Evolutionary Ecology (2021) 35:443–462
https://doi.org/10.1007/s10682-021-10107-y

ORIGINAL PAPER

# Rapid morphological changes as agents of adaptation in introduced populations of the common myna (*Acridotheres tristis*)

**Tali Magory Cohen[1,2] · Richard E. Major[3] · R. Suresh Kumar[4] · Manoj Nair[4] · Kyle M. Ewart[3] · Mark E. Hauber[5] · Roi Dor[6]**

Received: 20 September 2020 / Accepted: 11 February 2021 / Published online: 26 February 2021

## Abstract

Invasive species present an opportunity to test the association between selective forces and adaptive morphological traits because these species can experience rapid changes when introduced to new environments. One such invader is the common myna (*Acridotheres tristis*), a broadly ranging avian species that has been introduced on most continents and many oceanic islands. Here, we studied morphological variability in native and introduced populations of common mynas to identify the key environmental variables correlated with local phenotypic variation during biological invasions. In particular, we aimed to determine whether similar selective pressures acted on populations in the native range and the introduced ranges, and whether the same factors shaped morphological variation in different introduced populations. We recorded eight morphological measurements from 1,331 individuals across sites throughout most of the common myna's range, as well as climatic, topographic and anthropogenic environmental data, sex and age of individuals, and years since local introduction. We found inconsistent signals of morphological adaptation in the native population, representing different patterns between females and males. Conversely, urbanization was a significant explanatory factor of phenotypic shifts in introduced populations, especially with regards to foraging-related traits. Moreover, we found that adaptation occurred differently across two focal introduced populations (Sydney, Australia and Israel). Therefore, caution is required in studies relating to evolutionary adaptations and predictions made regarding characteristics of invasive populations within a limited range of their introduced ranges. Our results also indicate a major role for urbanization in impacting the shape and size of foraging-related features in this broadly-distributed invasive species, emphasizing the impact of human-induced environmental changes upon the trajectories of biological invasions and, ultimately, their effects on native biodiversity.

**Keywords** Common myna · Invasive species · Morphology · Spatial sorting · Urbanization

---

✉ Tali Magory Cohen
talimc@tauex.tau.ac.il

Extended author information available on the last page of the article

## Introduction

Morphology represents a subset of phenotypic adaptations to local environmental conditions. Traditionally, spatial patterns of morphological variation have been explained by ecogeographical rules (e.g., Bergmann's rule, Bergmann 1848; Salewski and Watt 2017; Gloger's rule, Gloger 1833; Delhey 2017), according to which endothermic species should differ in their morphological traits in different environmental conditions such as humidity and temperature (but see Meiri et al. 2004, 2007; Feldman and Meiri 2014). This variation can occur at different taxonomic levels, and morphometric differences among populations of a single species resulting from local adaptation have been described comprehensively (Blondel et al. 1999; Sæther et al. 2007; Badyaev et al. 2008; Magory Cohen et al. 2018). However, the rate at which these differences arise and the strength of the selective pressures leading to morphological evolution remain unclear in populations that experience non-directional or slow modifications in their environments. Therefore, focal studies where rapid environmental changes take place, e.g., when species invade new environments, present an opportunity to test the associations between selective forces and adaptive morphological traits (including, for example, relaxed selection, Lahti et al. 2009).

A relatively recent selective force now widely operating on phenotypic variation in some populations of wild animals is urbanization. Urbanization-induced processes have been shown to instigate morphological changes in several animal lineages, including birds (Badyaev et al. 2008; Liker et al. 2008; Giraudeau et al. 2014), mammals (Tomassini et al. 2014; Yu et al. 2017), and fishes (Kern and Langerhans 2018; Alter et al. 2020). Specifically, differences in diet composition between urbanized areas and natural environments were suggested to cause changes in traits related to foraging such as bill size and shape in birds (Badyaev et al. 2008; Giraudeau et al. 2014) and cranial size in mammals (Tomassini et al. 2014). Whether these trends reflect general patterns across a species' complete range, or necessitate an acute environmental change, remains unclear.

Invasive species can experience rapid morphological changes when introduced to new environments (Phillips et al. 2006; Alford et al. 2009; Mathys and Lockwood 2011; Cardilini et al. 2016; Gleditsch and Sperry 2019). The realized phenotypes can be advantageous in promoting invasive dispersal at range fronts (Phillips et al. 2010; Berthouly-Salazar et al. 2012, 2013; Hudson et al. 2016), responding to novel conditions by improving (Sol et al. 2005) and facilitating cognitive skills (Magory Cohen et al. 2020), exploiting new food resources (Hudson et al. 2016), or adapting to new climatic conditions (Baker and Moeed 1979; Cardilini et al. 2016). These resulting local adaptations possibly occur independently of each other. For example, whereas longer wings may allow for greater dispersal distances during range expansion (Berthouly-Salazar et al. 2012), an increase in head size, which may be associated with improved cognition in new environments (Lefebvre et al. 2004), may not occur (Berthouly-Salazar et al. 2012). Therefore, the ability of an invasive species to respond to locally different selective pressures may predetermine its invasion success (Cerwenka et al. 2014). Consequently, biological invasions provide an opportunity to study the link between rapid phenotypic adaptation to novel environments and invasion success on a microevolutionary timescale (Phillips and Shine 2005; Clarke et al. 2019).

Tests of correlations between morphological characters and environmental conditions can benefit from studying a widespread invader that occupies multiple introduced areas, allowing for repeatedly independent assessment across different environments. One such invader is the common myna (*Acridotheres tristis*), a broadly ranging avian species that has been introduced on every continent except for Antarctica, and on many oceanic islands (Magory Cohen et al. 2019). Previous studies suggest that different selective pressures act on common myna populations in various parts of the species' expanded range. For example, in an introduced population of common mynas in New Zealand, evidence of early morphological local adaptation was found to match two biogeographical rules of morphological variation (i.e., Bergmann rule and Gloger rule; Baker and Moeed 1979). However, across its native populations in India, no evidence was found to support Bergmann's rule and, instead, a trade-off between bioclimatic factors and inter-specific competition for food resources was suggested to explain size variation (Baker and Moeed 1980). In another introduced population in South Africa, Berthouly-Salazar et al. (2012) found evidence of spatial sorting in traits related to dispersal, whereas foraging-related traits were correlated with environmental variables, including urbanization. Because introductions of common mynas varied in space and time (i.e., earliest known introductions were mid-nineteenth century in Hawaii and Australia: Cramp & Perrins 1994; Long 1981; the most recent ones occurred in Spain and Portugal: Saavedra et al. 2015, and in Italy: Mori et al. 2020), they constitute an ideal study system to explore local adaptations across contemporary time scales and under diverse geographic conditions.

Despite accumulating evidence of local morphological adaptations in a multitude of invasive species (Ross and Baker 1982; Phillips and Shine 2006; Berthouly-Salazar et al. 2012; Bitton and Graham 2015; Hudson et al. 2016; Gruber 2017), whether these adaptive changes occur similarly across a species' different invasive ranges remains uncertain. Here, we studied morphological variations in native and introduced populations of common mynas across several continents in order to identify the key environmental variables correlated with local adaptation during biological invasions. In particular, we aimed to determine whether similar selective pressures acted on populations in the native range and the introduced ranges and whether the same factors shaped morphological variation in different introduced populations.

We measured morphological traits from a combination of wild-caught live birds, carcasses from culled birds following conservation management, and museum specimens to investigate changes in morphology across the native and the introduced ranges of the common myna. Native populations have been subjected to diverse environmental conditions throughout their evolutionary history. We expected that the morphological traits of native and introduced populations will change in similar directions in response to the impacts of particular environmental predictors (albeit that the magnitude of environmental conditions experienced by disparate populations may differ). For example, we predicted that morphological traits related to thermoregulation will be negatively correlated with mean annual temperatures across both native and introduced ranges (Johnston and Selander 1964; Baker and Moeed 1979; Grant 1979). Additionally, because urbanization has been shown to be an important explanatory predictor of the global distribution of common mynas (Magory Cohen et al. 2019; Magory Cohen and Dor 2019), and urban areas offer different dietary opportunities than semi-urban or rural areas, we predicted that morphological character shifts related to foraging will increase with the intensity of urbanization (Badyaev et al. 2008; Norazlimi and Ramli 2015). In turn, we expected that characters related to invasiveness will be highest in populations at the invasion range's front, and decrease as a function of the time since introduction, as mynas from the range front were shown to be more innovative and less neophobic than their native conspecifics (Magory Cohen et al. 2020).

