Ornis Fennica 87:93–98. 2010

Morphological shifts in the House Sparrows *Passer domesticus* of Helgoland: insular syndrome or founder effects?

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Received 15 January 2009, accepted 16 April 2010

Islands are natural laboratories for the study of evolution and help us to explain the patterns of diversification at large spatial scales. The colonisation of an island by a bird species inevitably involves divergence from the mainland mother population due to non-selective and selective evolution. On the island of Helgoland, House Sparrows *Passer domesticus* established a resident island population in 1958 which now numbers over 100 breeding pairs. We compared measurements of ringing data between Helgoland and two nearby mainland populations (length of 8th primary, body mass) and found a significantly higher body mass and lower P8 length/ body mass ratio on the island. Further, we found that P8 length and body mass significantly increased between the years 1989 and 2008 in Helgoland, indicating that the population changed in size towards larger individuals. This morphological shift might best be explained by the "insular syndrome" theory, which predicts increasing size of island birds as a result of reduced predation risk, reduced dispersal and increased intraspecific competition due to high population densities. On the other hand, founder effects could have added to the shift in the P8/ body mass ratio, assuming that the founder individuals yet showed this feature and the population had not much exchange with the mainland since the colonisation in 1958. Future molecular analyses of the population structure may help to reveal more details on the isolation, colonisation process and geographical origin of the Helgoland House Sparrow population.

1. Introduction

Few songbird species have established stable populations on the small off-shore island of Helgoland in the German North Sea in the last hundred years. Besides the Blackbird *Turdus merula* (Sacher *et al.* 2006), one of the most successful colonizers is the House Sparrow *Passer domesticus*. From the information available (Gätke 1900, Vauk 1972), it appears that House Sparrows settled on Helgoland around 1900. This population increased to 50 pairs between 1939 and 1942, but subsequently became extinct during the extensive bombardment at the end of the Second World War in 1952 (Jungfer 1956, Vauk 1962). Recolonisation, well documented by Vauk (1962), took place in 1958 when 30 founder individuals attempted to overwinter on Helgoland. Only 8 of these survived and two pairs initiated breeding in 1959. Thereafter, the population grew quickly as the number of ringed birds demonstrates (16 individuals ringed in 1959; 37 in 1960; 35 in 1961; Vauk 1962), which reached 50 pairs in 1967 (Hoffmann & Vauk 1969) and a maximum of 250–300 pairs in 1976 and 1979 (Dierschke *et al.* 2003). Nowadays 80–180 pairs breed annually on the island (e. g. 140 in 2008; Dierschke *et al.* 2009). The House Sparrows of Helgoland are completely resident, although before the Second World War reports claimed that they were migrating from the island during winter (Gätke 1900, Vauk 1972).

Island birds often differ in several morphological and ecological traits from their mainland counterparts, and these differences have played an important role in stimulating ecological and evolutionary theory in the past (Scott *et al.* 2003). The modifications are the result of local adaptation as a response to both, non-selective (founder effect, genetic drift) and selective evolution during the colonisation process of an island, which includes changes in morphology (size and shape), demography (age-specific fecundity, survival, dispersal) and behaviour, often summarized under the term "insular syndrome" (Blondel 2000). Recent studies on House Finches *Carpodacus mexicanus* have shown that morphological differentiation, e.g. of the wing-tip shape, among populations can take place even on a microevolutionary time scale (Egbert & Belthoff 2003). Similarly wing morphology of Blackcaps *Sylvia atricapilla* was found to have changed within less than 30 generations due to the development of a new migratory route and assortative mating (Rolshausen *et al.* 2009).

Given that the time span since the first colonisation of Helgoland by House Sparrows would be large enough to cause such microevolutionary changes, we studied their morphological characteristics by means of ringing data from the "Vogelwarte Helgoland" at the Institute of Avian Research. We compared available measurements (length of the 8th primary, i.e., P8, and body mass) between the island and two nearby mainland populations. Following the general assumption of the development of larger size due to the insular syndrome (Clegg & Owens 2002, Scott *et al.* 2003), we expected Helgoland House Sparrows to show larger P8 length and higher body mass than their mainland congeners.

