen, closed population estimate, migration stopover, leg flags, intertidal zone

INTRODUCTION

The Spoon-billed Sandpiper *Calidris pygmaea* is one of the world's most threatened migratory bird species and is categorized as Critically Endangered on the IUCN Red List (BirdLife International 2018). It breeds along a discontinuous strip of 4,500 km of coastal

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tundra in the north-east arctic and subarctic zones of the Russian Federation in the Chukotka Autonomous Okrug and northern Kamchatka Krai. During autumn and spring migration, concentrations of Spoon-billed Sandpipers are known from a relatively small number of sites around the Yellow Sea (People's Republic of China, Democratic People's Republic of Korea and Republic of Korea). After their post-breeding moult, birds move to wintering grounds in south-east Asia, between Bangladesh and south China (Zöckler *et al.* 2016). Coastal mudflats, including estuaries, are the main habitat in the non-breeding season.

The Dongtai-Rudong mudflats, on the south-west coast of the Yellow Sea (Fig. 1), stretch for about 150 km from Jianggang, Dongtai County in the north via Yangkou to Dongling, both in Rudong County, Jiangsu Province, China. Spoon-billed Sandpipers were first recorded there in 2008, and 103 were counted in October 2011 (Tong *et al.* 2012). Since then up to 225 birds (sum of site-specific maxima from counts at Tiaozini, Yangkou and Dongling in 2014; Fig. 1) have been counted in the post-breeding migration season and the species is also present during the spring migration (Peng *et al.* 2017).

At Dongtai-Rudong, Spoon-billed Sandpipers are dispersed within large flocks of similarly coloured small shorebirds of other species and are therefore difficult to locate and count, especially when the birds are roosting and the distinctive bill is hidden in the back feathers. The time-consuming nature of survey fieldwork means that only a small number of roosts can be checked during a single high tide period. Although Spoon-billed Sandpipers can also be observed on the mudflats of falling and rising tides, they are then dispersed over a large area, so it is difficult to conduct a co-ordinated count. Hence, current co-ordinated count methods provide estimates of the minimum numbers of Spoon-billed Sandpipers present, but their accuracy and repeatability in representing the true numbers of birds present is unknown.

A reliable method for estimating numbers of Spoon-billed Sandpipers is vital for conservation because of the perilous conservation status of the species and the recent rapid changes occurring in the extent and quality of its mudflat habitat in Jiangsu Province and more widely in the Yellow Sea area. Considerable areas of mudflat in Jiangsu Province have disappeared in recent land claim projects to create harbours, industry zones, wind and solar power generation farms, aquaculture ponds and ricefields (Li *et al.* 2017). In addition, Smooth Cordgrass *Spartina alterniflora* has spread rapidly over many mudflats along the coast of China (Zuo *et al.* 2012), including those in Jiangsu (Zhang *et al.* 2004). *Spartina* cover renders mudflats unsuitable for foraging by most shorebird species (Gan *et al.* 2009, Li *et al.* 2009). Large losses and degradation of intertidal shorebird habitat throughout much of the Yellow Sea area have occurred in recent decades (Murray *et al.* 2014, 2019, Melville *et al.* 2016). A short section of southern Jiangsu coastline at Tiaozini (Fig. 1) is known to be of particular importance for Spoon-billed Sandpipers (Peng *et al.* 2017). In this paper, we report results from a population survey at this site by a closed-population method not used previously for this species. We assess its reliability and repeatability in the post-breeding moult periods of two consecutive years.

METHODS

Study area

We conducted surveys at Tiaozini during 2–10 October 2017 and 5–15 September 2018. These periods were both centred on the highest tides of a neap-spring-neap cycle (6 October 2017 and 11 September 2018). The selection of periods with the highest tides made the birds easier to see when concentrated at roosts on the landward side of the seawall at high tide and

on the upper part of the intertidal zone during rising and falling tides. The parts of the intertidal zone where we conducted surveys are delineated in Fig. 1. During the entire tidal cycle, Spoon-billed Sandpipers used larger areas of mudflats than the polygons shown, but our surveys were restricted to the upper flats to minimise the risk of the observers drowning. Roosts were on unvegetated areas of rice fields and on land recently claimed from the intertidal zone and being converted to aquaculture ponds within 1.5 km landward of the seawall and located immediately to the west of the polygons shown in Fig. 1. Ten observers were involved: nine in 2017 and eight in 2018; seven participated in both years. Observers worked as individuals within sight of others, or in pairs.

