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DOI: <https://doi.org/10.1002/ece3.9217>

Posted at the Zurich Open Repository and Archive, University of Zurich

ZORA URL: <https://doi.org/10.5167/uzh-220648>

Journal Article

Published Version



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Originally published at:

Hüppi, Evelyn; Geiger, Madeleine (2022). Fast-paced city life? Tempo and mode of phenotypic changes in urban birds from Switzerland. *Ecology and Evolution*, 12(8):e9217.

DOI: <https://doi.org/10.1002/ece3.9217>

RESEARCH ARTICLE

Fast-paced city life? Tempo and mode of phenotypic changes in urban birds from Switzerland

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Funding information

FAN Research Talent Development Fund/
Fonds zur Förderung des akademischen
Nachwuchses; Schweizerischer
Nationalfonds zur Förderung der
Wissenschaftlichen Forschung, Grant/
Award Number: 31003A_169395

Abstract

Humans' large influence on the environment has constructed many new ecological niches, such as in urban areas. Phenotypic changes, including morphological ones related to human influence, are known from a small number of bird species. The amount of change in a given time period, that is, the rate of change, may vary. Rates of change (both evolutionary and through phenotypic plasticity) are reportedly rapid in human-influenced settings, although this is disputed. We present new data on changes in beak dimensions and rates of change over historical time periods in four urban bird species (Common Chaffinch, European Greenfinch, Eurasian Blackbird, House Sparrow) from three Swiss cities (Basel, Bern, Geneva). Our study shows that beak dimensions have changed little in most investigated urban bird populations over the past century. Only in Genevan Blackbirds there was evidence for an increase in beak length over the past 65 years; Bernese Chaffinches appear to be trending toward a decrease in beak width over the past 55 years. Rates of change in our sample in comparison with literature records showed that compared to populations less influenced by humans, urban evolutionary rates appear to be similar. Although in accordance with previous findings about other urban bird species, our study exemplifies the difficulty to find universal patterns in tempo and mode of phenotypic evolution in urban areas, even when considering the same taxa. Our data contribute to the expanding field of urban evolutionary biology, which is particularly important regarding the growing urban habitats worldwide.

KEYWORDS

aves, darwins, haldanes, morphological change, rate of evolution, urban evolution

TAXONOMY CLASSIFICATION

Urban ecology; Zoology

1 | INTRODUCTION

Although humans have influenced environments since prehistoric times, it was not until the second half of the 18th century that industrialization caused urban areas to grow enormously (Antrop, 2000). This process

accelerated in the second half of the 20th century (Antrop, 2004). Recent developments show that urbanization is a major cause of extinction (Alberti, 2015; Biamonte et al., 2011; Fattorini, 2011; Hamer & McDonnell, 2010) and contributes significantly to the current biodiversity crisis (Aronson et al., 2014; McKinney, 2002).

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Nevertheless, some species survive and thrive even in the relatively extreme urban habitats. Specific environmental characteristics of these urban areas determine the faunal elements that settle there (Erz, 1966; French et al., 2018; Hamer & McDonnell, 2008; Jones & Leather, 2012; Klausnitzer, 1988; McCleery, 2010) and expose them to new selection pressures (Santini et al., 2019; Seress & Liker, 2015). Hundreds of different animal species are known to inhabit urban areas worldwide (Ineichen et al., 2012; Schilthuizen, 2013; Szulkin et al., 2020), among which are many birds.

Phenotypic changes related to urbanization are known for an increasing number of bird species and include changes in behavior (Cooke, 1980; Hu & Cardoso, 2010; Møller, 2010a; Patricelli & Blickley, 2006), physiology (Audet et al., 2016; Brzek et al., 2009; Giraudeau & McGraw, 2014; Partecke et al., 2006) and life history (Bailly et al., 2016; Møller, 2009; Richner, 1989). Morphological changes, as those recorded in the shape and size of the skull or beak, have also been shown in numerous bird species (Badyaev et al., 2008; Hendry et al., 2006; Hutton & McGraw, 2016; McNew et al., 2017; Riyahi et al., 2013). While skull volume scales with brain size (Bonaparte et al., 2011; Iwaniuk & Nelson, 2002; Møller, 2010b) and is associated with cognitive performance (Sol et al., 2005), beak shape and size are mainly related to diet, such as the type of food (Francis & Guralnick, 2010; Lovette et al., 2002) or feeding ecology (Beecher, 1951; Kulemeyer et al., 2009), as well as phylogeny (Bright et al., 2016; Cooney et al., 2017), which in turn influence song characteristics (Demery et al., 2021; Giraudeau et al., 2014). The phenotypes changing in response to an increasingly human-dominated environment are thus fundamentally linked to survival and fitness, and understanding these changes is important regarding conservation efforts in the long term.

One further aspect of phenotypic change is its rate, that is, the amount of change over a given period of time. Darwin (1859) had suggested that rates of evolution are too slow to be recordable in historical time. However, more recent studies suggest that rates of change, both evolutionary and via phenotypic plasticity, could be fast (Cooney et al., 2017), particularly in urban environments (Alberti et al., 2017; Pergams & Lawler, 2009; Yeh, 2004).

Urban evolutionary biology is an emerging field (Szulkin et al., 2020) and so far not many studies have comparatively examined the quality and pace of morphological change in response to the urban habitat within species (Littleford-Colquhoun et al., 2017; Thompson et al., 2016; Winchell et al., 2016; Yakub & Tiffin, 2017).

Therefore, the study of morphological characteristics in further urban species and populations would contribute valuable information to elucidate patterns of urban evolution. In this pilot study, we quantified changes in beak morphology of four urban bird species in three Swiss cities across historical time periods to contribute new evidence concerning morphological changes, as well as on the rate of these changes in response to urban evolution. This is the first study investigating the same phenotypic characteristics in the same species across different populations, allowing for the investigation of common trends due to urbanization.

We tested the hypothesis that the high selection pressure of the urban habitat, which is strongly influenced by humans, leads to morphological changes and that the estimated rates of change of these phenotypic changes are relatively high, as in other anthropogenic contexts.

2 | MATERIALS AND METHODS

2.1 | Sample

In total, we sampled 116 specimens from four bird species (Eurasian Blackbird, *Turdus merula*; Common Chaffinch, *Fringilla coelebs*; European Greenfinch *Chloris chloris*; House Sparrow, *Passer domesticus*; hereafter only simplified common species names are used) from three urban areas in Switzerland (Basel, Bern, Geneva), covering time intervals ranging from the late 19th to the early 21st century (Table 1). Here, we refer to the time series of one species within one of the study cities as “population,” assuming that birds of one species found within one urban area in different years belong to the same population. For this study, we used bird skins, that is preserved skins of dead birds including feathers and the original skull and the beak inside the skin (Chapin, 1929; Winker, 2000).