2. Material and methods

Helgoland lies in the North Sea, about 60 km off the German coast (54°12'N, 07°56'E) with a size of approximately 1 km². As described above, House Sparrows recolonised the island in 1958 (Vauk 1962). We compared standard wing measurements (P8 length) and body mass obtained from the ringing data collection of the Institute of Avian Research of juvenile House Sparrows in July and August on Helgoland (HEL, 1989–2008; $n = 272$), with comparable data from two populations of the nearby German mainland: Langförden (52°47' N, 8°15' E) and Horumersiel (53°41' N, 8°01' E), Niedersachsen (NDS; 2006–2008, $n = 20$), and Neuwittenbeck (54°22' N, 10°01' E) and Pohnsdorf (54°14' N, 10°14' E), Schleswig-Holstein (SH; 2003–2008; $n = 49$). In order to demonstrate that Helgoland House Sparrows were significantly heavier in relation to their P8 length, we calculated additionally the ratio of P8 length and body mass.

We are aware of the fact that body size of juvenile sparrows is increasing with time after fledging (Lepczyk & Karasov 2000) and that the measurements may vary between years. Therefore, in order to control for year and seasonal effects, we standardised our data by conducting a GLM analysis with year and day of the year as continuous variables. The residuals were calculated and summed to the average values of the whole population, obtaining standardised P8 and body mass values for each individual. We had to exclude adult birds from our analyses since the sample size for the different areas was to low and the data was strongly biased by date. Other measurements such as tarsus length could not be included in our analyses since these data were unfortunately not available in the ringing data base.

To compare juvenile House Sparrows from the three areas (HEL, SH, NDS), we conducted ANOVAs for the period from 1989 to 2008 and for 2003 to 2008 (for the latter period data from all three study sites were available). Post hoc analyses were conducted with sequential Bonferroni corrections. Furthermore, by a linear regression we evaluated possible change in the P8 length and body mass in Helgoland over the period from 1989 to 2008. We used SPSS 12.0 for all statistical analyses and SigmaPlot for the graphs.

Table 1. Comparison of standardized (by date and year) P8 length, body mass and the P8 length / body mass ratio between juvenile House Sparrows from Helgoland (HEL) and from two mainland populations (Schleswig-Holstein = SH, Niedersachsen = NDS) during (a) 1989–2008 and (b) 2003–2008; numbers in the respective columns show mean ± SE. For juveniles, only individuals captured from July to August before post-juvenile moult are included. The *F* and *p* columns show ANOVA results (df between groups = 2; df within groups for (a) = 338 and for (b) = 148); the Bonferroni column shows *p* values after Bonferroni correction (significant results are in bold).

Measurement	HEL (n for (a) = 272 and for (b) = 82)	SH (n=49)	NDS (n=20)	*F*	*p*	Bonferroni
(a) 1989–2008						
P8 (mm)	55.84±0.11	55.45±0.30	53.17±0.73	16.33	<0.001	HEL vs SH p = 0.640 HEL vs NDS **p <0.001** SH vs NDS **p <0.001**
Body mass (g)	29.07±0.13	27.28±0.27	26.10±0.53	31.25	<0.001	HEL vs SH **p <0.001** HEL vs NDS **p <0.001** SH vs NDS p = 0.102
P8 /body mass (mm/g)	1.93±0.01	2.04±0.02	2.05±0.05	19.03	<0.001	HEL vs SH **p < 0.001** HEL vs NDS **p <0.001** SH vs NDS p = 1.000
(b) 2003–2008						
P8 (mm)	55.93±0.18	55.45±0.30	53.17±0.73	14.61	<0.001	HEL vs SH p = 0.58 HEL vs NDS **p <0.001** SH vs NDS **p <0.001**
Body mass (g)	29.54±0.22	27.28±0.27	26.10±0.53	33.15	<0.001	HEL vs SH **p <0.001** HEL vs NDS **p <0.001** SH vs NDS p =0.091
P8 /body mass (mm/g)	1.90±0.01	2.04±0.02	2.05±0.05	17.61	<0.001	HEL vs SH **p < 0.001** HEL vs NDS **p <0.001** SH vs NDS p = 1.00

