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Crypsis in a polymorphic mammal along an urbanization gradient

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Abstract
Urbanization transforms landscapes and may alter background matching for polymorphic species that rely on cryptic coloration for survival, potentially generating urban–rural clines in traits related to coloration. Such clines are evident in eastern gray squirrel (*Sciurus carolinensis*) populations, for which a melanic morph is currently more prevalent in cities but was historically more prevalent in rural woodlands prior to urbanization. We compared the degree of crypsis between the two primary color morphs of gray squirrels – gray and melanic – among the suite of habitats that predominate along an urbanization gradient to test whether an altered visual environment may contribute to the maintenance of an urban–rural cline in morph prevalence. Detectability of taxidermy mounts of each morph against their backgrounds in replicate sites within each habitat was quantified with human observers and image pixel classification. The melanic morph was more conspicuous than the gray morph in all habitat types and across seasons, as evidenced by greater detection probabilities by human observers and lower background matching. Coat color in gray squirrels likely mediates visual detection by predators, potentially resulting in selection against the more conspicuous, melanic morph in rural woodlands where predation is the primary constraint on survival. The greater conspicuity of the melanic morph on road surfaces may be beneficial in cities where vehicular collisions are the primary cause of squirrel mortality. We conclude that differential crypsis between color morphs across the habitat continuum of urban–rural gradients may play an important role in maintaining urban–rural clines in coat color in eastern gray squirrels.

Keywords Animal color · Camouflage · Citizen science · City · Evolution · Squirrel

Introduction

Urban areas are the most rapidly expanding of any ecosystem on Earth (United Nations 2018). Urbanization often reduces biodiversity through habitat transformations that include increased impervious surfaces, ambient temperature, artificial light, and noise (Grimm et al. 2008; Rivkin et al. 2019). Yet urban areas can also represent new habitat for some species, driving novel evolutionary trajectories that can affect trait variation (Hahs et al. 2023), as evidenced in many species by morphological variation between urban and rural populations (Wandeler et al. 2003; Weller and Ganzhorn 2004; Vakhlamova et al. 2014; Diamond et al. 2017). The evolution of trait variation along urbanization gradients can have important implications for ecosystem function via eco-evolutionary feedbacks (e.g., Brans et al. 2022), as well as conservation of unique forms of biodiversity (i.e., novel trait variants).

The mechanistic processes causing trait differentiation between urban and rural areas are often unknown. Non-adaptive evolution, driven by genetic drift or gene flow may play a role (Miles et al. 2021), whereas fitness differences between urban populations and surrounding, rural populations might also lead to adaptive evolution. Color pattern affects individual fitness in many species by mediating the degree to which individuals are concealed or revealed to predators in different environments (Hultgren and Stachowicz 2008; Cook et al. 2012; Zimova et al. 2014; Troscianko et al. 2016). Crypsis is a potential component involved in selection that might be mediated by urbanization via altered visual environments (reviewed by Leveau 2021). Replacement of vegetation with impervious cover dramatically

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reshapes the landscape in cities versus rural areas, which may amplify or weaken selective pressures on conspicuity in species that rely on it for survival. For example, urban grasshoppers show biased movement to pavement that best matches their coloration to avoid predation (Edelaar et al. 2019). Conversely, bold coloration in cities may be advantageous for some species, where greater visibility to humans on roads could reduce the likelihood of being struck by motorists (Kreling 2023).

Here we explore drivers of morphological evolution in eastern gray squirrels (*Sciurus carolinensis*), an arboreal rodent common in urban and rural woodlands within its native range of eastern North America. The species exhibits two distinct coat color morphs (Fig. 1): gray and melanic (black) morphs associated with a 24-bp deletion allele on the melanocortin-1 receptor gene (MC1R; McRobie et al. 2009). Urban–rural clines in melanism have been documented in northern parts of the gray squirrel's range where melanism is regionally common (Cosentino and Gibbs 2022). The prevalence of squirrel melanism declines with increasing distance from urban centers, a pattern that appears to be explained in part by selection favoring the gray morph in rural woodlands (Cosentino et al. 2023); however, the selective forces generating these clines are not known.

