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Article

Urban links to molt schedule, body condition and carotenoid-based coloration in the house finch *Haemorhous mexicanus*

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Animals in urban environments are exposed to novel conditions, such as habitat and dietary alterations, and night-time light pollution, that can shift the timing and expression of life-history traits. Birds are popular urban-ecological study subjects, and in these feathered animals regular plumage molt is a critical process for maintenance of feather quality and their associated functions (e.g. thermoregulation, aerodynamics and communicative coloration). We hypothesized that environmental changes associated with urbanization might affect the timing and progression of molt. As molt is energetically and nutritionally costly, we also tested whether putative urban–rural molt differences might be explained by indirect effects of urban environments on aspects of health (i.e. body condition, sexually selected plumage color). We tracked body molt intensity during molt onset, peak and completion in both sexes of urban and rural house finches *Haemorhous mexicanus*, and related this to body condition and sexually selected carotenoid-based plumage coloration. We found that urban birds began molting earlier, peaked at a lower molt intensity and ended molt later than rural conspecifics. We also find that both body condition and plumage hue in males explain variation in body molt intensity differently for urban and rural populations at various points during the molting period. Overall, we demonstrate that songbird molt patterns and the development of carotenoid-based sexual ornaments can be altered in urban environments, and that rapid urbanization may have broader implications for molt dynamics, annual life-history traits and sexual selection.

Keywords: carotenoids, feather growth, life history trade-offs, plumage coloration, urban ecology

Introduction

Animals inhabiting urban areas are exposed to many unique environmental conditions, such as night light pollution, background noise (e.g. cars, construction) and changes in predator abundance and food availability (Cinzano et al. 2001, Isaksson and Andersson 2007, Slabbekoorn 2013, Gaston et al. 2015, Dominoni et al. 2016, Machovsky-Capuska et al. 2016). Recent work at the intraspecific level has shown that anthropogenic activities can rapidly shift animal behaviors, physiology, morphology and life history (Mills et al. 1989, Kark et al. 2007, Hendry et al. 2008, Desrochers

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2015). To better understand human impacts on organismal fitness, we must comprehensively investigate the range of behavioral and physiological life-history investments made by urban animals.

Animals have evolved to time their demanding annual activities (e.g. breeding, migration) to proper environmental cues and resource availability, and we already know that urban environments advance the timing of breeding and migration (Deviche and Davies 2013, Tryjanowski et al. 2013, Visser and Gienapp 2019). Anthropogenic activity may also perturb other annual self-maintenance activities, including replacement of the integument (e.g. feather molt in birds). Molt is energetically and nutritionally demanding, and is often limited by access to food in wild birds (Hill and Montgomerie 1994), or exposure to parasites (Marzal et al. 2013). Anthropogenically induced alterations to the environment could therefore affect the timing and extensiveness of molt, and feather quality, that could ultimately limit the effectiveness of plumage in thermoregulation, flight and mate attraction (Brush 1978, Swaddle and Witter 1997, Badyaev and Landeen 2007, Vézina et al. 2015). Disruptions to molt timing and progression could also interfere with other key life-history traits like breeding (including by affecting sexually selected plumage colors, Badyaev and Vleck 2007) or migration (Svensson and Nilsson 1997).

Multiple urban-related environmental factors may alter the molt schedule of birds. For example, light pollution at night advanced primary feather molt in European blackbirds (*Turdus merula*; Dominoni et al. 2013a, b). Additionally, metal pollution may reduce the growth rates of feathers and result in irregular (e.g. asymmetric) development (Talloen et al. 2008, Sillanpaa et al. 2010). Dietary differences in urban environments might also provide better or worse nutritional and energetic conditions. Surprisingly, despite an explosion of urban-ecological studies, only one has focused on molt dynamics of wild birds in the city (Hope et al. 2015). These authors found that urban Carolina chickadees *Poecile carolinensis* began molting their primary feathers earlier and molted fewer feathers simultaneously (a lower 'molt intensity') than rural chickadees, but that the duration of molt did not differ based on urbanization. Here we extend these findings in a different songbird species by asking if and how the urban environment relates to the growth dynamics of body feathers in both males and females.

