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Signals of local adaptation across an environmental gradient among highly connected populations of the Dead Sea Sparrow *Passer moabiticus* in Israel

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Populations found at the edge of a species range often have decreased genetic diversity, which together with high gene flow may reduce the ability of a species to adapt to local environmental conditions. The Dead Sea Sparrow *Passer moabiticus* occupies a disjointed range, where the Israeli populations are considered peripheral and fragmented. The species is also thought to have undergone a recent range expansion. We aimed to describe the genetic and morphological variation of the Israeli populations and to determine the extent of gene flow among them. We expected that because of the small latitudinal gradient across Israel and the recent range expansion of the species that Dead Sea Sparrow populations would show no significant morphological adaptation to local environmental conditions, and that considerable gene flow would be taking place among populations. Our findings indicate the existence of gene flow, suggesting high connectivity among populations, but recovered no support for a recent range expansion, possibly due to insufficient time since expansion for mutations to have accumulated. However, despite recurrent gene flow among populations, latitudinal variation in wing length (male and female) and body mass (male) was indicative of local adaptation across Israel, in accordance with Bergmann's rule.

Keywords: gene flow, genetic diversity, peripheral populations, phenotypic variation, population structure, range expansion.

Populations found at the edge of a species range often exhibit decreased genetic diversity and high genetic differentiation (Mayr 1966, Eckert *et al.* 2008), although several exceptions have been documented (e.g. Vucetich & Waite 2003, Dai & Fu 2011, Assis *et al.* 2013). Genetic diversity is expected to decrease, the greater the distance from the centre of the species' range, which is most often attributed to reduced gene flow towards the range edge due to lower rates of dispersal, selection against unfavourable genotypes at the range periphery or strong genetic drift in small populations (García-Ramos & Kirkpatrick 1997, Vucetich & Waite 2003, Eckert *et al.* 2008, Dai & Fu 2011). In addition, as species tend to be more abundant towards the centre of a species distribution (Brown 1984), gene flow will be directed toward smaller, peripheral populations, thereby introducing genotypes which may not be beneficial to populations at the range boundary and thereby limit the capacity for local adaptation (García-Ramos & Kirkpatrick 1997, Lenormand 2002). When peripheral populations are growing, as in the case of range expansion, they are expected to exhibit genetic patterns that include relatively stable allele frequencies, high frequencies of rare alleles and low frequency of mutations, and an excess of homozygosity relative to the number of observed alleles (Tajima 1989, Excoffier *et al.* 2009). Typically, a gradual loss of genetic diversity will occur towards the range expansion front (Excoffier *et al.* 2009). Hence, decreased genetic variation together with high gene flow among populations may reduce the ability of populations to adapt to local environmental conditions (Hartl & Clark 1997).

However, divergent selection of traits related to local adaptation can contribute to population differentiation. One such adaptation is described by

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Bergmann's rule, according to which the body size of homoeothermic animals is larger in colder climates than in warmer ones, with the underlying mechanism pertaining to the need for optimal temperature control (Bergmann 1848, Salewski & Watt 2017). Evidence of morphometric differences among populations as a result of local adaptation has been described in many avian species, including neighbouring populations (Blondel *et al.* 1999, Badyaev *et al.* 2008, Ben Cohen & Dor 2018) or geographically distant ones (Saether *et al.* 2007). These differences can be accompanied either by genetic differentiation in neutral markers (Le Corre & Kremer 2012), suggesting genetic drift as the main mechanism for this divergence, or by low neutral genetic variation (Saether *et al.* 2007, Badyaev *et al.* 2008, Antoniazza *et al.* 2010, Le Corre & Kremer 2012), which suggest local adaptation as the primary evolutionary mechanism (Merilä & Crnokrak 2001, Leinonen *et al.* 2008). Hence, mechanisms such as phenotypic plasticity may contribute to population divergence without modifying the genetic diversity of the population (Grenier *et al.* 2016).

The Dead Sea Sparrow *Passer moabiticus* is one of the smallest species in the genus. It was first described south of the Dead Sea and it currently occupies a highly disjointed range extending from southwest Afghanistan in the east, through Iran, Pakistan, Iraq, Syria, Jordan, Israel, Turkey and Cyprus in the west (Clement *et al.* 1993, IUCN 2017; Fig. 1). The species preferred habitat is that of semi-desert regions with high ambient temperatures adjacent to water resources (Summers-Smith