Individually-marked Spoon-billed Sandpipers

To estimate population size, we recorded the presence or absence and identity of individual marks on the Spoon-billed Sandpipers at Tiaozini. Nearly all of the marks consisted of coloured plastic leg flags applied to the right or left tibia and engraved with two black alphanumeric characters (Clark *et al.* 2005). Most were applied to adults and chicks on the breeding grounds at Meinypil'gyno (Chukotka) in the Russian Federation, including wild birds and 'head-started' chicks reared artificially and released there as recently fledged juveniles (Clark *et al.* 2014). In each year 2015–2018, Spoon-billed Sandpipers were also captured and marked in Jiangsu Province, mostly at Tiaozini. We captured and applied leg flags to two birds at Tiaozini during the observation period in 2017 and marked 12 more in the observation period in 2018. In addition to applying flags to these birds, we also marked them on the breast feathers with a green permanent marker pen (2017) or with a light green colour ring (2018). By using these additional marks, we were able to distinguish sightings of birds marked at Tiaozini in the periods when our surveys were in progress from those marked there in previous years. We recorded a few birds with other individually-identifiable leg flags or colour ring combinations applied at sites in arctic and subarctic Russia and the Republic of Korea.

Scan surveys and flag reading

We found flocks of small shorebirds using binoculars or spotting scopes. Roosts were located by plotting flight lines of flocks flying from the mudflats over the seawall as high tide approached. We searched flocks for Spoon-billed Sandpipers using spotting scopes. To estimate the proportion of birds in the local population that had individually identifiable markings, we watched each Spoon-billed Sandpiper that we located to establish whether or not it had a leg flag or other marks. Observations eligible for inclusion in the scan survey analysis were those in which the bird was seen well enough and at short enough range for the observer to be sure that both tibiae were seen clearly. It was often necessary to watch birds for several minutes to do this. Resting birds were excluded from the scan sample if they remained sitting and their legs could not be seen. It was also often necessary to watch actively foraging birds for a considerable time because the tibiae were often concealed by the belly feathers when using some foraging methods, but clearly visible when using other methods. It was therefore often necessary to await a change in behaviour to see both of a bird's tibiae. The presence or absence of flags was assessed whenever the observer found what seemed to be a new individual. Observers did not disregard birds if they realised, by reading the flag, that they had previously recorded the same marked individual recently nearby, with the same rule being applied to unmarked birds suspected as being the same as ones seen previously. This resulted in some marked and unmarked individuals being scanned many times during our surveys, particularly when moving around on rising and falling tides. Although this introduces pseudo-replication, the rule was necessary in order to avoid bias in estimating the proportion of marked birds.

When a flagged individual was seen, the colour of the flag (light green, white or yellow), its location (left or right tibia) and the presence of plastic colour rings on the other tibia or on the tarsi were noted. This information was sufficient to establish whether the bird had been marked at Tiaozini during the current scan survey, even if the flag inscription could not be read. Observers made every effort to read the inscriptions on leg flags, but it was not always possible to do this despite the colour and location of the flag being readily apparent. The age of all sightings of birds seen well enough during scan surveys (1,439 sightings in 2017 and 946 in 2018) was determined as juvenile (hatching year) or older using plumage characteristics (Clark *et al.* 2018). The date and time was recorded for all scan survey and flag reading observations.

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Closed population estimates of the number of marked individuals present

We used a combination of closed population capture-recapture models and the Lincoln-Petersen estimator to estimate the size of the local population (Lukacs 2018). We were unable to use closed population capture-recapture models on their own to estimate the size of the local population because it was not possible to read flag inscriptions during many of the sightings, only to see that the bird was marked (above). Hence, we instead estimated population size in two stages: (1) the number of individually-marked birds present and (2) the proportion of birds that were individually-marked from scan surveys. This section describes the analyses in Stage 1.