## Materials and methods

### Sample collection

We measured 1331 individuals from the majority of the common myna distribution range, using a combination of field sampling in Israel, Australia, and India (between the years of 2014–2018) and specimens collected globally which were deposited in ornithology museum collections between the years 1836–2018 (Fig. 1, Table S1). Live-caught or culled specimens collected in Israel and Australia represent the introduced range (introduced in 1997 and mid-nineteenth century, respectively), whereas samples collected in India represent the native range. In total, we collated data from 1,015 individuals from the introduced ranges and 316 from the native range.

In the field, birds were trapped via specific myna traps and opportunistic mist-netting (Israel and India), occasional shooting by authorized individuals or rangers (Israel and Australia) or a direct collective culling effort (Australia). Birds trapped in India were subsequently banded and released at the point of capture, whereas invasive birds captured in Israel and Australia were transferred to the Israel Nature and Parks Authority or euthanized, respectively, according to local permits. Collected carcasses were frozen for measurement at a later date. All animal care procedures were approved by the Tel Aviv University ethics committee (permit nos. L-15–033 and 04-17-056), the Israel Nature and Parks Authority (permit numbers 2015/40,828 and 2017/41,780), the Australian Museum Animal Care and Ethics Committee (approval number 15–03), and the Wildlife Institute of India Animal Welfare committee and Uttarakhand State Forest department permit (L. No. 1258/5–6). Global positioning system (GPS) coordinates were recorded for each bird caught. When a museum specimen or a bird collected from culling had not been assigned coordinates, then coordinates of the nearest town or reference point were recorded using an online tool (https://www.gps-coordinates.net/). Records for which the sampling locality was too coarse (i.e., were not specific enough, such as large cities or regions) were omitted from the data set.

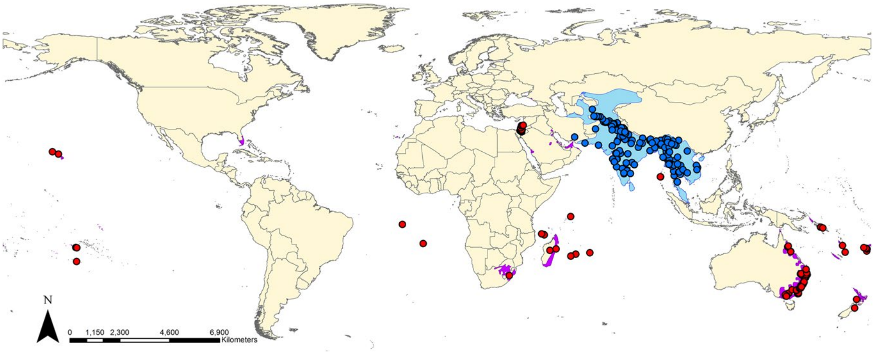


**Fig. 1** Sampling records of common mynas used in this study. The light blue shading represents the known native range of the species, while the purple shading represents its introduced range (according to IUCN data; IUCN 2019). Sampling records are marked with red (introduced, n = 1015) and blue (native, n = 316) circles. Additional details of samples used in this study are found in Table S1. This map lacks the most recent local introductions in Italy, Spain, and Portugal (see main text)

## Morphological measurements

We aged birds by their plumage (Cramp and Perrins 1994) and classified them as either adults (After Hatching Year–AHY) or juveniles (Hatching Year–HY). Birds sampled during field sampling were sexed anatomically (Australia) or via Polymerase Chain Reaction (PCR) by amplifying sex-specific coding regions (chromo-helicase-DNA binding protein; CHD) on the Z (male and female) and W (female-only) avian sex chromosomes with the primers F2250 and R2718 (Fridolfsson and Ellegren 1999) or CHD1-i16-F and CHD1-i16-R (Suh et al. 2011) (Israel and India). We recorded eight measurements following Berthouli-Salazar et al. (2012) and Baker and Moeed (1979), including wing chord, hereafter wing length (carpal joint to tip of the longest primary flattened), tarsus length (tibio-tarsus joint to the distal end of the tarso-metatarsus), bill length (bill tip to the nasal-frontal hinge), bill depth (at the proximate edge of the nostrils), bill width (at the proximate edge of the nostrils), head length (tip of the bill to the back of the head minus bill length), middle toe length (distal inter-condylar fossa to the tarsometatarsal facet of phalanx I), and premaxilla length (tip of the bill to the anterior border of the nostrils). Wing length was only used in the analysis if the individual was not molting its 7th or 8th primary (the longest primary feathers). All measurements were recorded with a 0.1 mm-unit dial caliper except for wing length that was recorded with a 1 mm-unit flat ruler. All measurements were taken by a single person (TMC), except for 13 Indian specimens taken by RSK after careful steps were taken to confirm that the measurements did not differ systematically.

## Environmental variables

We extracted a set of environmental variables that had been determined biologically important in shaping the global common myna distribution (Magory Cohen et al. 2019). Because the temporal scale of the examined specimens spanned approximately 150 years, it was crucial that the environmental data reflect the time period in which the specimen was collected. Therefore, we used data with a yearly resolution for climatic variables that included mean temperature (TMP), annual average precipitation (PRE), potential evapotranspiration (PET), and diurnal temperature range (DTR) (Harris et al. 2014; 0.500 degree resolution). In addition, we included a topographic variable (altitude, ALT, METI/NASA 2011; 0.004 degree resolution) and two proxies of urbanization: constructed impervious surface area (IMP [density for each grid cell as a percentage of the total area in km$^2$], Elvidge et al. 2007; 0.008 degree resolution) and human population density (HD [number of people per cell * $10^5$], CIESIN 2014; 0.008 degree resolution). Both IMP and HD were previously shown to effectively capture urbanization with regards to common mynas (Magory Cohen et al. 2019). To correctly model the temporal changes in morphology, we used historic human density extracted for the specific year of the record. We achieved this by calculating the factor by which the population has increased from the year the record was taken to modern day estimates (Roser and Ortiz-Ospina 2018), and dividing the current human density (per location) by this factor. We applied the same transformation to impervious surfaces in the absence of historical measurements, assuming that anthropogenic changes have occurred in a similar direction and order of magnitude. In addition, we estimated the time since the invasion based on previous documentation and museum records (TIME).

## Statistical analyses

Since common mynas are sexually dimorphic in size (males being larger, Cramp and Perrins 1994), the analyses were conducted for each sex separately. In addition, only adult specimens were analyzed to avoid signal loss in traits that stabilize in adulthood. None of the response variables (i.e., morphological traits) were highly correlated (Pearson's $|r| \leq 0.64$, Table S2), therefore we modeled each of the eight measurements separately. This modelling approach is better suited for interpreting biological results because it allows for independent consideration of each trait. Similarly, none of the environmental variables were highly correlated (Pearson's $|r| \leq 0.75$). We treated the urbanization predictor variables (HD, IMP) both as linear and quadratic terms ($HD^2$, $IMP^2$) so that simple nonlinear relationships could be detected. We expected that nonlinear association may occur between anthropogenic predictors and morphological traits because the urban environment may give rise to multidirectional selective forces that act on the same trait in dissonance; for example, dietary changes in urban environments may favor longer bills (Badyaev et al. 2008; Giraudeau et al. 2014), while bill shape may be limited by acoustic requirements for song to overcome anthropogenic noise (Giraudeau et al. 2014). Ultimately, we standardized response variables and continuous predictors by subtracting the mean and dividing by the standard deviation using the 'stdize' function in R package 'MuMIn' version 2.7–0 (Barton 2018). We tested the correlation between each morphological trait (response) and standardized climatic (TMP, PRE, PET, DTR), topographic (ALT) and urbanization (IMP, HD) variables by employing General Linear Models (GLM) and General Linear Mixed Models (GLMM; 'Country' being the random factor in analyses that included multiple countries) using R statistical software (R Core Team 2019).