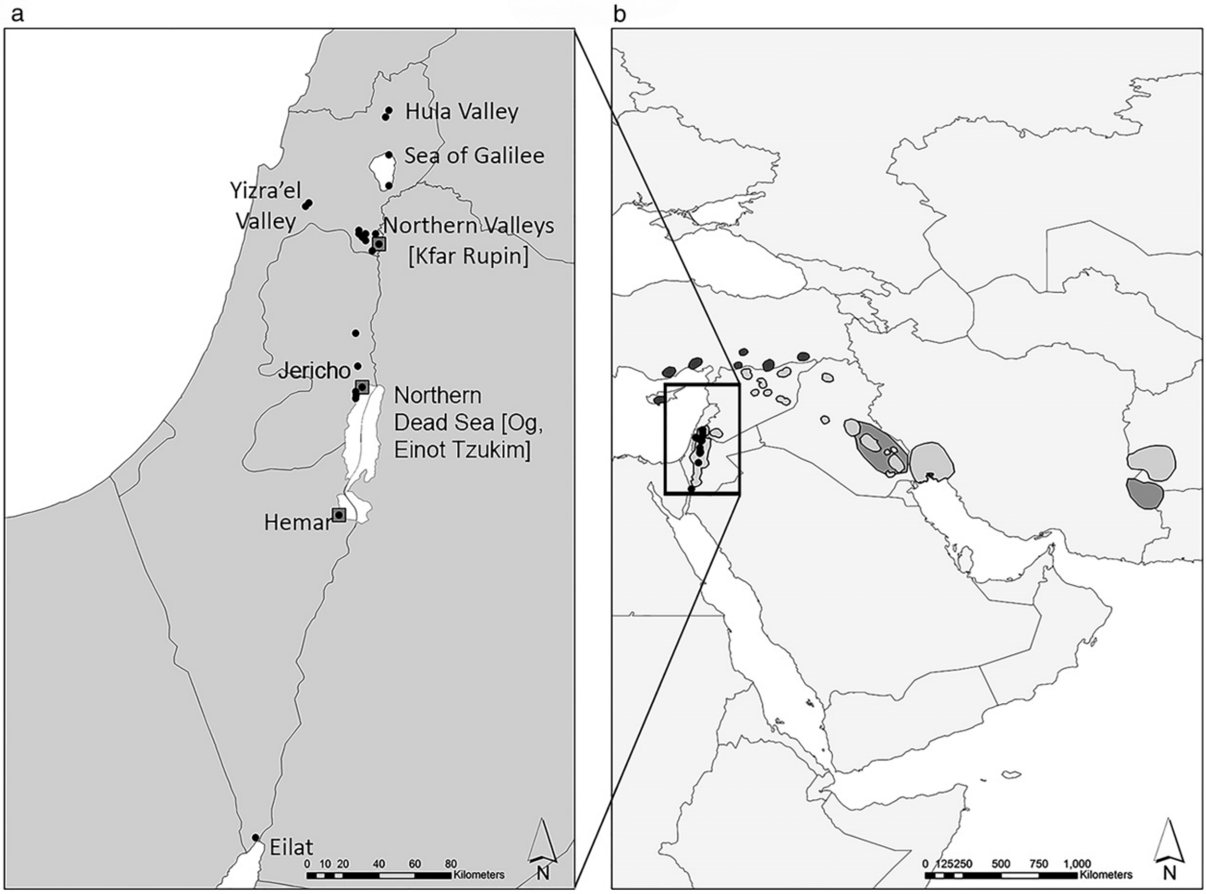

Figure 1. (a) Sampling locations of Dead Sea Sparrow populations in Israel. Grey squares represent locations where genetic samples were collected. (b) Breeding and non-breeding range of populations of the Dead Sea Sparrow in its complete range. Black circles represent locations from which morphological samples were available for the study. Range specification as follows: dark grey – Extant (breeding); medium grey – Extant (non–breeding); light grey – Extant (resident). Adapted from BirdLife International and Handbook of the Birds of the World (2016) *Passer moabiticus*. The IUCN Red List of Threatened Species. Version 2017–1.

1988), although the species' recent expansion also includes well-vegetated cultivated areas (Snow & Perrins 1998). Expansion of its distribution range with resulting increase in abundance has been documented from both Israel and Jordan, as well as from northern Iraq to Syria, Turkey and, more recently, to Cyprus. This expansion has in part been attributed to changes in resource availability resulting from the development of new human settlements (Yom-Tov *et al.* 1976, Summers-Smith 1988). There is uncertainty whether this recent range expansion is simply a result of an increase in observer effort or a true increase in distribution range.

In Israel, where the nominate subspecies *P. m. moabiticus* occurs, the species is known to have originated in the southern parts of the Dead Sea but has since expanded its breeding range deep into the Rift Valley from Eilat in the south to the Hula Valley in the north, and has been reported from the western valleys of Esdraelon (Yizra'el) to the Zvulun Valley near the Mediterranean coast (Yom-Tov *et al.* 1976). Previous studies have suggested that this range expansion may have been the result of anthropogenic changes that led to both the destruction of the original habitat and the creation of new advantageous ones for the species, with irrigated agriculture and fish ponds being constructed for new settlements (Yom-Tov *et al.* 1976, Yom-Tov & Ar 1980). Being a social species, the Dead Sea Sparrow nests in loose colonies of 10–100 nests established by males on tree branches (Mendelssohn 1955). Females then join the males at the breeding grounds and pairs demonstrate high nest-site fidelity (75.1%, R. Haran unpubl. data). Outside the breeding season, the Dead Sea Sparrow lives in flocks of up to hundreds of individuals, sometimes in mixed flocks together with Spanish Sparrows *Passer hispaniolensis* and House Sparrows *Passer domesticus* (Shirihai 1996, Yosef *et al.* 2004). Seasonal migration from the breeding grounds has been described during the non-breeding season and is considered mostly local in nature, but little is known about the migratory behaviour of this species (Summers-Smith 1988, Shirihai 1996). Although reports of the species are disjointed, leading to what seemingly is a fragmented distribution range of *P. m. moabiticus*, the Israeli populations most likely represent the species' southwestern border, i.e. representing a series of peripheral populations (Fig. 1).

To elucidate the status of the Israeli population of the Dead Sea Sparrow, in light of the evidence of its recent range expansion, we aimed to describe the genetic and morphological structure of the Israeli populations and to determine the level of connectivity among them. We sought to investigate local movement behaviour of this species. We hypothesize that in light of the small latitudinal gradient and the recent nature of the range expansion, the Israeli populations of the Dead Sea Sparrow would show no significant morphological adaptations to the local environment. In addition, in light of the known seasonal migratory behaviour of this species, we expect gene flow to occur among populations. This study contributes to the unveiling of the changes brought about by the recent range expansion of the species, both by increasing our knowledge regarding population connectivity and gene flow, and by delineating the morphological variation stemming from isolation-by-distance among populations as well as variable environmental conditions.

METHODS

Sample collection

Birds were captured following standard mist-netting procedures for banding, measurements and blood sampling. Blood was taken by puncturing the brachial vein and drawing up to 50 μL of blood from each individual, and was preserved in a blood lysis buffer (modified from White & Densmore 1992). In total, 61 *P. m. moabiticus* individuals were sampled during the breeding season (March–August) in 2014–2015, representing three localities along the Rift Valley (~150 km; Fig. 1a): 14 individuals from Kfar Rupin (KR; latitude: 32.45°N, longitude: 35.57°E), 28 from Og (OG; latitude: 31.75°N, longitude: 35.48°E) and 19 from Hemar Reservoir (HE; latitude: 31.13°N, longitude: 35.37°E). An additional 47 individuals were sampled outside of the breeding season at Og ($n = 43$) and Einot Tzukim (ET; $n = 4$; latitude: 31.7°N, longitude: 35.45°E; Table S1). Maximum wing length was recorded with a ruler (1 mm) by flattening and straightening the wing (Eck *et al.* 2011) and body mass was measured with a 0.1-g scale.

Additional morphometric data were available from data deposited at The Israeli Bird Ringing Centre (IBRC) during 1981–2015 ($n = 875$), which included data pertaining to sex, age, wing length, body mass and fat percentage of the ringed bird. Data were also obtained by measuring *P. moabiticus* specimens at the British Museum Bird Collection at Tring ($n = 51$) and at The American Museum of Natural History in New York ($n = 9$). The total number of samples available for morphological comparisons was therefore 1039, for which coordinates were only ascertained for 1020 individuals, representing 24 localities. Of these, 924 specimens were available from Israel, for which data on sex, age and wing or body mass measurements were available for 379 males (10 juveniles, 323 adults) and 297 females (18 juveniles, 243 adults; Table S1, Appendix S1, Fig. 1a).

DNA extraction and amplification

A subsample of birds from three breeding populations, representing most of the breeding range in Israel, was used for the genetic study, comprising only breeding individuals: 18 from Hemar, 26 from Og and 13 from Kfar Rupin (Fig. 1). DNA was extracted using a Qiagen DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA, USA). We polymerase chain reaction (PCR)-amplified a 691-base pair fragment of the mitochondrial gene cytochrome oxidase unit I (COI) with the primers avianCOIF1-f (5′-CTGTAAAAAGGACTACAGC CTAACGC-3′) and avianCOIR1-r (5′-GGTTCG ATTCCTTCCTTTCTT-3′). The 25-μL volume solution used for PCR comprised 3 μL of DNA extract, 2.5 μL 10× PCR buffer, 2.5 μL 0.2 mM of dNTPs, 2.5 μL of 20 mM $MgCl_2$, 0.5 μL of forward and reverse primers (10 mM) and 0.5 U/reaction of Hy-Taq DNA Polymerase (Hylabs, Rehovot, Israel). The PCR programme comprised an initial denaturation step at 94 °C for 2 min followed by 35 cycles of 30 s at 94 °C, 1 min at 62 °C and 1 min elongation at 72 °C, with a final extension time of 10 min at 72 °C. The successfully amplified samples were genotyped or sequenced at the ZABAM Instrumentation and Service Center of Tel Aviv University on an ABI 3500xl Genetic analyser (Applied Biosystems, Foster City, CA, USA). All sequence data are deposited in GenBank (Accession numbers MF767303–MF767304).