3. Results

An ANOVA with Bonferroni correction for the period from 1989–2008 revealed no significant difference in the length of P8 of juvenile House Sparrows between the birds from Helgoland and Schleswig-Holstein, but it indicated significant differences between Schleswig-Holstein and Niedersachsen and between Helgoland and Niedersachsen (Table 1a). Furthermore, we found a significant difference in body mass among the three areas, with the heaviest juveniles being on Helgoland, lighter individuals in Schleswig-Holstein, and the lightest ones in Niedersachsen. Differences in the ratio of P8 length and body mass were also highly significant (Table 1a, Fig. 1). The results remained similar when we considered only the period for which we had samples from both, the island and the mainland (2003–2008; Table 1b).

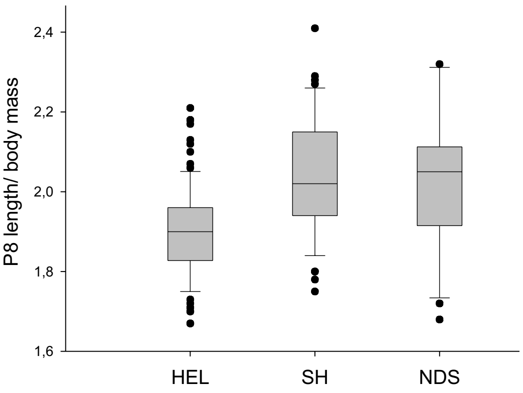

Fig. 1. The P8 length/body mass ratio of House Sparrows on Helgoland (HEL), Schleswig-Holstein (SH) and Niedersachsen (NDS). Data standardized by date and year. Box plots for juveniles (HEL: *n* = 272; SH: *n* = 49; NDS: *n* = 20) with median, interquartlile range and outliers are shown. For statistical comparisons, see text and Table 1a.

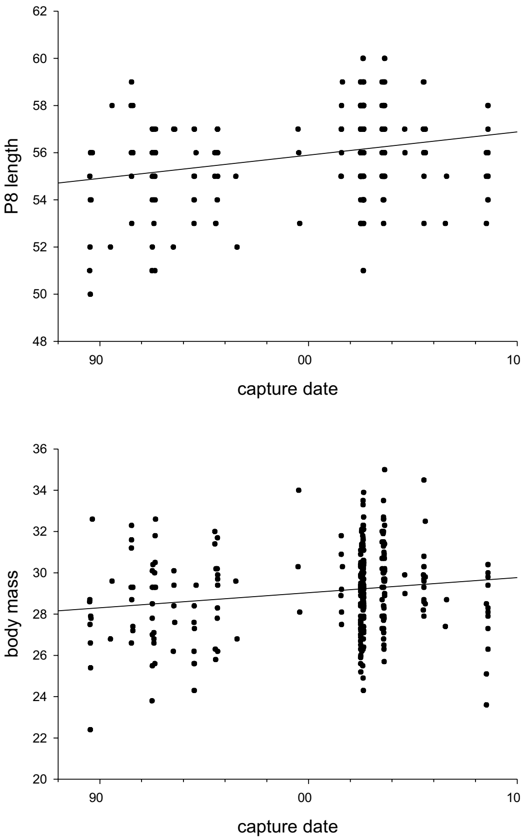

Fig. 2. Top: time series 1989–2008 for P8 length in juvenile House Sparrows *Passer domesticus* on Helgoland island captured in the months of July and August. Down: time series 1989–2008 for body mass in juvenile House Sparrows *Passer domesticus* on Helgoland island captured in the months of July and August. For statistical values, see text.