We chose species that are known to breed in urban areas (Klausnitzer, 1988) and exhibit a reduced migratory behavior (Evans et al., 2012; Jascur & Döbelin, 2014), in order to avoid those that are only occasionally using urban habitats and would probably not represent a population. Most of the samples studied had been collected during the breeding season. The two migratory species were represented by about 22% specimens collected in the winter months (November to February; Chaffinch, $n = 12$; Greenfinch, $n = 13$). Thus, some of the specimens may represent winter visitors and thus

Species	Cities					
	Basel		Bern		Geneva	
	<i>n</i>	Years	<i>n</i>	Years	<i>n</i>	Years
Common chaffinch	7	1870–2000	9	1958–2013	6	1951–2016
Eurasian blackbird	9	1853–1986	4	1978–1995	25	1950–2015
European greenfinch	10	1899–1983	5	1969–1991	9	1969–2012
House sparrow	14	1870–2018	4	1969–2008	14	1899–2009

TABLE 1 Investigated time series of urban birds from Swiss cities with respective sample sizes (n) and investigated time periods (in years; alphabetically ordered by city and common species name).

not the breeding population. However, a considerable proportion of the breeding population in these two species remains in their breeding habitat during winter and we thus considered these populations as true. Species were chosen according to the availability of a relatively large number ($n \geq 4$) of appropriate specimens in the three study cities complying with certain criteria. Criteria for the selection of specimens were availability of (1) information on the date (at least to the year) and (2) locality of finding (within a defined urban area, see below), and (3) on sex. Furthermore, we included a species if (4) it was represented by specimens collected in different years.

We classified the collection localities as “urban” if sealed surfaces and buildings dominated the area and green space such as forests and agricultural fields were not present in the immediate vicinity (Parsons et al., 2020). For this purpose, contemporary maps accessed using the “journey through time” tool [available on the online topographic map viewer of the Swiss government, Maps of Switzerland (2021)] were used to evaluate each find location in the corresponding year. A more sophisticated classification of collection localities, for example, according to quantitative characteristics and throughout historical time was not possible due to the lack of information.

To minimize the influence of ontogenetic variation, only adult specimens were considered. Adulthood was defined to be attained if the specimens exhibited adult plumage. To minimize potential variation due to sexual dimorphism, we considered only specimens of one sex per population, chosen according to a higher number of specimens of one sex in that population.

The used specimens were housed at the Muséum d'Histoire Naturelle Genève, Switzerland (MHNG), the Naturhistorisches Museum Basel, Switzerland (NMB), and the Naturhistorisches Museum Bern, Switzerland (NMBE). For this study, we did not use any living specimens and no birds were sacrificed.

2.2 | Measurements

Three linear measurements, beak length, depth, and width, following Eck et al. (2011; Figure 1), were taken by one observer (EH) with digital calipers to the nearest 0.01 mm. The complete dataset can be found on Dryad <https://doi.org/10.5061/dryad.8cz8w9gtv>. To account for potential measurement errors, about 50% of the specimens ($n = 59$) randomly chosen from the sample were measured twice, once at the beginning of the measurement period and a second time later on the same day. The replicates were used to assess whether the measurements were reproducible and constant. For each measurement, we calculated the standard deviation of the two replicates in each of the repeated test specimens. The mean of these standard deviations per measurement was then compared to the mean standard deviation of all specimens in that time series (with respect to that measurement). This procedure was repeated for all measurements (Geiger, 2021). The standard deviation among the replicates (errors implied by the observer and/or the measurement device) were on average 10.12 times lower for beak length (minimum

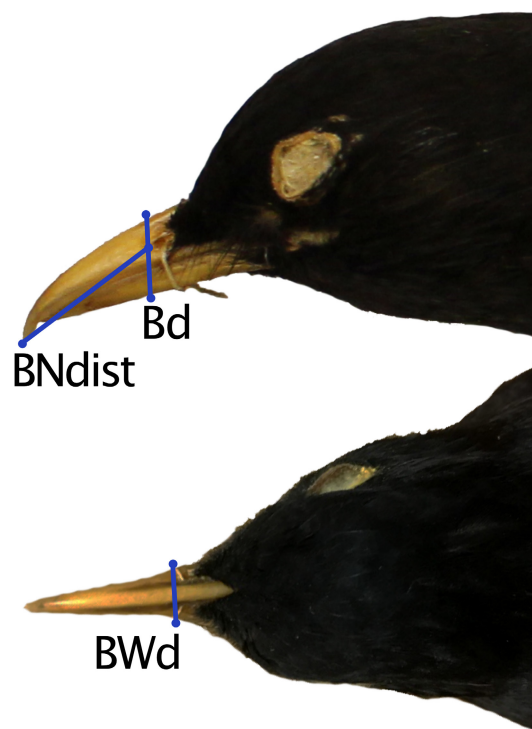


FIGURE 1 Linear measurements. Skin of a Eurasian Blackbird (MHNG 1759.79) in lateral view (top) with indicated beak depth (Bd) and beak length (BNdist) measurements, and in dorsal view (bottom), with indicated beak width measurement (BWd). Bd, distance from the top to bottom of beak at distal margin of nostrils; BNdist, distance from distal (anterior) edge of nostrils to tip of beak, measured on the left and on the right side; BWd, width from left to right side of beak measured at distal margin of nostrils.

3.09 times, maximum 19.99 times), 5.88 times lower for beak depth (minimum 1.50 times, maximum 18.10 times), and 2.56 times lower for beak width (minimum 1.36 times, maximum 6.08 times), than the standard deviation among the specimens. We therefore interpreted the observer error to be negligible compared to the intraspecies variation.

2.3 | Analyses of time series and rates of change

We used the individual values of beak depth (Bd) and beak width (BWd) and calculated the average of the left and the right side prior to the analyses for beak length (BNdist). To infer potential changes over time in beak dimensions in the urban bird populations studied (Table 1), we compared individual logarithmized beak dimensions (Figure 1) across years using linear regressions. The negative or positive signs of the slopes (a) indicate whether beak measurements tended to become smaller or larger over time (Table 3).

To estimate the rates of change of beak dimensions over time in the populations, we calculated darwin estimates (darwins) and haldane estimates (haldanes) as standard metrics of evolutionary rates (Gingerich, 1993; Haldane, 1949). Since darwins and/or haldanes are used in studies of evolutionary rates, we used both

metrics to compare our results with as many studies as possible. The darwin metric is suitable for measuring change over time and from the perspective of human interest because it shows proportional change over the years. However, to understand the response of a population to environmental change, the haldane metric is recommended because it accounts for standardization by trait variation and uses a time scale relevant to the organism (generations; Hendry & Kinnison, 1999). Darwins for every measurement were calculated using a linear regression of the natural logarithm of beak dimensions, used as the dependent variable, and time in millions of years was taken as the independent variable (Hendry & Kinnison, 1999). Haldanes for every measurement were estimated using a linear regression of the natural logarithm of beak dimensions divided by the pooled standard deviation as the dependent variable and generations since the first collection as the independent variable (Hendry & Kinnison, 1999). Since the generation length estimate for a given species may vary

depending on the method used and therefore has a major influence on estimates of rates of evolution in haldanes, we calculated haldanes of a given species using two different generation length estimates. First, as a minimum assumption for generation length in a given species (Gingerich, 2019), we used the age at sexual maturity from the literature (Tacutu et al., 2018; Table 2). Second, as a more sophisticated assumption, we used estimates for generation length based on life tables, including adult survival, age at first breeding, and maximum longevity, provided by Bird et al. (2020; Table 2). The same procedures were repeated for all measures and for each species studied. For the interpretation of the magnitude of the changes, only the absolute values of the darwin and haldane estimates were used.