Many avian species have ornamental body plumage colors, which can serve as sexual signals of viability and condition (Cuthill et al. 2017). Interestingly, multiple recent studies have shown that urban environments reduce the quality of plumage color signals (reviewed by Hutton and McGraw 2016b). Molting birds might have to choose between investing limited energy towards new feather synthesis or color development, in which case we might expect a negative relationship between molt rate and signal quality. Alternatively, birds that are in better condition might have both more rapid feather synthesis and develop higher quality color signals (Hill and Montgomerie 1994). Urban environments could alter the nutritional, energetic and metabolic conditions under which feather synthesis and color development occur, thereby affecting basic relationships between color and molt. Though quality of color ornamentation predicts both tail feather molt onset and nutritional condition in house finches *Haemorhous mexicanus* (Hill and Montgomerie 1994), we are unaware of any studies that have tested how urbanization alters the links between body condition, molt and coloration. Thus, in this study we tested the effects of urbanization on both color and body condition, and their links to body molt.

Based on the observation that environmental changes due to urban development might shift the cues and energetic conditions that trigger molt, we predict that: 1) urban environments alter the pace and timing of molt, 2) urban environments alter the body condition (measured as the scaled mass index) of birds during the molt process and 3) urban environments reduce intensity of color developed during molt. We also predicted that, because females invest little into ornamental coloration, 4) females may have more energy to invest in maintaining overall body condition and feather synthesis. Because females invest less energy in coloration, they likely experience a weaker energetic trade-off between investment towards coloration and feather growth during molt, and therefore we may expect relatively minor effects of urbanization on female molt and body condition.

We studied the house finch, which is a common bird native to the desert in the southwestern United States. The house finch also inhabits many urban environments, and thus is a popular organism for studies of urban organismal ecology (Fernández-Juricic et al. 2005, Valcarcel and Fernández-Juricic 2009, Giraudeau and McGraw 2014, Hasegawa et al. 2014, Adelman et al. 2015). Male finches display ornate carotenoid-based plumage, which varies in hue from yellow to orange to red, and females prefer to mate with redder males (Hill 1990, 1991, 2000, Hill and Montgomerie 1994). Following breeding, house finches enter a post-nuptial molt around mid-July (typically shorter and less extensive molts occur during postjuvenal molt; Michener and Michener 1940), which lasts for approximately 105 days (Badyaev et al. 2012), at which time circulating carotenoid pigments are deposited into ornamental crown, breast and rump feathers. We have recently found that urban male house finches are less red than rural finches (Hasegawa et al. 2014, Giraudeau et al. 2018). House finches are strongly sexually dichromatic, with females displaying little to no coloration. Thus, in this study we focused on male color exclusively.

Methods

Field methods

We studied house finches within a 1 km radius at four sites along a gradient of habitat urbanization in Phoenix, Arizona, USA (two urban sites: Downtown Phoenix and Arizona State University Tempe Campus; two rural sites: South Mountain Regional Park and Estrella Mountain Regional Park; Hasegawa et al. 2014, Hutton and McGraw 2016b). These urban and rural sites differ in both human population density and numerous metrics of land-use and land-cover, such as coverage by vegetation, disturbed commercial/industrial area and water (Giraudeau et al. 2014). During prebasic molt (11 Jul–9 Oct 2014), we visited each site every two weeks (in total 7 sampling periods) to capture birds between sunrise and 11:00 a.m. using baited basket traps. We fitted captured finches with a numbered metal United States Geological Survey band to identify individuals. We captured a total of 634 house finches (after hatch year (AHY) male = 42, hatch year (HY) male = 218, AHY female = 17, HY female = 242, HY birds of unknown sex = 111; from Phoenix = 118, from Tempe Campus = 203, from South Mountain Regional Park = 159, from Estrella Mountain Regional Park = 152), 535 of which were unique individuals and 72 were captured at least twice. This capture success resulted in an average of 22.64 finches (range = 12–84) trapped per site per sampling period.