We also found that the P8 length and the body mass of juvenile Helgoland House Sparrows significantly increased between the years 1989 and 2008 (Fig. 2), indicating that the population apparently changed in size towards larger individuals during this time span (P8 length: $R = 0.24$, $F = 16.48$, df = 1, $p<0.001$; body mass: $R = 0.17$, $F = 8.05$, df = 1, $p = 0.005$). Unfortunately data from the years before 1989 are lacking to test if this constitutes a general trend since the arrival of the founder individuals or a more recent shift in morphology.

We found evidence that House Sparrows move between Helgoland and the mainland. Recovery data from the ringing centre at the Institute of Avian Research, “Vogelwarte Helgoland”, Wilhelmshaven, demonstrate that some House Sparrows ringed on Helgoland had reached the mainland. In total 12 recoveries between 1937 and 2008 are known, which spread along the coastline and nearby islands between Denmark and the Netherlands (Fig. 3). In contrast, during the same period only one alien bird was found on Helgoland which stemmed from the island of Neuwerk, an extremely low number regarding the rather high trapping effort on the island.

4. Discussion

We found that the juvenile House Sparrows of Helgoland were significantly heavier than their mainland congeners. The length of the 8th primary was not significantly different compared to the mainland population of Schleswig-Holstein, but larger than the Niedersachsen population. As a result, Helgoland birds differed significantly from both mainland populations by having a lower P8 length / body mass ratio, while there was no difference in this ratio between the two mainland populations. Further, we found that juvenile House Sparrows slightly increased in body mass and P8 length within the period of 1989–2008.

The observed pattern supports the “insular syndrome”, which predicts larger size of birds on islands. According to this theory, island birds experience reduced risk of predation, show reduced dispersal and increased intraspecific competition due to high population densities compared with mainland counterparts (e.g., Blondel 2000, Clegg & Owens 2002, Scott *et al.* 2003). In the case of the Helgoland House Sparrows, all three factors might have played a major role in shaping the morphology of the actual population.

Lower predation risk for House Sparrows on Helgoland seems a robust assumption, since outside the migration periods the island is nearly free of any avian predator whereas avian predators are resident on mainland populations. This reduced predation risk will likely favour heavier birds. For example, abundance of the main avian predator, the Sparrowhawk *Accipiter nisus*, has been shown to influence the body mass of other House Sparrow populations (MacLeod *et al.* 2006). An alternative explanation might be that a bias in dispersal

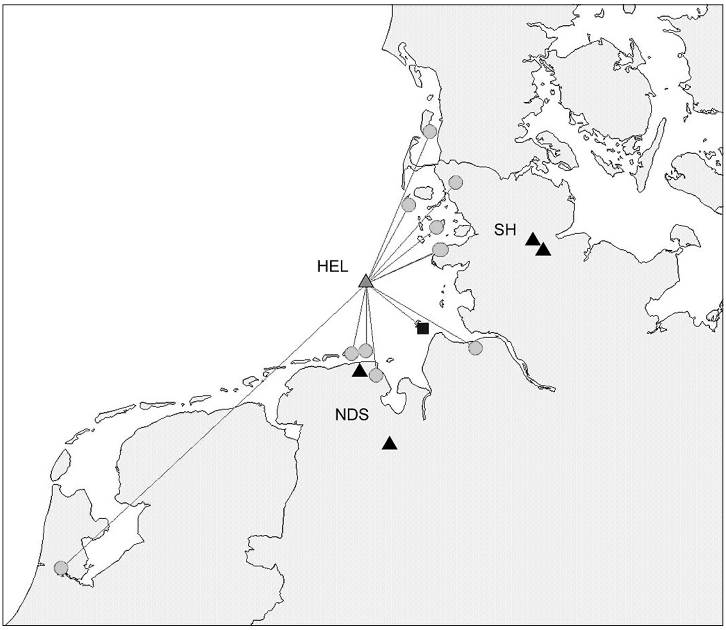

Fig. 3. Recoveries of House Sparrows *Passer domesticus* ringed on Helgoland island between 1937 and 2008 (circles). No birds from the mainland were found on Helgoland. The only recovery from outside Helgoland refers to a bird ringed on Neuwerk island (square). The triangles indicate Helgoland (HEL; filled grey) and the studied mainland populations of Niedersachsen and Schwleswig-Holstein (NDS and SH, respectively; filled black).