Additionally, to measure temporal change in traits through time, we analyzed two populations for which we had large sample sizes: Israel ($n = 286$) and Sydney, Australia ($n = 233$). The Israel population was recently introduced (approximately 23 years ago) while the Sydney population represents an older invasion (approximately 150 years ago). Ewart et al. (2018) recently demonstrated that the two separate known introductions of common mynas in Australia in Sydney and Melbourne resulted in multiple, genetically distinct groups. Therefore, we compared only the Sydney population, for which our data set was larger, to the Israeli population. Given that common mynas reach sexual maturity approximately within a year (Eddinger 1967), sufficient time for detectable selection would have occurred (Grant and Grant 1995) across the multiple generations produced even in the recently introduced population in Israel. To account for the differences among the introduction times, we included standardized time since introduction (TIME) as an additional explanatory variable. Since temporal data as to the time since invasion was unavailable for most of the local spreads from Melbourne, this was another reason for excluding Melbourne from this comparison. For these subsets, we again modeled each morphological trait separately (Pearson's $|r| \leq 0.70$, Table S2). However, one of the environmental variables (potential evapotranspiration) was highly correlated (Pearson's $|r| > 0.80$) in both the Israeli subset (with diurnal temperature range, Pearson's $|r| = 0.90$) and the Australian one (with annual average precipitation, Pearson's $|r| = 0.82$). Therefore, we excluded potential evapotranspiration (PET) from these models. Additionally, two more predictor variables were highly correlated in the Australian subset (human density and impervious surface area, Pearson's $|r| = 0.86$). In order for the two subsets to be comparable, we included the correlated predictor variables in the

Australian model. However, we ran separate models omitting one of the two correlated predictor variables each time to validate the results of the model with all of the predictors. Our results showed that all model outputs were very similar (Table S3).

For each of the morphological traits, alternative models with different combinations of environmental predictors were produced using an all-subsets approach, including the null model. We fitted the models based on the Shapiro–Wilk test of normality (Shapiro and Wilk 1965), and used General Linear Models (GLM) or General Linear Mixed Models (GLMM) if a random factor was used. We opted against models that account for spatial autocorrelation for two reasons. Firstly, Spatial Autocorrelation Regression models require aggregation of the observations that were collected at the same coordinates. Our dataset consisted of many localities from which multiple measurements were available for a single pair of coordinates only, as was often the result of historical museum record keeping and/or collection, as well as of culling efforts. Secondly, evidence for spatial autocorrelation (Moran's I, calculated via the 'ape' R package (Paradis and Schliep 2018) was variable and partial (Table S4). Therefore, we accounted for some of the spatial autocorrelation by including 'country' as a random factor in our models. We then evaluated the models using the Akaike information criterion (AIC), and selected the best models ($\Delta\text{AIC} \leq 2$). We employed model averaging over the best models that were selected using the R package MuMIn (Barton 2018). To describe the statistical significance of the predictor variables, we calculated 95% confidence intervals (CIs) and determined coefficients significant if they did not overlap zero (Barton 2018). In addition, we calculated the relative importance of each explanatory variable across averaged models via the R package MuMIn (Barton 2018).

## Results

### Local adaptation in the native range

We found inconsistent signals of morphological adaptation in the native population, whereby different trait patterns were evident between males and females. (Tables 1, S5). For example, in males and females, morphological characters related to foraging (bill length, bill width, head length) were correlated with both climatic and urbanization predictors, although the same traits were explained by different variables in the different sexes; bill length in females was best explained by mean temperature (estimate ± SE = 0.12 ± 0.04, CI: 0.04–0.21), whereas in males it was best explained by impervious surfaces coverage (estimate ± SE = 3.86 ± 1.77, CI: 0.39–7.34). Morphological traits considered to be proxies of body size (wing length, tarsus length, toe length) were explained by urbanization variables in females (e.g., tarsus length: impervious surface area: estimate ± SE = −3.03 ± 1.22, CI: −5.42 to −0.64) but by climatic variables in males (e.g., wing length: mean temperature: estimate ± SE = −2.32 ± 0.66, CI: −3.62 to −1.02).

### Morphological variation in the introduced range

There was a set of more consistent signals in the introduced population, especially with regards to foraging-related traits. Urbanization was a significant explanatory factor in introduced populations globally in five morphological characters in females and four in males. Most traits were inversely proportional to impervious surfaces, or coalesced

**Table 1** Statistically significant predictor variables explaining the variance in morphological characters of common mynas in native and introduced populations, as analyzed with General Linear Mixed Models

| | Bill depth | Bill length | Bill width | Head | Premaxilla | Tarsus | Toe | Wing |
|---|---|---|---|---|---|---|---|---|
| *Native* | | | | | | | | |
| Females | | TMP (+) | TMP (+) | HD (−) | PET (−), TMP (+) | IMP (−), IMP$^2$ (−) | IMP$^2$ (+), PET (+) | HD$^2$ (+), PRE (+) |
| Males | | IMP$^2$ (+) | | ALT (+), DTR (+), PRE (+) | | | TMP (−), PET (+) | DTR (+), TMP (−) |
| *Introduced* | | | | | | | | |
| Females | DTR (+), HD (+), HD$^2$ (−), IMP (−), PET (−) | | HD (+), HD$^2$ (−), IMP (−), PRE (+), PET (−) | IMP (−) | ALT (−), IMP (−) | | HD (+), IMP (−) | |
| Males | TMP (+) | DTR (+) | ALT (-), IMP (−), HD (+), HD$^2$ (−) | IMP (−) | IMP (−), ALT (−), PET (−) | | IMP (−) | |

Signs in parentheses mark whether the trait has increased (+) or decreased (−) with respect to the explanatory variable based on estimates detailed in Tables S5 and S6. Results shown here were obtained by model averaging. Statistical significance was determined by confidence intervals not overlapping zero.

Predictor abbreviations are as follows: mean temperature (TMP), annual average precipitation (PRE), potential evapotranspiration (PET), diurnal temperature range (DTR), topographic variable (ALT), linear and quadratic terms of constructed impervious surface area (IMP, IMP$^2$, respectively) and linear and quadratic terms of human population density (HD, HD$^2$, respectively) towards an optimal value, depending on human density (Tables 1, S6). For example, bill width and bill depth had a parabolic relationship with human density (Fig. 2a, d, respectively), while premaxilla and head length decreased as impervious surfaces increased (Fig. 2b, c, respectively) in females (this trend was missing for bill depth in males, where temperature was a significant explanatory predictor; mean temperature: estimate ± SE = 0.12 ± 0.04, CI: 0.05–0.20). One body size related trait (the middle toe length) also decreased as impervious surfaces increased (in both sexes; Tables 1, S6). However, no significant explanatory predictor variable was found for traits related to the remaining body size-related traits in either sex (tarsus length and wing length; see Table 1, S6). Some variance in foraging-related traits was also explained by climatic factors (e.g., males, bill length, diurnal temperature range: estimate ± SE = 0.31 ± 0.10, CI: 0.10–0.50, but these represented no significant predictors in females).