For each bird, we measured the mass to the nearest 0.1 g with a digital scale (Smart Weigh, Chestnut Ridge, NY) and tarsus length to the nearest 0.01 mm using digital calipers (Neiko Tools, Homewood, IL). We then used these measurements to calculate an estimate of body condition, the scaled mass index $(\hat{M}_i) = M_i \times \left[\frac{L_0}{L_i}\right]^{b_{\mathrm{SMA}}}$, where M_i = mass of individual i, L_0 = the arithmetic population mean of tarsus length, L_i = tarsus length of individual i and b_{SMA} = the slope of the standardized major axis regression of ln M on ln L (Peig and Green 2010, Warton et al. 2012). Sex (male, female or unknown) was determined according to plumage characteristics (Hill 1993). Age was assigned (hatch–year or after–hatch–year) using plumage characters and/or the extent of skull pneumatization (Pyle 1997). To estimate the intensity of body molt, we counted the number of actively molting feathers (pinfeathers, feathers in sheath and unsheathed but incompletely grown feathers) in each region that can grow colorful body feathers (crown, breast and rump) (Hill and Montgomerie 1994, Yuri and Rohwer 1997, Butler 2013). This method was highly repeatable ($n = 22$, $r = 0.996$), as estimated from duplicate scores of the same bird (without identity being known) by our one observer (PH). In this study, because we studied only body molt and not other molting regions (e.g. tail, wing), note that any shorthand reference to our 'molt' data concerns body molt only.

Although some birds (about 35%) had begun body molt at the onset of our study, it is likely that inter-populational differences in molt intensity can be used to estimate interpopulation differences in molt onset and completion. First, avian molt intensity typically follows a predictable parabolic trajectory (Hope et al. 2015). Second, birds appear to modulate overall molt rate primary by altering molt intensity; Pap et al. (2008) found that experimental food restriction reduced molt rate by reducing only molt intensity, but not the growth rate of individual feathers. Third, when birds are restricted in the amount of time they have to molt, they increase molt intensity, but not growth rate of individual feathers (Hall and Fransson 2000). Finally, an interspecific study of molt in birds found that molt intensity explained ~60% of the variation in molt duration, whereas the growth rate of individual feathers accounted for only 4.4% (Rohwer and Rohwer 2013). So, while growth rate of individual feathers can vary, that variation likely contributes little towards overall molt rate. Therefore, in our study we believe molt intensity to be a good proxy for overall molt rate, and that molt intensity near the beginning and end of molt will be a good proxy for molt onset and completion, respectively.

Following Giraudeau et al. (2013), for all individuals that expressed carotenoid coloration on the crown, breast or rump, we took two photos of that region with a digital Sony Cybershot DSC-W800 camera (Sony, Tokyo, Japan). The photos were then processed in Photoshop CS6, by using the magic wand tool to separately select the growing plumage areas containing carotenoid pigmentation. To minimize color variation due to illumination, all photos were taken equidistant to the subject, with constant camera settings, and in a shaded area. We also corrected photos in Photoshop CS6 using a color/gray standard (Lendvai et al. 2013). We then extracted the hue values, and hue values from the two photos per body region per bird were averaged. All photos were analyzed by only one person (JM) who was blind to the capture site of each animal. Hue scores among body regions were significantly and highly correlated within a bird (all $r > 0.72$), so we averaged them across all color patches to obtain a single mean hue score per bird. Note that lower hue values indicate redder plumage hues.

The photographic method for measuring plumage color likely reflects house finch visual sensitivities for a few reasons. In a prior study, total carotenoid content of feathers (which was also related to 3-hydroxy-echinenone content, the main red ketocarotenoid in male house finch feathers) was significantly predicted by spectroradiometric tristimulus hue values, as well as hue θ values calculated from both non-UV sensitive and UV-sensitive avian visual models (Butler et al. 2011). Additionally, total carotenoid content of feathers was not significantly predicted by hue φ, which represents stimulation of ultraviolet-sensitive cones. Together, these results suggest that, in male house finches, visual (i.e. non-ultraviolet sensitive) hue values are sufficient to explain carotenoid-based plumage hue variation as detected by the avian visual system. As many cameras (including the model used in this study) do not capture ultraviolet light, the photographic method in this study is based on the visible light spectrum and likely captures hue variation similar to tristimulus hue values recorded by a spectroradiometer. Additionally, this photographic method has the added benefit of allowing us to obtain holistic hue values from the large carotenoid-colored patches of house finches, rather than from small areas within patches. Among-feather variation in hue can sometimes be considerable within patches, so photographic methods might better and more easily capture among-individual hue variability.