favours birds with a lower P8/ body mass ratio on the island, due to heightened emigration of birds with longer wings and/or lighter body mass to the mainland. However, other House Sparrow populations disperse quite rarely and irrespective of body mass or condition (Altwegg *et al.* 2000), and our long-term ringing data show that recoveries of Helgoland House Sparrows on the mainland are quite scarce (Fig. 3). Another possibility is that the quite high population density of House Sparrows on the island has led to an assortment of more competitive and therefore larger individuals, following the hypothesis that strong intraspecific competition selects for larger body sizes on islands. This would be in accordance with the finding that body mass is an important determinant of dominance in the House Sparrow (Liker & Barta 2001).

An alternative to these potential island selection pressures is that the changes in Helgoland House Sparrow morphology have nothing to do with microevolution, but might simply reflect the body characteristics of the founder individuals (founder effect). Vauk (1962) reported that of the 30 birds overwintering on the island in 1958/1959, only eight survived and two pairs started to breed (only four founder birds). It seems possible that only the birds in the best condition (e.g., those with most fat reserves) survived the harsh winter, passing these traits (e.g., large body mass) to the island descendants. As ringing recoveries suggest that immigration of House Sparrow individuals to Helgoland is a rare event, founder effects could have persisted since the initial colonisation and would explain the observed pattern. However, the observed change in body mass and P8 length within the short period of 1989–2008 towards larger individuals argues against morphology having remained stable since the founder event and provides stronger support for island-specific selection.

Unfortunately, morphological data from the colonisation period around 1958 till the eighties are lacking to evaluate how the morphology of the House Sparrows on Helgoland has changed since the colonization. Future long-term studies on the development of morphology and body mass in Helgoland House Sparrows may reveal insights on the ongoing evolution processes. Further, genetic analyses may clarify the possible founder effects, gene flow and inbreeding, and may allow determining the geographical origin of the colonisation of Helgoland by the House Sparrow.

Acknowledgements. All data from Niedersachsen, Helgoland and Schleswig-Holstein stem from the ringing data archive at the Institute of Avian Research, “Vogelwarte Helgoland”. The manuscript was much improved by the comments of Franz Bairlein, Esther del Val and two anonymous referees.

Morfologiset siirtymät Helgolandin varpusilla: saari- vai perustajavaikutus?

Saaret soveltuvat evoluutiotutkimukseen ja auttavat selvittämään eriytymisen vaikutuksia suuressa mittakaavassa. Lintulajin asuttaessa saaren seuraa väistämättä erojen kasvu mantereen lähtöpopulaatioon nähden johtuen valikoimattomista ja valikoivista evoluutiopaineista. Varpuset asettuivat Helgolandin saarelle 1958, kannan ollessa nykyään yli sata paria.

Vertasimme varpusten rengastusaineiston mittatietoja Helgolandin ja kahden mannerpopulaation välillä (käsisulan P8 pituus, ruumiinpaino) ja havaitsimme merkitsevästi alhaisemman P8 pituuden ja ruumiinpainon suhteen Helgolandilla. Havaitsimme myös P8 pituuden ja ruumiinpainon kasvaneen saarella 1989–2008, mikä viittaa yksilöiden keskikoon kasvuun. Tämän kasvun selittää mielestämme parhaiten saarivaikutusteoria, jonka mukaan saariyksilöiden kasvava koko johtuu alentuneesta petojen saalistusriskistä ja yksilöiden levittäytymisestä, ja toisaalta kasvaneesta lajinsisäisestä kilpailusta korkean yksilötiheyden vuoksi.

Toisaalta perustajavaikutus on saattanut vaikuttaa havaittuun kohonneeseen P8 ja ruumiinpainon suhteeseen, olettaen että perustajayksilöillä oli kyseinen ominaisuus ja ettei saaripopulaation ja mannerpopulaatioiden välillä ole juuri tapahtunut yksilönvaihtoa sitten saaren asuttamisen 1958. Populaatiorakenteen molekyylitutkimus saattaa paljastaa lisää yksityiskohtia Helgolandin varpuspopulaation eristyneisyydestä, asuttamishistoriasta ja maantieteellisestä alkuperästä.