In addition, 10 microsatellite markers known to be highly variable in the House Sparrow were PCR-amplified using primers in two sets of multiplex reactions (multiplex 1: CAM01, CAM17, Pdo05; multiplex 2: CAM10, CAM05, Pdo01, CAM15) and singleplex markers (Pdo08, CAM20 and CAM02; Neumann & Wetton 1996, Griffith *et al.* 1999, 2007, Dawson *et al.* 2013). PCR was carried out in 25-μL volumes which comprised 3 μL of DNA extract, 100× PCR buffer, 0.2 mM of dNTPs, $MgCl_2$, forward and reverse primers and 0.5 U/reaction of Hy-Taq DNA Polymerase (Hylabs). $MgCl_2$ and primer volumes varied with the markers and are detailed in Table S2. The PCR programme was similar to that used for amplification of the mitochondrial marker, with the exception of marker Pdo08 (PCR Touch Down programme consisted of an initial denaturation at 94 °C for 2 min followed by a total of 40 cycles of 30 s at 94 °C, 30 s annealing (Table S2) for 1 cycle each at 66–55 °C, and 30 cycles at 55 °C, and 1 min elongation at 72 °C, with a final extension time of 10 min at 72 °C).

Population genetic analyses

Microsatellite genotypes (Appendix S2) were examined and determined using the software GeneMarker (Holland & Parson 2011). Deviations from Hardy–Weinberg equilibrium were evaluated, as was evidence of linkage disequilibrium using Arlequin 3.5.1.3 (Excoffier & Lischer 2010). The presence of null alleles was examined with Cervus 3.0 (Kalinowski *et al.* 2007). Population genetic analysis was performed with GenAlEx 6.5b2 (Peakall & Smouse 2001). This comprised an estimation of allele frequencies for each locus relevant to each population and the calculation of expected (H_e) vs. observed (H_o) heterozygosity values. An analysis of variances (AMOVA) test was performed to examine the variable distribution within and between populations and to determine F_{ST}. Assignment tests were employed to determine the likelihood of individual genotypes being assigned to the population from which they had been sampled. Furthermore, allelic richness was calculated with 9999 bootstraps using the ‘diveRsity’ R package (Keenan *et al.* 2013).

Clustering analysis, using principal coordinates analysis (PCoA), was calculated on the basis of a pairwise, individual-by-individual ($N \times N$) genetic distance matrix via GenAlEx (Peakall & Smouse 2001). Population structure was detected with STRUCTURE 2.3.4 (Pritchard *et al.* 2000) using a Bayesian clustering method with 1 million Markov chain Monte Carlo (MCMC) repetitions and a burnin period of 0.1 million iterations. Microsatellite allele frequencies were considered to be correlated among populations. STRUCTURE was run under the admixture model, with correlated allele frequencies from $K = 1$ to $K = 7$ with three iterations for each K-value to explore the probability of assignment of individuals to different populations. We examined the means of the posterior probability distribution ($Ln\ P\ (D)$) in order to find the largest value for different numbers of genetic groups (K) over three runs per K-value by applying STRUCTURE HARVESTER (Earl 2012).

Observed demographic range expansion, as well as the fragmented nature of the species range, and the recent observed reduction in breeding success necessitated a search for evidence of a population bottleneck. To do so, we utilized the program BOTTLENECK 1.2.0.2 (Cornuet & Luikart 1996, Piry *et al.* 1999) using data from the microsatellite markers. Both the two-phase model of mutation (TPM; Di Rienzo *et al.* 1994, Primmer *et al.* 1998) and the SMM model were employed, using 10 000 replicates, as no prior information regarding the mutation model of the loci used in this study was available. The TPM model was run once with 95% single-step mutations and once with 80%, with a variance among multiple steps of 12. To identify gene diversity excess, a one-tailed Wilcoxon signed-rank test was applied (Luikart 1997) and a qualitative descriptor of the allele frequency distribution ('mode-shift' indicator) was employed to discriminate bottlenecked populations from stable populations (Luikart & Cornuet 1998). Significance levels were adjusted using the Sidak correction: the corrected P-value was calculated as the significance level (0.05) divided by the number of loci (9) ($P = 0.005$). In addition, we tested for departures from constant population size using the COI marker employing Fu's Fs statistic (Fu 1997) and R_2 statistics (Ramos-Onsins & Rozas 2002), as well as Tajima's D test (Tajima 1989), and tested their significance using 1000 coalescent simulations. We employed all of these tests via DnaSP v. 5.0 (Librado & Rozas 2009).

To estimate contemporary gene flow by comparing migration rates among the populations we utilized the program BAYESASS v. 3.0 (Wilson & Rannala 2003) using data from the microsatellite markers. BAYESASS uses a Bayesian approach to infer migration rates ('m') by employing an MCMC sampling procedure. After initial trials showed appropriate acceptance rates (20–60%, Rannala 2007), we used 10^7 iterations, a burnin of 10^6 steps and a sampling interval of 1000 steps between samples being drawn from the MCMC distribution. Additionally, we employed multiple runs ($n = 10$) with changing seed numbers to ascertain consistency of the results. The results we present are averaged over the 10 runs.

Morphometric analyses

Because body size measurements vary significantly between the breeding and non-breeding season, and due to local seasonal movement during the winter, intraspecific comparisons were also limited to samples collected during the breeding season alone.

Data analysis was carried out using R v. 3.3.2 (R Core Team 2016). Multifactorial analysis was applied to examine the effect of fixed environmental predictors on wing length and body mass, including latitude, elevation (https://www.gps-coordinates.net/), the age and sex of the bird, and interactions between sex and latitude, as the migration behaviour of this species may be related to the sex of the individual. Initially, the analysis included mean temperature of the warmest quarter and maximum temperature of the warmest month as explanatory variables (CHELSA Climate, ver. 1.1; Karger *et al.* 2017). However, these predictors were highly correlated with latitude (Pearson's $r = -0.879$ and $r = -0.89$, respectively, $P < 0.001$) and with each other (Pearson's $r = 0.999$, $P < 0.001$). As latitude potentially entails a collection of environmental changes along the gradient (including also precipitation, vegetation index and more; Mittelbach *et al.* 2007), and as these are also highly correlated, we included latitude as the explanatory factor rather than temperature (but see Supporting Information for separate analysis for both variables; Fig. S1). Because none of the response variables had a normal distribution, this was achieved by using a generalized linear mixed-effects model (GLMM) with Gaussian error and log link function ('glmmPQL' function in the package 'MASS', Venables & Ripley 2002) with a random factor of 'year', which corresponded to the effect of the individual who had recorded the measurements and because ringers have changed over the course of the period during which the dataset was generated (36 years). Continuous predicting factors were standardized to increase comparability (Schielzeth 2010) using the stdize function in the r-package 'MuMIn' (Barton & Barton 2018). As neither rescaled nor log-transformed response variables had a normal distribution, original values were used in the model to enable easy interpretation of the results. All models were run with the complete set of factors in a step-wise manner, omitting the factor with the high P-value until all coefficients were significant ($P < 0.05$). In addition, models were also run separately for males and females to examine the difference between the two sexes. Because of difficulties in determining the exact age of juveniles in the field, this analysis was only applied to birds aged as adults. Additionally, a Wilcoxon rank-sum test was employed to determine statistical differences between males and females.

