Systematic revision of the 'diminutive' Kentish Plover (Charadriidae: *Charadrius*) with the resurrection of *Charadrius seebohmi* based on phenotypic and genetic analyses

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The Kentish Plover *Charadrius alexandrinus* Linnaeus 1758 is a common shorebird in Eurasia and North Africa that breeds in a variety of habitats, exhibits different extents of migratory behaviour and is an emerging model species of breeding system evolution. Here we focus on the resident population found across the southern tip of India and Sri Lanka, and re-evaluate its systematic status based on phenotypic and genetic distinctiveness from a sympatric migrant, *Charadrius alexandrinus sensu stricto*, and the recently elevated closely related *Charadrius dealbatus* in East Asia. We show that the Sri Lankan and South Indian (South Asian) population differs in body size, moulting pattern and plumage coloration from C. *alexandrinus* and C. *dealbatus*. Furthermore, based on two mitochondrial, two sex-linked and 11 autosomal microsatellite markers from 378 individuals, we show that these three taxa have moderate genetic differentiation (F_{st} 0.078–0.096). The South Asian taxon is sister to the clade of C. *alexandrinus sensu stricto* and C. *dealbatus* with an estimated divergence time of 1.19 million years ago. We also examined ornithological records of major museum collections in Asia, Europe and North America for the south Asian taxon to evaluate its biogeographical and taxonomic status. Based on differences in genotype, phenotype, allochronic migratory pattern and breeding range, we resurrect the most suitable synonym, *Charadrius alexandrinus seebohmi* Hartert and Jackson, 1915, and elevate the nomen to the species level with the proposed English name 'Hanuman Plover'.

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Species with broad geographical ranges are exposed to a variety of physical barriers and environmental variation, and therefore often have population substructuring (Peñalba et al. 2019, Liu et al. 2020). Such taxa tend to consist of multiple geographical populations that have distinct morphological characters, with some taxa in need of taxonomic revision (Price 2008). Subspecies could exhibit substantial genetic differentiation and eventually diverge into a full species, such as in the Barn Swallow Hirundo rustica (Scodato & Safran 2014), gulls (Larus: Liebers-Helbig et al. 2001) and wagtails (Motacilla: Harris et al. 2018). In wagtails, for example, the widespread Yellow Wagtail Motacilla flava has numerous subspecies and has recently been split into two species, Western Yellow Wagtail Motacilla flava and Eastern Yellow Wagtail Motacilla tschutschensis, based on breeding range separation and phylogenetic differences (Sangster et al. 1999, Alström et al. 2003, Dickinson & Christidis 2014, Gill et al. 2021).

The Kentish Plover Charadrius alexandrinus is a cosmopolitan species complex, consisting of four currently recognized taxa: C. a. alexandrinus, C. a. nivosus, C. a. dealbatus and C. a. seebohmi, separated geographically with some subtle morphological and plumage differences (Swinhoe 1870, del Hoyo et al. 2021a, 2021b, Kennerley et al. 2008). Geographical barriers, like islands, impact the level of genetic diversity and population genetic differentiation in this species complex (Küpper et al. 2009, 2012, Almalkl et al. 2016, Küpper & dos Remedios 2019). Recent studies that evaluated the taxonomic status of the Snowy Plover C. a. nivosus (Küpper et al. 2009) and the White-faced Plover C. a. dealbatus (Rheindt et al. 2011, Sadanandan et al. 2019, Wang et al. 2019a, 2019b) recommended that these taxa be elevated to species based on their genetic and phenotypic distinctiveness, a treatment that has now been adopted (e.g. Gill et al. 2021, del Hoyo et al. 2021a, 2021b).

The wide geographical distribution of C. alexandrinus sensu stricto, which includes inland lakes, grasslands, high plateaus and coastal beaches (Meininger & Székely 1997, del Hoyo et al. 2021a, 2021b), as well as several offshore and oceanic islands (e.g. Canary Islands, Azores, Cape Verde; Almalkl et al. 2016) provide excellent opportunities for testing speciation hypotheses. Furthermore, C. alexandrinus hybridizes with C. dealbatus, enabling evaluation of the importance of genetic introgression in species diversification (Wang et al. 2019a). Different populations of C. alexandrinus often exhibit different mating systems and parenting (Carmona-Isunza et al. 2015, Eberhart-Phillips et al. 2017), and a series of experimental and observational studies have uncovered the evolutionary costs and benefits, and neuroendocrine basis of these different strategies (Kosztolányi et al. 2012, Song et al. 2020). The C. alexandrinus species complex is also an emerging model species for breeding system evolution (Székely 2019).

Here we focus on a diminutive non-migratory form of C. alexandrinus sensu lato (C. alexandrinus seebohmi), found in Sri Lanka and the Palk Bay region of south India (Seebohm 1887), which has long been considered a distinct subspecies based on differences in body size and plumage (Latham 1801, Seebohm 1887, Hartert & Jackson 1915, Whistler & Kinnear 1936; Fig. 1). As C. alexandrinus breeds in northern Asia (above 40°N) and migrates to equatorial regions in the non-breeding season (Küpper et al. 2009), both migratory (C. alexandrinus sensu stricto) and resident (C. alexandrinus sensu lato) populations are found in South Asia during the non-breeding season. However, in the breeding season (in May–July), only the resident C. alexandrinus sensu lato breeds in these equatorial regions (Legge 1880, Ali & Ripley 1983, Henry 1998, Rasmussen & Anderton 2005, del Hoyo et al. 2021a, 2021b). These morphological, plumage and migratory differences suggest that the South Asian population may be a distinctive lineage of C. alexandrinus sensu lato and could be considered as a nominal species.

To fill this gap in the taxonomy and biogeography of the C. alexandrinus species complex in South Asia, we assessed the level of divergence using morphometric measurements, plumage and molecular DNA data from mitochondrial, sex-linked loci and autosomal microsatellite markers, for C. a. alexandrinus sensu lato in Sri Lanka, C. a.

Figure 1. Adult male (a) and female (b) *Charadrius seebohmi* from Mannar Island, Sri Lanka, and adult male (c) and female (d) *Charadrius alexandrinus sensu stricto* from Bohai Bay, China. Open wings of (e) *C. seebohmi* and (f) *C. alexandrinus sensu stricto*. Photo credits: (a, b, e: JJN, c, d: PQ, f: Chenjing Huang).

alexandrinus sensu stricto and C. *dealbatus*. In addition, we also examined the historical literature and specimens in museum collections to elucidate the conflicting nomenclature and to evaluate the taxonomic position of the South Asian population of C. *alexandrinus sensu lato*.

METHODS

Sample and data collection

We captured seven female and six male nesting C. *alexandrinus sensu lato* from Mannar Island (near the type locality, Arippu), Sri Lanka (9°05′15.7″ N, 79°41′58.6″E), between May and August 2019, and collected blood samples and morphological data from them. Another six blood samples and associated morphological data were collected through the National Bird Ringing Programme from Bundala National Park (Hambantota), Sri Lanka (6°10′52.62″N, 81°14′5.46″E) in June and August between 2013 and 2020 (Fig. 2). Sampling was carried out using mist-nets and funnel traps (as described elsewhere: Karr 1981, Székely et al. 2008). The captured birds were processed at the capture location and released immediately with a coloured leg band for later behavioural observations (Hjort & Lindholm 1978).

This study was conducted under the permit of WL/3/2/37/19 (DWLC) and the Ministry of Defence, Sri Lanka MOD/MLO/02/01-A3-27.

A 50-µL sample of blood was collected from the brachial vein and samples were stored in cryogenic vials filled with 500 µL of Queen's lysis buffer (Owen 2011). Body measurements (weight, head length (the back of the skull to the front of skull above the beak), bill length (length of the culmen from the base of the beak to the tip), bill height (height of the beak at the distal end of nostril) and width (width of the beak at the distal end of nostril), length of the tarsus of the right leg, the flattened wing length, tail length, and length of each primary, secondary and tertiary feather of the left wing) were taken with Vernier callipers (±0.02 mm), a stopped wing ruler (±0.1 mm) and a spring scale (±1.0 g) as in Seneviratne et al. (2012). Body measurements and genetic data from 11 populations of C. *a. alexandrinus* and eight populations of C. *dealbatus* were obtained
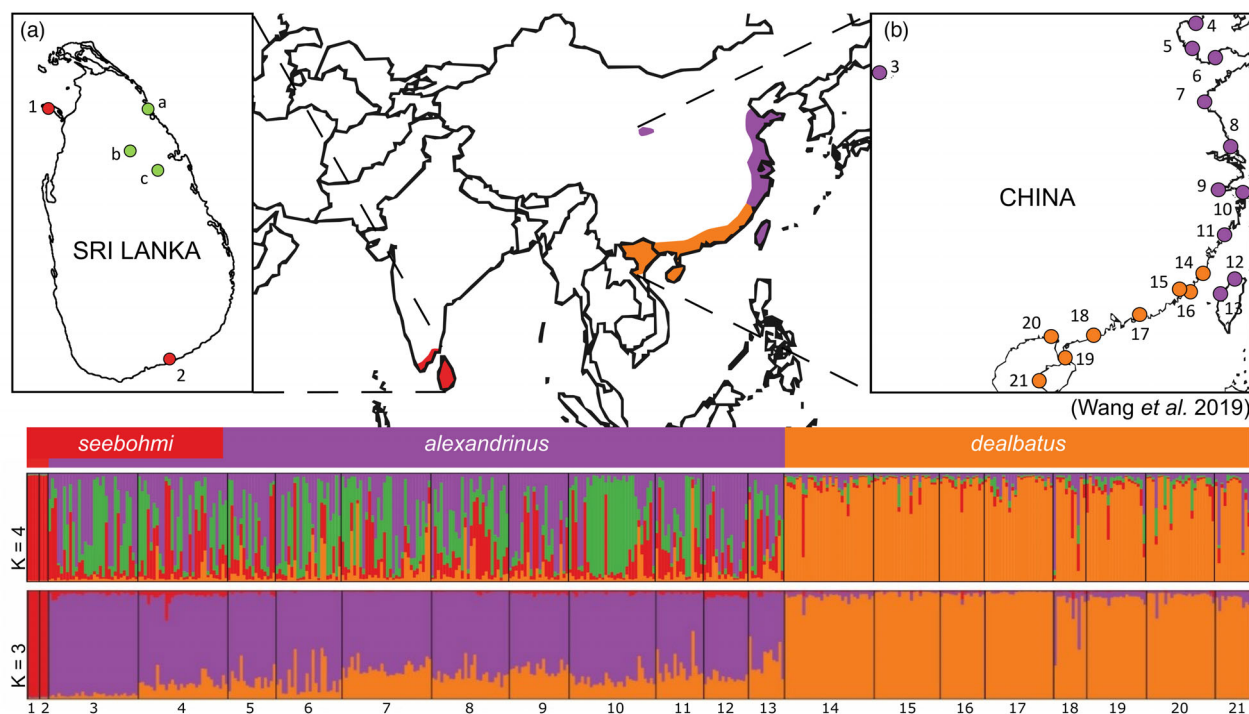
Figure 2. Map of Asia (top) illustrating the breeding range of *Charadrius seebohmi*, *Charadrius alexandrinus sensu stricto* and *Charadrius dealbatus*. Insets depict field sites in Sri Lanka (a) and China (b). Structure plots (bottom) of Bayesian genetic clustering for three subspecies; K = 4 (above) and K = 3 (below) with respect to their sampling locations. Numbers represent Mannar (1) and Hambantota (2; Sri Lanka), C. *alexandrinus sensu stricto* populations (3–13) and C. *dealbatus* populations (14–21; China). Letters a–c indicate locations of museum specimens at NMSL: a – Kokkilai, b – Pulmude, c – Kanthale, Sri Lanka.

from the Chinese coast, Qinghai Lake and Taiwan (Wang *et al.* 2019a, 2019b). In addition to the measurements from live specimens, key morphometric data from 12 museum specimens of *C. alexandrinus sensu lato* from Sri Lanka (six males and six females) were obtained from the National Museum of Natural History, Sri Lanka (NMSL). We identified subspecies by considering the differences in plumage characters (colour of loral stripe, facial plumage and crown colour) and the wing length (mean 101.4, range 96–106 mm), as described in Hartert and Jackson (1915), Rasmussen and Anderton (2005) and Kennerley *et al.* (2008) (Table 1).