We used records in which a Spoon-billed Sandpiper was identified as an individual by its marks (hereafter, *reads*), both from scan surveys and opportunistic observations, to estimate the number of marked individuals N present at Tiaozini during the survey periods separately for 2017 and 2018 (N_{2017} and N_{2018}) using closed population capture-recapture models (Lukacs 2018). Birds captured and flagged part-way through the scan survey period were excluded from both the closed population analysis and treated as unmarked in the scan survey analysis (below). In using closed population capture-recapture models, we assumed that the local population was closed during the survey, with no arrivals, departures, or deaths. This seems reasonable given that most birds were undergoing wing moult and the surveys were of short duration (Table 1). We divided each survey into non-overlapping periods, usually each of one day in duration, and obtained a resighting history for each bird which identified the periods in which it was and was not recorded. In a few cases, we merged data for two or three consecutive days into one period to avoid numbers of individuals detected per period being less than five (Table 1). Closed population models use changes across successive periods in the numbers of individuals detected for the first time during a survey, relative to the numbers of birds recorded that were already detected in previous periods of the survey. A large number of model formulations are possible (Lukacs 2018), but we considered that two formulations in particular were most applicable to our data. In Model A, we assumed that the probability of first detecting a marked bird present in the local population (*first-time read*) differed among the periods constituting the survey. We knew that search effort and conditions varied among periods, so we considered it unrealistic to fit models in which all periods were assumed to have the same detection probability. Within a given period, we assumed that the probability of recording an individual seen in a previous period (*repeat-read*) was the same as for a first-time read. We expected that this model would be appropriate for our data because we had designed the fieldwork so that observers would not disregard or be particularly likely to read marks on birds that had already been recorded previously during the survey (above). However, the possibility of an unintended difference in the probability of reading a mark for the first time from that for a repeat-read could not be excluded, so we also fitted Model B. In

this model, the probability of first detecting a marked bird present in the local population differed among periods, as for Model A, but the odds of recording a bird already seen in a previous period were assumed to be given by multiplying the odds of recording a bird for the first time during that period by a constant factor, which we call the *odds multiplier*. We assumed that the same value of the odds multiplier applied to all periods in both years. Note that it is not possible to assume detection probabilities that differ among all periods independently for first-time and repeat-reads. N is not identifiable for that model structure – it is necessary to constrain the relationship between first-time and repeat-read probabilities in some way to estimate N (Lukacs 2018). Model A is a special case of Model B, in that the odds multiplier in Model A is fixed at a value of 1 (i.e. first-time and repeat-read odds of detection are assumed equal), whereas it is estimated from the data in Model B and may differ from 1. We fitted both Models A and B using the maximum-likelihood methods given by Lukacs (2018) and using the Huggins conditional likelihood formulation (Huggins 1989). We then used weights derived from small-sample Akaike Information Criterion values for the two models (AIC_c weights) to calculate model-averaged estimates of N for each year and the odds multiplier common to both years (Burnham & Anderson 2002). We used a bootstrap procedure (Manly 2006) to obtain 95% confidence intervals for our estimates. We performed resampling, at random and with replacement, from the sighting histories of the n individuals recorded in a given survey year, so that we obtained a bootstrap sample of n sighting histories. We repeated this to obtain 1,000 bootstrap samples and then performed the analyses described above on each of them. We took the central 950 values of the bootstrap estimates to define the 95% confidence interval of each parameter.