RESULTS

Genetic diversity

All 10 microsatellite markers originally used to genotype the House Sparrow populations were successfully PCR-amplified in the Dead Sea Sparrow. All loci were polymorphic, but the levels of polymorphism varied among markers, with as few as two alleles per locus for some markers (CAM02, CAM17 and CAM20) and as many as nine in others (Pdo08; Table S2). The average number of alleles per locus was 5.4 and no linkage disequilibrium was found between any of the markers when adjusting for multiple comparisons using the Bonferroni correction. No statistically significant deviations from Hardy–Weinberg were recovered for loci across populations, with the exception of the locus Pdo08, for which null alleles were detected. However, when analyses were performed with this locus omitted, similar results were recovered. Nonetheless, the marker was excluded from the final analyses. One locus (CAM20) was found to be monomorphic in the Hemar population.

PCR-amplification of a region of the COI gene in 39 individuals from the three populations yielded an identical sequence for 38 individuals (H1; Accession number MF767303), representing low genetic diversity. Only one sequence from the Hemar population was different at one nucleotide position from the other sequences (H2; Accession number MF767304).

Genetic variability was estimated according to the observed and expected heterozygosity of microsatellite markers among the three populations and was found to be moderate to high (Table 1), suggesting a genetically diverse population in which out-breeding and dispersal probably take place. This was also supported by low fixation index values, indicating that random mating is likely to occur (0.001–0.136). Allelic richness was similar in all three populations (range 5.3–5.7). Assignment tests yielded low self-assignment values, suggesting a high rate of gene flow among populations (Table 1). Moreover, F_{ST} values were low between all paired comparisons ($0.000 < F_{ST} < 0.006$) and the results were not significant (Table S3).

Population structure, demographic history and gene flow

The optimal number of clusters recovered was one, i.e. a single population ($K = 1$: mean Ln$P(D) = -1020.4$; Fig. S2). The recovery of a single population was also supported by the clustering analysis using PCoA (Fig. 2).

We did not recover evidence for a signature of a recent range expansion or a bottleneck, when analysing the populations separately or as a single population. The Wilcoxon signed-rank tests found no evidence of a significant population size change in either of the analyses, indicating no significant excess of heterozygosity or a deficit of heterozygotes in either of the models used (Table S4). In addition, mitochondrial DNA frequency-based tests did not show any significant signal of departures from stable population size in either the total population (Fu's $Fs = 0.000$, $P = 0.499$; $R_2 = 0.131$, $P = 0.817$; Tajima's $D = -1.089$,

Table 1. Estimates of genetic diversity of the Israeli populations of the Dead Sea Sparrow as determined using nine microsatellite markers.

Population	N	N_a	A_R	H_e	H_o	F	Assign (%)
Kfar Rupin	13	4.5	5.7	0.582	0.565	0.001	7.69
Og	26	4.6	5.7	0.555	0.490	0.090	19.23
Hemar	18	4.2	5.3	0.527	0.439	0.136	44.44
Total	57	4.4	6.3	0.555	0.498	0.074	24.56

N, sample size; N_a, average number of alleles over all loci; A_R, allelic richness over all loci; H_e, unbiased expected heterozygosity; H_o, observed heterozygosity; F, fixation index; Assign, assignment test score.

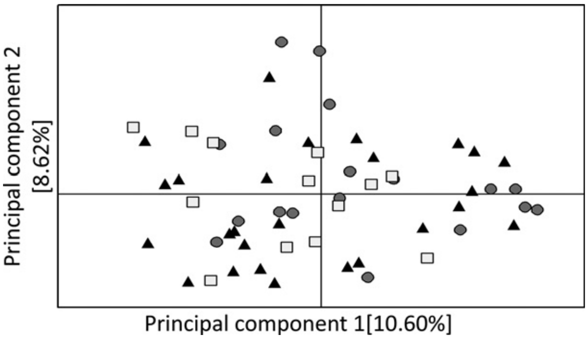

Figure 2. Principal coordinates analysis of Dead Sea Sparrow individuals from different localities as illustrated for nine microsatellite markers. Geographical regions are marked by colours and shapes as follows: light grey square – Kfar Rupin; black triangle – Nahal Og; dark grey circle – Hemar reservoir. Axes represent the percentage of total variation of the markers explained for each principal coordinate.

$P = 0.128$) or for the Hemar population, the only population with more than one haplotype (Fu's $Fs = 0.000$, $P = 0.775$; $R_2 = 0.229$, $P = 0.551$; Tajima's D = -1.165, $P = 0.077$).

Gene flow estimates generated by BAYESASS revealed asymmetrical estimates of migration ('*m*'), as north-to-south migration (KR → OG: $m = 0.16 \pm 0.11$, KR → HE: $m = 0.15 \pm 0.11$, OG → HE: $m = 0.17 \pm 0.12$) was more frequent than south-to-north migration (HE → KR: $m = 0.04 \pm 0.04$, HE → OG: $m = 0.15 \pm 0.11$, OG → KR: $m = 0.04 \pm 0.04$). However, confidence intervals (CI) for all of the pairwise comparisons overlapped with zero, suggesting that these results should be interpreted with caution. In addition, whereas BAYESASS has previously been shown to provide accurate estimates of migration rates when $F_{ST} \geq 0.05$ (Faubet *et al.* 2007), the current estimates of F_{ST} of the studied populations did not meet this assumption ($0.000 < F_{ST} < 0.006$); therefore migration estimates could be underestimated.

Morphological analyses

Data for 333 males (323 adults, 10 juveniles) and 261 females (243 adults, 18 juveniles) were available for the morphological study of the Israeli population. Whereas male adult birds had longer wings than females (mean: 62.87 ± 1.47 and 60.89 ± 1.35 mm, respectively, $P = 0.035$), during the breeding season, female adult birds had greater body mass (14.30 ± 1.22 g) than males (13.96 ± 0.97 g; Fig. 3). Both wing length and body mass differed significantly between the two sexes ($W = 64\ 149$ and $W = 24\ 776$, $P < 0.001$ and 0.002, respectively, Wilcoxon rank sum test). In addition, sex, age and latitude had a significant effect on wing length, with northern adult males having the longest wings (GLMM; Table 2). Conversely, body mass was only significantly affected by sex and age, with female adults weighing the most (GLMM; Table 2).

When analysing the sexes separately, the increase in wing length as explained by latitude of adult males (estimate: 0.0052 ± 0.0017, $P = 0.003$) was more prominent than that in adult females (estimate: 0.0030 ± 0.0015, $P = 0.044$), but was also affected by elevation (estimate: 0.0044 ± 0.0017, $P = 0.012$). The body mass of adult males was also dependent on latitude (estimate: 0.0267 ± 0.0052, $P < 0.001$), but none of the other explanatory variables was found to be significant.