Phenotypic data collection and analysis

Morphological data of 31 *C. alexandrinus sensu lato* from Sri Lanka and South India, 379 *C. alexandrinus sensu stricto* and 163 *C. dealbatus* from Eastern Asia were used in phenotypic comparisons. Only four morphological measurements were available for the latter two taxa, and therefore subsequent analyses were based on bill length, tarsus length, wing length and tail length.

To compare morphometrics and body size, analysis of variance (ANOVA) and Tukey's honest significant difference test (Tukey 1949) were used. A principal component analysis (PCA) was carried out for body measurements to visualize the biometric space of the three taxa using only individuals with complete sets of measurements. Plumage comparisons were conducted using the same set of individuals (above). Due to the possible differences in the patterns of moulting in breeding birds in South Asia, plumage variables were not analysed quantitatively (see Results).

Morphology, behaviour, ecological variables and geographical separation were compared using objective criteria to assess taxonomic status (Tobias *et al.* 2010). Cohen's *d* effect size (Cohen 1988)

was calculated using means of morphological variables to determine the magnitude score of each biometric measurement (Tobias *et al.* 2010). In addition to the known plumage variations, comparisons of photographs published by the Oriental Bird Club (http://orientalbirdimages.org/birdimages.php; $n = 20$) and eBird (https://ebird.org/; $n = 20$) were used to characterize plumage differences.

All statistical analyses were conducted in R Ver. 4.0.5 (R Core Team 2017) using RSstudio Ver. 2021.09.1 + 372 (RStudio Team 2020).

DNA sequencing and genotyping

Blood samples from breeding males were used for the genetic analysis to help ensure that only the South Asian breeding population (*C. alexandrinus sensu lato*) was sampled. Genomic DNA was extracted using the phenol–chloroform method (Burke & Bruford 1987, Fernando *et al.* 2016).

Extracted DNA of *C. alexandrinus sensu lato* individuals from Mannar ($n = 5$) and Bundala ($n = 5$) was used for polymerase chain reactions (PCRs) to amplify a total of 19 genetic markers including two mitochondrial loci partial D-loop of the mitochondrial control region (CR) (Wenink *et al.* 1994), NADH dehydrogenase subunit 3 (ND3) (Chesser 1999), two Z chromosome-linked regions (Z4 and Z45) (Ji *et al.* 2014) and 13 autosomal microsatellite loci (Calex 01, 04, 05, 08, 11, 18, 19, 22, 23, 32, 37, 39 and 45 (Küpper *et al.* 2007), C204 (Funk *et al.* 2007) and Hru2 (Primmer *et al.* 1995)) following methods described in Wang *et al.* (2019a, 2019b) and optimizations from Funk *et al.* (2007) and Küpper *et al.* (2007). The PCRs were carried out using a MultiGene™ OptiMax Thermal Cycler (Labnet International Inc., Edison, NJ, USA). The samples from 10 successfully PCR-amplified individuals were sequenced by Macrogen Inc. (Seoul, South Korea). Raw electropherograms were manually

Table 1. Summary of descriptive statistics on measurements of *Charadrius seebohmi*, *Charadrius alexandrinus sensu stricto* and *Charadrius dealbatus* from Sri Lanka and eastern China. Data are given as mean ± standard deviation.

	C. seebohmi ($n = 23$)	*C. alexandrinus* ($n = 291$)	*C. dealbatus* ($n = 127$)
Bill length (mm)	16.84 ± 1.67	16.74 ± 1.02	18.00 ± 1.00
Tarsus (mm)	26.10 ± 1.89	28.57 ± 1.09	28.11 ± 1.18
Wing length (mm)	100.88 ± 3.45	115.18 ± 3.18	117.41 ± 3.97
Tail length (mm)	45.96 ± 4.87	48.66 ± 2.07	50.03 ± 1.85

checked and edited using Chromas (Ver. 2.6.6; McCarthy 1997). Microsatellite genotyping was carried out using capillary gel electrophoresis on an ABI 3500 dx (Applied Biosystems, Waltham, MA, USA) with 440–902 base-pair size standards. Individual microsatellite traces and peak calls in electropherogram files were analysed using Geneious (Ver. 1.4.6; Kearse et al. 2012) along with the Microsatellite Analysis External Plug-in.

We compared our dataset with Wang et al. (2019b), which included 219 C. alexandrinus sensu stricto from 11 populations and 131 C. dealbatus from eight populations along the Chinese coast and Taiwan. All the laboratory work for this study was carried out at the Laboratory for Molecular Ecology and Evolution at the Department of Zoology and Environment Sciences, University of Colombo.

Phylogenetic analyses

To determine the phylogenetic position of C. alexandrinus sensu lato from Sri Lanka, we used sequence data from four genes, CR, ND3, Z4 and Z45, and additional sequences from NCBI GenBank (MK830765–MK830815, MK830754–MK830764, AM941556–AM941555 and KM001420–KM001422) representing members of the C. alexandrinus complex (Küpper et al. 2009, Rheindt et al. 2011). Kittlitz's Plover Charadrius pecuarius was used as the outgroup.

Sequences were loaded into MEGA (Ver. 7.0.26; Kumar et al. 2016) and nucleotides were aligned using the MUSCLE algorithm (Edgar 2004). Aligned nucleotide sequences were translated into a protein coding codon sequence to check that no stop codons were present (Wickramasinghe et al. 2017). Before concatenation, two separate maximum likelihood trees for each marker were built to see if the trees were congruent. Concatenated phylogenetic trees were built using both maximum likelihood and Bayesian inference approaches. Maximum likelihood trees were built using IQ-TREE (Ver. 1.6.12) with 10 000 standard bootstrap replicates (Nguyen et al. 2014). A Bayesian tree was built using MrBayes (Ver. 3.2) with two simultaneous 1 000 000 generation runs (Ronquist et al. 2012), with the first 25% of trees discarded as the burn-in. Best-fit models for gene partitions were investigated using PartitionFinder (Ver. 1.1.0: Lanfear et al. 2012) under the Bayesian Information Criterion instead of Akaike Information Criterion because of the lower complexity in

the dataset (Chen & Chen 2008). FigTree (Ver. 1.4.4) was used to visualize phylogenetic trees (Andrew 2006). We built haplotype networks for all four loci (CR, ND3, Z4 and Z45) separately according to the median joining network algorithm (Bandelt et al. 1999) in PopArt (Ver. 1.7) with the ε value of 0 (Leigh & Bryant 2015). Sequences from CR, ND3 and Z-chromosome linked loci Z4 and Z45, as well as data from Rheindt et al. (2011) and Wang et al. (2019a, 2019b), were used to construct haplotype maps to represent genetic variation among closely related Charadrius plovers.

Divergence time estimation

A time-calibrated phylogeny was reconstructed using the CR region in BEAST (Ver. 2.5.1; Bouckaert et al. 2014, Drummond & Bouckaert 2015). We determined the optimal nucleotide substitution model to use with jModelTest 2.1.4 based on the Bayesian Information Criterion (Darriba et al. 2012). The best model HKY + I was implemented in the BEAST analyses. A Yule model was selected as the tree prior and a relaxed uncorrelated lognormal distribution was used as the clock model. The clock rates were set at 0.013 substitutions/site/million years based on the estimated substitution rate for the mitochondrial Control Region (Weir & Schluter 2008). The chain length of Markov chain Monte Carlo (MCMC) runs was set at 10 million generations, with sampling frequency of every 1000 generations. Two independent runs were performed. Tracer (Ver. 1.7; Rambaut et al. 2018) was used to assess convergence among the two independent runs and to confirm adequate effective sample sizes of the parameters (where effective sample size was ≥200). The two runs were then combined using LogCombiner (Ver. 2.4.7; Drummond & Bouckaert 2015) with 20% burn-in. The trees comprising the posterior distribution were summarized to produce a maximum clade credibility tree with TreeAnnotator (Ver. 1.8.2; Rambaut & Drummond 2007). We also calculated the mean genetic divergence between taxa within the C. alexandrinus species complex in MEGA11 (Tamura et al. 2021) with a K2P model.

Population genetic analyses

Using the 11 autosomal microsatellite loci, Bayesian clustering was performed in STRUCTURE (Ver. 2.3.4; Jonathan et al. 2000) to identify

genetic clustering among the three taxa. STRUC-TURE runs were performed as individual simulations with a manual input of population number (K) from 1 to 10, in 100 000-step MCMC runs with a burn-in of 10 000 steps. Each value of K was iterated 10 times to increase accuracy and to obtain ΔK to determine the best K-value (Falush *et al.* 2003, Evanno *et al.* 2005) using STRUC-TURE Harvester (Ver. 0.6.94; Earl & Von-Holdt 2012). Two runs under the best K-value were repeated in STRUCTURE with 1 000 000-step MCMC runs and a burn-in of 100 000 steps (Rheindt *et al.* 2011), with results illustrated as bar plots using Distruct (Ver. 1.1; Rosenberg 2004).

GenAlex (Ver. 6.5; Peakall & Smouse 2006) was used to calculate pairwise F_{st} values using the Weir and Cockerham (1984) formula for genetic distance. Significance was assessed based on 1000 permutations with significance levels adjusted for multiple testing using a sequential Bonferroni procedure (Hochberg 1988). All figures were retraced and illustrated using Inkscape (Ver. 1.1; Bah 2007).

RESULTS

Body measurements

Body measurements clustered into three distinct groups in the PCA (Fig. 3e), and the first three principal components explained 98% of the variance in meristic characters (Tables 1 and 2). Breeding *C. seebohmi* adults of both sexes (Fig. 1) were smaller than *C. alexandrinus sensu stricto* and *C. dealbatus* (Table 2).

Charadrius seebohmi was smaller than *C. alexandrinus sensu stricto* and *C. dealbatus* in bill length, tarsus length, wing length and tail length (ANOVA: $F_{2, 138} = 317.05$, $P < 0.001$). *Charadrius seebohmi* had shorter wings than *C. alexandrinus sensu stricto* (Tukey–Kramer test $P < 0.001$, 95% confidence interval (CI) –15.80 to −12.79) and *C. dealbatus* ($P = 0.000$, 95% CI –18.12 to −14.95). The assumption of homogeneity of variance was not met for the tarsus, bill and tail lengths, so we used Welch's adjusted F-ratios. *Charadrius seebohmi* had the shortest tarsus (Games–Howell test; $P < 0.001$, 95% CI –3.38 to −1.56). Bill length was longer in *C. dealbatus* ($F_{2, 75.64} = 88.95$, $P < 0.001$), but not different between *C. seebohmi* and *C. alexandrinus sensu stricto* (Games–Howell test; $P = 0.939$, 262 95% CI –0.65 to 0.85). Similarly, tail length differed only in *C. dealbatus* (Welch's $F_{2, 56.59} = 1942.79$, $P < 0.001$), whereas it did not differ between *C. seebohmi* and *C. alexandrinus sensu stricto* (Games–Howell test: $P = 0.165$, 95% CI –7.85 to 1.08).

Plumage

Unlike *C. alexandrinus sensu stricto* and *C. dealbatus*, *C. seebohmi* does not have a rufous cap during the breeding season. Adult breeding male *C. seebohmi* have rufous buff mixed in with their paler cap, dark incomplete breast patches (complete in *C. alexandrinus sensu stricto*) and a black forehead stripe. The breast patches and forehead stripe become paler in the non-breeding plumage. *Charadrius seebohmi* also has an incomplete front eye-lore which becomes darker in the breeding plumage. It has dark grey legs in both sexes (*C. alexandrinus sensu stricto* has black legs). Female *C. seebohmi* resemble female *C. alexandrinus sensu stricto*, but lack the warm tone in the forehead stripe, ear coverts, front eye-lore and breast patches in breeding plumage.

