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Body condition and poxvirus infection predict circulating glucose levels in a colorful songbird that inhabits urban and rural environments

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Abstract

There is widespread contemporary interest in causes and consequences of blood glucose status in humans (e.g., links to diabetes and cardiovascular disease), but we know comparatively less about what underlies variation in glucose levels of wild animals. Several environmental factors, including diet, disease status, and habitat quality, may regulate glucose circulation, and we are in need of work that assesses many organismal traits simultaneously to understand the plasticity and predictability of glucose levels in ecological and evolutionary contexts. Here, we measured circulating glucose levels in a species of passerine bird (the house finch, *Haemorhous mexicanus*) that has served as a valuable model for research on sexual selection, disease, and urban behavioral ecology, as these animals display sexually dichromatic ornamental coloration, harbor many infectious diseases (e.g., poxvirus, coccidiosis, mycoplasmal conjunctivitis), and reside in both natural habitats and cities. We tested the effects of sex, habitat type, body condition, coccidiosis and poxvirus infections, and expression of carotenoid plumage coloration on blood glucose concentrations and found that the body condition and poxvirus infection significantly predicted circulating glucose levels. Specifically, birds with higher blood glucose levels had higher body condition scores and were infected with poxvirus. This result is consistent with biomedical, domesticated-animal, and wildlife-rehabilitation findings, and the premise that glucose elevation is a physiological response to or indicator of infection and relative body weight. The fact that we failed to find links between glucose and our other measurements suggests that blood glucose levels can reveal some but not all aspects of organismal or environmental quality.

KEYWORDS

blood sugar, disease, *Haemorhous mexicanus*, house finch, wildlife health

1 | INTRODUCTION

As humans have massively modified the planet in recent decades, there has been mounting interest in studying rapid environmental impacts on the health and well-being (i.e., quality) of organisms (Acevedo-Whitehouse & Duffus, 2009), including humans (Cable et al., 2017; Watts et al., 2018). Many metrics of organismal quality have been considered, including obesity and cardiovascular health in human populations (Roth et al., 2017; Swinburn et al., 2019) and a variety of phenotypic and fitness metrics in non-human captive and wild animals (Hill, 2011; Manteca, Amat, Salas, & Temple, 2016; Wilson & Nussey, 2011). The fact that these metrics largely have differed for humans and non-humans, however, has limited our ability to compare impacts of single or collective ecological factors on a range of living things. Instead, we need comparable methods for assessing responsiveness and well-being, to develop holistic understandings of how ecosystems of organisms (humans and non-humans) respond to ongoing rapid environmental change.

One such translatable metric among animals may be glucose status. The rapid rise in human hyperglycemia and diabetes since the industrial revolution has led many to focus on glucose status as a critical indicator of the modern diet, inactive lifestyles, cardiovascular disease risk, and overall lifespan (Sami, Ansari, Butt, & Hamid, 2017). As glucose levels are thought to respond to several forms of stress (Marik & Bellomo, 2013), they may in fact broadly capture an organism's responses to or tolerance of many environmental and physiological challenges. Although empirical studies on blood sugar in wild animals has lagged behind those in humans, some recent findings in animals are consistent with the idea that circulating glucose concentrations reflect variation in the phenotypic and physiological quality of animals, especially in birds (where metabolic demands and energy turnover are high; Scanes & Braun, 2013). For example, body size/mass is a strong predictor of avian glucose circulation, both within (Lill, 2011) and among bird species (Braun & Sweazea, 2008); smaller species tend to circulate higher levels, on average (Tomasek, Bobek, Kralova, Adamkova, & Albrecht, 2019), though this mass–glucose relationship is positive within some species (including in young nestling birds; Kalinski et al., 2014; Lill, 2011). Species with higher glucose levels also tend to migrate shorter distances but invest more in individual reproductive bouts (i.e., clutch mass; Tomasek et al., 2019). Within some bird species, changes in plasma glucose status have also been linked to food deprivation (i.e., in yellow-legged gulls, *Larus cachinnans*; Alonso-Alvarez & Ferrer, 2001), anemia (i.e., in whiskered terns, *Chlidonias hybrida*; Minias, 2014), as well as nest ectoparasitism and habitat type (i.e., in natural versus urban sites in great tit nestlings, *Parus major*; Gladalski et al., 2018). In one of the more comprehensive ecological studies of variation in blood glucose, Kalinski et al. (2014) found that nestling blue tits (*Cyanistes caeruleus*) with higher circulating glucose levels were heavier, found more often in urban habitats, and had decreased survival. Thus, though it appears that several environmental factors, including body size, diet, health state, and habitat quality, can regulate glucose circulation in different systems, we are in need of more intraspecific work, especially in free-ranging animals, that assesses many organismal traits simultaneously to understand plasticity and predictability of glucose levels in ecological and evolutionary contexts.