Due to the small sample size, nonparametric Kruskal–Wallis tests were used to compare rates of change within the urban sample. Differences in darwins and haldanes between different beak dimensions in urban birds were tested at species level (estimates of specific beak dimensions for each species from all three cities).

To set the here estimated darwins and haldanes into context, we compared our rate estimates of urban birds with rate estimates from other bird populations from the literature. Bird-specific evolutionary rate estimates were extracted from the “evolutionary rate database” of Hendry et al. (2008), who extracted rate estimates from various literature sources (Baker et al., 1990; Clegg et al., 2002; Conant, 1988; Cooch et al., 1991; Grant & Grant, 2002; Johnston & Selander, 1964; Larsson et al., 1998; Smith et al., 1995; Zink, 1983). In addition, two more recent and relevant rate estimates were obtained directly from the primary literature (Bosse et al., 2017; Rolshausen et al., 2009).

TABLE 2 Generation length estimates for the four bird species (alphabetically ordered) according to Tacutu et al. (2018; sexual maturity) and Bird et al. (2020; life tables).

Species	Generation time estimates	
	Sexual maturity (years)	Life table (years)
Common chaffinch	1	5.0
Eurasian blackbird	1	4.0
European greenfinch	1	2.7
House sparrow	1	3.7

TABLE 3 Slopes and 95% bootstrapped confidence intervals (CI) of linear regressions of investigated beak dimensions over the observed time periods in urban bird species (alphabetically ordered by common species name, grouped by beak dimension and city).

	Basel		Bern		Geneva	
	Slope	95% CI	Slope	95% CI	Slope	95% CI
Beak length						
Common chaffinch	0.00014	−0.00013, 0.00035	0.000001	−0.00099, 0.00090	−0.00004	−0.00057, 0.00283
Eurasian blackbird	−0.00016	−0.00105, 0.00008	0.00076	−0.00230, 0.02401	0.00075**	−0.00002, 0.00159
European greenfinch	−0.00033	−0.00079, 0.00082	−0.00148	−0.00323, −0.00022	−0.00006	−0.00049, 0.00037
House sparrow	0.00003	−0.00031, 0.00046	−0.00148	−0.00383, 0.00029	−0.00003	−0.00037, 0.00029
Beak depth						
Common chaffinch	−0.00011	−0.00037, 0.00054	0.00017	−0.00091, 0.00134	−0.00001	−0.00011, 0.00037
Eurasian blackbird	0.00009	−0.00031, 0.00057	0.00074	−0.00086, 0.00233	0.00034	−0.00018, 0.00086
European greenfinch	0.00006	−0.00042, 0.00118	0.00060	−0.00542, 0.02080	−0.00019	−0.00144, 0.00064
House sparrow	−0.00007	−0.00041, 0.00051	0.00030	−0.01617, 0.00180	−0.00018	−0.00069, 0.00019
Beak width						
Common chaffinch	0.00005	−0.00041, 0.00042	−0.00052*	−0.00122, −0.00005	−0.00008	−0.00116, 0.00830
Eurasian blackbird	0.00007	−0.00030, 0.00033	−0.00188	−0.01690, −0.00022	0.00010	−0.00070, 0.00089
European greenfinch	0.00025	−0.00033, 0.00081	−0.00011	−0.00318, 0.00154	0.00016	−0.00067, 0.00102
House sparrow	−0.00005	−0.00054, 0.00012	−0.00176	−0.00491, 0.00455	−0.00022	−0.00049, 0.00007

Note: Asterisks indicate a significant correlation on a 5%-level (**) or a trend on a 10%-level (*).

For these comparisons, we focused on rate estimates from studies in a natural context and in urban and nonurban anthropogenic contexts. Categorization of natural and anthropogenic contexts was adopted from the authors' description of the study context and/or as given by Hendry et al. (2008). A context was defined as "natural" if a given environment or habitat was without obvious human influence or if the dispersal of the population in question was natural subsequent to human introduction. A context was defined as "non-urban anthropogenic" if human activity influenced conditions in a given environment or habitat. The "urban anthropogenic" context studied here is assumed to be a special case of the anthropogenic context and was analyzed separately from the two other groups. In one study, we classified the context as natural even though it was indicated by Hendry et al. (2008) as anthropogenic. We assumed, as with the Common Chaffinch (Baker et al., 1990) and House Sparrow (Johnston & Selander, 1964), that the Laysan Finch (Conant, 1988) dispersed naturally after human introduction.

For comparability of rates of change among our and the literature studies, we limited included studies to the ones reporting on the same taxon (birds), similar anatomical structures (skull and beak dimensions), and similar time intervals (within 10–167 years). For comparison of our haldane estimates with the literature data, we used rates calculated with age at sexual maturity (Tacutu et al., 2018) and rates based on life table data (Bird et al., 2020). These databases were chosen because they provide generation estimates on all of the here investigated bird species. Different approaches to estimate generation length have also been used to calculate rates in the literature (Hendry et al., 2008, Table 3). The choice of approach plays a role in the rate comparisons because the haldane estimate depends on the estimates of the time interval in generations. Generation lengths from literature studies were adopted as noted by the authors, with the exception of two studies. In the case of the Great Tit from the anthropogenic context, generation length was not explicitly mentioned in the study (Bosse et al., 2017). Here, we assumed that haldanes were calculated