Moult patterns

Our observations based on photos of banded birds suggest that the moulting pattern of *C. seebohmi* is more closely aligned with that of *C. dealbatus*, probably driven by their similar non-migratory behaviour. These taxa probably undergo a very early moult into breeding plumage during September or October, much earlier than any population of *C. a. alexandrinus sensu stricto* (the latter moults into breeding plumage from January to March). *Charadrius seebohmi* start moulting into non-breeding plumage just before breeding in April and seem to suspend this moult as they start to breed. This suspended moult is variable, and in some individuals the contour and flight feathers are partially moulted before they start breeding. This suspended moult allows *C. seebohmi* to acquire partial non-breeding plumage before the breeding season (Fig. 1), in the same manner as *C. dealbatus*, but in the latter only contour feathers are concerned.

Genetic analyses

A concatenated dataset of 927 bases from the CR and ND3 regions fully supported the separation of *C. seebohmi* from *C. alexandrinus sensu stricto* with
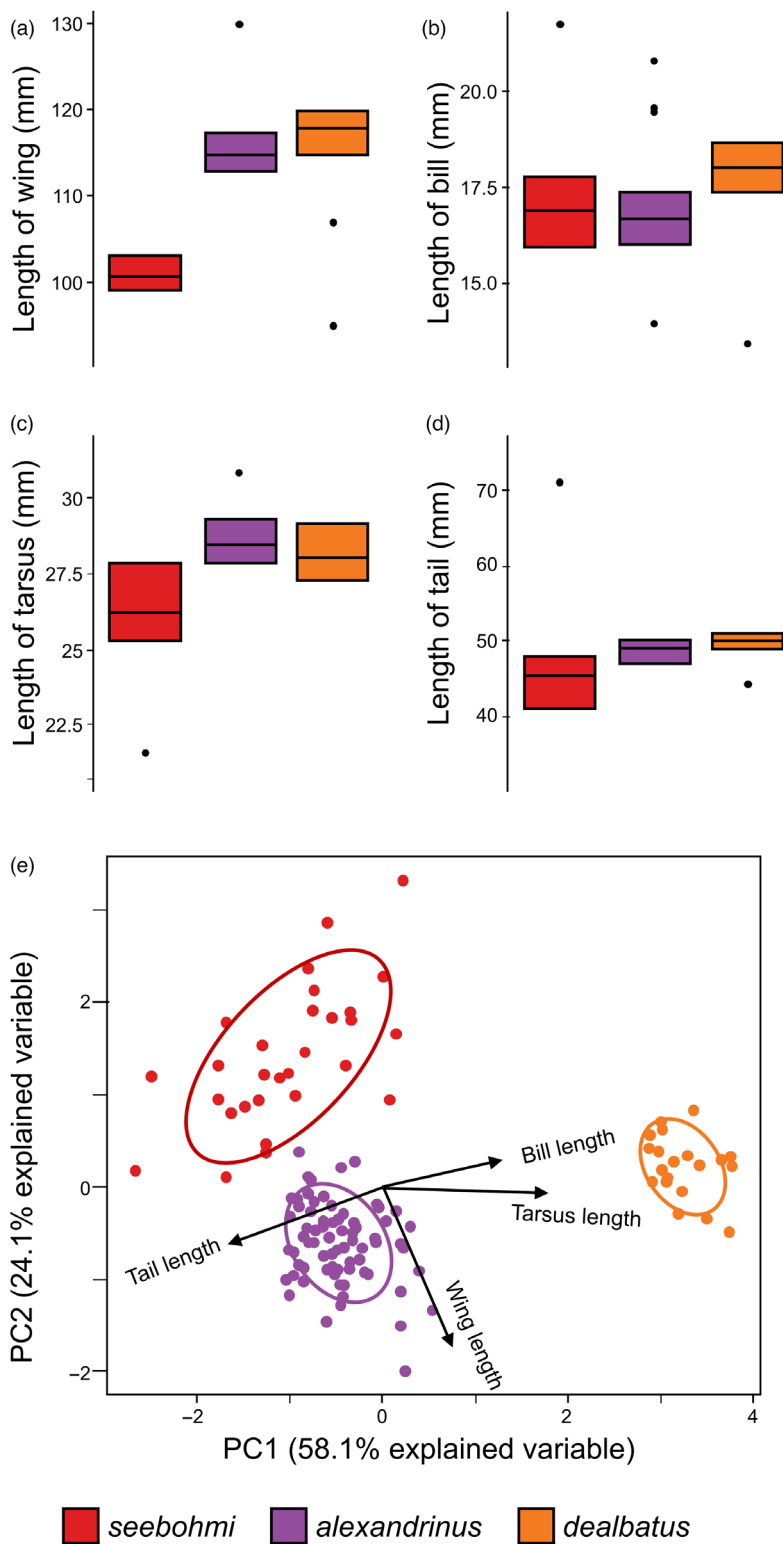
Figure 3. (a–d) Summary of differences among *Charadrius seebohmi*, *Charadrius alexandrinus sensu stricto* and *Charadrius dealbatus* in body-size variables. (e) Ordination from principal components analysis (PCA) on the same variables (see text for summary of PCA results).

Table 2. Eigenvalues and percentage of variance of the principal components analysis of *Charadrius seebohmi*, *Charadrius alexandrinus sensu stricto* and *Charadrius dealbatus*.

	PC1	PC2	PC3	PC4
Eigenvalues (sd^2)	2.32	0.96	0.64	0.07
Percentage of variance	58.12	24.07	16.08	1.73
Cumulative percentage of variance	58.12	82.18	98.26	100.0

PC1, first principal component; sd, standard deviation.

a bootstrap value of 100 in the maximum likelihood tree and a posterior probability value of 0.9976 in the Bayesian tree (Fig. 4). We used sequences from 345 individuals of *C. alexandrinus* and *C. dealbatus* across their range, and gradually reduced the number of sequences to avoid polytomy formation between *C. alexandrinus* and *C. dealbatus*. Within the *C. alexandrinus* species complex, *C. seebohmi* is sister to the *C. alexandrinus* and *C. dealbatus* sister pair (Fig. 4). The genetic
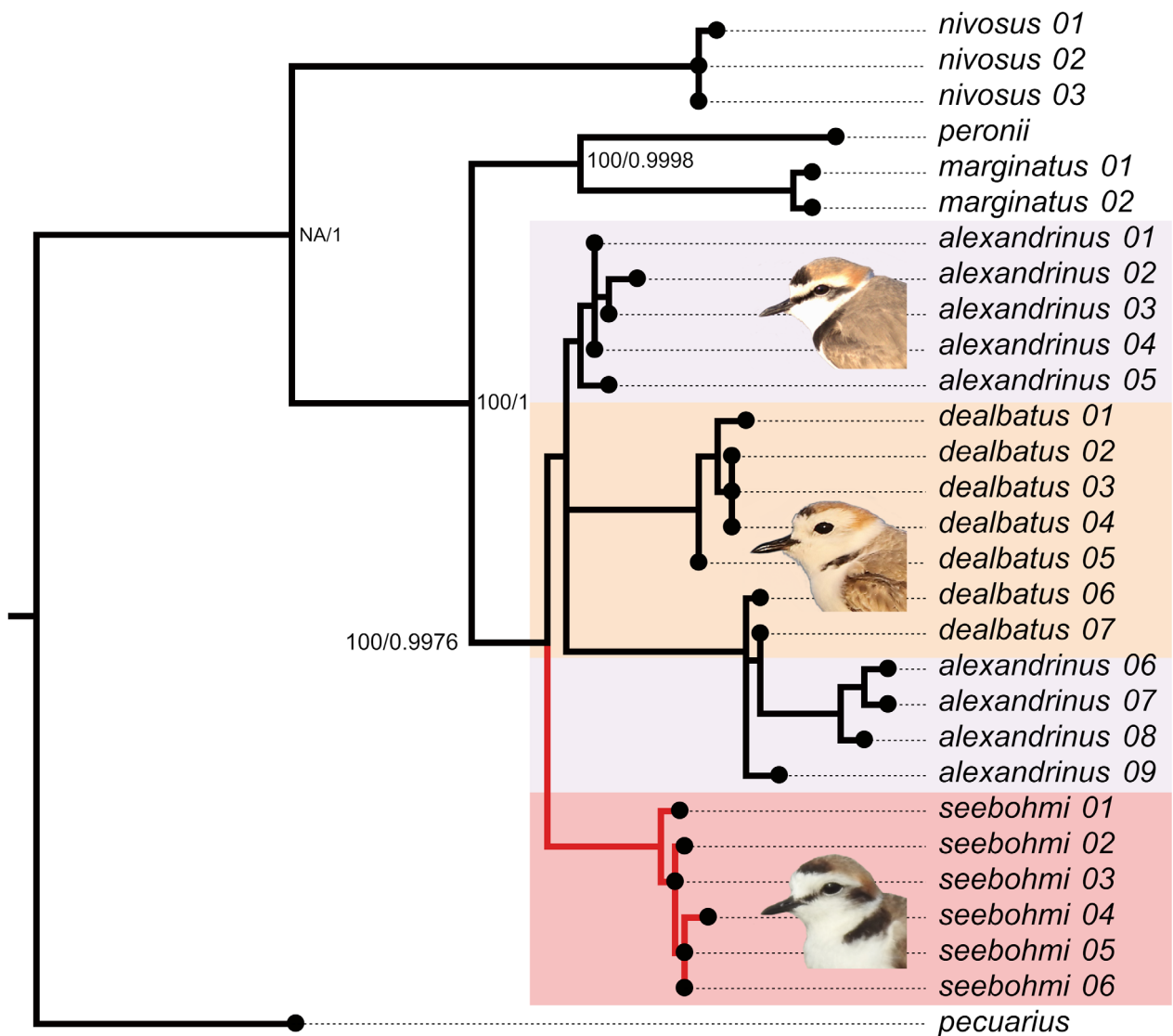
Figure 4. Phylogenetic affinities in the *Charadrius alexandrinus* complex generated using the mitochondrial CR and ND3 regions. The first value indicates bootstrap values in a maximum likelihood framework, and the second values indicate posterior probabilities in a Bayesian framework.

divergence between different taxa was as follows: *alexandrinus–seebohmi* 3.79%; *dealbatus–seebohmi* 3.86%; *alexandrinus–dealbatus* 0.1%. Divergence time estimation for *C. seebohmi* from *C. alexandrinus* using CR sequences was estimated as 1.19 million years ago (95% highest posterior density 0.46–2.10).

Haplotype networks for *C. seebohmi* and four other closely related taxa in the *C. alexandrinus* species complex showed a clear and distinct diversity in *C. seebohmi* at the CR region (Fig. 5) with a nucleotide diversity (π) of 0.02907, and was separated from the other taxa by at least 10 steps. The ND3 region showed the least diversity (π = 0.01645) for *C. seebohmi*. A concatenated sequence of CR, ND3, Z4 and Z45 of 2327 bp had a nucleotide diversity (π) of 0.00184, forming reciprocally monophyletic clusters in the haplotype network. The level of genetic polymorphism of *C. seebohmi* against its closely related taxa is summarized in Table S1.

About 16 variations in alleles (repeat motifs) were seen among the three taxa where *C. seebohmi* was separated from *C. alexandrinus sensu stricto* and *C. dealbatus* (Table S2). Genetic cluster analysis in STRUCTURE segregated *C. seebohmi* into a distinct cluster from *C. alexandrinus* and *C.*

dealbatus (for both K = 3 and K = 4) (Fig. 2). Results of pairwise F_{st} between groups (0.078–0.095: adjusted $P < 0.01$) showed a moderate level of genetic differentiation of *C. seebohmi* compared with *C. alexandrinus sensu stricto* and *C. dealbatus*, which isolates *C. seebohmi* from other members of the *C. alexandrinus* cluster (Table 4).

Species delimitation

Taking all phenotypic data together, following Tobias *et al.* (2010) we obtained a magnitude value of 11 (Table 3), which is consistent with considering *C. seebohmi* as a distinct species (Tobias *et al.* 2010). The relative sequence divergence between the taxa being split (*alexandrinus–seebohmi*) was 3.79% and the levels of sequence divergence between other species pairs in the *C. alexandrines* species complex (*dealbatus–seebohmi* and *alexandrinus–dealbatus*) were 3.86% and 0.1%, respectively (see above), which further supports *C. seebhomi* being considered as a distinct species.