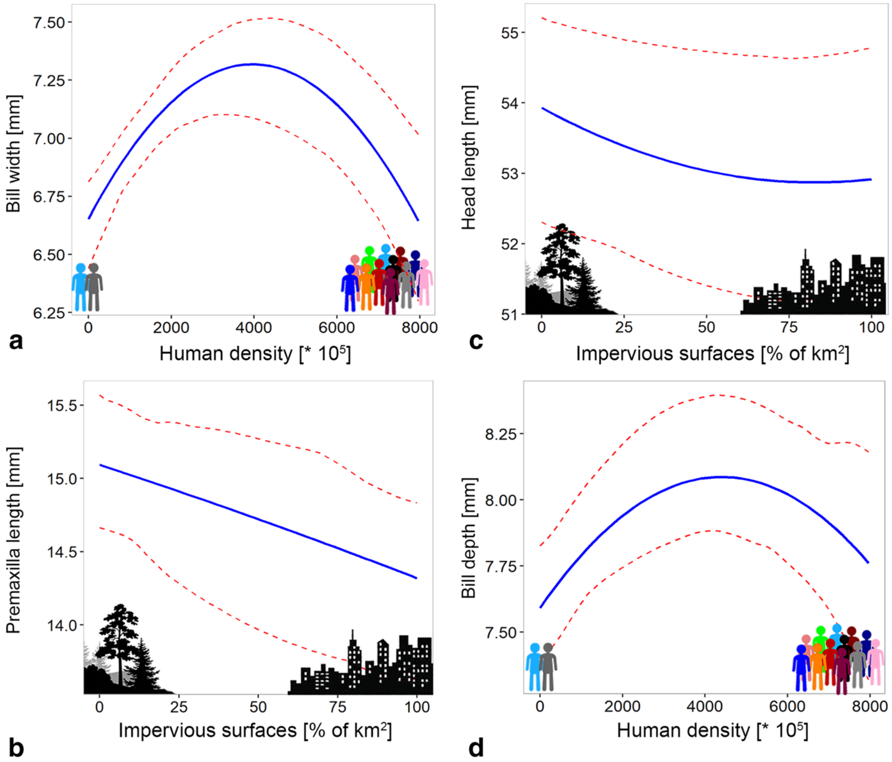
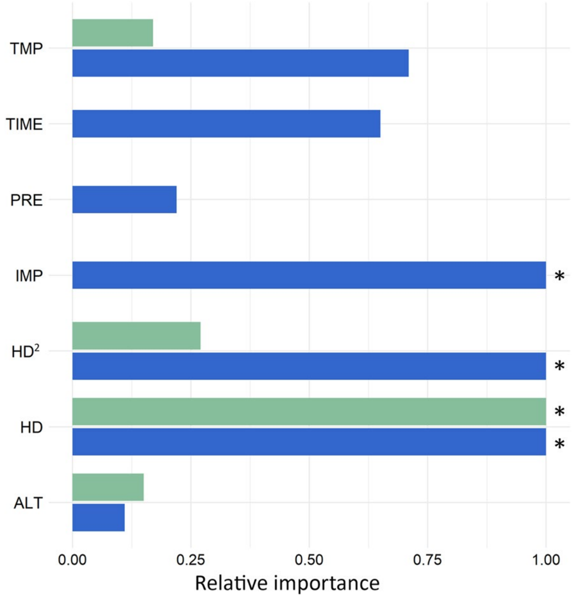


**Fig. 2** Morphological traits in female common mynas as model outputs of the function of anthropogenic factors. **a** Bill width [mm] as a function of human density [number of people per cell * $10^5$] **b** Premaxilla length [mm] as a function of impervious surfaces [density for each grid cell as a percentage of the total area in $km^2$] **c** Head length [mm] as a function of impervious surfaces [density for each grid cell as a percentage of the total area in $km^2$] **d** Bill depth [mm] as a function of human density [number of people per cell * $10^5$]. All other factors were kept constant. Dashed red lines represent upper and lower 95% confidence intervals

**Fig. 3** Relative importance of each of the predictors used to model male premaxilla length in the models selected for the population in Israel and Sydney, Australia. Models were selected using the Akaike information criterion (AIC) and averaged over the best models ($\Delta$AIC $\leq$ 2). Israel is represented by blue bars and Sydney, is represented by light green bars. Significant explanatory variables (determined by confidence intervals not overlapping 0) are marked with an asterisk. Abbreviations are as follows: mean temperature (TMP), years since the introduction (TIME), annual average precipitation (PRE), constructed impervious surface area (IMP), human population density (HD), and altitude (ALT)



## Putative adaptation in two introduced populations (Sydney, Australia and Israel)

We detected morphological shifts that varied between two focal introduced populations (Sydney, Australia and Israel) (Table S7, Fig. 3). Most traits were best explained by different factors or combinations of variables; for example, wing length in females was best explained in the Sydney population by human density (estimate ± SE = 0.63 ± 0.31, CI: 0.01–1.25), impervious surface area (estimate ± SE = 0.92 ± 0.57, CI: − 0.21–2.05) and its quadratic term (estimate ± SE = -0.32 ± 0.29, CI: − 0.89–0.25), time since the invasion (estimate ± SE = 1.14 ± 0.62, CI: − 0.09–2.38) and annual precipitation (estimate ± SE = 0.23 ± 0.38, CI: − 0.54 to − 0.99), whereas in the Israeli population, the best explaining factors included diurnal temperature range (estimate ± SE = − 3.39 ± 1.21, CI: − 5.79 to − 0.99), mean temperature (estimate ± SE = 7.03 ± 2.91, CI: 1.27–12.79), time since the invasion (estimate ± SE = 10.51 ± 3.93, CI: 2.72–18.30) and human density (estimate ± SE = − 0.34 ± 0.39, CI: − 1.12–0.43). Additionally, there was an inverse relationship between measurements in different populations for traits that were best explained by the same factors (e.g., premaxilla length in females, impervious surface area: Sydney: estimate ± SE = − 0.33 ± 0.15, CI: − 0.63 to − 0.02; Israel: estimate ± SE = 0.45 ± 0.19, CI: 0.08–0.83). Generally, most of the statistically significant explanatory factors were anthropogenic (impervious surface area or human density). Furthermore, in both populations, some traits were significantly correlated with the time since the introduction event. In Israel, two out of eight traits were significantly correlated with the time since the invasion in at least one of the sexes (bill depth in males, estimate ± SE = 1.77 ± 0.53, CI: 0.72–2.83, and wing length in females, estimate ± SE = 10.51 ± 3.93, CI: 2.72–18.30), whereas in Sydney this occurred in three traits (e.g., head length in both males and females, Fig. 4).

## Discussion

This study aimed to determine how morphological traits are shaped during biological invasions, and whether similar environmental conditions may act as selective pressures on native and/or introduced populations. We explored how morphological variation may evolve in different environments by comparing different introduced populations. Our main findings infer a major role of urbanization in predicting the shape and size of foraging-related traits in introduced populations, while selective pressures appear to vary across geographically disjunct populations.

Similarly to previous reports (Baker and Moeed 1979, 1980; Berthouly-Salazar et al. 2012), sexual dimorphism in size metrics was evident in mynas across the species' range. We found that different explanatory predictors often explained the variation in females vs. males in both native and introduced populations. Previous studies also reported sex-specific patterns in response to environmental conditions (Ball and Ketterson 2008; Honnen et al. 2016; Bezler et al. 2019; Tolla and Stevenson 2020). For example, in white-crowned sparrows (*Zonotrichia leucophrys*), higher baseline corticosterone levels were detected in urban males, but not in urban females (Bonier et al. 2007); urban male house finches (*Haemorhous mexicanus*) were more parasitized than desert males, but not urban females (Sykes et al. 2020); and urban female tree lizards (*Urosaurus ornatus*) had longer snout-vent length than females at semi-natural and natural sites, but no significant differences were found among males (French et al. 2008). Intraspecies sex-specific difference to environmental cues may stem from a multitude of factors including behavior, endocrine profile, spatial preferences and morphological constraints (Ball and Ketterson 2008; Tolla and Stevenson 2020). We suggest that morphological patterns in response to environmental conditions be examined with respect to sex both in dimorphic and monomorphic species.

### Difference in selective pressures among native and introduced populations.

General biogeographic patterns have been shown to explain morphological variation both within and among species, including birds (Meiri and Dayan 2003; Salewski and Watt

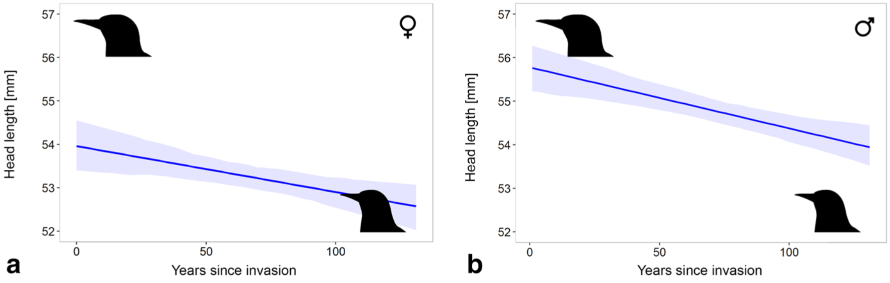


**Fig. 4** Head length [mm] as a function of the number of years since invasion in females **a** and males **b** in the Sydney population as predicted by General Linear Mixed Models that were run with the other fixed predictors as constant at their respective means. The fixed factors were those included in the model averaged over the best models per each sex (Table S7). Shaded areas are upper and lower 95% confidence intervals. Models were run with 100 bootstraps (with function 'boot' from the 'car' R package, (Fox and Weisberg 2019)) over an expanded grid

2017; Andrew et al. 2018; Nwaogu et al. 2018). In turn, whereas in native populations the environmental conditions have been in place for evolutionary-scaled time periods (with the exception of more recently induced changes, such as climate change and urbanization), introduced populations are subjected to additional factors, such as time since introduction, and/or a reduction in genetic diversity due to founder effect (Gibson et al. 1984; Phillips and Shine 2005). Therefore, comparing morphological variation between native and introduced populations can reveal invasion-induced phenotypes that may be beneficial in the introduced range, under the constraints of unknown genetic origins. Here we report morphological traits in native populations are associated with different explanatory predictors (Tables 1, S5) to that of traits in introduced populations (Tables 1, S6).