Here, we tested the degree to which several morphological, physiological, and life-history traits predict circulating glucose levels in a free-ranging songbird species—the house finch (*Haemorhous mexicanus*)—that has been commonly studied in the context of sexual selection and individual quality (Badyaev, Belloni, & Hill, 2020; Hill, 2002). Males have more colorful carotenoid-based plumage than females, and females use variation in male coloration in mating decisions and select the reddest males as partners (Hill, 1990). Redder males are in better condition (Hill & Montgomerie, 1994), have fewer parasites/pathogens (like coccidiosis and poxvirus; Brawner, Hill, & Sundermann, 2000; Thompson, Hillgarth, Leu, & McClure, 1997) and are more often found in rural/natural habitats compared to urban locations (Giraudeau, Chavez, Toomey, & McGraw, 2013; Giraudeau, Toomey, Hutton, & McGraw, 2018; Hasegawa, Ligon, Giraudeau, Watanabe, & McGraw, 2014). However, to our knowledge, no study has linked this classic form of a condition-dependent trait to glucose levels in any system. We specifically examined whether blood glucose levels in house finches varied as a function of several quality-related metrics—plumage coloration, habitat urbanization, body condition, sex, and infections with poxvirus and endoparasitic coccidians—to continue to assess if and how glucose levels may serve as a valuable metric for comparing effects of rapid environmental change within and among species.

2 | MATERIALS AND METHODS

We used sunflower-seed-baited basket traps to capture 58 house finches (37 male and 21 female) from 20 to 23 December 2018 at three of our common study sites in Maricopa County, AZ (Weaver, Ligon, Mousel, & McGraw, 2018)—one urban (Arizona State University campus in Tempe, AZ; lat 33°25′11.4″N, long 111°55′59.3″W), one suburban (residential backyard in Tempe, AZ; lat 33°20′41.1″N, long 111°55′49.5″W), and one rural (South Mountain Regional Park in Phoenix, AZ; lat 33°21′01.9″N, long 112°04′33.6″W). These sites are >10-km apart and differ in both urban land-use/land-cover metrics and in human population density (Giraudeau, Mousel, Earl, & McGraw, 2014). Ages of the birds in this study were unknown because, at this time of year, we could not distinguish hatch-years versus after-hatch-years based on plumage characters or skull pneumatization (Pyle, 1997).

At capture, we determined the sex of each bird based on plumage coloration (Hill, 2002) and measured body mass (to the nearest 0.01 g with a digital scale) and tarsus length (to the nearest 0.01 mm with digital calipers) so that we could calculate a residual mass index, based on a regression of tarsus on mass (which was statistically significant and positive; $r^2 = .20$, $p = .0004$), as our metric of body condition (Hutton, Wright, DeNardo, & McGraw, 2018). A single observer blind to the hypotheses being tested estimated presence/absence of poxvirus infection based on the occurrence of lesions on eyes, beak, or legs (Giraudeau et al., 2014); as we did not detect multiple lesions on any bird in this particular study (i.e., we have noted seasonal and annual variation in poxvirus infection prevalence/severity in our populations), we scored this trait only as present versus absent here.

Also at capture, we used an Accu-Chek® Guide blood glucose meter (Roche Diabetes Care Inc., Indianapolis, IN) to measure the levels of circulating glucose (in mg/dl) in each captured bird. Recent work (Mohsenzadeh, Zaeemi, Razmyar, & Azizzadeh, 2015) has shown that results obtained in rock pigeons (*Columbia livia*) with this glucometer are comparable to those using traditional biochemistry autoanalyzer methods (also see work on passerines by Tomasek et al., 2019 using a different hand-held glucometer). We measured glucose from a drop of blood taken from each finch from the alar vein using a 26-gauge needle; we restrained birds by hand for blood draws and drew blood within 5 min of capture in the trap. We took duplicate glucose readings for a subset (n = 27) of individuals and found that circulating glucose levels were significantly and highly repeatably measured using this technique (r^2 = .92, $F_{1,25}$ = 271.0, p < .0001). As glucose levels did not covary with time of capture (r^2 = .04, p = .13), we did not include time of day in our statistical models (see below).