DISCUSSION

Charadrius alexandrinus was described by Linnaeus 1758, based on specimens from the Nile
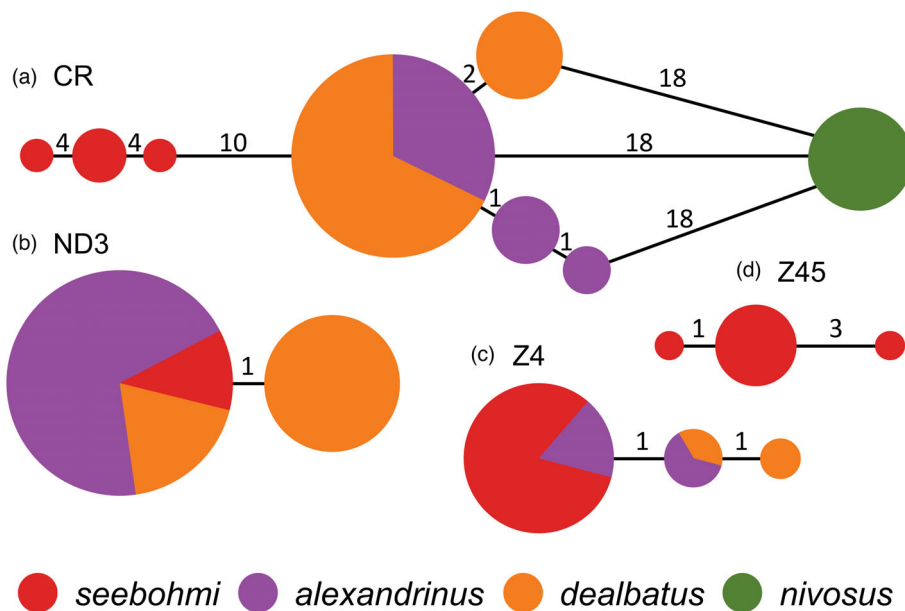
Figure 5. Haplotype map of CR (a), ND3 (b), Z4 (c) and Z45 (d). Numbers along the branches correspond to the number of mutational steps observed between haplotypes; the size of the circles corresponds to the number of populations for each haplotype. The colour indicates the respective species.

Table 3. Phenotypic character segregation of *Charadrius seebohmi* and *Charadrius alexandrinus sensu stricto*, as indicated in Tobias *et al.* (2010) character delimitation.

	seebohmi	alexandrinus	Magnitude score	Score
Body measurements	Shorter wing	Longer wing	Effect size d = 4.31 Moderate – magnitude score of 2	2
	Slightly longer bill	Slightly shorter bill	Effect size d = 0.07 Magnitude score of 0	0
	Slightly shorter tail	Slightly longer tail	Effect size d = 0.72 Minor – magnitude score of 1 (co-varying with wing length)	0
	Slightly shorter tarsus	Slightly longer tarsus	Effect size d = 1.60 Minor – magnitude score of 1 (co-varying with wing length)	0
Plumage characters and bare body parts	Dull brown cap of breeding males	Rufous cap of breeding males	Different colour and tone of strongly demarcated body part Major – magnitude score of 3	3
	Dull brown (washed) upperparts	Dull dark brown upperparts	Different tone of significant area of feathering Moderate – magnitude score of 1	1
	Showing a marked difference in moulting strategy		Partial moulting into non-breeding plumage before breeding and arrest of moulting in breeding season. Moderate – magnitude score 2	2
	Discontinuous eye-lore of male in breeding plumage	Continuous eye-lore of male in breeding plumage	Weak divergence in a plumage feature minor – magnitude score of 1	1
Ecological and behavioural characters	On average inhabits softer mud and dry grasslands	On average inhabits softer mud along tidal channels (Rheindt *et al.* 2011)	No magnitude score	0
Geographical characters	Resident subspecies in Sri Lanka and south-east India	Migration during winter, no overlapping breeding ranges with *C. a. seebohmi*	Parapatric geographical distribution Moderate – magnitude score of 2	2
Total assigned value				11

Table 4. The estimates of evolutionary divergence over sequence pairs between *Charadrius seebohmi*, *Charadrius alexandrinus sensu stricto* and *Charadrius dealbatus*. Above diagonal: pairwise F_{st} between taxa. Below diagonal: estimates of sequence divergence between taxa.

	C. seebohmi	C. dealbatus	C. alexandrinus
C. seebohmi		0.095	0.078
C. dealbatus	0.021		0.013
C. alexandrinus	0.020	0.002	
C. nivosus	0.067	0.049	0.050

River basin in Egypt depicted by Hasselquist (Hasselquist & Linnaeus 1757). Latham (1801) described another closely related species, *Charadrius cantianus*, from New Holland (= Australia, note: C. *alexandrinus* is a vagrant in Australia) mostly based on a specimen(s). Pallas (1811) named *Charadrius minutus* in the vicinity of the Red Sea in his *Zoographia Rosso-Asiatica*, which was later synonymized with *Charadrius dubius* Scopoli, 1786 by Seebohm (1887) – a species outside the C. *alexandrinus* complex and commonly known as the Little Ringed Plover. Seebohm (1887) recognized the distinctiveness of the population in the vicinity of the Red Sea and the South Indian population *sensu* Latham (1801) plus that from Sri Lanka, and hence he proposed the trinomen C. *cantianus minutus* (nec. C. *minutus* Pallas 1811), which is a primary homonym *sensu* Article 57 of the Code (ICZN 1999). According to Articles 52.2 and 52.3 (ICZN 1999), the

relative precedence of primary homonyms in the case of species-group names is determined by applying the relevant provisions of the Principles of Priority. Therefore, the senior homonym *C. minutus* Pallas 1811 has priority over *C. cantianus minutus* Seebohm 1887. The date of Pallas's publication is variously dated as 1811, 1827 and 1831; however, for bird references, the year 1811 should be used (*fide* Dickinson *et al.* 2011). Later, Hartert and Jackson (1915) correctly applied the principle of priority and proposed a replacement name for Seebohm's (1887) trinomen, as *C. alexandrinus seebohmi*. Furthermore, they restricted the type locality of *C. a. seebohmi* to Aripo, N. Ceylon (Arippu, northwestern Sri Lanka) based on one of its syntypes.

Whistler and Kinnear (1936) rejected the terra typica restriction of Hartert and Jackson (1915) and synonymized Seebohm's trinomen (i.e. *C. a. seebohmi*) with the forma typica in Africa (i.e. *C. alexandrinus sensu stricto* Zulla – Gulf of Zula between the Red Sea and Nile River Basin in Egypt). Therefore, they proposed a new trinomen for the Sri Lankan population of *Charadrius* with a placement to a different genus, as *Leucopolius alexandrinus leggei*.

Seebohm (1887) clearly recognized four subspecies including *C. cantianus minutus* from Sri Lanka (*C. a. seebohmi* auct.), South India and the Red Sea area, and the remaining subspecies (*C. cantianus dealbatus* and *C. cantianus nivosus*) are currently accepted and treated as distinct species (Küpper *et al.* 2009, Wang *et al.* 2019a, Gill *et al.* 2021, del Hoyo *et al.* 2021a, 2021b), while the nominotypical subspecies of *C. cantianus* is a junior subjective synonym of *C. alexandrinus sensu stricto*. The confusion appeared because Seebohm (1887) included both the Red Sea and Sri Lanka (plus South India) as the geographical range for *C. cantianus minutus*, though the description is consistent with the Sri Lankan population. Hence, Whistler and Kinnear (1936) considered *C. cantianus minutus* conspecific with *C. alexandrinus sensu stricto* in the Gulf of Zula. Although Seebohm (1887) included 'Red Sea' for part of the geographical range of his subspecies, he stated that he had several specimens from Sri Lanka (at least three specimens from Holdsworth's (1872) collection), so it is likely that the type series represented multiple species. However, no type of *C. alexandrinus* from the Red Sea could be located by us. Therefore, following Hartert and Jackson (1915), we restrict the type locality of *C. cantianus minutus* Seebohm (1887; i.e. *C. a. seebohmi* auct.) to Sri Lanka, *contra* Whistler and Kinnear (1936).

Based on the inability to identify the complete syntypic series of *C. cantianus minutus* and in order to associate the nomen with a name-bearing type specimen, we believe it is essential to designate a lectotype with a precise type locality for further taxonomic clarifications of the genus. Therefore, the specimen from Arippu, Sri Lanka (American Museum of Natural History (AMNH) 736757), which was also the syntype examined by Hartert and Jackson (1915) used to restrict the type locality, is designated here as the lectotype of *C. cantianus minutus* Seebohm 1887 (i.e. *C. alexandrinus seebohmi* Hartert & Jackson 1915), confirming that it is one of the original type series specifically identified from the series of Holdsworth (1872) (*fide* Seebohm 1887). Based on distinctive morphological and genetic evidence compared with *C. alexandrinus*, we further elevate this trinomen to the species level as *C. seebohmi* Hartert & Jackson 1915. This lectotype designation is consistent with the conditions of Article 74.7 of the Code (ICZN 1999). Finally, after comparing the designated lectotype of *C. seebohmi* stat. nov. with the holotype of *Leucopolius alexandrinus leggei* (Natural History Museum, Tring, UK (NHMUK) 1896.7.1.545, collected from Hambantota, Southern Province, Sri Lanka, by Legge in 1873), we find that these two taxa are morphologically conspecific: there are no diagnostic characters to separate them. Therefore, in accordance with the principle of priority (Article 23 of the Code: ICZN 1999) we synonymize *Leucopolius a. leggei* with *C. seebohmi*. It is clear that both populations in northwestern (Mannar) and southeastern (Hambantota) Sri Lanka represent a single species, *C. seebohmi*.

Using body measurements, plumage characteristics, breeding distribution and molecular data, we demonstrated the phenotypic and genetic distinctiveness of the resident population of Kentish Plover, *C. seebohmi*, of Sri Lanka and the Palk Bay region of southern India. Its sister taxa, *C. alexandrinus sensu stricto* and *C. dealbatus*, are larger in size, differ in plumage and genetic signature, and do not share the breeding ranges with *C. seebohmi*. The small size, shorter wing length, different moult pattern and timing, lack of rufus crown and broken loral stripe during the breeding season

separate *C. seebohmi* from *C. alexandrinus sensu stricto* and *C. dealbatus* in the field (Fig. 1).

These results are important for three reasons. First, they provide evidence of cryptic speciation in the genus *Charadrius* (Küpper & dos Remedios 2019, Wang *et al.* 2019a, Wei *et al.* 2022), presenting a possible case of incipient divergence due to spatial segregation in breeding range (Tang *et al.* 2022). Second, based on the substantial genetic and phenotypic differences between *C. seebohmi* and other *Charadrius* populations, we suspect that some of the unstudied phenotypic traits, such as vocalization, courtship display and moulting patterns, of *C. seebohmi* might also be different from the well-studied European and Chinese plover populations (Almalkl *et al.* 2016, Sadanandan *et al.* 2019, Székely 2019, Wang *et al.* 2019b, Song *et al.* 2020). Third, from a broader perspective, endemic and range-restricted taxa in the Global South are a major asset in defining and managing natural resources that are unequally distributed (IRP 2019). The recognition of such unique biota, therefore, is a vital first step in biodiversity conservation (Avise 2000), because such taxa can act as flagship species to draw conservation attention for critical ecosystems (BirdLife International 2004).

Phenotypic patterns

The smaller body size of *C. seebohmi* could be attributed to the latitudinal variation in size and selection pressures as suggested in other plovers (Ji *et al.* 2014, Wang *et al.* 2019a, 2019b). The shorter legs and bill of *C. seebohmi* are indicative of allometry of smaller overall size. Its shorter wings, however, could be attributable to the non-migratory nature of the tropical population (Lovette & Fitzpatrick 2016, de la Hera *et al.* 2020).