In the native range, variation in morphological traits was explained by different factors and the patterns were relatively inconsistent. These results are in accordance with morphometric variation described in common myna populations in India, where size variation was not related linearly to environmental factors (Baker and Moeed 1980). Baker and Moeed (1980) speculated that interspecific competition and food particle size may act as selective pressures in different regions, leading to the lack of observed pattern. Because of the global resolution of our study, data on local species composition or resource availability is difficult to obtain, and therefore we cannot exclude their effect on the data analysis. Moreover, our results support the presence of factors other than climate or topography that give rise to these variable patterns across their native range, including urbanization related factors. Conversely, urbanization (i.e., impervious surfaces or human population density) was the best explanatory predictor for five morphological traits in females in introduced populations, and four traits in males (Table 1, S6). Berthouly-Salazar et al. (2012) reported similar results in an introduced population of common mynas in South Africa, where characters associated with foraging were significantly correlated to urbanization intensity (but also vegetation). The impact of urbanization on morphology has been reported in many species (e.g., house finch (Giraudeau et al. 2014); Puerto Rican crested anole, *Anolis cristatellus* (Hall and Warner 2017); and house sparrow, *Passer domesticus* (Meillére et al. 2015)), and some studies suggested that this trend extends to introduced populations (e.g., European starling, *Sturnus vulgaris* (Bitton and Graham 2015); brown rat (*Rattus norvegicus*) (Puckett et al. 2020); and red fox, *Vulpes vulpes* (Stepkovitch et al. 2019)). The importance of factors additional to those in the native range, that explain morphometric patterns in the introduced populations (mainly anthropogenic), suggests that different selective forces act on native and invasive populations. Therefore, consideration is required in studies relating to evolutionary adaptations and predictions made when characterizing invasive populations across their introduced ranges, morphometric or other.

Natural drivers of phenotypic variation have been largely displaced by anthropogenic impacts, leading to an alteration of natural macroecological patterns (Santini et al. 2017). Human-dominated landscapes can cause habitat homogenization (Frishkoff et al. 2016), alter land surface temperatures (Ma et al. 2016) and precipitation levels (Seress and Liker 2015), modify nutrient cycles (Western 2001), become "ecological traps" (i.e., inappropriate habitat selection and behavioral and life-history decisions) (Rodewald et al. 2011) and mask original biogeographical drivers (Di Marco and Santini 2015). These changes can induce character displacement in urban populations that increase fitness. For example, house sparrows in more urbanized habitats had reduced body size and body mass compared to their rural conspecifics (Meillére et al. 2015), urbanization intensity affected wing pointedness in common blackbirds (*Turdus merula*) (Saccavino et al. 2018), and human behavior combined with ongoing urbanization has started changing niche differences that would otherwise support adaptive radiation in Darwin's finches on one of the Galápagos

Islands (De Leon et al. 2018). In particular, urban environments offer different food items or require different foraging techniques, which has been shown to affect the morphology of foraging-related traits such as bill length (Badyaev et al. 2008; Giraudeau et al. 2014; Bosse et al. 2017). In introduced populations of common mynas, we found that foraging-related characters (bill width, premaxilla length, head length in both sexes and bill depth in females) were mostly negatively correlated with urbanization proxies (i.e., impervious surfaces and human population density), suggesting that urbanized areas offer characteristic nutrition that favors certain phenotypes (size-related traits), irrelevant of the climatic conditions present. Our findings provide global support to Berthouly-Salazar et al. (2012), who showed a correlation between urbanization and bill shape in an introduced population in South Africa.

The presence of significant correlations between urbanization and foraging-related traits, but not body size proxies (e.g., tarsus length), suggests that urban selective drivers act on specific morphological characters that facilitate adaptation to resource availability in introduced common myna populations. We recently demonstrated that the probability of common myna presence increases as the environment becomes more impervious (i.e., more urbanized) (Magory Cohen et al. 2019). Our present findings suggest that this habitat preference may be aided by rapid morphological adaptation to urban diet or foraging requirements. This association may be more evident in the introduced range for several reasons. Firstly, introductions often happen in urban areas, hence the first invaders must cope with and survive in urbanized environments. Secondly, even after invading, few introduced common myna populations currently occur outside of urban or sub-urban areas (Old et al. 2014), whereas native populations were traditionally described from agricultural areas as well (Long 1981). Lastly, despite a comprehensive data-set, most of the native specimens we recorded were collected before the first half of the twentieth century, before urbanization increased greatly, therefore limiting our temporal perspective of the native range. Nonetheless, the signal observed in the introduced populations is statistically significant with a large effect size and maximal relative importance in most cases. Therefore, our findings indicate that morphological adaptations to urbanization have occurred in foraging-related traits in common mynas in introduced populations, possibly allowing the species to remain commensal throughout most of its invasive range.

To test whether local adaptation occurred similarly across the introduced range while controlling for time since introduction, we searched for patterns shared by introduced populations while accounting for the different invasions stages that they are in (i.e., the latency in years since the introduction). Our results lack consistent patterns across most traits and across sexes, in that different predictor variables explained the observed patterns. In a morphometric study on introduced common myna populations in Australia, New Zealand, Fiji and Hawaii, Gibson et al. (1984) noted that despite results indicating qualitatively similar selection among populations, there was variably intense stabilizing selection, leading to differences among populations introduced to different geographic localities. Gibson et al. (1984) suggested that the simple within-population covariation structure they observed may be a consequence of the small founding populations, or alternatively, the limited time since the introduction. The differences between the patterns among introduced populations may be the result of temporal (i.e., time sufficient for selection or plastic response), environmental or genetic (e.g., founder effect, introduction origin) constraints that emphasize the need to account for local-scale responses. However, in both populations, the majority of predictive factors that best described the morphometric variation were anthropogenic, indicating that the global trend can also be detected in higher local resolutions.

## Invasion-induced morphological variation

The challenges raised by novel environments require certain adjustments to be made, particularly during the initial establishment and subsequent dispersal invasion stages (Blackburn et al. 2011). Some invaders show significant character displacement between the native and the invasive range (Erfmeier and Bruelheide 2004; Zou et al. 2007), whereas others differ in fewer morphological traits (Polačik et al. 2012). These changes can occur in certain parts of the invasive range (i.e., at the invasion front, where a species had recently colonized) or throughout the entire population if sufficient time has passed for adaptation to occur (Shine et al. 2011).

Previous research has indicated that certain phenotypic traits that enhance rates of dispersal, such as longer limb length (Phillips and Shine 2005; Phillips et al. 2006) or wing length (Simmons and Thomas 2004; Berthouly-Salazar et al. 2012; Bitton and Graham 2015), accumulate at expanding range edges, a process referred to as 'spatial sorting' (Shine et al. 2011). This evolutionary mechanism is thought to operate as a subset of natural selection, that is based on differentials in dispersal rate through space rather than differentials in survival rate or reproductive success through time (Shine et al. 2011). Because the adaptive value of these traits is expected to aid first invaders in expanding the invasion range, spatial sorting is expected to constantly progress along the expanding invasion front, and its effect is dependent on the time since the arrival of colonizing individuals (i.e., time since invasion). In this study, we did not include a variable of distance from the introduction core because common myna spread had occurred unevenly throughout some regions in our dataset (e.g., in Israel, where spread occurred along the urban coast earlier than it did along a more natural altitudinal cline). In such cases, distance from the source does not correlate with differences between the core and the range front and hence may bias the analyses. However, time since the invasion reflects whether the locality is a range front, and therefore describes spatial sorting more accurately, we employed it as a proxy for identifying range fronts. Alternatively, if a range expansion occurs in a continuous manner equally across a landscape, the distance between the core population and the invasion front can be utilized to investigate traits related to dispersal. In an introduced population of common mynas in South Africa, Berthouly-Salazar et al. (2012) found that head length, wing length and wing loading were positively correlated with distance from the source of the invasion in females, indicating spatial sorting. Our analyses show evidence of spatial sorting (a significant increase in head length in the range front) in the Sydney population (long-term introduction) but not the Israeli population (recent introduction) (Table S7). It is possible that in the recently introduced Israeli population, there was insufficient time since the first colonialization event (less than 25 years) for the traits to stabilize in the core population. Alternatively, the use of time since invasion to define the range front, however plausible, may not represent the spatial sorting processes sufficiently. Revisiting this data in the future could possibly enable a better perspective on this mechanism in recently introduced populations.