DISCUSSION

Local adaptation despite low genetic differentiation

Examination of the genetic structure of the local Dead Sea Sparrow population in Israel revealed no significant degree of genetic differentiation among populations (Table S3, Fig. 2). STRUCTURE analyses revealed that each sample had a similar probability of being assigned to a theoretical cluster, suggesting a panmictic population. Additionally, low assignment tests scores and fixation index values, as well as moderate to high observed heterozygosity within populations (Table 1) suggests that gene flow is ongoing. However, despite low genetic differentiation among geographically distinct populations, evidence of local adaptation of individual populations sampled across Israel was found in the wing length of adults of both sexes and body mass of adult males (Table 2). Northern birds, both males and females, had longer wings, in agreement with Bergmann's rule (Bergmann 1848, Salewski & Watt 2017). This result is in accordance with wing length being previously shown to be a proxy for body size in birds (Nolan & Ketterson 1983, Wiklund 1996, Gosler *et al.* 1998). Although wing length has also been associated with mean ambient temperature (Allen's rule, Welty 1962), and was found to decrease with

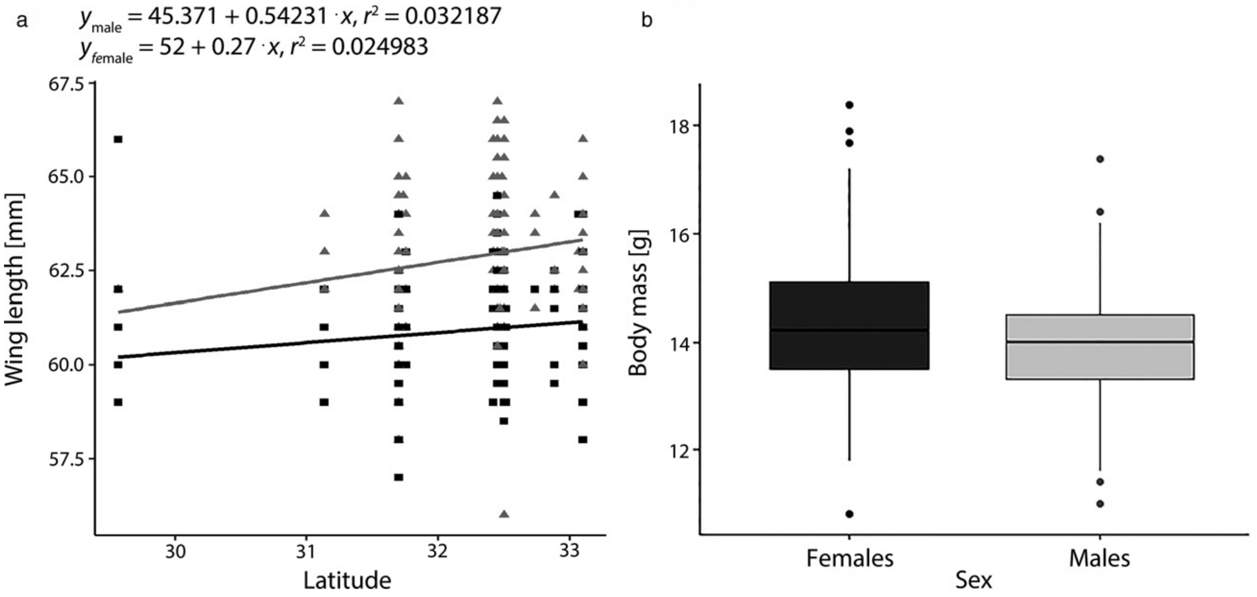

Figure 3. (a) The effect of sex on wing length and (b) body mass in adult female and male Dead Sea Sparrows as depicted by a single factorial analysis. Values of adult males are shown in grey triangles and those of adult females are shown in black squares. The boxes are drawn with widths proportional to the square-roots of the number of observations in each group.

Table 2. Results of the generalized linear mixed-effects model (GLMM) with Gaussian error and log link function testing the effects of age, sex and latitude on wing length ($n = 589$) and body mass ($n = 523$) in Dead Sea Sparrows during the breeding season between 1981 and 2015.

	Wing length (mm)				Body mass (g)			
	Estimate	se	*t*-value	*P*	Estimate	se	*t*-value	*P*
Intercept	4.109	0.002	1953.29	< 0.001	2.653	0.008	349.93	< 0.001
Age (Juveniles)	−0.01	0.005	−2.01	0.046	−0.043	0.018	−2.42	0.016
Sex (Males)	0.031	0.002	16.1	< 0.001	−0.023	0.007	−3.42	0.001
Latitude[a]	0.005	0.001	4.05	< 0.001	–	–	–	–

'Year' was employed as a random factor to represent the effect of the individual who recorded the measurements. All models were run with the complete set of factors in a step-wise manner, omitting the factor with the highest *P*-value until all coefficients were significant ($P < 0.05$). [a]Standardized.

decreasing temperatures in some birds (Yom-Tov *et al.* 2006, McCollin *et al.* 2015), this trend was not reflected in our results. In contrast to wing length, variance in body mass was only significantly explained by latitude in adult males, presumably because of physiological changes, which include an increase in female body mass during the breeding season. Alternatively, Blanckenhorn *et al.* (2006) have shown in an extensive review that male latitudinal body size clines were steeper than those of females for a large number of species, representing what they term 'a latitudinal version of Rensch's rule'.

To confirm that our present results did not stem from differences in sample size between the genetic and the morphological datasets, we conducted a separate morphometric analysis for the samples used in the genetic analysis and observed similar trends. This result suggests that local adaptation has taken place under the distinctive environmental conditions that exist over a relatively short geographical distance in Israel, and which are also demonstrated in the ambient average temperature during the breeding season: mean temperatures in the warmest quarter range between 27.7 °C at the northernmost locality to 32.1 °C at the southernmost locality. Although evidence of high gene flow is traditionally thought to limit adaptive variation among local populations due to ‘gene swamping’ (Haldane 1930, Lenormand 2002), the interplay between stabilizing genetic pressure and divergent selection remains unclear (Seehausen 2004, Savolainen *et al.* 2013, Tigano & Friesen 2016). The occurrence of local adaptation despite low genetic differentiation has been described previously in plants (Sambatti & Rice 2006, Gonzalo-Turpin & Hazard 2009), fish (Saint-Laurent *et al.* 2003, Hemmer-Hansen *et al.* 2007, Nielsen *et al.* 2009) and birds (e.g. Dor *et al.* 2011, Poelstra *et al.* 2014). Several mechanisms have been suggested to support the presence of phenotypic variation among closely related populations, including non-random gene flow (Edelaar & Bolnick 2012, Richter-Boix *et al.* 2013), specific loci that experience reduced gene flow due to natural selection (Matsubayashi *et al.* 2010, Sousa *et al.* 2013), phenotypic plasticity (Crispo 2008), sexual selection (Wilkins *et al.* 2016) and migration–selection–drift balance (Bridle & Vines 2007, Yeaman & Whitlock 2011). In general, the extent of evolutionary change is dictated by directional selection, gene flow, the ecological gradient and the heritability of the trait (García-Ramos & Kirkpatrick 1997).