Lincoln-Petersen estimate of the total number of birds

This section describes Stage 2 of our analysis (above). We estimated the proportion F of Spoon-billed Sandpipers in the local population that were marked by dividing the number of sightings of marked birds on scan surveys in each year by the total number of scans of all birds. In both years, some birds were captured and flagged part-way through the scan survey period (above). Attempting to include them would complicate the analysis, so we treated them as unmarked in the scan survey analysis. We divided the model-averaged estimate N of the number of marked birds present from Stage 1 by the estimate of F for that year, to give a Lincoln-Petersen estimate of the total number of birds present (Lukacs 2018). We obtained 95% confidence intervals for the total population size and F by using a bootstrap procedure. We placed all the scan observations by each observer in chronological order and assigned each of the scan records to a group of consecutive records. We assigned sets of at least 20 consecutive records by the same observer to a group, with all records assigned to the same time being placed in the same group (Table 1). We then obtained 1,000 bootstrap samples, of size n , of these groups by randomly resampling, with replacement, from the n scan survey groups for each survey year. We then calculated F for each of the bootstrap samples and took the central 950 values of the bootstrap estimates to define the 95% confidence interval of F . We then aligned the 1,000 bootstrap estimates of model-averaged N (above), in random order, with the 1,000 bootstrap estimates of F , also in random order, and calculated the total population size from each pairing of N and F . We took the central 950 values of the bootstrap estimates to define the 95% confidence interval of population size. Confidence intervals for the mean and ratio of N across the two years were calculated in the same way. Calculations were performed using Program MARK (see Lukacs 2018), programs specifically written for the purpose in the language BBCBASIC and in Microsoft Excel.

Justification for the assumption that the local population was closed during the surveys

Valid application of the closed-population method assumes that there were no arrivals, departures, or deaths of birds at our study site during the survey periods, so that it could be treated as a ‘closed population’ for the purpose of population estimation. Surveys were timed so that they were conducted within the period between the mean autumn arrival (19 August \pm 11 days) and departure (24 October \pm 6 days) dates of Spoon-billed Sandpipers on the Jiangsu coast, modelled by Li *et al.* (2017). In addition, our survey dates lie between the mean start date (7 August) and the mean end date (13 October) estimated by Li *et al.* (2017) for the period of primary feather moult of adult Spoon-billed Sandpipers on the Jiangsu coast. We consider it unlikely that Spoon-billed Sandpipers would move substantial distances during their moult. Two other sites in Jiangsu Province known to be used by significant numbers of Spoon-billed Sandpipers are sufficiently distant from Tiaozini (Yangkou – 27 km; Dongling – 74 km; Fig. 1) that we consider movements to and from them to be infrequent. Although some deaths would be expected within our survey periods, they were sufficiently short (7 days for 2017 and 9 days for 2018) that we expected there to be only a few. Assuming that the annual survival rate of 0.76 for adult Spoon-billed Sandpipers estimated by Zöckler *et al.* (2010) applies uniformly throughout the year, it would be expected that only 0.5% to 0.7% of adults would die during these short periods.

Justification for the assumption that the local population was well mixed

Our method also assumes that the population we sampled was sufficiently well-mixed that the probability of encountering any individual could be regarded as uniform. Had there been parts of the population we sampled to a lesser extent than others, and which did not often exchange individuals with the sampled parts, we would have underestimated the number of individually-marked birds at Tiaozini and that would lead to underestimation of the total population size. We considered attempting to model heterogeneity of survey coverage using variants of the closed population capture-recapture models described by Lukacs (2018), but did not do so because our sample sizes of marked birds were small. In addition, the results obtained from these methods are sensitive to the assumptions made about the way in which the probability of sighting varies among individuals (Lukacs 2018). We think it unlikely that there was substantial heterogeneity in our survey coverage because observers ranged widely across the mudflats near the seawall (Fig. 1) and we conducted our surveys around high tide, when the birds could not access mudflats we could not visit, such as the Dongsha shoals which extend up to 50 km offshore to the east of the coastline shown in Fig. 1 (see map in Fig. 1 of Peng *et al.* 2017). We believe that all of the large high-tide roosts were detected and sampled, though our coverage of each roost was certainly incomplete. However, we accept that there could have been some heterogeneity. If present, it would lead to our estimates being too low.

RESULTS

Closed population estimates of the number of marked individuals present

Models A and B both estimated that our flag-reading programme detected most of the marked individuals present in both years (95% and 98% detected for Models A and B, respectively, in 2017, and 85% and 97%, respectively, in 2018). Using the model-averaged estimates of N indicated that 98% of marked individuals present were detected in 2017 and 95% in 2018 (Table 2). Our mark-reading results are shown in Fig. 2, in which the cumulative number of marked birds detected is plotted against the cumulative number of mark reads, arranged in chronological order. This diagram indicates that the cumulative number of birds detected tended to level off markedly as the cumulative number of reads increased, especially in 2017,

which supports the conclusion from the closed population analysis that high proportions of marked birds were detected in both years.