We also used our standard digital-photographic techniques (Giraudeau et al., 2013; Giraudeau, Toomey, & McGraw, 2012) to measure carotenoid-based plumage coloration (as hue, saturation, and brightness), namely for rump patches of females and for the crown, breast, and rump patches of males. As plumage hue, saturation, and brightness were all significantly intercorrelated (all|r| > 0.53, all p < .0001), we used principal components analysis to collapse these into a single principal component, which had an eigenvalue of 2.25 and explained 75% of the variation in the tristimulus scores. Hue loaded negatively (−0.83) and saturation and brightness loaded positively (0.91 and 0.86, respectively) with PC1, such that higher PC1 scores denote redder, more saturated, and brighter plumage. Lastly, after 1600 hr, we obtained a fecal sample from each bird so that we could use fecal float and microscope slide preparations later in the lab (using compound light microscopy) to estimate the severity of infection with coccidian endoparasites (*sensu* Brawner et al., 2000; Giraudeau et al., 2014). Fresh feces were preserved in a 1 ml solution of 2.2% potassium dichromate, and at the time of analysis, we transferred the sample contents into a fresh 9 ml culture tube and filled it to the top with Sheather's sugar solution (RICCA, Arlington, TX). We placed a microscope coverslip atop the convex meniscus of the solution on the tube mouth and centrifuged for 5 min at 3,000 RPM. We then transferred the coverslip to a microscope slide, and two independent scorers examined the slide under a light microscope (Olympus BX60) at ×40 magnification with constant (i.e., equal brightness and contrast) microscope settings and ranked oocyst load (i.e., degree of infection) on a 0–5 integer scale (0 = no oocysts; 1 = 1–10 oocysts; 2 = 11–100; 3 = 101–1,000; 4 = 1,001–10,000; 5 = >10,000; Brawner et al., 2000; Costa & Macedo, 2005).

To evaluate predictors of blood glucose levels in house finches, we used an Akaike information criterion, model-averaging approach (*sensu* Ligon & McGraw, 2013; Simpson & McGraw, 2018). We created a global model with residual body mass, sex, capture site, coccidia estimate, poxvirus presence, and plumage coloration as our fixed effects. As the blood glucose data were not normally distributed, we used a Box-Cox transformation to acquire the best-fit, normally distributed transformation (λ = −1.038). We then calculated a summed Akaike weight, or relative importance (RI), and average beta value for each fixed effect from our global model, and for all possible models nested within our global model. To avoid misinterpretation of RI values, we created a final linear model of blood glucose levels using only fixed effects with an RI > 0.5 and only interpreted the effects that were significant in this final model (Galipaud, Gillingham, David, & Dechaume-Moncharmont, 2014). To test for the possible influence of collinearity between variables, we calculated the variance inflation factors from our global model and found that only sex and color had generalized variance inflation factors (GVIF) >5 (GVIF = 6.63 and 6.30, respectively; all others <.5), which corresponds to standard sex differences in plumage color for this species (Badyaev et al., 2020). However, neither sex nor coloration ended up as a strong effect in our analyses (see Section 3), so we are confident that our results were not influenced by collinearity.

3 | RESULTS

Glucose levels in free-ranging urban, suburban, and rural house finches averaged 269.30 mg/dl (±5.65 SEM) and ranged from 168 to 467 mg/dl (see more information in Table S1, available online). We found that residual body mass (RI = 0.99) and poxvirus presence (RI = 0.96; Figure 1) were strong predictors of blood glucose levels, and both variables were significant in the final model (linear regression: r^2 = 0.41, $F_{2,39}$ = 13.49, p < .001; Table 1). Specifically, we found a positive relationship between residual body mass and blood glucose concentration (Figure 2), such that individuals in better body condition (i.e., greater body mass for a given skeletal size) had higher