The Kentish Plover *C. alexandrinus sensu stricto* starts breeding in mid-April to May in higher latitudes (northwest Europe), but in tropical regions in Africa it breeds as early as mid-November (e.g. on Socotra Island; Porter & Suleiman 2014), January (Cape Verde; Snow & Perrins 1998), February (northeast Africa) and in March (northwest Africa and Iraq; Hanane 2011, del Hoyo *et al.* 2021a, 2021b), and therefore the earlier transition to breeding plumage might be an adaptation of *C. alexandrinus* in tropical latitudes. Tropical breeding *C. dealbatus* moults into breeding plumage as early as October (Kennerley *et al.* 2008).

Morphological and genetic differentiation among Kentish Plover

The moulting pattern of *C. seebohmi* differs from that of *C. alexandrinus sensu stricto* (Jonathan Martinez unpubl. data), and therefore comparisons of breeding and non-breeding plumages are not feasible with the available anecdotal information on their moulting. Our observations suggest that the moulting pattern in *C. seebohmi* is like that of *C. dealbatus* (Kennerley *et al.* 2008) by starting to moult into non-breeding plumage just before breeding in April. However, unlike *C. dealbatus* (del Hoyo *et al.* 2021a, 2021b), *C. seebohmi* appears to have a suspended primary moult in June, from which they acquire partial non-breeding-like plumage before the breeding season. Therefore, *C. seebohmi* moulting into non-breeding plumage results in the fading of ornamentation and forming less contrast among plumage patches observed, especially in males.

Potential causes of divergence in *Charadrius seebohmi*

The closest relatives of *C. seebohmi*, *C. alexandrinus sensu stricto* and *C. dealbatus*, diverged at about 0.6 million years ago (Sadanandan *et al.* 2019, Wang *et al.* 2019a). Despite their genetic and phenotypic distinctiveness (Wang *et al.* 2019b), they have a considerable amount of gene flow in parapatry (Wang *et al.* 2019a), and hence a narrow hybrid zone emerged on the southeastern Chinese coast (Sadanandan *et al.* 2019, Wang *et al.* 2019b). The separation of *C. seebohmi* from its sister clade had taken place much earlier, 1.19 million years ago (Fig. 4). The climatic conditions of the mid-Pleistocene (Berger & Jansen 1994) might have triggered this divergence in the ancestral continental populations in South Asia, as shown in other avian groups in the region (Wickramasinghe *et al.* 2017, Jha *et al.* 2021). Like its East Asian sister pair, the disjunct breeding distribution of the South Asian pair (*C. alexandrinus* and *C. seebohmi*) suggests spatial differences in breeding range. The sympatry in non-breeding (winter) months and the occurrence of non-breeding *C. alexandrinus* as 'summer loiterers' in the tropical breeding grounds of *C. seebohmi*, however, suggest a possibility for introgression between these phylogenetically distinct taxa. A detailed future study aiming at much

broader sampling of these seemingly allopatric plovers in Sri Lanka and south-central India would shed more light into the population genetic structure of *C. seebohmi*.

Allopatric speciation, in which physical barriers restrict gene flow between two populations, facilitating the initiation of divergence through selection (Mayr 1963) or genetic drift (Coyne & Price 2000), is the prevalent mode of speciation in birds (Price 2008). If populations remain isolated for a long enough period after divergence has been established, genome-wide differentiation can be accumulated (Schluter & Conte 2009, Nosil & Schluter 2011). The accumulation of genomic changes can be drastic or subtle, but such changes, even in narrow genomic tracts, can contribute to strong reproductive isolation (Grossen *et al.* 2016). Allopatry due to migratory divides or allochronic differences in migratory behaviour, therefore, would contribute to prezygotic isolation and divergence (Delmore *et al.* 2016, Taylor & Friesen *et al.* 2017, van Bemmelen *et al.* 2019).

Wang *et al.* (2019b) found genetic and phenotypic distinctiveness along the Chinese coast in the closest relatives of *C. seebohmi*. The divergence of *C. dealbatus* from *C. alexandrinus* had been facilitated by sea-level fluctuations in the Pleistocene, character displacement and associated ecological niche differentiation (Wang *et al.* 2019b). Sexually mediated traits such as plumage coloration aimed at mate attraction (Andersson 1994) can act as key divergent forces in reinforcing such speciation events (Price 2008). Hindrance of gene flow through allopatry can also play a role. As suggested by previous phenotypic (Kennerley *et al.* 2008) and genetic (Sadanandan *et al.* 2019) studies, these plovers maintain allopatry in breeding ranges. The breeding population of *C. seebohmi*, for example, is separated from the closest breeding populations of *C. alexandrinus sensu stricto* by ~1200 km and from *C. dealbatus* by about ~1000 km (del Hoyo *et al.* 1996).

Charadrius alexandrinus sensu stricto exhibits high gene flow due to dispersal between breeding sites (Küpper *et al.* 2012). Lack of dispersal is key to hindrance of gene flow (Funk *et al.* 2007) where *C. seebohmi* is severely limited, first by the latitudinal segregation and then by the limited linear coastal habitat in Sri Lanka and southern tip of peninsular India. Furthermore, the two subspecies are mostly allopatric in the breeding season. Local adaptations might further limit dispersal and facilitate divergence (Rheindt & Edwards 2011).

Taxonomic redescription

Charadrius seebohmi stat. nov. Hartert & Jackson 1915

Charadrius cantianus Latham (1801) [*Partim*]

Aegialites cantianus [*Partim*] – Holdsworth 1872, Gould 1873,

Aegialites cantiana [*Partim*] – Legge 1878

Charadrius cantianus minutus Seebohm 1887 [*Partim*; nec. *C. minutus* Pallas 1811]

Aegialites alexandrina [*Partim*] – Cat. Birds British Mus. Lond. 1896

Charadrius cantianus minor (sic) – Cat. Birds British Mus. Lond. 1896

Charadrius alexandrinus seebohmi Hartert & Jackson 1915 (nom. nov. for *C. c. minutus* Seebohm 1887), – Hartert 1922, Cat. Birds British Mus. Lond. 1896

Leucopolius alexandrinus [*Partim*] – Whistler & Kinnear 1936

Leucopolius alexandrinus leggei Whistler & Kinnear 1936, – Pollock 2015

Charadrius alexandrinus seebohmi – Henry 1998, Rasmussen & Anderton 2005, Kasambe 2007, Abeyrama & Seneviratne 2017, 2018, Kotagama & Ratnavira 2017, Wijesundara *et al.* 2017, Rao *et al.* 2018, Warakagoda *et al.* 2020

Lectotype designation

American Museum of Natural History (New York, USA), AMNH 736757, male, collected from Aripo, northern Ceylon [=Arripu, Sri Lanka: 8°47′48.8″N, 79°55′28.1″E], March 1869, by E.W.H. Holdsworth, from the Rothschild collection.

Remarks: Since Holdsworth misidentified this specimen as *Ægialites cantianus*, he described it as a juvenile without full plumage, but with a black bill, dark brown irides, dark grey feet and paler legs. When Hartert and Jackson (1915) described this specimen, it was at Walter Rothschild's private collection in Tring, UK. Rothschild sold his collection to the American Museum of Natural History in the 1930s, where the specimen is now permanently deposited (Greenway 1978; Fig. 6a–c).

Paralectotypes

AMNH 736758 (female, wing length = 99.2 mm), collected from Aripo (Arripu, Sri Lanka) by E.W.H. Holdsworth on 15 January 1870; AMNH 736759 (male, wing length = 94.6 mm), collected
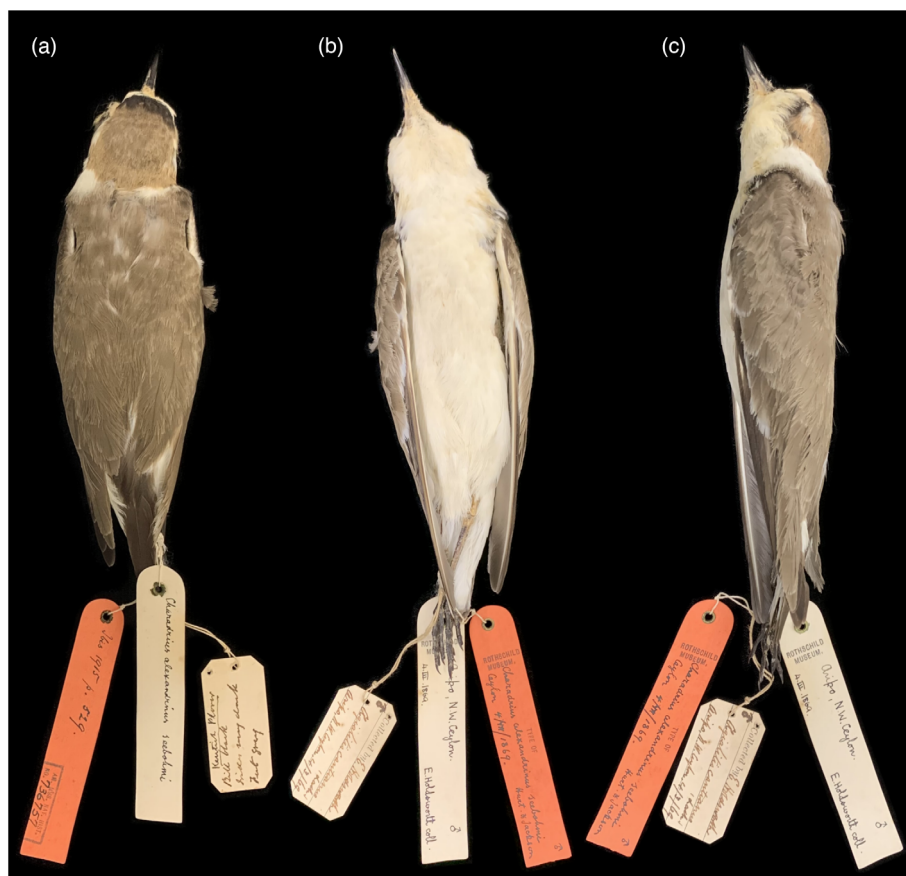
Figure 6. Lectotype: AMNH 736757: a male *Charadrius seebohmi*, collected in 1872 from Arippu (near Mannar), Sri Lanka by E.W.H. Holdsworth. Dorsal (a), ventral (b) and side aspects (c). (Photo credit Paul R Sweet: American Museum of Natural History (AMNH).)

from NW Ceylon (northwestern Sri Lanka), by E.W.H. Holdsworth on 30 March 1869; NHMUK 1896.7.1.545 (male) collected from Hambanthota, Sri Lanka, by W.W.V. Legge on 27 June 1873 (also the holotype of *Leucopolius alexandrinus leggei* (Whistler & Kinnear 1936) – now a junior subjective synonym of *Charadrius seebohmi*); in addition, there are 10 more specimens collected from Sri Lanka during 1873–1949, plus one with a questionable origin collected by R. Meinertzhagen (Dalton 2005) at the Natural History Museum, Tring, UK, possibly part of the paralectotype series. Furthermore, the National Museum of Natural History, Sri Lanka (NMSL) houses 13 skin specimens from Sri Lanka, collected during 1881–1979, that might also be paralectotypes (see Appendix S1).

Redescription of lectotype

A male specimen. Culmen is black; incomplete dark grey eye-lore expanding from culmen to the eye; head is white except for the grey cap and grey ear coverts; a distinguishable darker forehead stripe demarcates the grey cap from the white forehead; a white hindneck collar at the end of the grey cap connected to the white breast; grey-brown shoulder patches are bordering the white collar; shoulder patches are disconnected by white breast; upperparts, grey; legs, dark grey; feet, do not have distinguishable colour differences from the dark grey tibiotarsus and tarsometatarsus; upper-wing and tail, overall grey-brown with no distinct patterns; length of the flattened wing, 101 mm (range 93–107 mm, n = 28 skins from other collections).

Diagnosis

Hanuman Plover (C. *seebohmi* stat. nov.) is a small plover compared with C. *alexandrinus sensu stricto* and C. *dealbatus*. It has white underparts and grey upperparts, dark grey legs, and a white hind neck collar. It has an incomplete front eye-lore which becomes darker in the breeding plumage in contrast to C. *alexandrinus sensu stricto* which has a complete black line. It does not have a rufous cap in the breeding season. The adult breeding male has a brown cap, dark incomplete breast patches and a black forehead stripe. Female C. *seebohmi* resembles female C. *alexandrinus sensu stricto*. It lacks black in the forehead stripe, ear coverts, front eye-lore and breast patches in both breeding and winter plumages.