Statistics

All data were analyzed in the R computing environment (<www.r-project.org>). Given our focus on urban-rural differences within sexes, we did not include birds that we could not sex in the analyses. Therefore, analyses were run separately for males ($n = 260$) and females ($n = 261$). Given that in our initial analysis sites within each habitat type did not differ from one another (i.e. Phoenix versus Tempe and South Mountain versus Estrella Mountain, all differences $p > 0.57$), sites were pooled into 'urban' and 'rural' habitats for final analysis. To investigate the effect of habitat urbanization on body molt intensity, we modeled the data with generalized linear models (GLMs) using the *glm()* command with a Poisson error distribution (Pinheiro et al. 2015). For each model we examined diagnostic plots (normal Q–Q plots, and plots of residuals versus fitted values) to ensure that we met the assumptions of linear mixed models. Because for some individuals we obtained data from multiple time-points, we at first attempted to include individual identity as a random factor in our models. However, these models would not converge, so for individuals with multiple replicates we randomly chose a single replicate and removed others from the dataset, thereby avoiding pseudoreplication (Zuur et al. 2009). Removal of replicates reduced the sample size for these analyses to $n = 216$ females and 207 males. We used a Poisson error distribution as opposed to a normal ('Gaussian') error distribution because, our data are ultimately count data, and at low levels of molt (e.g. weeks 0 and 12), the data were zero-inflated and right-skewed. Additionally, at peak times of molt, the distribution was approximately normal; it is known that Poisson distributions with high levels of the parameter k approximate a normal distribution (Zuur et al. 2009), so a Poisson error distribution was appropriate for all molt periods. We checked to ensure that, at each site and each time period, a Poisson distribution was appropriate. In the GLM, we used molt intensity as the response variable, and habitat type (urban versus rural), time (weeks 0–12) and their interaction as predictors.

To investigate the effects of habitat on body condition, we created linear mixed-effect models with a normal error distribution, keeping all factors and covariates the same as previous, except for changing the response variable to the scaled mass index. Body condition models did not experience similar convergence problems as the molt models (above), so we included the entire dataset and controlled for pseudoreplicates by including individual as a random effect. Finally, to investigate co-variation between time and color as a function of habitat, we created similar models to the body condition models, except with plumage hue as a response variable. For all models, if there was a significant interaction between habitat and time, we examined pairwise differences between the urban and rural group within each time point using Tukey's method for multiple comparisons. As 59 of the 535 (11%) unique individuals that we captured were adults, we initially included age as a covariate in all models but then removed it because it was not significant in any model (all $p > 0.05$). This is consistent with prior studies of house finches showing no age differences in molt (Hill and Montgomerie 1994).

Next, we investigated how body condition and color (for males only) predict molt intensity for birds from urban versus rural sites. We did so by first collapsing multiple weeks of data, based roughly on the inflection points of the parabolic molt intensity curve (which may reveal different trade-offs between molt and color or condition), into three major periods of molt (weeks 0–2: beginning; weeks 4–8: peak; weeks 10–12: end). We then generated three GLMMs (Poisson error distribution, as above), one for each period of molt, with molt intensity as the response and habitat, body condition and the habitat × body condition interaction as predictors. Next, we used three similar GLMMs to investigate the relationship between molt intensity and male plumage hue, but with habitat, hue and the habitat × hue interaction as predictors.

Results

Urban effects on molt dynamics

Urban and rural populations differed significantly in body molt intensity and timing over the course of the study (Fig. 1a–b, Table 1). Specifically, for males, we found a significant interaction between habitat and time on body molt (Fig. 1a, Table 1). Urban males had greater molt intensity than

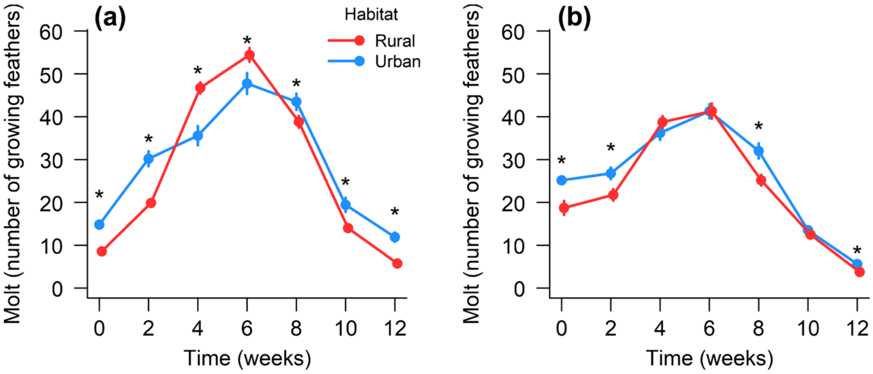

Figure 1. Change in molt intensity over time is dependent on habitat urbanization for both (a) males and (b) females. Points are least square means and error bars represent ± 1 SEM. Asterisks indicate the time periods when urban and rural birds differed in the given parameter. Red points and lines represent the rural population, and blue points and lines represent the urban population.