Estimates from Models A and B of the number of marked birds present N were similar to each other (Table 2). The AIC_c score was lower for Model A than Model B, but given the small difference between the two models ($\Delta AIC_c = 0.826$), we averaged the model results to estimate the value for the odds multiplier. The model-averaged estimate of the odds multiplier was 0.936, which is close to the value 1 expected if per-period probabilities of first-time and repeat-read detections had been the same. However, the confidence interval for the odds multiplier was wide (Table 2).

Lincoln-Petersen estimate of the total number of birds

The estimates of the total population size of Spoon-billed Sandpipers at the Tiaozini study area were similar in 2017 (220) and 2018 (224). The confidence interval of the ratio of the population estimates for the two years overlapped 1, indicating that there was no evidence for population change between the years. Hence, it seems reasonable to use the mean of the two estimates, 222 birds (95% CI: 196–258), as the best estimate of the number of Spoon-billed Sandpipers at Tiaozini. Nearly all of the birds observed were one calendar year old or more (i.e. not juveniles). In 2017, 2.5% were juveniles and in 2018 none were juveniles. Hence, our population estimates refer almost entirely to adults.

DISCUSSION

Our findings highlight the importance for Spoon-billed Sandpipers of the Jiangsu coast, and Tiaozini in particular. Clark *et al.* (2018) used scan surveys and Jolly-Seber estimates of numbers of leg-flagged birds to estimate the world population of Spoon-billed Sandpipers in their second calendar year or older in the autumn of 2014 as 533 individuals. If this estimate is taken to apply to 2017 and 2018, then about 40% of the world population of adults (second calendar year or older) was at Tiaozini in those autumns. The maximum-count estimates of Spoon-billed Sandpiper numbers for Yangkou in 2014 and 2015 by Peng *et al.* (2017) were 37 and 25 and, for Dongling, 44 and 38. The mean of these estimates is 72 for both sites combined. If the maximum-count estimates at Yangkou and Dongling underestimate the true numbers to the extent that we think is likely for Tiaozini, this would suggest that the numbers of Spoon-billed Sandpipers at Yangkou and Dongling combined might have been about 130 birds. This would make the total across all three sites about 350 individuals, which represents over 60% of the world population of adults on the Jiangsu coast in autumn. However, we recommend that surveys like those we conducted at Tiaozini should also be made at Yangkou and Dongling to replace this approximate extrapolation. The location of the remaining 40% of the world population of adult Spoon-billed Sandpipers during the post-breeding moult is unknown, but we think that parts of the Dongtai-Rudong mudflats other than Tiaozini, Yangkou and Dongling have been surveyed thoroughly enough that the region probably does not hold any undetected large concentrations of birds. However, there are areas of remaining intertidal mudflats elsewhere around the Yellow Sea where substantial numbers of Spoon-billed Sandpipers might occur and have not yet been counted (Murray *et al.* 2019). A possible post-breeding moult site in the Democratic People's Republic of Korea has recently been identified by satellite-tracking of two adults (Green *et al.* 2018), but surveys have not yet been conducted there. We observed very few juvenile Spoon-billed Sandpipers at Tiaozini, which is in accord with previous studies (Li *et al.* 2017). Unpublished leg-flag resighting data indicate that individually-marked young of the year are seen at wintering sites further south without having been recorded in autumn at Tiaozini, or elsewhere at Dongtai-Rudong, and

may be seen thereafter as adults at Dongtai-Rudong in subsequent autumns. Hence, juveniles appear to have a different route for their first autumn migration from that of adults.