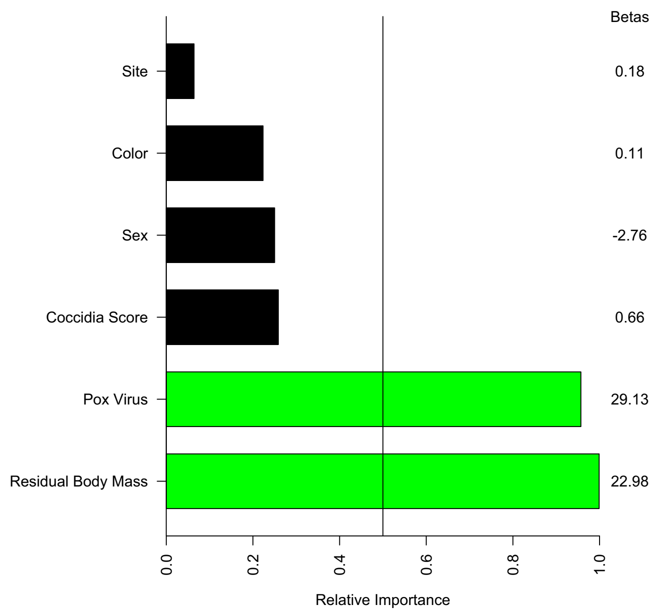

FIGURE 1 Information-theoretic model-averaging results depicting the relative importance (RI) values and average beta coefficients for each of the predictor variables in our model of glucose variation in house finches during winter. Bars in green represent variables for which RI values exceeded the 0.5 cutoff; black bars denote variables with RIs < 0.5 [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Blood glucose was strongly predicted (relative importance [RI], >0.5) by residual body mass and poxvirus presence, and both variables were statistically significant in our final linear model

Fixed effect (RI)	Estimate	Standard error	*t* Value	*p* Value
Intercept	83,064.7	6.1	13,603.1	<.001
Residual body mass	22.9	5.2	4.4	<.001
Poxvirus presence	30.7	10.1	3.0	.004

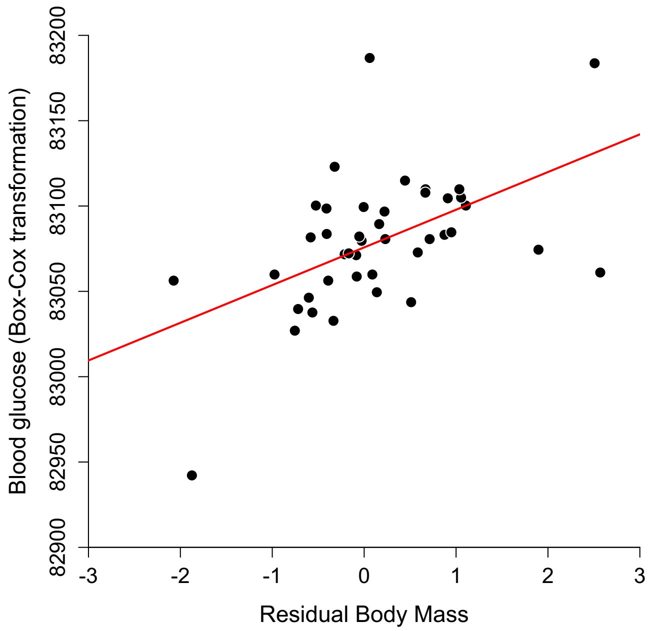

FIGURE 2 Scatterplot showing the positive significant relationship (best-fit line in red) between residual body mass and circulating glucose levels in house finches. Higher residual mass values indicate greater body mass for a given structural/skeletal size, and we show the Box–Cox-transformed values for blood glucose [Color figure can be viewed at wileyonlinelibrary.com]

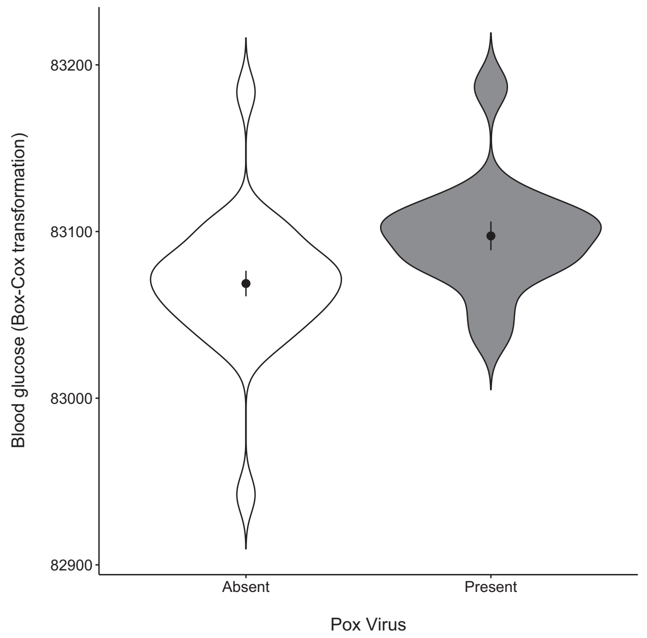

FIGURE 3 Violin plot showing the pairwise difference in circulating glucose levels (Box–Cox-transformed values) between house finches that had poxvirus lesions versus those that did not present lesions. Finches with poxvirus had higher levels of circulating glucose. Black dots = means; vertical black lines = standard errors of the means; white- and gray-shaded areas = distribution of glucose levels (along *y*-axis) and density of points per glucose level (thickness of shaded region at a given location on the *y*-axis)