References

Altwegg, R., Ringsby T. H. & Saether B.-E. 2000: Phenotypic correlates and consequences of dispersal in a metapopulation of house sparrows *Passer domesticus*. — Journal of Animal Ecology 69: 762–770.

Blondel, J. 2000: Evolution and ecology of birds on islands: trends and prospects. — Vie & Milieu 50: 205–220.

Clegg, S. M. & Owens, I. P. F. 2002: The ‘island rule’ in birds: medium body size and its ecological explanation. — Proceedings of the Royal Society of London B 269: 1359–1365.

Dierschke, J., Dierschke, V., Jachmann, F. & Stühmer, F. 2003: Ornithologischer Jahresbericht 2002 für Helgoland. — Ornithologischer Jahresbericht Helgoland 13: 64. (In German)

Dierschke, J., Dierschke, V., Schmaljohann, H. & Stühmer, F. 2009: Ornithologischer Jahresbericht 2008 für Helgoland. — Ornithologischer Jahresbericht Helgoland 19:7. (In German)

Egbert, J. R. & Belthoff, J. R. 2003: Wing shape in house finches differs relative to migratory habit in eastern and western North America. — Condor 105: 825–829.

Gätke, H. 1900: Die Vogelwarte Helgoland. 2. Auflage. — Braunschweig. (In German)

Hoffmann, H. J. & Vauk, G. 1969: Die Brutvögel Helgoland 1964–1967. — Vogelwelt 90: 140–145. (In German)

Jungfer, W 1954: Helgoländer Brutvögel 1953. — Vogelwelt 75: 191–194. (In German)

Lepczyk, C.A. & Karasov, W.H. 2000: Effect of ephemeral food restriction on growth of house sparrows. — Auk 117: 164–174.

Liker, A & Barta, Z. 2001: Male badge size predicts dominance against females in house sparrows. — Condor 103: 151–157.

MacLeod, R., Barnett, P., Clark, J. & Cresswell, W. 2006: Mass-dependent predation risk as a mechanism for house sparrow declines? — Biological Letters 2: 43–46.

Pérez-Tris, J. & Tellería, J.L. 2001: Age-related variation in wing shape of migratory and sedentary Blackcaps *Sylvia atricapilla*. — Journal of Avian Biology 32: 207–213.

Rolshausen, G., Segelbacher, G., Hobson, K.A. & Schaefer, H.M. 2009: Contemporary evolution of reproductive isolation and phenotypic divergence in sympatry along a migratory divide. — Current Biology 19: 1–5.

Sacher, T., Engler, J., Gorschewski, A., Gottschling, M., Hesler, N., Bairlein, F. & Coppack, T. 2006. Die Helgoländer Amselpopulation: ein Modell für Populationsgenetik und Zugbiologie. — Ornithologischer Jahresbericht Helgoland 16: 76–84. (In German)

Scott, S.N., Clegg, S.M., Blomberg, S.P., Kikkawa, J. & Owens, I.P.F. 2003: Morphological shifts in island-dwelling birds: the roles of generalist foraging and niche expansion. — Evolution 56: 2313–2321.

Seki, S.I., Sakanashi, M., Kawaji, N. & Kotaka, N. 2007: Phylogeography of the Ryukyu robin (*Erithacus komadori*): population subdivision in land-bridge islands in relation to the shift in migratory habit. — Molecular Ecology 16: 101–113.

Vauk, G. 1962: Beobachtungen über Zugbewegungen und Wiederansiedlung des Haussperlings *Passer d. domesticus* auf Helgoland. — Schriften Naturwissenschaftlichen Verein Schleswig Holstein 33: 33–36. (In German)

Vauk, G. 1972: Die Vögel Helgolands. — Paul Parey, Hamburg und Berlin. (In German)