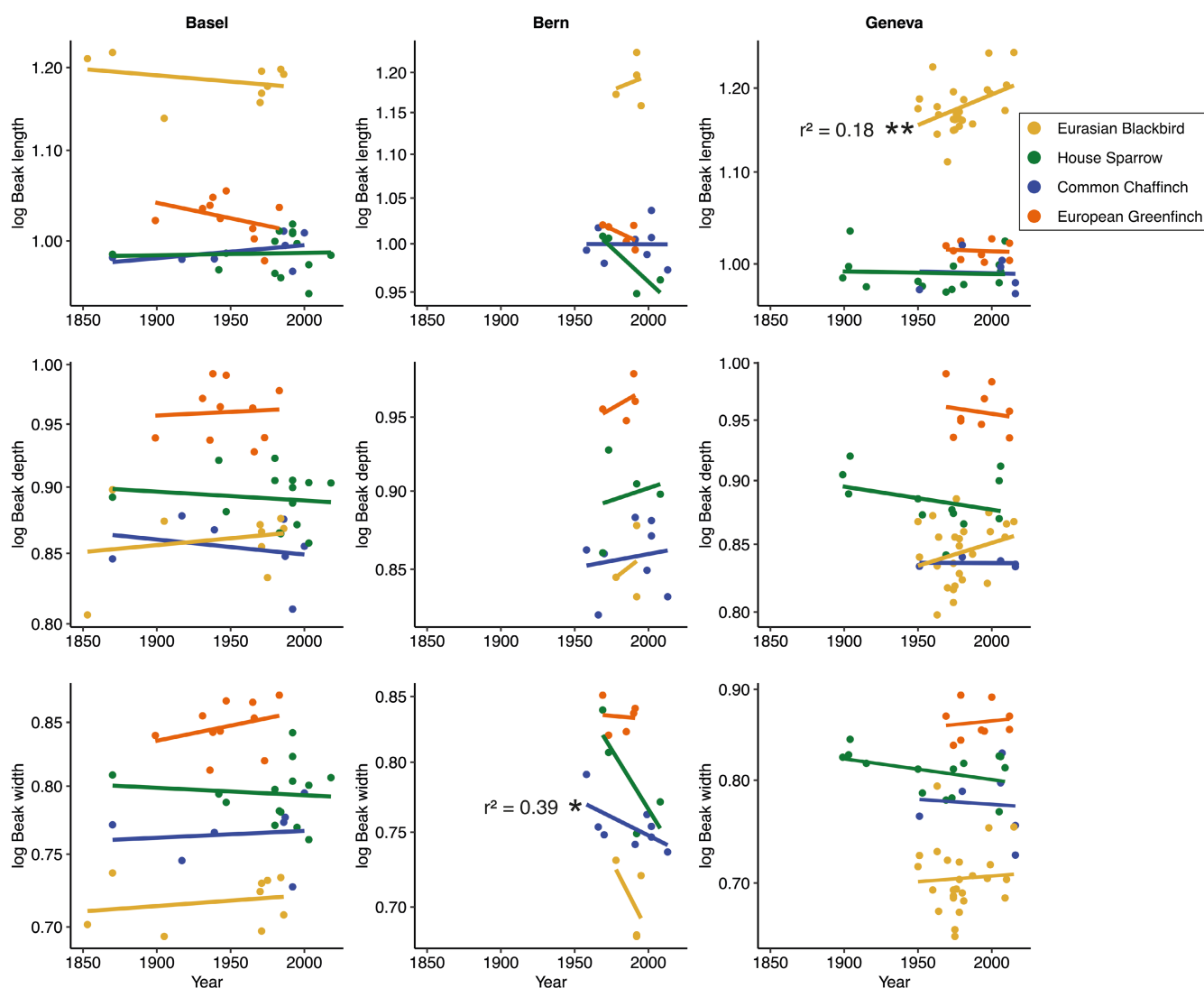


FIGURE 2 Regressions of logarithmized beak dimensions of four bird species in three Swiss cities versus year (collection years). The significant increase in beak length ($p < .05$) in Genevan Blackbirds is indicated with two asterisks (**) and the trend decrease in beak width ($p < .1$) in Bernese Chaffinches is indicated with one asterisk (*).

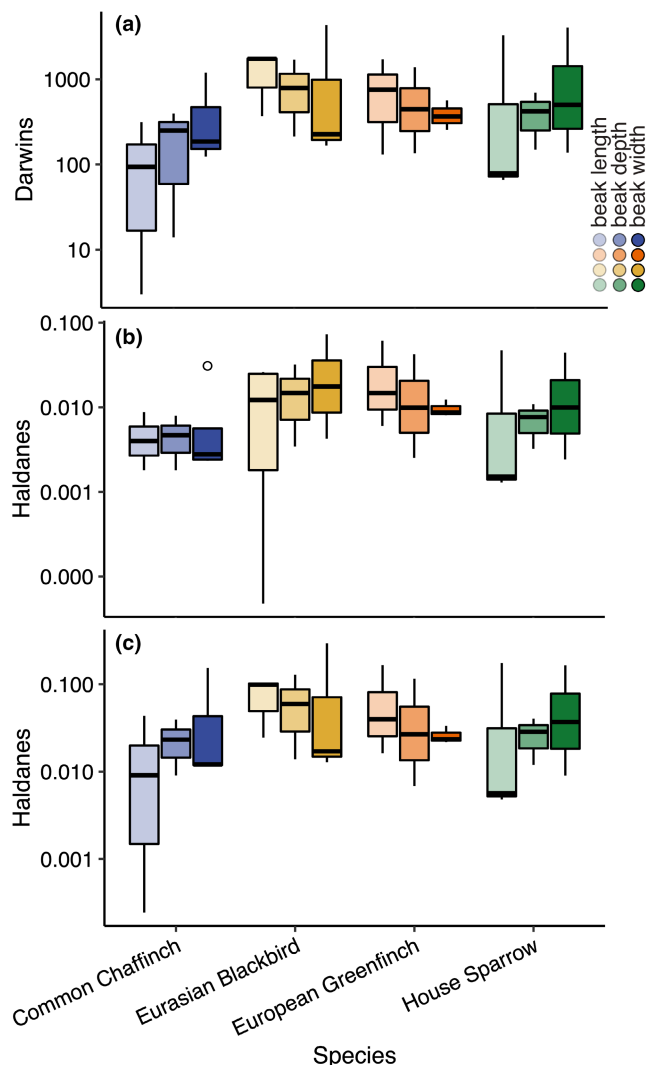


FIGURE 3 Estimates of rates of phenotypic change of beak dimensions for the four investigated bird species. Estimates were pooled for Basel, Bern plus Geneva in darwins (a) and haldanes (b and c). Haldane estimates were calculated based on age at sexual maturity as generation length estimate (Tacutu et al., 2018) in b, and based on life table estimates (Bird et al., 2020) in c. Each box represents the three cities' pooled estimates for each bird species (alphabetically ordered by species) and each beak dimension. The outlier is indicated by an open circle.

based on age at sexual maturity. In the case of the Darwin finches, the number of generations stated in the original article and the review was ambiguous. Here, we assumed that instead of the stated one generation in the review (Hendry et al., 2008; Table 3), 30 generations were meant, which corresponds to the observation period in the primary literature (Grant & Grant, 2002). Differences between urban, nonurban anthropogenic, and natural contexts were tested on a species-level (species means over all reported skull and beak dimensions) using nonparametric Kruskal–Wallis tests due to the small and unequal sample sizes among the contexts.

All analyses were performed using Past version 4.03 (Hammer et al., 2001), R version 3.6.3 (R Core Team, 2020), and RStudio version 1.1.463 (RStudio Team, 2020).

3 | RESULTS

3.1 | Phenotypic change of beak dimensions in urban birds over time

Most of the changes over time were not marked and not significant in most species and cities. For beak length, the slopes (a) of the regressions of beak dimensions over time in the four species and the three cities ranged from 0.000001 to 0.0015 (Table 3). For beak depth, a ranged from 0.00001 to 0.0007 and for beak width from 0.00005 to 0.0019 (Table 3). The changes of beak dimensions over time were most pronounced in the city of Bern (Figure 2, Table 3).

However, beak length of Genevan Blackbirds changed significantly over time ($t_{25} = 2.255$, $p = .03$, $r^2 = .181$, 95% CI $[-0.00002, 0.00159]$), with beak length increasing from 14.95 mm in the oldest specimen (died in 1950) to 17.59 mm in the youngest specimen (died in 2015). This corresponds to an increase of about 17% within 65 years, which corresponds to 65 generations (sexual maturity estimate; Table 2) or 16.25 generations (life table estimate; Table 2). Furthermore, we found a trend toward a decrease of beak width in Bernese Chaffinches ($t_8 = 1.952$, $p = .099$, $r^2 = .388$, 95% CI $[-0.00122, -0.00005]$, Figure 2). In these Chaffinches, beak width decreased from 6.18 mm in the oldest specimen (died in 1958) to 5.45 mm in the youngest (died in 2013), reflecting a decrease of about 12% within 55 years and corresponding to either 55 generations (sexual maturity estimate; Table 2) or 11 generations (life table estimate; Table 2).