It is possible that other selective forces masked the effect of spatial sorting. Time since invasion was correlated with traits unrelated to dispersal, including bill length and head length in both sexes and with bill width in females in the Sydney population, and with bill depth in males in the Israeli population (Table S7). Classical natural selection may have acted on these traits in response to habitat quality or resources availability, also known as the 'resource rule' (McNab 2010). Yom-Tov and Geffen (2011) argue that weather-driven food supply may affect body size directly or indirectly, in the same way as population size fluctuates with resource availability, either via adaptive genetic changes or plastic responses. Food availability has been shown to be correlated with body size in amphibians (Green and Middleton 2013), mammals (Gür and Kart Gür 2012; Boast et al. 2013; Schiaffini et al. 2019), birds (Salewski et al. 2014; Sun et al. 2017) and reptiles (Jessop et al. 2016), and has been suggested to drive phenotypic variation in an invasive mink (*Neovison vison*) (Zalewski and Bartoszewicz 2012). Because we did not (i) sample individuals more than once, (ii) estimate their genetic and transcriptomic makeup, or (iii) perform common garden experiments, we cannot determine whether the phenotypes documented here arose from genetic adaptation or a plastic response. Most of the traits measured likely change very little throughout an individual life span once the individual has reached adulthood (e.g., tarsus length), but others may change more readily under certain environmental conditions such as stress (e.g., wing length, (Butler et al. 2010)). Since natural selection requires time, traits would appear to change over the course of several generations. Therefore, given the observed correlations between time since invasion and morphological traits unrelated to dispersal, we favor the explanation of natural selection generating these phenotypes in the context of biological invasions, although our data cannot fully exclude the role of phenotypic plasticity.

Many factors, both intrinsic and extrinsic, can influence the morphological composition of an individual, including inter- and intra-specific competition, resource availability, wildlife management (including hunting pressure), and developmental and growth rates (as well as those previously discussed; Yom-Tov and Geffen 2011). In invasive species, the morphological profile also depends on limiting factors such as the original gene pool of the founding population and time since introduction combined with rates of phenotypic change (through local adaptation or plasticity) (Phillips and Shine 2006). In particular, the genetic makeup of the founding population may dictate the rate and direction of selection (Mayr 1963, 1982). Our efforts to explain morphological patterns in native and introduced populations of common mynas did not incorporate these details, and therefore cannot exclude the possibility that they contribute to explaining the patterns we describe. Due to the large scale of our study that included many introductions of largely unknown origins, the genetic makeup of the introduced individuals and the variation among introduced populations may amplify particular signals. In addition, though extensive in its geographical sampling, this study was also limited by the availability of specimens collected in the native range, especially in recent years. Moreover, we corrected only partially for spatial autocorrelation in our data, making the observed trends potentially non-independent. However, we believe that the magnitude and geographic extent of our sample size somewhat decreases bias stemming from spatial autocorrelation, especially in an avian species, like the myna, with varying home ranges. Despite these caveats, we show consistent global trends relating urbanization to morphological changes in introduced common myna populations that were not found in native populations. Our results emphasize the impact of human-induced environmental changes on the trajectory of biological invasions, ultimately affecting biodiversity.

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s10682-021-10107-y.

**Acknowledgements** The authors wish to thank Eyal Deri, Mark Katz, Ohad Hatozfe, Giselle Hazan, Doron Nissim, Gonen Bahir, Ori Linial, Asaf Kaplan, Eran Hymes, Gal Bismuth, Amir Shafir, Zehava Siegal and other rangers of the Israel Nature and Parks Authority, and Manju Siliwal, Yotam Ghendler, Yoav Motro, Yonatan Veronski, Asaf Yitzhaki, Sveta Weismann, Darren Burns, Snir Halle, Hala Kasis, Imam Hussain, Mohammad Rafi, Deven Mehta, Hareendra Baraiya, Sarabjeet and Ankita Bhatt and the many colleagues and volunteers who helped collect samples.

**Author's contributions** TMC designed the study, contributed to data collection, carried out the analyses and drafted the manuscript; RM contributed to data collection and drafted the manuscript; RSK contributed to data collection and drafted the manuscript; MN contributed to data collection and drafted the manuscript; KE helped with data analsis and drafted the manuscript; MEH helped with data interpretation and drafted the manuscript; and RD designed the study and drafted the manuscript.

**Funding** This work was supported by the Tel Aviv University Global Research & Training Fellowship in Medical and Life Sciences (GRTF) fund, The Smaller-Winnikow Fellowship Fund for Environmental Research, The Rieger Foundation-Jewish National Fund fellowship, and the Heredity Fieldwork Grant of the Genetics Society UK. This research was also supported by Grant No. 2017285 from the United States-Israel Binational Science Foundation (BSF; to RD and MEH). RSK and MN were provided an in-house grant of the Wildlife Institute of India for undertaking fieldwork in India. MEH was supported by the Hanse-Wissenschaftskolleg (Institute for Advanced Study), Germany, during the preparation of the manuscript. RSK and MN were provided an in-house grant of the Wildlife Institute of India for undertaking fieldwork in India.

**Data availability and material** Sampling locations and morphological data are available in Figshare https://doi.org/10.6084/m9.figshare.13302242.

### Declarations

**Conflict of interest** The authors declare no conflicts of interest.

**Consent for publication** All authors gave final approval for publication.

**Ethical approval** All animal care procedures were approved by the Tel Aviv University ethics committee (permit nos. L-15-033 and 04-17-056), the Israel Nature and Parks Authority (permit numbers 2015/40828 and 2017/41780), the Australian Museum Animal Care and Ethics Committee (approval number 15–03), and the Wildlife Institute of India Animal Welfare committee and Uttarakhand State Forest department permit (L. No. 1258/5–6).

## References

Alford RA, Brown GP, Schwarzkopf L et al (2009) Comparisons through time and space suggest rapid evolution of dispersal behaviour in an invasive species. Wildl Res 36:23–28

Alter SE, Tariq L, Creed JK, Megafu E (2021) Evolutionary responses of marine organisms to urbanized seascapes. Evol Appl 14(1):210–232

Andrew SC, Awasthy M, Griffith AD et al (2018) Clinal variation in avian body size is better explained by summer maximum temperatures during development than by cold winter temperatures. Auk 135:206–217

Badyaev AV, Young RL, Oh KP, 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

Baker AJ, Moeed A (1979) Evolution in the introduced New Zealand population of the common myna. Can J Zool 57:570–584

Baker AJ, Moeed A (1980) Morphometric variation in Indian samples of the Common Myna, *Acridotheres tristis* (Aves: Sturnidae). Bijdr tot Dierkd 50:351–363

Ball GF, Ketterson ED (2008) Sex differences in the response to environmental cues regulating seasonal reproduction in birds. Philos Trans R Soc B Biol Sci 363:231–246

Barton K (2018) MuMIn: Multi-model inference. R package version 0.12. 2/r18.

Bergmann C (1848) Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. Göttinger Stud, pp. 595–708.