Table 1. Outputs for the main models in which we tested temporal progression in molt intensity (generalized linear model with Poisson error term), body condition (linear mixed model) and hue (linear mixed model) of carotenoid-based plumage over the molt period for both males and females. p-values in bold are considered statistically significant predictors at $\alpha < 0.05$. 'Week' refers to our biweekly sampling interval for analyses of males (Methods for additional details).

Response	Sex	Predictors	df	χ^2	p
Molt	Male	Habitat	1	23.33	**< 0.001**
		Week	6	1623.26	**< 0.001**
		Habitat × Week	6	106.26	**< 0.001**
	Female	Habitat	1	10.66	**0.0011**
		Week	6	1503.01	**< 0.001**
		Habitat × Week	6	24.83	**< 0.001**
Condition	Male	Habitat	1	8.24	**0.0041**
		Week	6	129.18	**< 0.001**
		Habitat × Week	6	12.48	**0.052**
	Female	Habitat	1	0.16	0.68
		Week	6	15.93	**0.014**
		Habitat × Week	6	14.61	**0.023**
Hue	Male	Habitat	1	5.92	**0.015**
		Week	6	33.81	**< 0.001**
		Habitat × Week	6	6.04	0.42

rural birds at weeks 0 and 2 (Tukey contrasts, $p < 0.001$ for both weeks), but rural males not only caught up, but overtook, urban birds during weeks 4 ($p = 0.001$) and 6 ($p = 0.027$), after which point urban males once again had greater molt intensity (week 8: $p = 0.043$; week 10: $p = 0.003$; week 12: $p < 0.001$). Given that urban males had greater molt intensity towards the beginning (weeks 0–2) and end (weeks 8–12) of molt, this indicates that males from the urban areas began molt earlier and ended later. Additionally, the broader curve and shallower peak in molt for urban relative to rural birds suggests that molt duration was longer in urban areas.

Female molt was also significantly affected by an interaction between habitat and time (Fig. 1b, Table 1). Urban females had greater molt intensity than rural females during the beginning of molt (week 0: $p = 0.0018$; week 2: $p = 0.0098$). However, during most of peak molt urban and rural females had similar molt intensity (week 4: $p = 0.23$; week 6: $p = 0.98$; week 8: $p = 0.0014$). Lastly, during the end of molt, urban and rural females tended to molt similarly, with the exception of the final week of data collection when urban females had slightly higher molt intensity (week 10: $p = 0.42$; week 12: $p = 0.014$). These results reveal that urban females began molt earlier and ended later (similar to males), but that, unlike in males, urban and rural females did not differ in molt intensity during peak molt.

Urban effects on body condition and their relations to molt

In males, we found a near-significant interaction between habitat and time on body condition (Fig. 2a, Table 1). Body condition was similar between urban and rural males from weeks 0 to 4 (all $p > 0.05$), after which time the two populations diverged, with rural males tending to maintain better body condition than urban males (week 6: $p = 0.023$; week 8: $p = 0.74$; week 10: $p < 0.001$; week 12: $p = 0.15$).

Females also showed a significant habitat-dependent change in body condition over time (Fig. 2b, Table 1). Though rural and urban females did not differ in body condition during the beginning and end of molt (weeks 0–2 and weeks 10–12; all $p > 0.05$), rural females were in significantly better body condition than urban females during the beginning of peak molt, after which this difference slowly disappeared (week 4: $p = 0.0089$; week 6: $p = 0.073$; week 8: $p = 0.31$).

Urban–rural variation in male carotenoid-based plumage coloration during molt

Male finches were reddest as molt peaked, and rural males were redder than urban males throughout the entirety of molt, as there was a significant effect of habitat but not the habitat × time interaction (Fig. 3, Table 1). These results are consistent with our two prior studies (both conducted outside of the molt period and only in males) showing that urban house finches are less red year-round (Hasegawa et al. 2014, Giraudeau et al. 2015).