3.2 | Rates of phenotypic change in beak dimensions in urban birds

The darwin estimates (darwins) for the different species, cities, and traits ranged from 3 to 4331 powers of e per million years (Figure 3a, Table 4). Differences between medians of different beak dimensions were not significant ($\chi^2 = 0.150$, $df = 2$, $p = .93$).

Haldane estimates (haldanes) of the beak dimensions calculated with age sexual maturity as generation length estimate (Table 2) ranged from 0.00005 to 0.073 standard deviations (SD) per generation (Figure 3b, Table 5). The haldanes calculated with life table estimates as generation length estimate (Table 2) ranged from 0.00002 to 0.295 SD per generation (Figure 3c, Table 5). The haldanes for the different beak dimensions, calculated with the generation length estimate of Tacutu et al. (2018; Figure 3b; $\chi^2 = 0.086$, $df = 2$, $p = .96$) and with the generation length estimate of Bird et al. (2020; Figure 3c) were not significantly different from each other ($\chi^2 = 0.006$, $df = 2$, $p = .99$).

3.3 | Rates of change in different environmental contexts

The darwins for the populations from the urban anthropogenic context (this study, 287–1254 powers of e per million years) were within

TABLE 4 Rates of change, measured in darwins (slopes) and 95 % bootstrapped confidence intervals (CI) for the different bird species (alphabetically ordered by common species name, grouped by beak dimension and city).

	Basel		Bern		Geneva	
	Slope	95% CI	Slope	95% CI	Slope	95% CI
Beak length						
Common chaffinch	315	−347, 853	−3	−2144, 2105	−94	−1256, 5768
Eurasian blackbird	−368	−3431, 161	1759	−5268, 55218	1737**	−19, 3510
European greenfinch	−755	−1802, 1984	−1708	−5834, −265	−131	−1085, 831
House sparrow	79	−710, 974	−3289	−8591, 422	−66	−879, 648
Beak depth						
Common chaffinch	−250	−897, 1315	397	−2031, 2444	−14	−186, 846
Eurasian blackbird	213	−772, 1294	1696	−1964, 5357	791	−433, 1972
European greenfinch	136	−861, 2718	1380	−12459, 47661	−445	−3032, 1465
House sparrow	−150	−1041, 1172	698	−37179, 4138	−421	−1566, 429
Beak width						
Common chaffinch	124	−995, 923	−1198*	−2728, −143	−186	−2479, 18206
Eurasian blackbird	167	−693, 767	−4331	−38863, −513	226	−1552, 2067
European greenfinch	566	−913, 1903	−255	−7319, 3540	366	−1712, 2189
House sparrow	−138	−1134, 338	−4055	−11310, 10490	−500	−1203, 123

Note: Asterisks indicate a significant correlation on a 5% level (**) or a trend on a 10% level (*).

the magnitude of rate estimates from the literature featuring populations from a natural context (81–2642 powers of e per million years; Hendry et al., 2008, and references cited therein; Table 6, Figure 4a). Although the median value of the darwin estimates was by trend higher in the urban context (841 powers of e per million years) compared to the natural one (250 powers of e per million years), the difference was not significant ($t(\chi^2 = 0.721, df = 1, p = .396)$).

Haldane estimates calculated based on a generation length of one year (i.e., age at sexual maturity; Table 7, Figure 4b), estimated for the nonurban anthropogenic (Bosse et al., 2017) and urban anthropogenic contexts overlapped with the estimates from the natural context (Table 7, Figure 4b). The rate estimate from the nonurban anthropogenic context (Bosse et al., 2017) were also within the magnitude of rate estimates of the urban anthropogenic context. There was no significant difference in species-level haldane estimates between urban anthropogenic, nonurban anthropogenic, and natural contexts ($\chi^2 = 1.767, df = 2, p = .41$). Haldane estimates calculated from life tables data (Table 7, Figure 4c) showed that the magnitude of rate estimates from the nonurban anthropogenic and urban anthropogenic contexts, with one exception, also overlapped with those from natural context (Figure 4c). The urban Blackbirds were estimated to change faster than populations from the natural context. However, the difference in haldane estimates between the different contexts were not significant ($\chi^2 = 0.273, df = 2, p = .87$).

The high rate estimates in urban populations are more evident when comparing the same species directly. Chaffinches and Sparrows in an urban context have higher rates than their counterparts in natural environments. Darwin estimates for both, the urban

Chaffinch and the urban Sparrow (this study), were about three to five times higher (Table 6), and haldanes were about twice as high (Table 7) compared to the estimates of their conspecifics from the natural environment (literature data; Table 7). (NB: the mean time interval in years, over which rate estimates were measured, was similar for the Sparrows from both contexts, but only half as long for the urban Chaffinch compared to the Chaffinch from the natural context).

4 | DISCUSSION

The aim of this study was to track beak dimensions of urban bird populations over time and test for changes. Darwin and haldane estimates were then compared to rates of change in bird populations from natural and nonurban anthropogenic contexts from the literature. Changes in beak dimensions over time were generally small in all species and cities and we found only an increase in beak length in Genevan Blackbirds and a trend of decrease in beak width in Bernese Chaffinches. Whether these differences are examples of phenotypic plasticity and/or are the result of genetic changes we cannot determine in this study. The estimates of rates of change of urban populations were generally within the magnitude of rate estimates from a natural context. However, single comparisons of the same species showed that urban rates were higher than those of conspecifics from the natural context.

Our study has the limitation that it is based on a small number of specimens overall and across years. Time series concerning single localities are generally scarce in museum collections and information of

TABLE 5 Rate of change, measured in haldanes (slopes) and 95 % bootstrapped confidence intervals (CI) for the different bird species (alphabetically ordered by common species name, grouped by beak dimension and city).