In the Dead Sea Sparrow, strong breeding site-fidelity suggests that despite seasonal movement, these individuals spend the better part of the year in the same area. This enables phenotypic divergence related to the effect of temperature to be selected, as wing length (and body mass in males), and by proxy body size, increases with the decrease in average temperature. Alternatively, preliminary data collected from individuals captured during the breeding season and recaptured during wintering (R. Haran unpubl. data) revealed seasonal movement patterns from north to south during wintering, as average temperatures decrease, suggesting a possible role of wing length in local migration distances in allowing birds with longer wings to travel longer distances (Förschler & Bairlein 2011). However, a deeper understanding of the mechanism underpinning geographical variation in wing length requires additional exploration of the genetic and genomic architecture of the selected traits.

Strong north to south directional migration was detected between the populations ($0.15 < m < 0.17$, $0.11 < \mathrm{sd} < 0.12$) and was consistent with the expected seasonal migration pattern (Summers-Smith 1988, Shirihai 1996). This result may reflect local wintering southward movement of the species that may be caused by the decreasing ambient temperature during the cold season, after which most individuals probably return to their original breeding grounds (R. Haran unpubl. data). Such migration behaviour may result in the gene flow pattern revealed here, should a fraction of the migrating individuals stay on their wintering grounds. However, northward migration was also detected, although to a lesser extent, suggesting that gene flow may occur in both directions.

Despite having found no evidence of a recent range expansion, this result may reflect seasonal migration patterns rather than the lack of an expansion event. High migration rates between adjacent populations, such as those found in this study, may result in populations with high genetic diversity despite a clear demographic expansion pattern (Excoffier *et al.* 2009). An alternative explanation may be the relatively short period of time since the documented range expansion (Yom-Tov *et al.* 1976, Summers-Smith 1988), which may impede a stronger genetic signal of population growth, as the number of variable sites between two DNA sequences is proportional to the time since the expansion began (Rogers & Harpending 1992). Increasing the genetic sample size may reveal additional haplotypes in these populations.

Implications for conservation

The conservation status of the Dead Sea Sparrow is difficult to determine, partly because of the difficulty inherent in studying the species across much of its distribution range. The Israeli population examined here is considered a peripheral population, located at the southwestern border of the species’ range (Fig. 1b). As such, it may become even smaller and more fragmented (Thomas & Kunin 1999), and gene flow from the centre of the species’ range may decrease, eventually leading to reduced fitness (Bridle & Vines 2007). Although gene flow can prevent peripheral populations from reaching the optimal trait phenotype through the introduction of poorly adapted immigrants (García-Ramos & Kirkpatrick 1997), high genetic variation can facilitate the emergence of adaptive alleles in a rapidly changing environment (Bridle & Vines 2007). However, if the rate of environmental change outpaces the extent of available genetic variation, including that which is introduced by migration, then the mean fitness and total density of the population are expected to decline drastically (Lenormand 2002, Bridle & Vines 2007). Therefore, although no evidence of a bottleneck was found in the present study, the fragmented nature of the range of *P. moabiticus* may require careful monitoring of the species' demographic and genetic variation, particularly in light of the morphological divergence found in the Israeli population. Moreover, additional research of the connectivity among populations across a larger part of the species' range may help to shed light on the current status of the species from a global perspective, which is presently that of 'Least Concern' but with signs of a decrease in population size (IUCN 2017).

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REFERENCES

Antoniazza, S., Burri, R., Fumagalli, L., Goudet, J. & Roulin, A. 2010. Local adaptation maintains clinal variation in melanin-based coloration of European barn owls (*Tyto alba*). *Evolution* **64**: 1944–1954.

Assis, J., Coelho, N.C., Alberto, F., Valero, M., Raimondi, P., Reed, D. & Serrão, E.A. 2013. High and distinct range-edge genetic diversity despite local bottlenecks. *PLoS One* **8**: e68646.

Badyaev, A.V., Young, R.L., Oh, K.P. & Addison, C. 2008. Evolution on a local scale: developmental, functional, and genetic bases of divergence in bill form and associated changes in song structure between adjacent habitats. *Evolution* **62**: 1951–1964.

Barton, K. & Barton, M.K. 2018. *Package 'MuMIn'*.

Ben Cohen, S. & Dor, R. 2018. Phenotypic divergence despite low genetic differentiation in House Sparrow populations. *Sci. Rep.* **8**: 394.

Bergmann, C. 1848. *Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse*. Göttinger Stud: 595–708.

Blanckenhorn, W.U., Stillwell, R.C., Young, K.A., Fox, C.W. & Ashton, K.G. 2006. When Rensch meets Bergmann: does sexual size dimorphism change systematically with latitude? *Evolution* **60**: 2004–2011.

Blondel, J., Dias, P.C., Perret, P., Maistre, M. & Lambrechts, M.M. 1999. Selection-based biodiversity at a small spatial scale in a low-dispersing insular bird. *Science* **285**: 1399–1402.

Bridle, J.R. & Vines, T.H. 2007. Limits to evolution at range margins: when and why does adaptation fail? *Trends Ecol. Evol.* **22**: 140–147.

Brown, J.H. 1984. On the relationship between abundance and distribution of species. *Am. Nat.* **124**: 255–279.

Clement, P., Harris, A. & Davis, J. 1993. *Finches and Sparrows: An Identification Guide*. Princeton, NJ: Princeton University Press.

Cornuet, J.M. & Luikart, G. 1996. Description and power analysis of two tests for detecting recent population bottlenecks from allele frequency data. *Genetics* **144**: 2001–2014.

Crispo, E. 2008. Modifying effects of phenotypic plasticity on interactions among natural selection, adaptation and gene flow. *J. Evol. Biol.* **21**: 1460–1469.

Dai, Q. & Fu, J. 2011. When central populations exhibit more genetic diversity than peripheral populations: a simulation study. *Chin. Sci. Bull.* **56**: 2531–2540.

Dawson, D.A., Ball, A.D., Spurgin, L.G., Martín-Gálvez, D., Stewart, I.R., Horsburgh, G.J., Potter, J., Molina-Morales, M., Bicknell, A.W., Preston, S.A. & Ekblom, R. 2013. High-utility conserved avian microsatellite markers enable parentage and population studies across a wide range of species. *BMC Genom.* **14**: 176.

Di Rienzo, A., Peterson, A.C., Garza, J.C., Valdes, A.M., Slatkin, M. & Freimer, N.B. 1994. Mutational processes of simple-sequence repeat loci in human populations. *Proc. Natl Acad. Sci. USA* **91**: 3166–3170.

Dor, R., Safran, R.J., Vortman, Y., Lotem, A., McGowan, A., Evans, M.R. & Lovette, I.J. 2011. Population genetics and morphological comparisons of migratory European (*Hirundo rustica rustica*) and sedentary East-Mediterranean (*Hirundo rustica transitiva*) barn swallows. *J. Hered.* **103**: 55–63.

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

Eck, S., Töpfer, T., Fiebig, J., Heynen, I., Fiedler, W., Nicolai, B., van den Elzen, R., Winkler, R. & Woog, F. 2011. *Measuring Birds*. Wilhelmshaven: Vögelvermessen Deutsche Ornithologen.

Eckert, C.G., Samis, K.E. & Lougheed, S.C. 2008. Genetic variation across species' geographical ranges: the central–marginal hypothesis and beyond. *Mol. Ecol.* **17**: 1170–1188.

Edelaar, P. & Bolnick, D.I. 2012. Non-random gene flow: an underappreciated force in evolution and ecology. *Trends Ecol. Evol.* **27**: 659–665.