circulating glucose levels. We also found a significant effect of poxvirus presence on blood glucose, such that individuals with poxvirus lesions had higher glucose levels than those without lesions (Figure 3). Body condition was not significantly related to poxvirus infection ($F_{1,56} = 0.69$, $p = .41$). We did not find strong effects of sex (RI = 0.25), plumage coloration (RI = 0.22), habitat of origin (RI = 0.06), or degree of coccidiosis infection (RI = 0.26) on blood glucose concentrations (Figure 1).

4 | DISCUSSION

Birds have emerged as an intriguing study system for investigating regulation and function of blood sugar concentrations in animals, as they circulate very high glucose levels compared to humans and other mammals and yet largely do not appear to experience diabetic complications (Braun & Sweazea, 2008; Li, 2017; Mello & Lovell, 2018). Much prior work on avian glucose circulation has focused on captive populations (Braun & Sweazea, 2008) but more recent work has centered on levels measured in wild birds (i.e., the comparative study of 30 songbird species; Tomasek et al., 2019). However, perhaps the most extensive intraspecific study on glucose levels in a wild-bird species was in young nestling birds (blue tits; Kalinski et al., 2014). Here, we studied free-ranging birds (of at least 5–8 months old, with many likely to be older, though they are not ageable at this time of year due to skull ossification of all age classes) to understand the degree to which a range of life-history, morphological, and physiological variables predicted circulating levels of glucose in house finches during winter. We found that body condition and poxvirus infection prevalence were both significant predictors of blood glucose concentrations and specifically that finches with higher glucose levels were in greater body condition and more likely to be infected with poxvirus. In contrast, we found that sex, plumage color expression, the extent of coccidiosis infection, and habitat of origin (urban vs. rural) did not explain significant variation in individual glucose titers.

As we did not find a relationship between poxvirus infection prevalence and body condition per se in these birds, our results suggest that body condition and viral infection had independent effects on circulating glucose titers. Body mass has been linked to glucose levels in several prior investigations of wild birds, but some studies show positive relationships (Jenni-Eiermann & Jenni, 1994; Kalinski et al., 2014; Lill, 2011), whereas others reveal negative relationships (Braun & Sweazea, 2008; Lill, 2011; Tomasek et al., 2019). However, when assessing an animal's nutritional or physiological condition, it can be important to consider not just body mass, but size-corrected mass (Peig & Green, 2010), and this variable has been less commonly used and compared to glucose circulation in the literature. Interestingly, in the two studies that examined body condition (as mass-tarsus residuals), they, like us, found a significant positive relationship between the condition and circulating glucose titers in nestling great cormorants (*Phalacrocorax carbo sinensis*; Minias & Kaczmarek, 2013) and breeding pale-bellied tyrant manakins (*Neopelma pallescens*; Azeredo, Oliveira, & Lopez, 2016). So, what might a positive body condition (i.e., more soft body mass for a given structural size) reveal in relation to glucose in these cases? Obesity is commonly linked to hyperglycemia in animals (Kanasaki & Koya, 2011; Niaz et al., 2018; Wong, Chin, Suhaimi, Fairus & Ima-Nirwana, 2016), but because we did not quantify body fat or muscle per se here, we cannot rule out that relative masses of other tissues/organs (not necessarily obesity) could contribute to this result. As free-ranging songbirds are generally so physically and metabolically active and presumed not to suffer from diabetes, it would be interesting now to determine whether or not commonly considered factors linked to obesity, such as diet and activity patterns, help explain this relationship between avian body condition and circulating glucose titers.