	Basel				Bern				Geneva			
	Sexual maturity		Life table		Sexual maturity		Life table		Sexual maturity		Life table	
	Slope	95%	Slope	95% CI	Slope	95% CI	Slope	95% CI	Slope	95% CI	Slope	95% CI
Beak length												
Common chaffinch	0.009	-0.0093, 0.0244	0.044	-0.0532, 0.1201	0.00005	-0.0464, 0.0395	-0.0002	-0.2254, 0.2028	-0.002	-0.0293, 0.1515	-0.009	-0.1459, 0.7293
Eurasian blackbird	-0.006	-0.0397, 0.0026	-0.024	-0.1658, 0.0119	0.026	-0.0774, 0.8114	0.105	-0.3115, 3.2891	0.025**	-0.0005, 0.0509	0.099**	-0.0051, 0.2102
European greenfinch	-0.015	-0.0364, 0.0377	-0.04	-0.0968, 0.1040	-0.061	-0.1536, -0.0091	-0.165	-0.5656, -0.0246	-0.006	-0.0508, 0.0388	-0.016	-0.1403, 0.1071
House sparrow	0.001	-0.0159, 0.0209	0.005	-0.0607, 0.0820	-0.047	-0.1224, 0.0060	-0.175	-0.4557, 0.0224	-0.002	-0.0200, 0.0157	-0.006	-0.0729, 0.0571
Beak depth												
Common chaffinch	-0.005	-0.0163, 0.0241	-0.023	-0.0822, 0.1060	0.008	-0.0411, 0.0558	0.04	-0.2139, 0.2540	-0.002	-0.030, 0.1207	-0.009	-0.1787, 0.6003
Eurasian blackbird	0.003	-0.0121, 0.0217	0.014	-0.0473, 0.0884	0.032	-0.0371, 0.1010	0.129	-0.1495, 0.4073	0.015	-0.0079, 0.0358	0.059	-0.0250, 0.1488
European greenfinch	0.003	-0.0165, 0.0497	0.007	-0.0494, 0.1385	0.043	-0.3844, 1.4724	0.115	-1.0385, 3.9798	-0.010	-0.079, 0.0307	-0.027	-0.1884, 0.0791
House sparrow	-0.003	-0.0199, 0.0252	-0.012	-0.0720, 0.0956	0.011	-0.5802, 0.0646	0.04	-2.1693, 0.2404	-0.008	-0.0270, 0.0075	-0.029	-0.1047, 0.0244
Beak width												
Common chaffinch	0.002	-0.0203, 0.0182	0.012	-0.0925, 0.0895	-0.031*	-0.0708, -0.0044	-0.154*	-0.3532, -0.0181	-0.002	-0.0328, 0.2239	-0.012	-0.1704, 1.1709
Eurasian blackbird	0.004	-0.0177, 0.0197	0.017	-0.0712, 0.0796	-0.073	-0.6556, -0.0087	-0.295	-2.656, -0.0360	0.003	-0.0228, 0.0303	0.013	-0.0916, 0.1139
European greenfinch	0.012	-0.0199, 0.0424	0.033	-0.0511, 0.1102	-0.009	-0.2495, 0.1028	-0.023	-0.6689, 0.3247	0.008	-0.039, 0.042	0.022	-0.0996, 0.1277
House sparrow	-0.002	-0.0256, 0.0062	-0.009	-0.0917, 0.0225	-0.044	-0.1232, 0.1141	-0.164	-0.4588, 0.4277	-0.010	-0.023, 0.002	-0.037	-0.0854, 0.0105

Note: Estimates for generation length based on Tacutu et al. (2018; sexual maturity) and Bird et al. (2020; life tables). Asterisks indicate a significant correlation on a 5% level (*) or a trend on a 10% level (*).

TABLE 6 Species-level darwin estimates for morphological changes of the skull and the beak of populations in urban anthropogenic (this study) and natural (literature) contexts (Ordered by context and within context alphabetically by common species name).

Species	Darwin estimates (species mean)	Context
Barnacle Goose	1161	Natural
<i>Branta leucopsis</i> ^a		
Common Chaffinch	81	Natural
<i>Fringilla coelebs</i> ^a		
House Sparrow	252	Natural
<i>Passer domesticus</i> ^a		
Iiwi	152	Natural
<i>Drepanis coccinea</i> ^a		
Laysan Finch	2642	Natural
<i>Telespiza cantans</i> ^a		
Red Fox-sparrow	217	Natural
<i>Passerella iliaca</i> ^a		
Silvereye	249	Natural
<i>Zosterops lateralis</i> ^a		
Snow Goose	1428	Natural
<i>Anser caerulescens</i> ^a		
Common Chaffinch	287	Urban anthropogenic
<i>Fringilla coelebs</i> ^b		
Eurasian Blackbird	1254	Urban anthropogenic
<i>Turdus merula</i> ^b		
European Greenfinch	638	Urban anthropogenic
<i>Chloris chloris</i> ^b		
House Sparrow	1044	Urban anthropogenic
<i>Passer domesticus</i> ^b		

^aRate estimates obtained from Hendry et al. (2008; see section 2 above).

^bThis study.

finding localities that is exact enough to allow for a categorization of specimens into an urban versus nonurban context is rare. However, attempts to use collection material to trace the evolutionary history of species over historical time periods has great potential, especially if sampling efforts can be targeted for a future expansion of studies. The great potential of our study lies in the parallel comparison of the same traits in the same species in different cities, allowing for the investigation of common trends across cities.

Although most of the changes over time were not marked and not significant in most species and cities (Figure 2), some patterns might reveal consistent patterns if investigated in a broader context and with a greater sample. Examples for this are the Greenfinch, the Blackbird, and the Sparrow, which exhibited a consistent, albeit nonsignificant, tendency of change of one of the investigated beak dimensions over time in all three cities (Greenfinch: beak length decrease; Blackbird: beak depth increase; Sparrow: beak width decrease;

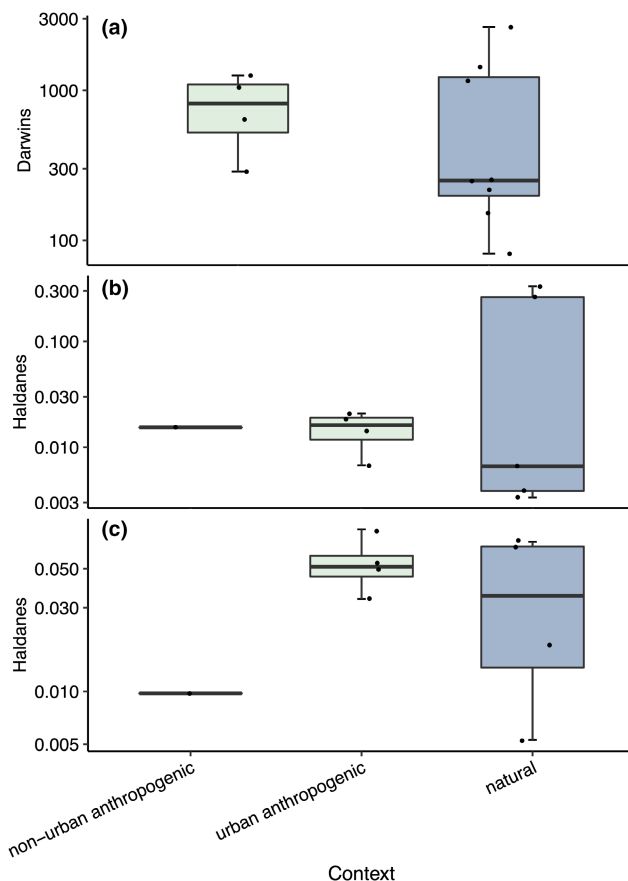


FIGURE 4 Comparison of species-level darwin and haldane estimates for morphological changes of the skull and/or the beak of bird populations in darwin (a) and haldane (b and c) estimates are shown for urban anthropogenic (this study), nonurban anthropogenic (literature data) and natural (literature data) contexts (Bosse et al., 2017; Hendry et al., 2008, and references therein; Rolshausen et al., 2009). The urban context is assumed to be a special case of an anthropogenic context. Haldane estimates with assumed generation length based on age sexual maturity (one year equals one generation (Tacutu et al., 2018) are shown in b, and those calculated with a generation length based on life tables data (urban context (Bird et al., 2020), nonurban anthropogenic or natural context (Hendry et al., 2008, Table 3) in c. Note that no darwin estimates concerning skull or beak changes in populations from a nonurban anthropogenic context were available from the literature.