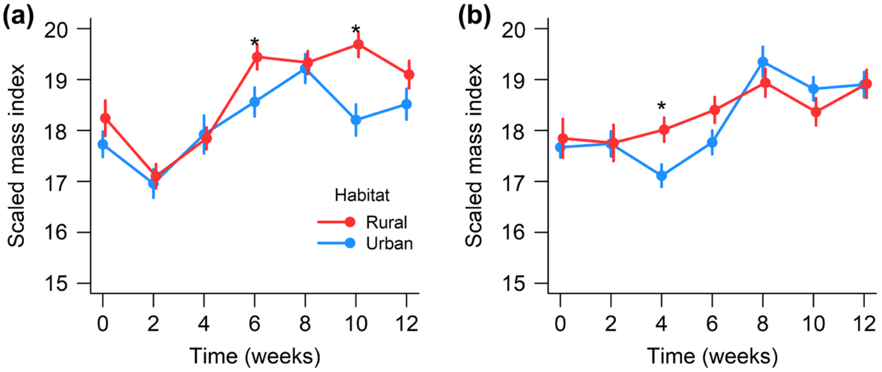

Figure 2. Change in body condition (measured as the scaled mass index) over time is dependent on habitat urbanization for both (a) males and (b) females. Points are least square means and error bars represent ± 1 SEM. Asterisks indicate the time periods when urban and rural birds differed in the given parameter. Red points and lines represent the rural population, and blue points and lines represent the urban population.

Dependence of molt intensity on body condition and plumage hue in urban and rural habitats

We investigated the dependence of molt on body condition in urban and rural males and females. In rural male finches, we found that condition significantly and positively predicted molt intensity during the beginning of molt which was not the case among urban males (Supporting information; Table 2). At peak molt, body condition did not predict molt intensity in either urban or rural males (Supporting information, Table 2). At the end of molt, body condition significantly and positively predicted molt intensity in both urban and rural males (Supporting information; Table 2).

In both rural and urban female finches, we found that body condition positively and significantly predicted molt intensity at the end of molt, but not during any other period (Supporting information, Table 2).

We also investigated the dependence of molt intensity on ornamental color in male finches. During the beginning of molt, redder males (regardless of habitat) had higher molt intensity (Supporting information; Table 2). However, during peak molt, redder males had higher molt intensity only in rural, but not urban, habitats (Supporting information; Table 2). Additionally, at the end of molt, the sign of this relationship changed and redder birds had lower molt intensity (Supporting information; Table 2). Given that redder males had greater molt intensity during the most intense periods of feather growth (beginning and peak) and that pattern was reversed at the end of molt, these results suggest that redder birds begin molt earlier and complete molt more quickly.

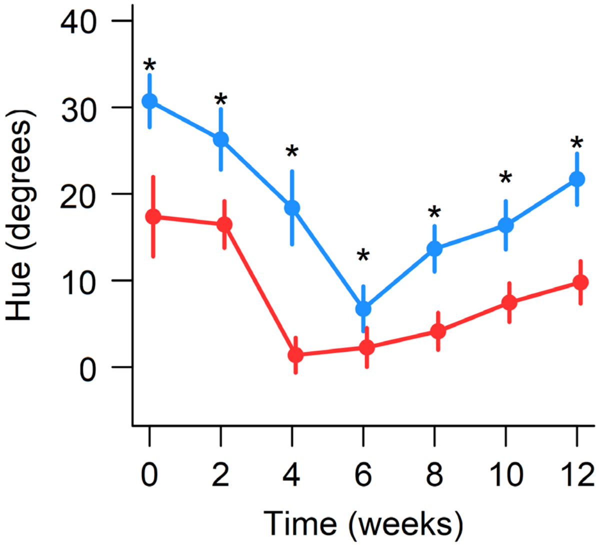

Figure 3. Carotenoid-based plumage hue is different between rural and urban male house finches. Points are least square means and error bars represent ± 1 SEM. Asterisks indicate the time periods when urban and rural birds differed in the given parameter. Red points and lines represent the rural population, and blue points and lines represent the urban population. Note that lower hue values indicate redder plumage, and higher values indicate yellower plumage.