To our knowledge, our finding that the presence of poxviral infection was associated with elevated circulating glucose levels in house finches is among the first to demonstrate a link between pathogen/parasite burden and glucose in wild birds. In both European starling (*Sturnus vulgaris*; Pryor & Casto, 2015) and great tit (Gladalski et al., 2018) nestlings, glucose levels were higher in birds exposed to more nest parasites; Norte et al. (2018), in contrast, found no effect of experimental infection with tick-borne spirochetes on glucose levels in captive blackbirds (*Turdus merula*). Our study is unique in its focus on viral infection and glucose in free-ranging birds, but there is supporting literature showing elevated glucose titers in virally infected domesticated birds (e.g., Newcastle virus in chickens, *Gallus domesticus*; Okorie-Kanu, Okorie-Kanu, & Okoye, 2016), as well as in other domesticated animals (e.g., bovine viral diarrhea; Lorenz, 2000) and humans (e.g., hepatitis C flavivirus; Lecube, Hernandez, Genesca, & Simo, 2006). Mechanistic explanations for the consistent link between disease and raised glucose concentrations have centered on stress hyperglycemia (McAllister et al., 2014), which involves the release of hormones (e.g., cortisol, glucagon, adrenaline) during a stress response that counteract insulin and, thus, interfere with glucose use/clearance. In the absence of an experimental approach and hormone measurements in our study, we now are in need of lab experiments to identify true causal links between body condition, viral infection status, blood glucose, and potentially mediating hormone actions in our study system.

Unlike our findings for body condition and poxvirus, it is interesting that plumage color and habitat urbanization were dissociated from circulating glucose levels, as we have previously shown that color expression and habitat type strongly relate to disease (including poxvirus) in our study population (Giraudeau et al., 2014, 2018). Carotenoid colors, including those in house finches that are the result of metabolically derived pigments (Inouye, Hill, Stradi, & Montgomerie, 2001), are thought to honestly reveal vital cellular and physiological (i.e., energy- and mitochondria-centered) processes (Hill, 2011), and maybe especially associated with glucose, given its metabolic role as mitochondrial fuel. However, it is noteworthy for this study that we did not sample these birds at the time when they develop their bright coloration (which occurs during molt from July–September), so a follow-up study would be useful to examine glucose levels alongside mitochondrial activity and development of ornamental coloration. Moreover, the urban environment is thought to exert pervasive impacts on avian traits often linked to hyperglycemia (e.g., diet, movement patterns, health state; Isakkson, Rodewald & Gil, 2018), and in great tit nestlings, urban birds circulate more glucose than rural birds (Gladalski et al., 2018). Perhaps, due to seasonal glucose variation (Remage-Healey & Romero, 2000) and to oft-detected environmental effects on glucose in nestling birds (Kalinski et al., 2014; Lill, 2011), future studies may uncover more complex season- (e.g., breeding), age-, and site-related variation in glucose circulation in house finches.

Finally, the absence of a link to coccidiosis suggests that gut coccidian parasites do not, at least at this time of year, preferentially steal glucose or significantly interfere with glucose regulation in these free-ranging birds. In domesticated animals (such as chickens; Ruff & Wilkins, 1980), glucose levels are often lower in individuals infected with coccidia, but perhaps coccidia were thieving other macronutrients in our house finches, or, as we conducted this study during a milder time of year than the extremely hot summer–fall in Arizona (which is when we conducted our prior study linking coccidiosis to urbanization in finches; Giraudeau et al., 2014), these finches were able to comparatively buffer or offset any effects of coccidiosis on physiological systems like glucose circulation than if we studied them earlier in the year. We now plan an upcoming, comprehensive assessment of circulating glucose levels during the summer–fall molt in our finch population.

In sum, we provide evidence here that two common predictors of hyperglycemia in humans—body condition and viral infection—also are related to blood glucose levels in a wild-bird species. In a clade like birds, which is generally resistant to diabetic complications, we must now further investigate the fitness consequences (e.g., survival, reproduction) of such hyperglycemic conditions on free-ranging animals, as has been done recently in captive zebra finches (*Taeniopygia guttata*, where survival is lower in birds with consistently higher glucose titers; Montoya, Briga, Jimeno, Moonen, & Verhulst, 2018). However, the fact that we found that sex, plumage coloration, habitat type, and endoparasitic infections were not linked to blood sugar levels in house finches during winter indicates that, whereas glucose status is commonly viewed as a general stress biomarker in humans

(Marik & Bellomo, 2013) and other animals (including domesticated, laboratory, and rehabilitating animals; Giridharan, 2018; Stacy & Innis, 2017), it can still vary independently of several salient forms of environmental and physiological variation in birds.

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

DATA AVAILABILITY STATEMENT

The datasets supporting this article will be made accessible in figshare upon publication.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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