Berthouly-Salazar C, Hui C, Blackburn TM et al (2013) Long-distance dispersal maximizes evolutionary potential during rapid geographic range expansion. Mol Ecol 22:5793–5804

Berthouly-Salazar C, van Rensburg BJ, Le Roux JJ et al (2012) Spatial sorting drives morphological variation in the invasive bird, *Acridotheres tristis*. PLoS ONE 7:1–9

Bezler A, Id FB, West SM et al (2019) Tissue- and sex-specific small RNAomes reveal sex differences in response to the environment. PLoS Genet 15:e1007905

Bitton PP, Graham BA (2015) Change in wing morphology of the European starling during and after colonization of North America. J Zool 295:254–260

Blackburn TM, Pyšek P, Bacher S et al (2011) A proposed unified framework for biological invasions. Trends Ecol Evol 26:333–339

Blondel J, Dias PC, Perret P et al (1999) Selection-based biodiversity at a small spatial scale in a low-dispersing insular bird. Science 285:1399–1402

Boast LK, Houser AM, Good K, Gusset M (2013) Regional variation in body size of the cheetah (*Acinonyx jubatus*). J Mammal 94:1293–1297

Bonier F, Martin PR, Sheldon KS et al (2007) Sex-specific consequences of life in the city. Behav Ecol 18:121–129

Bosse M, Spurgin LG, Laine VN et al (2017) Recent natural selection causes adaptive evolution of an avian polygenic trait. Science 358:365–368

Butler MW, Leppert LL, Dufty AM Jr (2010) Effects of small increases in corticosterone levels on morphology, immune function, and feather development. Physiol Biochem Zool 83:78–86

Cardilini APA, Buchanan KL, Sherman CDH et al (2016) Tests of ecogeographical relationships in a non-native species: what rules avian morphology? Oecologia 181:783–793

Cerwenka AF, Alibert P, Brandner J et al (2014) Phenotypic differentiation of Ponto-Caspian gobies during a contemporary invasion of the upper Danube River. Hydrobiologia 721:269–284

CIESIN FAO (2014) CIAT (Center for International Earth Science Information Network—CIESIN—Columbia University, United Nations Food and Agriculture Programme—FAO, and Centro Internacional de Agricultura Tropical—CIAT)(2005) Gridded Population of the World, Version 3 (GPWv3).

Clarke GS, Shine R, Phillips BL (2019) May the (selective) force be with you: Spatial sorting and natural selection exert opposing forces on limb length in an invasive amphibian. J Evol Biol 32:994–1001

Cramp S, Perrins CM (1994) The birds of the western Palearctic crows to finches. Oxford University Press, Oxford

De Leon LF, Sharpe DMT, Gotanda KM et al (2018) Urbanization erodes niche segregation in Darwin's finches. Evol Appl 12:1329–1343

Delhey K (2017) Gloger's rule. Curr Biol 27:R689–R691

Di Marco M, Santini L (2015) Human pressures predict species' geographic range size better than biological traits. Glob Chang Biol 21:2169–2178

Eddinger CR (1967) A study of the breeding behaviour of the Myna (*Acridotheres tristis* L.). Elepaio 28:1–12

Elvidge CD, Tuttle BT, Sutton PC et al (2007) Global distribution and density of constructed impervious surfaces. Sensors 7:1962–1979

Erfmeier A, Bruelheide H (2004) Comparison of native and invasive *Rhododendron ponticum* populations: growth, reproduction and morphology under field conditions. Flora 199:120–133

Ewart KM, Griffin A, Johnson RN et al (2018) Two speed invasion: assisted and intrinsic dispersal of common mynas over 150-years of colonization. J Biogeogr 46:45–57

Feldman A, Meiri S (2014) Australian snakes do not follow Bergmann's rule. J Evol Biol 41:327–335

Fox J, Weisberg S (2019) An R companion to applied regression, 3rd edn. Sage publications, Thousand Oaks

French SS, Fokidis HB, Moore MC (2008) Variation in stress and innate immunity in the tree lizard (*Urosaurus ornatus*) across an urban—rural gradient. J Comp Physiol B 178:997–1005

Fridolfsson A-K, Ellegren H (1999) A simple and universal method for molecular sexing of non-ratite birds. J avian Biol 30:116–121

Frishkoff LO, Karp DS, Flanders JR et al (2016) Climate change and habitat conversion favour the same species. Ecol Lett 19:1081–1090

Gibson AR, Baker AJ, Moeed A (1984) Morphometric variation in introduced populations of the common myna (*Acridotheres tristis*): an application of the jackknife to principal component analysis. Syst Zool 33:408–421

Giraudeau M, Nolan PM, Black CE et al (2014) Song characteristics track bill morphology along a gradient of urbanization in house finches (*Haemorhous mexicanus*). Front Zool 11:1–8

Gleditsch JM, Sperry JH (2019) Rapid morphological change of nonnative frugivores on the Hawaiian island of O'ahu. Evolution 73:1456–1465

Gloger CWL (1833) Das Abändern der Vögel durch Einfluss des Klimas. Breslau, Germany

Grant PR (1979) Ecological and morphological variation of Canary Island blue tits, *Parus caeruleus* (Aves: Paridae). Biol J ouml afthe Linn Soc 11:103–129

Grant PR, Grant BR (1995) Predicting microevolutionary responses to directional selection on heritable variation. Evolution 49:241–251

Green DM, Middleton J (2013) Body size varies with abundance, not climate, in an amphibian population. Ecography 36:947–955

Gruber JE (2017) Geographical divergence of behavioural traits in the invasive cane toad (*Rhinella marina*). Available from The University of Sydney eScholarship Repository. (430591572)

Gür H, Kart Gür M (2012) Is spatial variation in food availability an explanation for a Bergmannian size pattern in a North American hibernating, burrowing mammal? An information-theoretic approach. J Zool 287:104–114

Hall JM, Warner DA (2017) Body size and reproduction of a non-native lizard are enhanced in an urban environment. Biol J Linn Soc 122:860–871

Harris I, Jones PD, Osborn TJ, Lister DH (2014) Updated high-resolution grids of monthly climatic observations—the CRU TS3.10 Dataset. Int J Climatol 34:623–642

Honnen A, Johnston PR, Monaghan MT (2016) Sex-specific gene expression in the mosquito *Culex pipiens* f. molestus in response to artificial light at night. BMC Genomics. https://doi.org/10.1186/s12864-015-2336-0

Hudson CM, Brown GP, Shine R (2016) Athletic anurans: the impact of morphology, ecology and evolution on climbing ability in invasive cane toads. Biol J Linn Soc 119:992–999

IUCN (2019) The IUCN Red List of Threatened Species. Version 2019–1. http://www.iucnredlist.org. Accessed 16 May 2019

Jessop TS, Madsen T, Sumner J et al (2016) Maximum body size among insular Komodo dragon populations covaries with large prey density. Nord Soc Oikos 112:422–429

Johnston RF, Selander RK (1964) House sparrows: rapid evolution of races in North America. Science 144:548–550

Kern EMA, Langerhans RB (2018) Urbanization drives contemporary evolution in stream fish. Glob Chang Biol 24:3791–3803

Lahti DC, Johnson NA, Ajie BC et al (2009) Relaxed selection in the wild. Trends Ecol Evol 24:487–496

Lefebvre L, Reader SM, Sol D (2004) Brains, innovations and evolution in birds and primates. Brain Behav Evol 63:233–246

Liker A, Papp Z, Bókony V, Lendvai ÁZ (2008) Lean birds in the city: Body size and condition of house sparrows along the urbanization gradient. J Anim Ecol 77:789–795

Long JL (1981) Introduced birds of the world: The worldwide history, distribution and influence of birds introduced to new environments. Universe Books, New York

Ma Q, Wu J, He C (2016) Effects of urban impervious surfaces on land surface temperatures: Spatial scale dependence, temporal variations, and bioclimatic modulation. In: EGU General Assembly Conference Abstracts. pp EPSC2016–1802.

Magory Cohen T, Dor R (2019) The effect of local species composition on the distribution of an avian invader. Sci Rep 9:15861

Magory Cohen T, Haran R, Dor R (2018) Signals of local adaptation across an environmental gradient among highly connected populations of the Dead Sea Sparrow *Passer moabiticus* in Israel. Ibis 161:619–631

Magory Cohen T, Kumar RS, Nair M et al (2020) Innovation and decreased neophobia drive invasion success in a widespread avian invader. Anim Behav 163:61–72

Magory Cohen T, McKinney M, Kark S, Dor R (2019) Global invasion in progress: modeling the past, current and potential global distribution of the common myna. Biol Invasions 21:1295–1309

Mathys BA, Lockwood JL (2011) Contemporary morphological diversification of passerine birds introduced to the Hawaiian archipelago. Proc R Soc B Biol Sci 278:2392–2400

Mayr E (1963) Animal species and evolution. Harvard University Press, Cambridge

Mayr E (1982) Speciation and Macroevolution. Evolution 36:1119–1132

McNab BK (2010) Geographic and temporal correlations of mammalian size reconsidered: a resource rule. Oecologia 164:13–23

Meillére A, Brischoux F, Parenteau C, Angelier F (2015) Influence of urbanization on body size, condition, and physiology in an urban exploiter: a multi-component approach. PLoS ONE 10:e0135685

Meiri S, Dayan T (2003) On the validity of Bergmann's rule. J Biogeogr 30:331–351

Meiri S, Dayan T, Simberloff D (2004) Carnivores, biases and Bergmann's rule. Biol J Linn Soc 81:579–588

Meiri S, Yom-tov Y, Geffen E (2007) What determines conformity to Bergmann's rule? Glob Ecol Biogeogr 16:788–794

METI/NASA (2011) ASTER Global Digital Elevation. Model V002. In: NASA EOSDIS L. Process. DAAC, USGS Earth Resour. Obs. Sci. Center, Sioux Falls, South Dakota. https://lpdaac.usgs.gov. Accessed 23 Apr 2017.