Discussion

We evaluated the hypothesis that urbanization alters molt dynamics, body condition and carotenoid-based ornamental plumage during molt in house finches. In males, we found that urban finches had greater molt intensity at both molt onset and completion, but had lower molt intensity at peak molt than rural finches. In females, we found a similar trend, except that urban and rural populations did not differ in molt intensity at peak molt. This pattern of inter-population variation in molt intensity suggests that urban house finches, regardless of sex, molt earlier and more slowly than rural counterparts. These results closely resemble other studies comparing the impacts of urbanization on songbird molt. Hope et al. (2015) showed that urban Carolina chickadees began molting primary wing feathers earlier and had lower peak molt intensity than rural chickadees, though they found no difference in molt duration. Additionally, in a common-garden laboratory experiment on European blackbirds, Dominoni et al. (2013a, b) showed that urban birds began molting earlier relative to rural counterparts. In sum, there is increasing and consistent evidence that urban environments alter the molt patterns of birds, which adds this life-history trait to several others (i.e. breeding, migration) that are impacted by urbanization.

There are a few non-mutually-exclusive proximate explanations for why birds might molt differently in urban environments. First, the transition from breeding to molt is often driven by the decline of sex hormones and an increase in prolactin (Hahn et al. 1992, Deviche et al. 2000, Dawson 2006). Birds of some species tend to come into breeding condition and breed earlier in urban settings (Deviche and Davies 2013), and therefore might also transition from breeding into molt earlier (Dominoni et al. 2013a); thus, early molt might be caused by a frame-shift in annual life-history stages. However, our study included a mixture of after–hatch–year and hatch–year birds, with the majority of the sample being hatch–year birds. There is evidence in some birds that early-hatching juveniles molt less intensely, and complete molt less quickly (Helm and Gwinner 1999, Helm et al. 2005), which would be consistent with the observation that birds often breed earlier in urban environments. Therefore, the urban life-history frame-shift hypothesis has the potential to explain urban–rural differences in molt dynamics, and will be an interesting hypothesis to test in future studies. Secondly, urban environmental cues may explain our observed urban–rural variation in molt dynamics. There is experimental evidence that light pollution advances molt onset in European blackbirds (Dominoni et al. 2013b). Thus, light pollution may explain why urban birds begin molting earlier, despite being in similar body condition to rural birds. We need field studies of wild birds to test whether light pollution advances molt onset in the wild, and whether light-induced rapid early molt carries energetic costs.

In many birds, the most energetically and nutritionally costly period of molt is when the majority of body feathers are concurrently growing (Dolnik and Gavrilov 1979,

Table 2. Generalized linear mixed models (Poisson error term) showing the predictors of molt intensity at the beginning, peak and end of molt for urban and rural males and females. p-values in bold are considered statistically significant predictors at $\alpha < 0.05$. Slopes indicate the slope of the predictor (hue or condition) for urban and rural populations separately, as well as with both populations pooled. Slopes in bold indicate that the slope differed significantly from zero.

Sex	Molt period	Predictors	df	χ^2	p	Slope		
						Pooled	Urban	Rural
Male	Beginning	Hue	1	9.76	**0.0017**	**−0.016**	**−0.048**	**−0.013**
		Habitat	1	37.76	**< 0.001**			
		Hue × Habitat	1	21.14	**< 0.001**			
	Peak	Hue	1	47.67	**< 0.001**	**−0.0061**	−0.00093	**−0.011**
		Habitat	1	2.16	0.14			
		Hue × Habitat	1	20.82	**< 0.001**			
	End	Hue	1	27.35	**< 0.001**	**0.038**	**0.043**	**0.073**
		Habitat	1	0.21	0.64			
		Hue × Habitat	1	3.25	0.07			
	Beginning	Condition	1	9.25	**0.006**	0.02	−0.048	**0.093**
		Habitat	1	12.42	**< 0.001**			
		Condition × Habitat	1	10.29	**< 0.001**			
	Peak	Condition	1	1.08	0.29	NA	NA	NA
		Habitat	1	1.3	0.25			
		Condition × Habitat	1	0.92	0.34			
	End	Condition	1	21.21	**< 0.001**	**0.15**	**0.24**	**0.24**
		Habitat	1	0.77	0.37			
		Condition × Habitat	1	0.26	0.6			
Female	Beginning	Condition	1	0.11	0.73	NA	NA	NA
		Habitat	1	1.53	0.21			
		Condition × Habitat	1	2.19	0.13			
	Peak	Condition	1	0.5	0.47	NA	NA	NA
		Habitat	1	1.33	0.24			
		Condition × Habitat	1	1.75	0.19			
	End	Condition	1	4.71	**0.029**	**0.16**	**0.27**	**0.088**
		Habitat	1	7.31	**0.0067**			
		Condition × Habitat	1	8.56	**0.0034**			