Excoffier, L. & Lischer, H.E. 2010. Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. *Mol. Ecol. Resour.* **10**: 564–567.

Excoffier, L., Foll, M. & Petit, R.J. 2009. Genetic consequences of range expansions. *Annu. Rev. Ecol. Evol. Syst.* **40**: 481–501.

Faubet, P., Waples, R.S. & Gaggiotti, O.E. 2007. Evaluating the performance of a multilocus Bayesian method for the estimation of migration rates. *Mol. Ecol.* **16**: 1149–1166.

Förschler, M.I. & Bairlein, F. 2011. Morphological shifts of the external flight apparatus across the range of a passerine (Northern Wheatear) with diverging migratory behaviour. *PLoS One* **6**: e18732.

Fu, Y.X. 1997. Statistical tests of neutrality of mutations against population growth, hitchhiking and background selection. *Genetics* **147**: 915–925.

García-Ramos, G. & Kirkpatrick, M. 1997. Genetic models of adaptation and gene flow in peripheral populations. *Evolution* **51**: 21–28.

Gonzalo-Turpin, H. & Hazard, L. 2009. Local adaptation occurs along altitudinal gradient despite the existence of gene flow in the alpine plant species *Festuca eskia*. *J. Ecol.* **97**: 742–751.

Gosler, A.G., Greenwood, J.J.D., Baker, J.K. & Davidson, N.C. 1998. The field determination of body size and condition in passerines: a report to the British Ringing Committee. *Bird Study* **45**: 92–103.

Grenier, S., Barre, P. & Litrico, I. 2016. Phenotypic plasticity and selection: nonexclusive mechanisms of adaptation. *Scientifica (Cairo)* **2016**: 7021701.

Griffith, S.C., Stewart, I.R.K., Dawson, D.A., Owens, I.P.F. & Burke, T. 1999. Contrasting levels of extra-pair paternity in mainland and island populations of the house sparrow (*Passer domesticus*): is there an 'island effect'? *Biol. J. Linn. Soc.* **68**: 303–316.

Griffith, S.C., Dawson, D.A., Jensen, H., Ockendon, N., Greig, C., Neumann, K. & Burke, T. 2007. Fourteen polymorphic microsatellite loci characterized in the House Sparrow *Passer domesticus* (Passeridae, Aves). *Mol. Ecol. Notes* **7**: 333–336.

Haldane, J.B. 1930. Theoretical genetics of autopolyploids. *J. Genet.* **22**: 359–372.

Hartl, D.L. & Clark, A.G. 1997. *Principles of Population Genetics*, Vol. 116. Sunderland: Sinauer Associates.

Hemmer-Hansen, J., Nielsen, E.E., Frydenberg, J. & Loeschcke, V. 2007. Adaptive divergence in a high gene flow environment: Hsc70 variation in the European flounder (*Platichthys flesus* L.). *Heredity* **99**: 592–600.

Holland, M.M. & Parson, W. 2011. GeneMarker® HID: a reliable software tool for the analysis of forensic STR data. *J. Forensic Sci.* **56**: 29–35.

IUCN 2017. *The IUCN Red List of Threatened Species*. Version 2017-1. Available at: www.iucnredlist.org (accessed 2 July 2017).

Kalinowski, S.T., Taper, M.L. & Marshall, T.C. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Mol. Ecol.* **16**: 1099–1106.

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, H.P. & Kessler, M. 2017. Climatologies at high resolution for the earth's land surface areas. *Sci. data* **4**: 170122.

Keenan, K., McGinnity, P., Cross, T.F., Crozier, W.W. & Prodöhl, P.A. 2013. diveRsity: an R package for the estimation and exploration of population genetics parameters and their associated errors. *Methods Ecol. Evol.* **4**: 782–788.

Le Corre, V. & Kremer, A. 2012. The genetic differentiation at quantitative trait loci under local adaptation. *Mol. Ecol.* **21**: 1548–1566.

Leinonen, T., O'Hara, R.B., Cano, J.M. & Merilä, J. 2008. Comparative studies of quantitative trait and neutral marker divergence: a meta-analysis. *J. Evol. Biol.* **21**: 1–17.

Lenormand, T. 2002. Gene flow and the limits to natural selection. *Trends Ecol. Evol.* **17**: 183–189.

Librado, P. & Rozas, J. 2009. DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. *Bioinformatics* **25**: 1451–1452.

Luikart, G. 1997. *Usefulness of molecular markers for detecting population bottlenecks and monitoring genetic change*. Dissertation, University of Montana.

Luikart, G. & Cornuet, J.M. 1998. Empirical evaluation of a test for identifying recently bottlenecked populations from allele frequency data. *Conserv. Biol.* **12**: 228–237.

Matsubayashi, K.W., Ohshima, I. & Nosil, P. 2010. Ecological speciation in phytophagous insects. *Entomol. Exp. Appl.* **134**: 1–27.

Mayr, E. 1966. *Animal Species and Evolution*. Cambridge: Belknap Press of Harvard University Press.

McCollin, D., Hodgson, J. & Crockett, R. 2015. Do British birds conform to Bergmann's and Allen's rules? An analysis of body size variation with latitude for four species. *Bird Study* **62**: 404–410.

Mendelssohn, H. 1955. Biology and ethology of the Dead Sea Sparrow, *Passer moabiticus*, Tristram 1864. *Sallit* **1**: 27–36. (in Hebrew).

Merilä, J. & Crnokrak, P. 2001. Comparison of genetic differentiation at marker loci and quantitative traits. *J. Evol. Biol.* **14**: 892–903.

Mittelbach, G.G., Schemske, D.W., Cornell, H.V., Allen, A.P., Brown, J.M., Bush, M.B., Harrison, S.P., Hurlbert, A.H., Knowlton, N., Lessios, H.A., McCain, C.M., McCune, A.R., McDade, L.A., McPeek, M.A., Near, T.J., Price, T.D., Ricklefs, R.E., Roy, K., Sax, D.F., Schluter, D., Sobel, J.M. & Turelli, M. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecol. Lett.* **10**: 315–331.

Neumann, K. & Wetton, J.H. 1996. Highly polymorphic microsatellites in the house sparrow *Passer domesticus*. *Mol. Ecol.* **5**: 307–309.

Nielsen, E.E., Hemmer-Hansen, J., Poulsen, N.A., Loeschcke, V., Moen, T., Johansen, T., Mittelholzer, C., Taranger, G.L., Ogden, R. & Carvalho, G.R. 2009. Genomic signatures of local directional selection in a high gene flow marine organism; the Atlantic cod (*Gadus morhua*). *BMC Evol. Biol.* **9**: 276.

Nolan, V., Jr & Ketterson, E.D. 1983. An analysis of body mass, wing length, and visible fat deposits of Dark-eyed Juncos wintering at different latitudes. *Wilson Bull.* **95**: 603–620.

Peakall, R. & Smouse, P.E. 2001. *GenAlEx V5: Genetic Analysis in Excel. Population Genetic Software for Teaching and Research*. Canberra, ACT: Australian National University.

Piry, S., Luikart, G. & Cornuet, J.M. 1999. Computer note. BOTTLENECK: a computer program for detecting recent reductions in the effective size using allele frequency data. *J. Hered.* **90**: 502–503.