Mori E, Saavedra S, Menchetti M, Assandri G (2020) Past and present distribution of the Common Myna *Acridotheres tristis* in Italy: a review. Avocetta 44:32–36

Norazlimi NA, Ramli R (2015) The Relationships between morphological characteristics and foraging behavior in four selected species of shorebirds and water birds utilizing tropical mudflats. Sci World J. https://doi.org/10.1155/2015/105296

Nwaogu CJ, Tieleman BI, Bitrus K, Cresswell W (2018) Temperature and aridity determine body size conformity to Bergmann's rule independent of latitudinal differences in a tropical environment. J Ornithol 159:1053–1062

Old JM, Spencer R, Wolfenden J (2014) The Common Myna (*Sturnus tristis*) in urban, rural and semi-rural areas in Greater Sydney and its surrounds areas in Greater Sydney and its surrounds. Emu—Austral Ornithol 114:241–248

Paradis E, Schliep K (2018) Ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35:526–528

Phillips BL, Brown GP, Shine R (2010) Evolutionarily accelerated invasions: the rate of dispersal evolves upwards during the range advance of cane toads. J Evol Biol 23:2595–2601

Phillips BL, Brown GP, Webb JK, Shine R (2006) Invasion and the evolution of speed in toads. Nature 473:803

Phillips BL, Shine R (2005) The morphology, and hence impact, of an invasive species (the cane toad, *Bufo marinus*): Changes with time since colonisation. Anim Conserv 8:407–413

Phillips BL, Shine R (2006) Spatial and temporal variation in the morphology (and, thus, predicted impact) of an invasive species in Australia. Ecography 29:205–212

Polačik M, Janáč M, Vassilev M, Trichkova T (2012) Morphometric comparison of native and non-native populations of round goby *Neogobius melanostomus* from the River Danube. Folia Zool 61:1–8

Puckett EE, Sherratt E, Combs M et al (2020) Variation in brown rat cranial shape shows directional selection over 120 years in New York City. Ecol Evol 10:4739–4748

R Core Team (2019) R: A Language and Environment for Statistical Computing. R foundation for statistical computing, Vienna, Austria http://www.R-project.org.

Rodewald AD, Shustack DP, Jones TM (2011) Dynamic selective environments and evolutionary traps in human-dominated landscapes. Ecology 92:1781–1788

Roser M, Ortiz-Ospina E (2018) World Population Growth. In: OurWorldInData.org. https://ourworldindata.org/world-population-growth.

Ross WA, Baker AJ (1982) Variation in the size and shape of introduced starlings, *Sturnus vulgaris* (Aves: Sturninae), in New Zealand. Can J Zool 60:3316–3325

Saavedra S, Maraver A, Anadón JD, Tella JL (2015) A survey of recent introduction events, spread and mitigation efforts of mynas (*Acridotheres sp.*) in Spain and Portugal. Anim Biodivers Conserv 38:121–128

Saccavino E, Krämer J, Klaus S, Thomas D (2018) Does urbanization affect wing pointedness in the Blackbird Turdus merula? J Ornithol 159:1043–1051

Sæther SA, Fiske P, Ka JA (2007) Inferring local adaptation from QST–FST comparisons : neutral genetic and quantitative trait variation in European populations of great snipe. J Evol Biol 20:1563–1576

Salewski V, Hochachka WM, Flinks H (2014) Changes in Stonechat Saxicola torquata morphology: A response to climate change? J Ornithol 155:601–609

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

Santini L, González-Suárez M, Rondinini C, Di Marco M (2017) Shifting baseline in macroecology? Unravelling the influence of human impact on mammalian body mass. Divers Distrib 23:640–649

Schiaffini MI, Segura V, Prevosti FJ (2019) Geographic variation in skull shape and size of the Pampas fox *Lycalopex gymnocercus* (Carnivora: Canidae) in Argentina. Mamm Biol 97:50–58

Seress G, Liker A (2015) Habitat urbanization and its effects on birds. Acta Zool Acad Sci Hungaricae 61:373–408

Shapiro SS, Wilk MB (1965) An analysis of variance test for normality (complete samples). Biometrika 52:591–611

Shine R, Brown GP, Phillips BL (2011) An evolutionary process that assembles phenotypes through space rather than through time. Proc Natl Acad Sci 108:5708–5711

Simmons T (2004) Changes in dispersal during species' range expansions. Am Nat 164:378–395

Sol D, Uncan RP, Blackburn TM et al (2005) Big brains, enhanced cognition, and response of birds to novel environments. Proc Natl Acad Sci 102:5460–5465

Stepkovitch B, Martin JM, Dickman CR, Welbergen JA (2019) Urban lifestyle supports larger red foxes in Australia: an investigation into the morphology of an invasive predator. J Zool 309:287–294

Suh A, Kriegs JO, Brosius J, Schmitz J (2011) Retroposon insertions and the chronology of avian sex chromosome evolution. Mol Biol Evol 28:2993–2997

Sun Y, Li M, Song G et al (2017) The role of climate factors in geographic variation in body mass and wing length in a passerine bird. Avian Res 8:1–9

Sykes BE, Hutton P, McGraw KJ (2020) Sex-specific relationships between urbanization, parasitism, and plumage coloration in house finches. Curr Zool. https://doi.org/10.1093/cz/zoaa060

Tolla E, Stevenson TJ (2020) Sex differences and the neuroendocrine regulation of seasonal reproduction by supplementary environmental cues. Integr Comp Biol 60:1506–1516

Tomassini A, Colangelo P, Agnelli P et al (2014) Cranial size has increased over 133 years in a common bat, *Pipistrellus kuhlii*: A response to changing climate or urbanization? J Biogeogr 41:944–953

Western D (2001) Human-modified ecosystems and future evolution. Proc Natl Acad Sci 98:5458–5465

Yom-Tov Y, Geffen E (2011) Recent spatial and temporal changes in body size of terrestrial vertebrates: probable causes and pitfalls. Biol Rev 86:531–541

Yu A, Munshi-South J, Sargis EJ (2017) Morphological differentiation in white-footed mouse (Mammalia: Rodentia: Cricetidae: *Peromyscus leucopus*) populations from the New York City metropolitan area. Bull Peabody Museum Nat Hist 58:3–16

Zalewski A, Bartoszewicz M (2012) Phenotypic variation of an alien species in a new environment: the body size and diet of American mink over time and at local and continental scales. Biol J Linn Soc 105:681–693

Zou J, Rogers WE, Siemann E (2007) Differences in morphological and physiological traits between native and invasive populations of *Sapium sebiferum*. Funct Ecol 21:721–730

## Authors and Affiliations

**Tali Magory Cohen[1,2] · Richard E. Major[3] · R. Suresh Kumar[4] · Manoj Nair[4] · Kyle M. Ewart[3] · Mark E. Hauber[5] · Roi Dor[6]**

[1] School of Zoology, Faculty of Life Sciences, Tel Aviv University, 69978 Tel Aviv, Israel

[2] Steinhardt Museum of Natural History, Tel Aviv University, 69978 Tel Aviv, Israel

[3] Australian Museum Research Institute, Australian Museum, 1 William St, Sydney, NSW 2010, Australia

[4] Department of Endangered Species Management, Wildlife Institute of India, Dehradun, Uttarakhand 248 001, India

[5] Department of Evolution, Ecology, and Behavior, School of Integrative Biology, University of Illinois At Urbana-Champaign, Urbana, IL 61801, USA

[6] Department of Natural and Life Sciences, The Open University of Israel, 4353107 Ra'Anana, Israel