Etymology

The generic epithet *Charadrius* refers to a nocturnal waterbird where '*the sight of it would cure the jaundice*' (= an open country bird exposed to sun; *fide* Pande *et al.* 2009). The specific epithet was generated by Hartert and Jackson (1915) as a noun in the singular genitive case, honouring Henry Seebohm (1832–1895), the ornithologist who first identified the Sri Lankan breeding population as a possible distinct taxon (Seebohm 1887). The English name 'Hanuman Plover' and the vernacular Singhalese and Tamil names, *Hanuman Olaviya* and *Hanuman Uppukkothi*, respectively, refer to Hanuman, the ape-God of the Ramayana, a Sanskrit epic from ancient India, who helped Rama's ape-army to build the mythological bridge between southern India (Rameswaram) and Sri Lanka (Mannar Island), the type locality of C. *seebohmi*, to trespass to Sri Lanka. To celebrate the mythology as 'stories of the people of the native land of this plover', we suggest the name 'Hanuman Plover' as the English common name of this species.

Distribution

Charadrius seebohmi stat. nov. is found in coastal mudflats and adjacent grasslands in arid and dry zones of Sri Lanka and the southern tip of India. In Sri Lanka it is common in Rama's Bridge and Mannar, along the coast of northwestern, northern, eastern and southern provinces, including Chilaw, Kalpitiya, Veddithalathive, Irranathivu, Jaffna Peninsula, islands off Jaffna, Chundikulum National Park, Mullativu, Trincomalee, Batticaloa, Kumana and Yala National Parks, and the Hambanthota wetlands including Bundala National Park (Legge 1880, Henry 1998, Wijesundara *et al.* 2017). It can also be seen near large inland freshwater reservoirs in the dry zone (Henry 1998). In India, it is found in the coastal wetlands and grasslands of Kochi, Kerala, to Chennai, Tamil Nadu, including the coastal wetlands of Kollum, Rameswaram, Point Calemere, Cuddalore and Chengalpattu. Breeding has been reported in inland wetlands such as Vidarbha Maharashtra (Kasambe 2007) and Vani Vilasapuram, Karnataka (Rao *et al.* 2018).

The historical specimens we studied in collections from 1869 to 1980 (see Appendix S2) yielded C. *seebohmi* skins in Sri Lanka and South India, and C. *alexandrinus sensu stricto* skins from elsewhere. All the putative C. *seebohmi* specimens collected outside their current geographical range (e.g. YPM 42366 and YPM 42367 from Bihar, North India, and UMMZ 76855 from Sind, Pakistan) were reassessed to be C. *alexandrinus sensu stricto* based on the plumage characteristics and wing measurements.

Initial reports of the 'tropical' 'diminutive' form (Seebohm 1887) of the Kentish plover referred to 'Ceylon' [=Sri Lanka] and south India, as well as 'Somaliland' [=Somalia], 'Red Sea area' and Djibouti (summarized in Hartert & Jackson 1915). In their subspecies description, Hartert and Jackson (1915) stated 'Besides Ceylonese birds, some from Massaua [=Eritrea] and Somaliland in the British Museum undoubtedly belong to the "small race".' A female from Socotra (Gulf of Yemen), considered by Sharpe (1896) as C. *a. seebohmi* (now C. *seebohmi*), appears to be doubtful due to longer wing length (108 mm) and more contrasting facial plumage; therefore, we considered this west African specimen to be of C. *alexandrinus sensu stricto*. Based on three specimens, Friedmann (1930) stated that, 'It [C. *seebohmi*] is confined to the coast of the Indian Ocean from Ceylon to the Mouth of the Red Sea [Somali coast]. In Africa its range is restricted, as far as known, to the coast from Massawa [=Eritrea], to French Somaliland [=Djibouti]. The birds of southern Somaliland [=Somalia] are probably C. *alexandrinus* sensu stricto, as well as birds of Egypt, Syria, and Palestine. It is not known if C. *a. seebohmi* [= now C. *seebohmi*] is resident in the Somali coast or not, as all the specimens taken are

winter birds.' (Friedmann 1930). According to Whistler and Kinnear (1936), the most important difference of the Sri Lankan race is that it does not acquire the chestnut cap of the breeding plumage of the nominate race. 'This absence of a distinctive breeding plumage is a characteristic of other Cinghalease [= of Sri Lanka] race and is of great interest' (Whistler & Kinnear 1936). The skins from the Red Sea region came from winter months and as the body measurements and plumage characters were aligned to *C. alexandrinus sensu stricto*, so the subsequent authors considered the 'Kentish Plover of tropical North Africa' as *C. alexandrinus sensu stricto* (Peters 1931, Mackworth-Praed & Grant 1960, del Hoyo *et al.* 1996).

Conservation implications

Sri Lanka and southern India form a global biodiversity hotspot (Myers *et al.* 2000) and an area of high endemicity threatened with risk of extinction (Mittermeier *et al.* 2004). The range of *C. seebohmi* has one of the highest human population densities on the planet (Luck 2007, MoMD&E 2019), and therefore both breeding habitats and non-breeding sites of the species are severely threatened with encroachment, pollution, dogs and infrastructure such as highways, ports and wind farms (MoMD&E 2019). The description of *C. seebohmi* as a regional endemic could make this species a flagship species in conservation prioritization of some of the most important wetlands of the Central Asian Flyway in Sri Lanka (e.g. Mannar Island, Veddithalativu Nature Reserve and Kalametiya Sanctuary; Abeyrama & Seneviratne 2018). As conservation attention is mainly driven by a few charismatic megafauna and endemics in the tropics (Abeyrama & Seneviratne 2017), endemic-taxa-poor coastal wetlands such as the Palk Bay region and Mannar (critical overwintering sites for migratory waterbirds; Wetlands International 2020) would greatly benefit from such regional endemics in capturing much needed conservation attention for the benefit of millions of migratory and resident shorebirds.

AUTHOR CONTRIBUTIONS

Jude Janitha Niroshan: Data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); project administration (equal); software (equal); validation (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal). **Yang Liu:** Conceptualization (lead); formal analysis (equal); investigation (equal); methodology (equal); resources (equal); supervision (equal); validation (equal); writing – original draft (equal); writing – review and editing (equal). **Jonathan Martinez:** Investigation (equal); validation (equal); writing – original draft (equal); writing – review and editing (equal). **Pinjia Que:** Data curation (equal); formal analysis (equal); investigation (equal); writing – review and editing (equal). **Chentao Wei:** Data curation (equal); formal analysis (equal); methodology (equal); validation (equal); writing – review and editing (equal). **Sanjaya Weerakkody:** Formal analysis (supporting); methodology (supporting); software (supporting). **Gayomini Panagoda:** Investigation (equal); writing – review and editing (equal). **Jagathpriya Weerasena:** Formal analysis (equal); investigation (equal). **Thasun A. A. Amarasinghe:** Investigation (equal); methodology (equal); validation (equal); writing – original draft (equal); writing – review and editing (equal). **Tamas Szekely:** Methodology (equal);

validation (equal); writing – original draft (equal); writing – review and editing (equal). **Alexander L. Bond:** Formal analysis (equal); investigation (equal); writing – original draft (equal); writing – review and editing (equal). **Sampath S. Seneviratne:** Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (lead); resources (lead); supervision (lead); writing – original draft (lead); writing – review and editing (lead).

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ETHICAL NOTE

None.

Data Availability Statement

DNA sequences deposited at NCBI GenBank (https://www.ncbi.nlm.nih.gov/genbank/) under accession numbers OQ356320–OQ356325 for CR and OQ401332–OQ401337 for ND3. The phenotypic measurement data and raw microsatellite allele scores are available as Appendix S1.

REFERENCES

Abeyrama, D.K. & Seneviratne, S.S. 2017. Evolutionary distinctiveness of Sri Lankan Avifauna. *WildLanka* **5**: 1–10.

Abeyrama, D.K. & Seneviratne, S.S. 2018. Evolutionary distinctiveness of important bird areas (IBAs) of Sri Lanka: do the species-rich wet zone forests safeguard Sri Lanka's genetic heritage? *Ceylon J. Sci.* **46**: 89–99.

Ali, S. & Ripley, D.M. 1983. *The Handbook of the Birds of India and Pakistan*, Vol. **1-4**. Delhi: Oxford University Press.

Almalki, M., Kupán, K., Carmona-Isunza, M.C., López, P., Veiga, A., Kosztolányi, A. & Küpper, C. 2016. Morphological and genetic differentiation among Kentish Plover *Charadrius alexandrinus* populations in Macaronesia. *Ardeola* **64**: 3–16.

Alström, P., Mild, K. & Zetterström, D. 2003. *Pipits & Wagtails of Europe, Asia and North America*. London: Christopher Helm.

Andersson, M. 1994. *Sexual Selection*. Princeton, NJ: Princeton University Press.

Andrew, R. 2006. *FigTree*. Available at: http://tree.bio.ed.ac.uk/software/figtree/ (accessed 23 May 2020).

Avise, J.C. 2000. *Phylogeography: The History and Formation of Species*. Cambridge, MA: Harvard University Press.

Bah, T. 2007. *Inkscape: Guide to a Vector Drawing Program*. Hoboken, NJ: Prentice Hall Press.

Bandelt, H., Forster, P. & Röhl, A. 1999. Median-joining networks for inferring intraspecific phylogenies. *Mol. Biol. Evol.* **16**: 37–48.

van Bemmelen, R.S.A., Kolbeinsson, Y., Ramos, R., Gilg, O., Alves, J.A., Smith, M., Schekkerman, H., Lehikoinen, A., Petersen, I.K., Þórisson, B., Sokolov, A.A., Välimäki, K., van der Meer, T., Okill, J.D., Bolton, M., Moe, B., Hanssen, S.A., Bollache, L., Petersen, A., Thorstensen, S., González-Solís, J., Klaassen, R.H.G. & Tulp, I. 2019. A migratory divide among red-necked phalaropes in the Western palearctic reveals contrasting migration and wintering movement strategies. *Front. Ecol. Evol.* **7**: 86.

Berger, W.H. & Jansen, E. 1994. Mid-Pleistocene climate shift - the Nansen connection. In Johannessen, O.M., Muench, R.D. & Overland, J.E. (eds) *The Polar Oceans and Their Role in Shaping the Global Environment*. Vol. **85**: 295–311. Washington DC: American Geophysical Union Geophysical Monograph Series.

BirdLife International 2004. *Birds in the European Union: A Status Assessment*. Wageningen, The Netherlands: BirdLife International.

Bouckaert, R., Heled, J., Kühnert, D., Vaughan, T., Wu, C.-H., Xie, D., Suchard, M.A., Rambaut, A. & Drummond, A.J. 2014. BEAST 2: a software platform for Bayesian evolutionary analysis. *PLoS Comput. Biol.* **10**: e1003537.

Burke, T. & Bruford, M.W. 1987. DNA fingerprinting in birds. *Nature* **327**: 149–152.

Carmona-Isunza, M.C., Küpper, C., Serrano-Meneses, M.A. & Székely, T. 2015. Courtship behavior differs between monogamous and polygamous plovers. *Behav. Ecol. Sociobiol.* **69**: 2035–2042.

Catalogue of the Birds in the British Museum, London, 1874–98. 1896. Vol 24. Available at: https://www.biodiversitylibrary.org/item/34473 (accessed 10 June 2020).

Chen, J. & Chen, Z. 2008. Extended Bayesian information criteria for model selection with large model spaces. *Biometrika* **95**: 759–771.

Chesser, R.T. 1999. Molecular systematics of the rhinocryptid genus *Pteroptochos*. *Condor* **101**: 439–446.

Cohen, J. 1988. *Statistical Power Analysis for the Behavioral Sciences*. New York: Routledge.

Coyne, J.A. & Price, T.D. 2000. Little evidence for sympatric speciation in Island birds. *Evolution* **54**: 2166–2171.