Poelstra, J.W., Vijay, N., Bossu, C.M., Lantz, H., Ryll, B., Müller, I., Baglione, V., Unneberg, P., Wikelski, M., Grabherr, M.G. & Wolf, J.B. 2014. The genomic landscape underlying phenotypic integrity in the face of gene flow in crows. *Science* **344**: 1410–1414.

Primmer, C.R., Saino, N., Møller, A.P. & Ellegren, H. 1998. Unravelling the processes of microsatellite evolution through analysis of germ line mutations in Barn Swallows *Hirundo rustica*. *Mol. Biol. Evol.* **15**: 1047–1058.

Pritchard, J.K., Stephens, M. & Donnelly, P. 2000. Inference of population structure using multilocus genotype data. *Genetics* **155**: 945–959.

R Core Team 2016. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Available at: https://www.R-project.org/

Ramos-Onsins, S.E. & Rozas, J. 2002. Statistical properties of new neutrality tests against population growth. *Mol. Biol. Evol.* **19**: 2092–2100.

Rannala, B. 2007. *BayesAss Edition 3.0 User's Manual*. Davis, CA: University of California at Davis.

Richter-Boix, A., Quintela, M., Kierczak, M., Franch, M. & Laurila, A. 2013. Fine-grained adaptive divergence in an amphibian: genetic basis of phenotypic divergence and the role of nonrandom gene flow in restricting effective migration among wetlands. *Mol. Ecol.* **22**: 1322–1340.

Rogers, A.R. & Harpending, H. 1992. Population growth makes waves in the distribution of pairwise genetic differences. *Mol. Biol. Evol.* **9**: 552–569.

Saether, S.A., Fiske, P., Kålås, J.A., Kuresoo, A., Luigujoe, L., Piertney, S.B., Sahlman, T. & Höglund, J. 2007. Inferring local adaptation from Q_{ST}–F_{ST} comparisons: neutral genetic and quantitative trait variation in European populations of great snipe. *J. Evol. Biol.* **20**: 1563–1576.

Saint-Laurent, R., Legault, M. & Bernatchez, L. 2003. Divergent selection maintains adaptive differentiation despite high gene flow between sympatric rainbow smelt ecotypes (*Osmerus mordax Mitchill*). *Mol. Ecol.* **12**: 315–330.

Salewski, V. & Watt, C. 2017. Bergmann's rule: a biophysiological rule examined in birds. *Oikos* **126**: 161–172.

Sambatti, J.B. & Rice, K.J. 2006. Local adaptation, patterns of selection, and gene flow in the Californian serpentine sunflower (*Helianthus exilis*). *Evolution* **60**: 696–710.

Savolainen, O., Lascoux, M. & Merilä, J. 2013. Ecological genomics of local adaptation. *Nat. Rev. Genet.* **14**: 807–820.

Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. *Methods Ecol. Evol.* **1**: 103–113.

Seehausen, O. 2004. Hybridization and adaptive radiation. *Trends Ecol. Evol.* **19**: 198–207.

Shirihai, H. 1996. *The Birds of Israel*, Vol. 692. London: Academic Press.

Snow, D.W. & Perrins, C.M. 1998. *The Birds of the Western Palearctic. Concise Edition. Vol. 2. Non-Passerines*. Oxford: Oxford University Press.

Sousa, V.C., Carneiro, M., Ferrand, N. & Hey, J. 2013. Identifying loci under selection against gene flow in isolation-with-migration models. *Genetics* **194**: 211–233.

Summers-Smith, J.D. 1988. *The Sparrows: A Study of the Genus Passer*. Calton: T & AD Poyser.

Tajima, F. 1989. Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics* **123**: 585–595.

Thomas, C.D. & Kunin, W.E. 1999. The spatial structure of populations. *J. Animal Ecol.* **68**: 647–657.

Tigano, A. & Friesen, V.L. 2016. Genomics of local adaptation with gene flow. *Mol. Ecol.* **25**: 2144–2164.

Venables, W.N. & Ripley, B.D. 2002. *Modern Applied Statistics With S*, 4th edn. New York, NY: Springer.

Vucetich, J.A. & Waite, T.A. 2003. Spatial patterns of demography and genetic processes across the species' range: null hypotheses for landscape. *Conserv. Genet.* **4**: 639–645.

Welty, J.C. 1962. *The Life of Birds*. Philadelphia, PA: W.B. Saunders.

White, P.S. & Densmore, L.D. 1992. Mitochondrial DNA isolation. In Hoelzel, A.R. (ed.) *Molecular Genetic Analysis of Populations: A Practical Approach*: 50–51. Oxford: Oxford University Press.

Wiklund, C.G. 1996. Body length and wing length provide univariate estimates of overall body size in the Merlin. *Condor* **98**: 581–588.

Wilkins, M.R., Karaardıç, H., Vortman, Y., Parchman, T.L., Albrecht, T., Petrželková, A., Özkan, L., Pap, P.L., Hubbard, J.K., Hund, A.K. & Safran, R.J. 2016. Phenotypic differentiation is associated with divergent sexual selection among closely related Barn Swallow populations. *J. Evol. Biol.* **29**: 2410–2421.

Wilson, G.A. & Rannala, B. 2003. Bayesian inference of recent migration rates using multilocus genotypes. *Genetics* **163**: 1177–1191.

Yeaman, S. & Whitlock, M.C. 2011. The genetic architecture of adaptation under migration–selection balance. *Evolution* **65**: 1897–1911.

Yom-Tov, Y. & Ar, A. 1980. On the breeding ecology of the Dead Sea Sparrow, *Passer moabiticus*. *Isr. J. Zool.* **29**: 171–187.

Yom-Tov, Y., Mendelssohn, H. & Ar, A. 1976. Extension of range of the Dead Sea Sparrow *Passer moabiticus* and its effect on breeding success. *Isr. J. Zool.* **25**: 202–203.

Yom-Tov, Y., Yom-Tov, S., Wright, J., Jr, Thorne, C. & Du Feu, R. 2006. Recent changes in body weight and wing length among some British passerine birds. *Oikos* **112**: 91–101.

Yosef, R., Zduniak, P. & Tryjanowski, P. 2004. Age, sex and season related biometrics of the Dead Sea Sparrow *Passer moabiticus*. *Ardeola* **51**: 297–302.

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SUPPORTING INFORMATION

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

Data S1. Morphometric analysis for mean temperature of warmest quarter and maximum temperature of warmest month on wing length and body mass.

Figure S1. The effect of sex on wing length in adult female and male Dead Sea Sparrows as depicted by a single factorial analysis.

Figure S2. The mean posterior probability (Ln *P(D)*) of each assumed number of populations (K) generated by STRUCTURE HARVESTER (Earl 2012) indicating a single population.

Table S1. Information of Dead Sea Sparrow samples used in the study.

Table S2. PCR conditions and allele numbers and sizes for each microsatellite marker used in this study.

Table S3. Genetic differentiation (F_{ST}) between groups of Dead Sea Sparrows from different localities based on genotypic frequencies using nine microsatellite loci.

Table S4. Tests for genetic signatures of recent population bottlenecks in Dead Sea Sparrow populations in Israel.

Appendix S1. Morphology and location data table.

Appendix S2. Genetic data table.