Figure 2). Moreover, there were consistent tendencies of change in beak depth and beak width over time in all investigated Bernese species (Figure 2).

4.1 | Small changes and city trends in beak dimensions in urban birds

Habitat alteration due to human influence can have a strong impact on beak morphology and lead to rapid phenotypic changes (Badyaev et al., 2008). In the light of the few significant changes of beak traits over time found in the current study (Figure 2, Table 3), beak

TABLE 7 Species-level haldane estimates for different environmental contexts (ordered by context and within context alphabetically by common species name).

Species	Haldane estimates (sexual maturity)	Haldane estimates (life table)	Context	Generation length (years)
Barnacle Goose	0.066	0.066	Natural	2
<i>Branta leucopsis</i> ^a				
Common Cactus-finch	0.333	0.333	Natural	1
<i>Geospiza scandens</i> ^a				
Common Chaffinch	0.003	0.003	Natural	1
<i>Fringilla coelebs</i> ^a				
House Sparrow	0.007	0.007	Natural	1
<i>Passer domesticus</i> ^a				
Iiwi	0.004	0.004	Natural	3
<i>Drepanis coccinea</i> ^a				
Laysan Finch	0.071	0.071	Natural	2
<i>Telespiza cantans</i> ^a				
Medium Ground-finch	0.263	0.263	Natural	1
<i>Geospiza fortis</i> ^a				
Silvereye	0.019	0.019	Natural	3
<i>Zosterops lateralis</i> ^a				
Snow Goose	0.005	0.005	Natural	4
<i>Anser caerulescens</i> ^a				
Eurasian Blackcap	0.01	0.01	Nonurban anthropogenic	1.8
<i>Sylvia atricapilla</i> ^b				
Great Tit	0.015	0.015	Nonurban anthropogenic	na
<i>Parus major</i> ^c				
Common Chaffinch	0.007	0.034	Urban anthropogenic	5
<i>Fringilla coelebs</i> ^d				
Eurasian Blackbird	0.021	0.084	Urban anthropogenic	4
<i>Turdus merula</i> ^d				
European Greenfinch	0.018	0.05	Urban anthropogenic	2.7
<i>Chloris chloris</i> ^d				
House Sparrow	0.014	0.053	Urban anthropogenic	3.7
<i>Passer domesticus</i> ^d				

Note: In the urban sample, haldanes differ because rate estimates were calculated for the sample based on a generation length of one year (i.e., age at sexual maturity; Tacutu et al., 2018) and based on life tables data (Bird et al., 2020). The haldane estimates from the literature do not differ in the two columns because they were calculated using only the generation length specified by Hendry et al. (2008) or the respective primary study (see section 2).

^aRate estimates obtained from Hendry et al. (2008; see section 2 above).

^bRate estimates obtained from Rolshausen et al. (2009).

^cRate estimates obtained from Bosse et al. (2017).

^dThis study.

dimensions seem to be quite stable in the examined bird populations living in urban environments in Switzerland. There might be different reasons for the general scarcity of changes in beak dimensions.

First, the bird populations studied probably already lived in cities for a couple of generations prior to the time period studied here (Evans et al., 2010; Shaw et al., 2008). This implies that phenotypic changes due to the novel urban habitat may already be apparent even in the historically oldest of the birds studied, because changes

due to strong selection pressures at the beginning of an invasion can occur rapidly (Reznick & Ghalambor, 2001). However, urban areas in Switzerland have increased significantly in the 20th century (Federal Statistical Office, 2021). They have also increased in size and become more densely built-up (Federal Statistical Office, 2021), thus leading to a constantly changing habitat (Ineichen et al., 2012).

Second, while sparrows and blackbirds are known to show reduced migratory behavior in urban areas (Evans et al., 2012;

Vangestel et al., 2012), it is not known whether urban Chaffinch and urban Greenfinch populations inhabit urban areas in their breeding as well as winter habitats, and whether or not—as a consequence—they are exposed to anthropogenic influences year round. While it is generally assumed that urban bird populations become more sedentary due to warmer temperatures and food availability (Partecke & Gwinner, 2007), even as only seasonal exposure to an anthropogenic habitat might lead to morphological changes. For example, morphological changes of the beak have been shown in Eurasian Blackcaps and Great Tits that were fed by humans in their winter habitats, but not in their breeding habitats (Bosse et al., 2017; Rolshausen et al., 2009). Thus, seasonality of human influence might not play a role if selection pressure in the anthropogenic habitat is sufficiently large.

Third, urban bird populations may not be genetically isolated from nearby rural populations due to their high mobility, as is the case with well-studied urban populations of certain mammals (Kimmig et al., 2020; Wandeler et al., 2003), or they may serve as population sinks because of lower habitat quality in cities (Anderies et al., 2007; Demeyrier et al., 2016; Dias, 1996; Reynolds et al., 2017; Van Heezik et al., 2010; Vierling, 2000). Such constant admixture of urban and rural populations might dilute any plastic and/or adaptive effects of urbanization.

Nevertheless, certain tendencies could be observed. We found a significant increase in beak length of the urban Blackbirds from Geneva and a nonsignificant trend of decreasing beak width in Bernese Chaffinches.

Regarding the variation in beak length, there are several factors that may have an influence. On an individual level, season (Davis, 1954; Gosler, 1987; Matthysen, 1989) and, for certain species, age (Hussell, 1990; Mínguez et al., 1998) seem to play a role in beak length variation. In the case of Blackbirds both seem to be the case (Desrochers, 1992; Piliczewski et al., 2018). Furthermore, several studies showed that beak proportions change in relation to diet and/or acoustic properties of the environment. In populations living under greater human influence, beaks became larger overall in ground finches and house sparrows (McNew et al., 2017; Ravinet et al., 2018) and beak length increased in Eurasian blackcaps, house finches, and great tits (Bosse et al., 2017; Giraudeau et al., 2014; Rolshausen et al., 2009).

An increase in beak length in the Blackbirds studied here is thus in accordance with previous findings concerning different urban passerine species (Bosse et al., 2017; Giraudeau et al., 2014; Rolshausen et al., 2009). In these, an increased beak length has been associated with an advantage in handling larger food items and the production of lower frequency sound (Giraudeau et al., 2014). Specifically, studies on Eurasian blackcaps and great tits have shown that an increase in beak length may be associated with the use of bird feeders (Bosse et al., 2017; Rolshausen et al., 2009), because it facilitates the handling of larger seeds (Badyaev et al., 2008; Soobramoney & Perrin, 2007). Blackbirds are also among the bird species that frequent bird feeders (Reynolds et al., 2017). They generally feed on relatively soft foods such as oatmeal, fruits, and seeds up to peanut

size that they find on the ground beneath a bird feeder, or even trash in times of need (Von Blotzheim et al., 1966). Because this anthropogenic diet differs in its mechanical properties from this bird's natural winter diet, which consists mainly of berries (e.g., *Hedera helix*; Von Blotzheim et al., 1966) urban blackbirds might experience altered selection pressures compared to their rural conspecifics, which in turn might have an impact on urban blackbirds beak morphology. Whether there is a difference in song frequency in urban versus rural blackbirds, specifically a decrease of the minimum frequency due to the longer beak (Giraudeau et al., 2014), remains to be investigated.