Dalton, R. 2005. Ornithologists stunned by bird collector's deceit. *Nature* **437**: 7057.

Darriba, D., Taboada, G.L., Doallo, R. & Posada, D. 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nat. Methods* **9**: 772.

Delmore, K.E., Toews, D.P.L., Germain, R.R., Owens, G.L. & Irwin, D.E. 2016. The genetics of seasonal migration and plumage color. *Curr. Biol.* **26**: 2167–2173.

Dickinson, E.C. & Christidis, L. (eds) 2014. *The Howard and Moore Complete Checklist of the Birds of the World*, Vol. **2**, 4th edn. Eastbourne: Aves Press.

Dickinson, E.C., Overstreet, L.K., Dowsett, R.J. & Bruce, M.D. 2011. *Priority! The Dating of Scientific Names in Ornithology*. Northampton: Aves Press.

Drummond, A.J. & Bouckaert, R.R. 2015. *Bayesian Evolutionary Analysis with BEAST*. Cambridge, UK: Cambridge University Press.

Earl, D.A. & VonHoldt, B.M. 2012. STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conserv. Genet. Resour.* **4**: 359–361.

Eberhart-Phillips, L.J., Küpper, C., Miller, T.E.X., Cruz-López, M.K.H., dos Remedios, N., Stoffel, M.A., Hoffman, J.I., Krüger, O. & Székely, T. 2017. Adult sex ratio bias in snowy plovers is driven by sex-specific early survival: Implications for mating systems and population growth. *Proc. Natl Acad. Sci. USA* **114**: E5474–E5481.

Edgar, R.C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Res.* **32**: 1792–1797.

Evanno, G., Regnaut, S. & Goudet, J. 2005. Detecting the number of clusters of individuals using the software structure: a simulation study. *Mol. Ecol.* **4**: 359–361.

Falush, D., Stephens, M. & Pritchard, J.K. 2003. Inference of population structure using multilocus genotype data: linked loci and correlated allele frequencies. *Genetics* **164**: 1567–1587.

Fernando, S.P., Irwin, D.E. & Seneviratne, S.S. 2016. Phenotypic and genetic analysis support distinct species status of the Red-backed Woodpecker (Lesser Sri Lanka Flameback: *Dinopium psarodes*) of Sri Lanka. *Auk: Ornithol. Adv.* **133**: 497–511.

Friedmann, H. 1930. Birds collected by the Childs Frick expedition to Ethiopia and Kenya colony. *Bull. Smithsonian Inst.* **153**: 20.

Funk, W.C., Mullins, T.D. & Haig, S.M. 2007. Conservation genetics of snowy plovers (*Charadrius alexandrinus*) in the Western Hemisphere: population genetic structure and delineation of subspecies. *Conserv. Genet.* **8**: 1287–1309.

Gill, F., Donsker, D. & Rasmussen, P. (eds). 2021. *IOC World Bird List (v11.2)*. https://doi.org/10.14344/IOC.ML.11.2

Greenway, J.C. 1978. Type specimens of birds in the American Museum of Natural History. Part 2, Otididae, Jacanidae, Rostratulidae, Haematopodidae, Charadriidae, Scolopacidae, Recurvirostridae, Burhinidae, Glareolidae, Thinocoridae, Stercorariidae, Laridae, Alcidae, Pteroclididae, Columbidae, Psittacidae, Musophagidae, Cuculidae, Tytonidae, Strigidae, Podargidae, Nyctibiidae, Aegothelidae, Caprimulgidae, Apodidae, Hemiprocnidae, Trochilidae, Coliidae, Trogonidae, Alcedinidae, Momotidae, Meropidae, Leptosomatidae, Coraciidae, Upupidae, Phoeniculidae, Bucerotidae, Galbulidae, Bucconidae, Capitonidae, Indicatoridae, Ramphastidae, Picidae. *Bull. Am. Mus. Nat. Hist.* **161**: 1–305.

Grossen, C., Seneviratne, S.S., Croll, D. & Irwin, D.E. 2016. Strong reproductive isolation and narrow genomic tracts of differentiation among three woodpecker species in secondary contact. *Mol. Ecol.* **25**: 4247–4266.

Hanane, S. 2011. Breeding ecology of Kentish Plovers *Charadrius alexandrinus* in rocky and sandy habitats of north-West Morocco (North Africa). *Ostrich J. Afr. Ornithol.* **82**: 217–223.

Harris, R.B., Alström, P., Ödeen, A. & Leache, A.D. 2018. Discordance between genomic divergence and phenotypic variation in a rapidly evolving avian genus (*Motacilla*). *Mol. Phylo. Evol.* **120**: 183–195.

Hartert, E. & Jackson, A.C. 1915. Notes on some waders. *Ibis* **57**: 526–534.

Hasselquist, F. & Linnaeus, C. 1757. *Fredric Hasselquists . . . Iter Palæstinum, eller Resa til Heliga Landet, förrättad ifrån år 1749 til 1752, med beskrifningar, rön, anmärkningar, öfver de märkvärdigaste naturalier, på Hennes Kongl. Maj:ts befallning*. Stockholm: Trykt på L. Salvii kåstand.

Henry, G.M. 1998. *A Guide to the Birds of Sri Lanka*, 3rd edn. New Delhi: Oxford University Press.

de la Hera, I., Hernández-Téllez, I., Pérez-Rigueiro, J., Pérez-Tris, J., Rojo, F.J. & Tellería, J.L. 2020. Mechanical and structural adaptations to migration in the flight feathers of a Palaearctic passerine. *J. Evol. Biol.* **7**: 979–989.

Hjort, C. & Lindholm, C.G. 1978. Annual bird ringing totals and population fluctuations. *Oikos* **30**: 387–392.

Hochberg, Y. 1988. A sharper Bonferroni procedure for multiple tests of significance. *Biometrika* **75**: 800–802.

Holdsworth, E.W.H. 1872. Catalogue of the birds found in Ceylon: with some remarks on their habits and local distribution, and descriptions of two new species peculiar to the Island. *Proc. Zool. Soc. Lond.* **1872**: 404–483.

del Hoyo, J., Elliott, A. & Sargatal, J. 1996. *Handbook of the Birds of the World*, Vol. **3**. Barcelona: Lynx Edicions.

del Hoyo, J., Wiersma, P., Kirwan, G.M., Collar, N., Boesman, P.F.D. & Sharpe, C.J. 2021a. Kentish Plover (*Charadrius alexandrinus*). In Keeny, B.K. (ed) *Birds of the World Ver. 1.1*. Ithaca, NY, USA: Cornell Lab of Ornithology.

del Hoyo, J., Wiersma, P., Kirwan, G.M., Collar, N., Boesman, P.F.D. & Sharpe, C.J. 2021b. White-faced Plover (*Charadrius dealbatus*). In Billerman, S.M. (ed) *Birds of the World Ver. 1.0*. Ithaca, NY, USA: Cornell Lab of Ornithology.

International Commission on Zoological Nomenclature (ICZN) 1999. Anonymous [International Commission on Zoological Nomenclature]. International code of zoological nomenclature. In *International Trust for Zoological Nomenclature*, 4th edn. i–xxix + 1–306. London, UK: The Natural History Museum.

IRP 2019. *Global Resources Outlook 2019: Natural Resources for the Future We Want*. Nairobi, Kenya: A Report of the International Resource Panel. United Nations Environment Programme.

Ji, W., Zhang, G.R., Ran, W., Gardner, J.P.A., Wei, K.J., Wang, W.M. & Zou, G.W. 2014. Genetic diversity of and differentiation among five populations of blunt snout bream (*Megalobrama amblycephala*) revealed by SRAP markers: implications for conservation and management. *PLoS One* **9**: e108967.

Jha, A., Seneviratne, S., Prayag, H.S. & Vasudevan, K. 2021. Phylogeny identifies multiple colonisation events and Miocene aridification as drivers of South Asian bulbul (Passeriformes: Pycnonotidae) diversification. *Org. Divers. Evol.* **21**: 783–794.

Jonathan, K.P., Stephens, M. & Peter, D. 2000. Inference of population structure using multilocus genotype data. *Genetics* **155**: 945–959.

Karr, J.R. 1981. Surveying birds with mist nets. *Stud. Avian Biol.* **6**: 62–67.

Kasambe, R. 2007. First record of breeding of Kentish Plover (*Charadrius alexandrinus seebohmi*) from Vidarbha, Maharashta. *NLBW* **47**: 30.

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S. & Thierer, T. 2012. Geneious basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* **28**: 1647–1649.

Kennerley, P., Bakewell, D. & Round, P. 2008. Rediscovery of a long-lost *Charadrius* plover from South-East Asia. *Forktail* **24**: 63–79.

Kosztolányi, A., Küpper, C., Chastel, O., Parenteauc, C., Yılmaz, K.T., Miklósi, Á., Székely, T. & Lendvai, Á.Z. 2012. Prolactin stress response does not predict brood desertion in a polyandrous shorebird. *Horm. Behav.* **61**: 734–740.

Kotagama, S. & Ratnavira, G. 2017. *Birds of Sri Lanka an Illustrated Guide*. Colombo: Field Ornithology Group of Sri Lanka, University of Colombo.

Kumar, S., Stecher, G. & Tamura, K. 2016. MEGA7: Molecular evolutionary genetics analysis Ver. 7.0 for bigger datasets. *Mol. Biol. Evol.* **33**: 1870–1874.

Küpper, C. & dos Remedios, N. 2019. Defining species and populations: molecular genetic studies in plovers. In *The Population Ecology and Conservation of Charadrius Plovers*: 16–43. Boca Raton, FL: CRC Press.

Küpper, C., Horsburgh, G.J., Dawson, D.A., Ffrench-Constant, R., Székely, T. & Burke, T. 2007. Characterization of 36 polymorphic microsatellite loci in the Kentish plover (*Charadrius alexandrinus*) including two sex-linked loci and their amplification in four other *Charadrius* species. *Mol. Ecol. Notes* **7**: 35–39.

Küpper, C., Augustin, J., Kosztolányi, A., Burke, T., Figuerola, J. & Székely, T. 2009. Kentish versus snowy plover: Phenotypic and genetic analyses of *Charadrius alexandrinus* reveal divergence of Eurasian and American subspecies. *Auk* **126**: 839–852.

Küpper, C., Edwards, S.V., Kosztolányi, A., Alrashidi, M., Burke, T., Herrmann, P., Argüelles-Tico, A., Amat, J.A., Amezian, M., Rocha, A., Hötker, H., Ivanov, A., Chernicko, J. & Székely, T. 2012. High gene flow on a continental scale in the polyandrous Kentish plover *Charadrius alexandrinus*. *Mol. Ecol.* **21**: 5864–5879.

Lanfear, R., Calcott, B., Ho, S.Y.W. & Guindon, S. 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Mol. Biol. Evol.* **29**: 1695–1701.

Latham, J. 1801. A General synopsis of birds. *Leigh and Sotheby* **143**: 281–282.

Leigh, J.W. & Bryant, D. 2015. Popart: full-feature software for haplotype network construction. *Methods Ecol. Evol.* **6**: 1110–1116.

Legge, W.V. 1880. *A History of the Birds of Ceylon*. Vol. **1**: 198 London: W.V. Legge.

Liebers-Helbig, D., Helbig, A.J. & Knijff, P.D. 2001. Genetic differentiation and phylogeography of gulls in the *Larus cachinnans-fuscus* group (Aves: Charadriiformes). *Mol. Ecol.* **10**: 2447–2462.

Linnaeus, C. 1758. *Systema Naturæ*. 1: 150.

Liu, S., Liu, Y., Jelen, E., Alibadian, M., Yao, C.T., Li, X., Kayvanfar, N., Wang, Y., Vahidi, F.S., Han, J.L. & Sundev, G. 2020. Regional drivers of diversification in the late quaternary in a widely distributed generalist species, the common pheasant *Phasianus colchicus*. *J. Biogeogr.* **47**: 2714–2727.

Lovette, I.J. & Fitzpatrick, J.W. 2016. *Handbook of Bird Biology*. London: John Wiley & Sons.

Luck, G.W. 2007. A review of the relationships between human population density and biodiversity. *Biol. Rev.* **82**: 607–645.