Previous estimates of numbers of Spoon-billed Sandpipers on the Jiangsu coast in autumn have been obtained by collating maximum numbers encountered by observers at a given site. This was done for several days of fieldwork at each site and the maximum single date count taken as the estimate for the site. Using this method, Peng *et al.* (2017) estimated 144 Spoon-billed Sandpipers at Tiaozini in 2014 and 101 in 2015. These estimates are substantially lower than ours, averaging 55% of our mean value of 222 birds. Although the surveys were conducted in different years from ours, when numbers might have been different, we think it likely that their method underestimated the number of Spoon-billed Sandpipers at Tiaozini. The use of maximum counts to estimate total populations is open to error. Estimates will be biased too low if some high-tide roosts or feeding areas are not covered or partially covered by the observers and if some of the inconspicuous Spoon-billed Sandpipers are not detected within flocks of small shorebirds searched.

We speculate that the mudflats at Tiaozini may have special attributes important to foraging Spoon-billed Sandpipers, including a high tidal range, a large area of open mudflat available for the maximum time in the tidal cycle and surface sediments consisting of a thin layer of fine mud on top of firmer sand. The site may also have increased in importance because of displacement of birds from other areas by loss and degradation of habitat. Considerable losses of intertidal habitats to land claim have already occurred in this area and Smooth Cordgrass is still spreading over mudflats that are currently suitable for the species. Further efforts are urgently needed to safeguard Spoon-billed Sandpiper feeding and roosting habitats in this area. The Tiaozini mudflats lie within a small protected coastal area specified under the Dongtai Coastal Economic Zone, which protects them from further land claim. In January 2017, the Dongtai-Rudong mudflats were included on China's tentative list of World Heritage sites as part of a proposed serial nomination 'Migratory Bird Sanctuaries along the Coast of Yellow Sea-Bohai Gulf of China'. In January 2018, Jiangsu Yancheng National Nature Reserve was nominated as Phase I of this serial World Heritage nomination and the Yancheng Municipality Government announced in November 2018 that the Tiaozini site, and the Dongsha Shoals offshore from it, would be included within the nominated Yancheng World Heritage Site, which hopefully will be inscribed in July 2019. It is also hoped that the other key Spoon-billed Sandpiper sites along the Jiangsu coast will be included in the Phase II nomination in a few years' time.

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Table 1. Details of closed population and scan survey fieldwork at Tiaozini in 2017 and 2018. Data from groups of dates bracketed together were merged into one period to avoid sample sizes of less than five individuals detected. Period-detections are numbers of periods in which an individual was detected, summed across all individuals.

	2017	2018
<i>Closed population surveys</i>		
Number of periods	6	6
Dates in periods	(2/3/4), 5, 6, 7, 8, 9 October	(6/7), 10, 11, 12, (13/14), 15 September
Number of marked individuals recorded	22	24
Number of period-detections	54	45
<i>Scan surveys</i>		
Survey period	2–10 October	6–15 September
Number of scans	1,482	946
Number of mark detections	152	107
Number of groups for bootstrap resampling	54	35
Number of scans per group (range)	20–54	20–44

Table 2. Estimates of numbers of individually-marked Spoon-billed Sandpipers and total population size at Tiaozini, China, in 2017 and 2018. 95% bootstrap confidence intervals of parameter estimates are shown in brackets.

Parameter	2017	2018
<i>Closed population analysis</i>		
Number of marked birds \hat{N} (Model A)	23.1 (22.3–24.4)	28.1 (25.7–33.9)
Number of marked birds \hat{N} (Model B)	22.4 (22.0–24.5)	24.7 (24.0–25.2)
Number of marked birds \hat{N} (model-averaged)	22.5 (22.0–23.5)	25.3 (24.0–27.7)
Odds multiplier (model-averaged)	0.936 (0.424–1.655)	
<i>Lincoln-Petersen analysis</i>		
Proportion marked F	0.103 (0.085–0.121)	0.113 (0.093–0.134)
Population size N/F	220 (187–266)	224 (184–280)
Mean population size	222 (196–258)	
Ratio of 2018:2017 populations	1.018 (0.762–1.358)	

LEGENDS TO FIGURES

Fig. 1. Map of the Tiaozini, China, study area (left panel) showing intertidal mudflats (mid-grey shading) and sea (light grey) to the east of the seawall, and fishponds and ricefields to the west. The background image was obtained by the ESA Sentinel 2 satellite on 13 July 2018 at 02:36 GMT, 141 minutes before high tide. Hence, the area of intertidal mudflat shown is considerably smaller than that available to foraging birds at low tide, when exposed patches of mud and sand flats are present up to about 50 km east of this section of coastline on the Dongsha Shoals. The polygons show the outermost boundaries of the areas of intertidal mudflat in which scan surveys were conducted in 2017 (dotted line) and 2018 (solid line). The panels on the right show the location of Tiaozini within Jiangsu Province and the site's location within China (inset).