For beak width, two studies on urban house finches report contradictory results, maybe related to variable biotic and abiotic factors associated with the environments studied (acoustic environment vs. foraging pressure). House finches in and around urban Phoenix (Maricopa County, USA) showed a decrease of beak width with increasing urbanization, associated with a decrease in maximum song frequency (Giraudeau et al., 2014). In contrast, house finches on the campus of the University of Arizona in nearby Tucson showed an increased beak width compared to conspecifics in the desert. This result is presumably related to consumption of larger seeds from bird feeders (Badyaev et al., 2008), or cultivated crops (Ravinet et al., 2018), compared to house finches in a more natural habitat.

Chaffinches feed mainly on insects and other small animals in the warmer seasons and rely on plant seeds in winter (Von Blotzheim et al., 1966). In anthropogenic environments, they may additionally consume human food and frequent bird feeders (Von Blotzheim et al., 1966), especially in the cold season. The decrease in beak width in Bernese Chaffinches would indicate a decrease in bite force (Badyaev et al., 2008) and could be explained by the consumption of softer, human-derived food (De León et al., 2011), which is abundant in cities, and does not require a special beak size or bite force (De León et al., 2011). As in the blackbirds (above), potentially associated alterations of song frequency (Giraudeau et al., 2014) remain to be investigated.

In addition to the possibility of an influence of diet and acoustic characteristics of the environment on beak morphology, there may also be a relationship with body size. Potential body size changes due to urbanization might lead to associated changes in body proportions (allometry), such as beak shape. This could not be investigated here. However, other studies found no evidence for a relationship between a change in beak size and an increase in body size or tarsus length in different bird species (Badyaev et al., 2008; Bosse et al., 2017; Giraudeau et al., 2014; Gosler, 1987; Grant & Grant, 2006; McNew et al., 2017). Bird beaks are not insulated but are well vascularized, and thus could be important for heat exchange (Tattersall et al., 2017). Because climate-related geographic variation in beak size is likely the norm for many bird species, an increase in beak length could also be interpreted as an adaptation to warmer temperatures in cities. A similar correlation was suggested for urban brown rats in Manhattan, the United States (Puckett et al., 2020). Puckett et al. (2020) suspected that the enlarged nasal cavities of the brown rats could be related to the urban heat island effect.

Our results indicate that the diet of Blackbirds and Chaffinches and/or song characteristics might have changed with increasing urbanization in the past decades, and with it the beak morphology. Whether these changes are plastic and/or genetic cannot be determined here. To clarify this and also causalities and how diet and song characteristics might differ in natural versus urban habitats, further research, specifically also on a local scale, is needed. On the other hand, non-adaptive changes, for example, genetic drift due to small and relatively isolated populations in urban habitats might be the underlying reasons behind the observed changes of beak dimensions over time.

4.2 | Fast-paced city life?

Contrary to our expectations and the evidence for high evolutionary rates in populations living in human-influenced environments (Alberti et al., 2017; Hendry et al., 2008), the species-level rates of phenotypic change were not higher in urban and nonurban anthropogenic contexts than in a natural context (Figure 4). This finding indicates that (1) natural rates of change might be faster than previously assumed, depending on the magnitude of the environmental impact on the study population, (2) a methodological influence, and/or (3) a reporting bias (see next sections). However, the higher rate estimates in an urban context in comparisons with the same species from a natural context indicate that selection pressures might still be comparatively high for urban populations. These are yet single comparisons, and further studies on the same species in different environments will shed further light on rate estimates in urban vs. rural environments.

As for methodological influences (2): when comparing haldane estimates, it is important to consider the generation length or the resulting number of generations for a time interval (Hendry & Kinnison, 1999). Therefore, in selecting rate estimates from the literature, we restricted ourselves to those that covered a similar time interval as our urban sample. Within this selection, however, there were different generation lengths, based on either age at maturity or life tables data (Table 7). We found that urban haldane estimates were in the upper range of rate estimates from the natural context when calculated with life tables data for generation length (Figure 4c). However, when calculated with age at sexual maturity (Figure 4b), they tended to be in the lower range of the natural context. But regardless of which generation length was used to calculate the haldane estimates, the magnitude of rate estimates was greatest in the natural context, so urban and nonurban anthropogenic rates fall within this range (Figure 4b,c).

As for reporting bias (3): since exceptional circumstances are probably more likely to be reported than random "background" rates of change, the average rate of change in a natural context is likely relatively high, thus constituting a reporting bias influencing comparisons between a natural and an anthropogenic context.

5 | CONCLUSION

We showed that beak dimensions in urban birds in Switzerland have generally changed only slightly over time, yet clear trends in some species are discernible. And although the increase in beak length in urban blackbirds is in accordance with previous studies on some bird species in other urban habitats, these results show that there is no clear evidence of uniform across-city and across-species trends related to urbanization among the species and areas studied. However, certain tendencies suggest that an expanded sampling might reveal other patterns. Besides the need for the study of further taxa, larger samples and multiple species trends, as well as potential genetic bases for the observed patterns, future studies could also consider local variation of the cities' buildup and development, as well as human culture (e.g., bird feeding).

Estimates of rate of change in an urban context were high but similar to estimates from nonurban anthropogenic and natural contexts. This indicates that selection pressures in urban habitats might be strong, but so are selection pressures in the wild.

It would be informative if, in addition to urban or anthropogenic populations, nearby rural populations or the same species in different environments could be studied. Unfortunately, this was not possible in our case because of a lack of time series of rural populations of the same species. Further insights and more accuracy in the study of morphological changes would be provided by measuring skulls instead of bird skins. Uncertainties due to wear and seasonal differences in the rhamphotheca could thus be excluded and additional insights into skull proportions gained.

AUTHOR CONTRIBUTIONS

Evelyn Hüppi: Conceptualization (equal); formal analysis (lead); investigation (lead); methodology (equal); visualization (lead); writing – original draft (lead); writing – review and editing (equal). **Madeleine Geiger:** Conceptualization (equal); formal analysis (supporting); funding acquisition (lead); methodology (equal); supervision (equal); writing – review and editing (equal).

ACKNOWLEDGMENTS

We thank David Marques (NMB), Manuel Schweizer (NMBE), and Alice Cibois (MHNG) for access to collections, Marcelo R. Sánchez-Villagra for discussion, and Ana Balcarcel for help with the analyses. Further, we thank two anonymous reviewers for useful suggestions to improve an earlier version of this manuscript. This work was supported by SNF Swiss National Science Foundation 31003A_169395 to Marcelo R. Sánchez-Villagra and the Research Talent Development Fund (Fonds zur Förderung des akademischen Nachwuchses, FAN) to MG.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available at Dryad <http://doi.org/10.5061/dryad.8cz8w9gtv>.

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How to cite this article: Hüppi, E., & Geiger, M. (2022).

Fast-paced city life? Tempo and mode of phenotypic changes in urban birds from Switzerland. *Ecology and Evolution*, 12, e9217. <https://doi.org/10.1002/ece3.9217>