Mackworth-Praed, C.W. & Grant, H.C.B. 1960. *Birds of Eastern and North Eastern Africa: African Handbook of Birds*. London: Longmans.

Mayr, E. 1963. *Animal Species and Evolution*. Cambridge, MA and London, UK: Harvard University Press.

McCarthy, C. 1997. *Chromas*. Brisbane, QLD: Griffith Univ.

Meininger, P.L. & Székely, T. 1997. Kentish Plover – *Charadrius alexandrinus*. In Hagemeijer, W.J.M. & Blair, M.J. (eds) *The EBCC Atlas of European Breeding Birds: Their Distribution and Abundance*: 260–261. London: T & A D Poyser.

Mittermeier, R.A., Gil, P.R., Hoffmann, M., Pilgrim, J., Brooks, T., Mittermeier, C.G., Lamoreux, J. & da Fonseca, G.A.B. 2004. *Hotspots Revisited: Earth's Biologically Wealthiest and most Threatened Ecosystems*. México DF, Washington, D.C: CEMEX.

MoMD&E 2019. Biodiversity profile – Sri Lanka: Sixth National Report to the Convention on Biological Diversity. In Jayakody, S., Wikramanayake, E.D., Fernando, S., Wickramaratne, C., Arachchige, G.M. & Akbarally, Z. (eds) *Biodiversity Secretariat*: 211. Sri Lanka: Ministry of Mahaweli Development and Environment.

Myers, N., Mittermeier, R., Mittermeier, C., da Fonseca, G. & Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* **403**: 853–858.

Nguyen, L.T., Schmidt, H.A., von Haeseler, A. & Minh, B.Q. 2014. IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Mol. Biol. Evol.* **32**: 268–274.

Nosil, P. & Schluter, D. 2011. The genes underlying the process of speciation. *Trends Ecol. Evol.* **26**: 160–167.

Owen, J.C. 2011. Collecting, processing, and storing avian blood: a review. *J. Field Ornithol.* **82**: 339–354.

Pallas, P.S. 1811. *Zoographia Rosso-Asiatica*. Volumen Secundum, Petropoli: Academiae Sciantiarum Impress.

Pande, S., Sant, N. & Shivkumar, P. 2009. Avifaunal survey of south-and middle-Andamans, November 2009. *Indian BIRDS* **104**: 104–106.

Peakall, R. & Smouse, P.E. 2006. Genalex 6: genetic analysis in excel. Population genetic software for teaching and research. *Mol. Ecol. Notes* **6**: 288–295.

Peñalba, J.V., Joseph, L. & Moritz, C. 2019. Current geography masks dynamic history of gene flow during speciation in northern Australian birds. *Mol. Ecol.* **28**: 630–643.

Peters, J.L. 1931. *Checklist of the Birds of the World*. Cambridge, MA: Harvard University Press.

Pollock, A.W. 2015. *Binomial and Trinomial Index to The Auk, 1884–1940, Also Including the Nuttall bulletin, 1876–1883, and the A.O.U. Checklist of North American Birds*. Chicago, IL: American Ornithologists' Union.

Porter, R.F. & Suleiman, A.S. 2014. The populations and distribution of the breeding birds of the Socotra archipelago, Yemen: 2. Shearwaters to Terns. *Sandgrouse* **36**: 8–33.

Price, T. 2008. *Speciation in Birds*. CO, USA: Roberts and Co.

Primmer, C., Møller, A. & Ellegren, H. 1995. Resolving genetic relationships with microsatellite markers: a parentage testing system for the swallow *Hirundo rustica*. *Mol. Ecol.* **4**: 493–498.

R Core Team 2017. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Available at: http://r.meteo.uni.wroc.pl/web/packages/dplR/vignettes/intro-dplR.pdf (accessed 5 May 2020).

Rambaut, A. & Drummond, A.J. 2007. *TreeAnnotator*. Available at: http://beast.bio.ed.ac.uk/TreeAnnotator (accessed 18 March 2020).

Rambaut, A., Drummond, A.J., Xie, D., Baele, G. & Suchard, M.A. 2018. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Syst. Biol.* **67**: 901–904.

Rao, G.B., Babu, S., Kumara, H.N. & Bilaskar, M. 2018. Ceylon Kentish Plover *Charadrius alexandrinus seebohmi* breeding in Vani Vilasa Sagara, Hiriyur Taluka, Karnataka, India. *J. Threat. Taxa* **10**: 11237–11239.

Rasmussen, P.C. & Anderton, J.C. 2005. *Birds of South Asia: The Ripley Guide*. Barcelona, Spain: Lynx Edicions.

Rheindt, F.E. & Edwards, S.V. 2011. Genetic introgression: an integral but neglected component of speciation in birds. *Auk* **128**: 620–632.

Rheindt, F.E., Székely, T., Edwards, S.V., Lee, P.L.M., Burke, T., Kennerley, P.R., Bakewell, D.N., Alrashidi, M., Kosztolányi, A., Weston, M.A., Liu, W.T., Lei, W.P., Shigeta, Y., Javed, S., Zefania, S. & Küpper, C. 2011. Conflict between genetic and phenotypic differentiation: The evolutionary history of a 'lost and rediscovered' shorebird. *PLoS One* **6**: e26995.

Ronquist, F., Teslenko, M., Van Der Mark, P., Ayres, D.L., Darling, A., Höhna, S. & Huelsenbeck, J.P. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst. Biol.* **61**: 539–542.

Rosenberg, N.A. 2004. Distruct: a program for the graphical display of population structure. *Mol. Ecol. Notes.* **4**: 137–138.

RStudio Team 2020. *RStudio: Integrated Development for R*. PBC, Boston, MA: RStudio. Available at: http://www.rstudio.com/ (accessed 21 June 2020).

Sadanandan, K.R., Küpper, C., Low, G.W., Te Yao, C., Li, Y., Xu, T., Rheindt, F.E. & Wu, S. 2019. Population divergence and gene flow in two East Asian shorebirds on the verge of speciation. *Sci. Rep.* **9**: 1–9.

Sangster, G., Hazevoet, C.J., van den Berg, A.B., Roselaar, C.S. & Sluys, R. 1999. Dutch avifaunal list: Species concepts, taxonomic instability, and taxonomic changes in 1977-1998. *Ardea* **87**: 139–165.

Schluter, D. & Conte, G.L. 2009. Genetics and ecological speciation. *Proc. Natl Acad. Sci. USA* **106**: 9955–9962.

Scodato, S.C. & Safran, R.J. 2014. Geographic variation in sexual selection and implications for speciation in the Barn Swallow. *Avian Res.* **5**: 1–13.

Seebohm, H. 1887. *The Geographical Distribution of the Charadriidae, or the Plovers, Sandpipers, Snipes, and Their Allies*. London: Henry Sotheran & Co.

Seneviratne, S.S., Toews, D.P.L., Brelsford, A. & Irwin, D.E. 2012. Concordance of genetic and phenotypic characters across a sapsucker hybrid zone. *J. Avian Biol.* **43**: 1–12.

Sharpe, A. 1896. The geography and resources of British Central Africa. *Geogr. J.* **7**: 366–387.

Snow, D.W. & Perrins, C.M. (eds) 1998. *The Birds of the Western Palearctic*, Vol. **1**: Non-passerines. Oxford, UK: Oxford University Press.

Song, Z., Lin, X., Que, P., Halimubieke, N., Huang, Q., Zhang, Z. & Liu, Y. 2020. The allocation between egg size and clutch size depends on local nest survival rate in a mean of bet-hedging in a shorebird. *Avian Res.* **11**: 1–10.

Swinhoe, R. 1870. On the plovers of the genus Ægialites found in China. *Proc. Zool. Soc. London* **1870**: 136–142.

Székely, T. 2019. Why study plovers? The significance of non-model organisms in avian ecology, behaviour and evolution. *J. Ornithol.* **160**: 923–933.

Székely, T., Kosztolányi, A. & Küpper, C. 2008. *Practical Guide for Investigating Breeding Ecology of Kentish Plover Charadrius alexandrinus*. v 3. Unpublished Report. Bath: University of Bath.

Tamura, K., Stecher, G. & Kumar, S. 2021. MEGA11: molecular evolutionary genetics analysis Ver. 11. *Mol. Biol. Evol.* **38**: 3022–3027.

Tang, Q., Burri, R., Liu, Y., Suh, A., Sundev, G., Heckel, G. & Schweizer, M. 2022. Seasonal migration patterns and the maintenance of evolutionary diversity in a cryptic bird radiation. *Mol. Ecol.* **31**: 632–645.

Taylor, R.S. & Friesen, V.L. 2017. The role of allochrony in speciatio. *Mol. Ecol.* **26**: 3330–3342.

Tobias, J.A., Seddon, N., Spottiswoode, C.N., Pilgrim, J.D., Fishpool, L.D.C. & Collar, N.J. 2010. Quantitative criteria for species delimitation. *Ibis* **152**: 724–746.

Tukey, J.W. 1949. Comparing individual means in the analysis of variance. *Biometrics* **5**: 99–114.

Wang, X., Maher, K.H., Zhang, N., Que, P., Zheng, C., Liu, S. & Liu, Y. 2019a. Demographic histories and genome-wide patterns of divergence in incipient species of shorebirds. *Front. Genet.* **10**: 919.

Wang, X., Que, P., Heckel, G., Hu, J., Zhang, X., Chfiang, C.Y., Zhang, N., Huang, Q., Liu, S., Martinez, J., Pagani-Núñez, E., Dingle, C., Leung, Y.Y., Székely, T., Zhang, Z. & Liu, Y. 2019b. Genetic, phenotypic and ecological differentiation suggests incipient speciation in two *Charadrius* plovers along the Chinese coast. *BMC Evol. Biol.* **19**: 1–18.

Warakagoda, D., Inskipp, C., Inskipp, T. & Grimmett, R. 2020. *Birds of Sri Lanka*. London: Bloomsbury Publishing.

Wei, C.T., Schweizer, M., Tomkovich, P.A., Yu, V., Romanov, M., Jonathan Martinez, J., Lin, X., Halimubieke, N., Que, P.J., Mu, T., Huang, Q., Zhang, Z.W., Székely, T. & Liu, Y. 2022. Genome-wide data reveals paraphyly in the sand plover complex (*Charadrius mongolus/leschenaultii*). *Ornithology* **139**: 2.

Weir, B.S. & Cockerham, C.C. 1984. Estimating F-statistics for the analysis of population structure. *Evolution* **38**: 1358–1370.

Weir, J.T. & Schluter, D. 2008. Calibrating the avian molecular clock. *Mol. Ecol.* **17**: 2321–2328.

Wenink, P.W., Baker, A.J. & Tilanus, M.G.J. 1994. Mitochondrial control-region sequences in two shorebird species, the turnstone and the dunlin, and their utility in population genetic studies. *Mol. Biol. Evol.* **11**: 22–31.

Wetlands International. 2020. *Asia Waterbird Census*. Available at: https://south-asia.wetlands.org/our-approach/healthy-wetland-nature/asian-waterbird-census/ (accessed 11 October 2019).

Whistler & Kinnear 1936. The Vernay scientific survey of the Easter Ghats (ornithological section), part XV. *J. Bombay Nat. Hist. Soc.* **39**: 246–263.

Wickramasinghe, N., Robin, V.V., Ramakrishnan, U., Reddy, S. & Seneviratne, S.S. 2017. Non-sister Sri Lankan white-eyes (genus *Zosterops*) are a result of independent colonizations. *PLoS One* **12**: e0181441.

Wijesundara, C.S., Warakagoda, D., Sirivardana, U., Chathuranga, D., Hettiarachchi, T., Perera, N. & Weerakoon, G. 2017. Diversity and conservation of waterbirds in the northern avifaunal region of Sri Lanka. *Ceylon J. Science* **46**: 143.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Morphometric data and microsatellite data.

Appendix S2. Other specimens.

Table S1. Genetic polymorphism of *Charadrius seebohmi* and its closely related taxa.

Table S2. Number of repeat motifs of 13 microsatellite loci in various studies of *Charadrius* sp. plovers.