Fig. 2. Cumulative numbers of individually-marked Spoon-billed Sandpipers detected at Tiaozini in 2017 (black stepped line) and 2018 (grey stepped line) in relation to the cumulative number of mark reads, arranged in chronological order. Horizontal lines show the model-averaged estimates of the number of marked individuals present from Table 2.

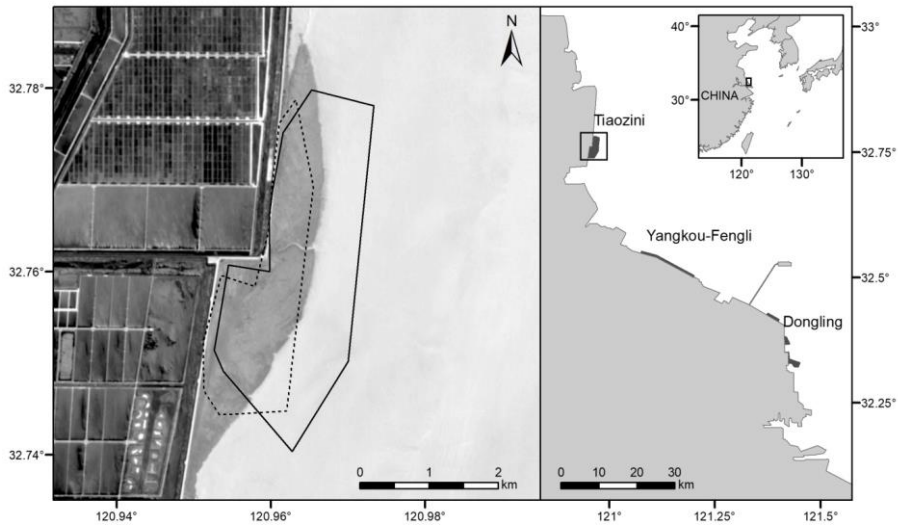


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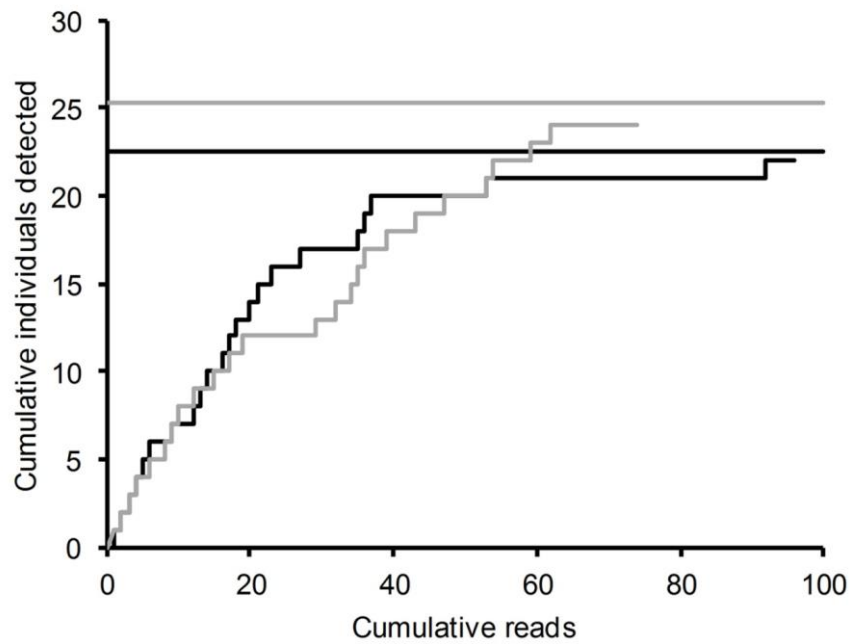


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