Hahn et al. 1992, Hill and Montgomerie 1994, Murphy 1996, Richardson and Kaminski 2008). During peak molt we found that rural males were both in better condition and had higher molt intensities than urban birds. Additionally, at the end of molt, rural males remained in better condition and had lower molt intensities. This suggests that body condition limits feather synthesis and overall molt duration during the peak and end of molt. Accordingly, recent behavioral studies of wild common mynas *Acridotheres tristis* suggest that urban birds may be deprived of access to high-protein diets, as they preferentially chose and competed for access to diets that were high in protein (Machovsky-Capuska et al. 2016). Thus, lack of nutrition in urban environments may limit peak molt rate and molt duration in urban birds. Future studies should examine how dietary differences between urban and rural populations of birds might limit molt duration and peak intensity.

We found evidence that urban birds may molt too quickly at the beginning of molt, given that they appear to incur an energetic cost in later stages of molt. Variation in molt speed may carry fitness consequences, and previous studies have shown that altered molt cycles can greatly influence the plumage quality and have potential fitness consequences (Nilsson and Svensson 1996). For example, experimentally quickened molt leads to reduced individual feather mass (Dawson 2004), reduced flight feather length, and increased prevalence of fault bars (Vágási et al. 2012). Indeed, a large multi-city regional study of house sparrows *Passer domesticus* in France demonstrated that individual feather density was lower in urban relative to rural sparrows (Meillère et al. 2017), suggesting that altered molt patterns in the urban environments may also impose additional costs to birds.

We investigated the relationship between plumage hue and molt patterns in males and found that hue tended to predict molt onset, completion and peak intensity. Hill and Montgomerie (1994) showed that redder male house finches grow tail and body feathers more rapidly, and here we bolster these earlier observations by showing that redder males initiate molt earlier, reach higher peak molt intensity (in rural, but not urban males), and complete molt sooner. This evidence supports previous hypotheses that early-molting males are in better nutritional condition and can allocate more energy to both feather synthesis and feather ornament production (Hill and Montgomerie 1994, Hill 2000, Maia and Macedo 2011). That urban males show no relationship between ornamentation and molt intensity at peak molt suggests that urban environments might unlink potential signal honesty-enforcing mechanisms. In this population, urbanization weakens the strength of female preference for male redness, further suggesting that urbanization can alter sexually selected communication, perhaps by affecting honesty enforcing mechanisms during molt (Hutton and McGraw 2016a).

To our knowledge, this is the first study to investigate how urbanization influences molt dynamics of ornamental and body feathers in a bird. Because of the fitness value of this life-history trait, we suggest that future investigations explore the environmental, life-history, behavioral and physiological mechanisms that regulate differences in timing, duration and intensity of molt of urban birds. Specifically, tracking of individuals with regards to breeding schedules and physiology (e.g. first/last clutch, gonadal recrudescence/quiescence and sex hormones) and molt schedule/physiology (sex hormones, molt onset, completion and intensity) will shed light on how the entire annual cycle is timed, linked or independently-regulated and if differentially so across an urban-ecological gradient. Secondly, experimental approaches that manipulate urban-like environmental factors (e.g. light, noise, chemical pollution, food) in 'natural' environments will provide the strongest test of this hypothesis. In sum, our results bolster those that suggest urban environments alter the physiology and life-history strategies of wild animals (Ditchkoff et al. 2006, Bonier et al. 2007).

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Pierce Hutton: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Project administration (supporting); Supervision (supporting); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Jennifer McKenna**: Data curation (supporting); Formal analysis (supporting); Investigation (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Kevin McGraw**: Conceptualization (supporting); Data curation (supporting); Formal analysis (supporting); Funding acquisition (lead); Investigation (supporting); Methodology (supporting); Project administration (lead); Resources (lead); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (supporting).

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Data availability statement

Data will be available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.f1vhhmgw5> (Hutton et al. 2021).

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