We compared the degree of crypsis between the two primary color morphs of gray squirrels – gray and melanic – among the suite of habitats that predominate along an urbanization gradient to test whether an altered visual environment may contribute to the maintenance of an urban–rural cline in morph prevalence. To do so, we examined relative crypsis of gray squirrel color morphs in relation to two axes of environmental change associated with urbanization that may most affect survival of these tree-dwelling animals: change in structure and composition of the forest habitats in which squirrels live, and visibility of each morph on road surfaces. In rural woodlands, predation is the primary cause of mortality in tree squirrels (Havera and Nixon 1980; Bowers and Breland 1996). Predators include a variety of raptors and mammalian carnivores, as well as human hunters (Benson 2013). Hunting pressure in rural areas can be intense, with > 1.5 million squirrel hunters in the U.S. (U.S. Fish and Wildlife Service 2016) and > 300,000 gray squirrels harvested annually in one state alone (Illinois; Williams and Miller 2018). In cities, vehicular collisions are the primary source of mortality. In one study on fox squirrels (*Sciurus niger*), > 60% of urban mortality was caused by vehicular collision, whereas < 5% of urban mortality was caused by predation (McCleery et al. 2008).

We imaged squirrels of each color morph in these representative habitats across the urbanization gradient and compared crypsis between morphs in two ways: 1) employing human observers in an online game to measure morph-specific detection probabilities and 2) using image pixel-classification to measure morph-specific background matching. Because human hunters and motorists are important sources of gray squirrel mortality, images were taken in the human visual range (400–700 nm) for which trichromatic color vision is typical. Although we recognize color vision in avian predators (e.g., tetrachromat with ultraviolet sensitivity) and mammalian carnivores (e.g., dichromat) differs from human vision, the variation between gray and melanic squirrels is largely achromatic. Thus, we did not expect pronounced differences in morph-specific crypsis across visual systems.

Fig. 1 Gray (left) and melanic (right) color morphs of the eastern gray squirrel (*Sciurus carolinensis*). Image source: Elizabeth Hunter

Methods

Study area

We examined crypsis of gray squirrels in Syracuse, New York (43.04° N, – 76.14° W), a mid-sized city with an area of 65 km^2 and ca. 150,000 residents (U.S. Census Bureau 2023). The city hosts a well-documented cline in coat color of gray squirrels, with prevalence of melanic forms decreasing from ~ 50% in the city center to < 10% in nearby (< 20 km away) rural forests surrounding the city (Cosentino et al. 2023).

Experimental design and imaging

We used image analysis techniques common in animal coloration studies (Karpestam et al. 2013; Stevens et al. 2015; Troscianko et al. 2018a, b; Edelaar et al. 2019; Barnett et al.

2020) to compare background matching between melanic and gray morphs across the urbanization gradient. To do so we staged taxidermy models of each color morph at replicate locations (hereafter "scenes") across five habitat types (Table 1, Supplemental Table S1, Supplementary Figs. S1-S6): old growth forest, secondary growth forests, residential areas, urban parks, and urban developed (i.e., core city). This suite of habitats captured both a spatial sequence of land use change encountered along contemporary urban–rural land use gradients (secondary forest to urban core), as well as a historical sequence of land use change that has occurred within the gray squirrel's native range over the last 300 years (old growth forest to secondary growth forest). We also staged taxidermy models on residential road surfaces, as traffic collisions are a major source of squirrel mortality (McCleery et al. 2008) and are increasing in extent over both time and space in relation to urbanization (Medley et al. 1995; Meijer et al. 2018).

We used 12 taxidermy models for imaging (six of each color morph) sourced from the Roosevelt Wild Life Station at the State University of New York College of Environmental Science and Forestry. Models selected for imaging in each scene were standardized for size between morphs. In each habitat scene, squirrel models were staged in three postures: running on the ground, running on a branch or elevated structure, and climbing (Fig. 2A). For each posture location, images were taken from two viewpoints to mimic visual perspectives of ground (e.g., humans and

Table 1 Sampling frame used for examining crypsis of gray and melanic color morphs of the eastern gray squirrel along an urbanization gradient

Habitat	Scenes	Postures	Viewpoints	Total images
Old growth forest	20	Climb, branch, ground	Aerial, ground	480
Secondary forest	20	Climb, branch, ground	Aerial, ground	480
Urban park	10	Climb, branch, ground	Aerial, ground	240
Urban yard	10	Climb, branch, ground	Aerial, ground	240
Urban developed	10	Climb, branch, ground	Aerial, ground	240
Road surface	20	Ground	Ground	80

Images were taken of taxidermy models of both morphs in up to three postures (climbing, running on branch, running on ground) and two viewpoints (ground or aerial) during leaf-on (fall) and leaf-off (spring) seasons. In total, 12 images per non-road scene and two images per road scene across two seasons generated 1,760 unique images composed of 880 melanic-gray pairs

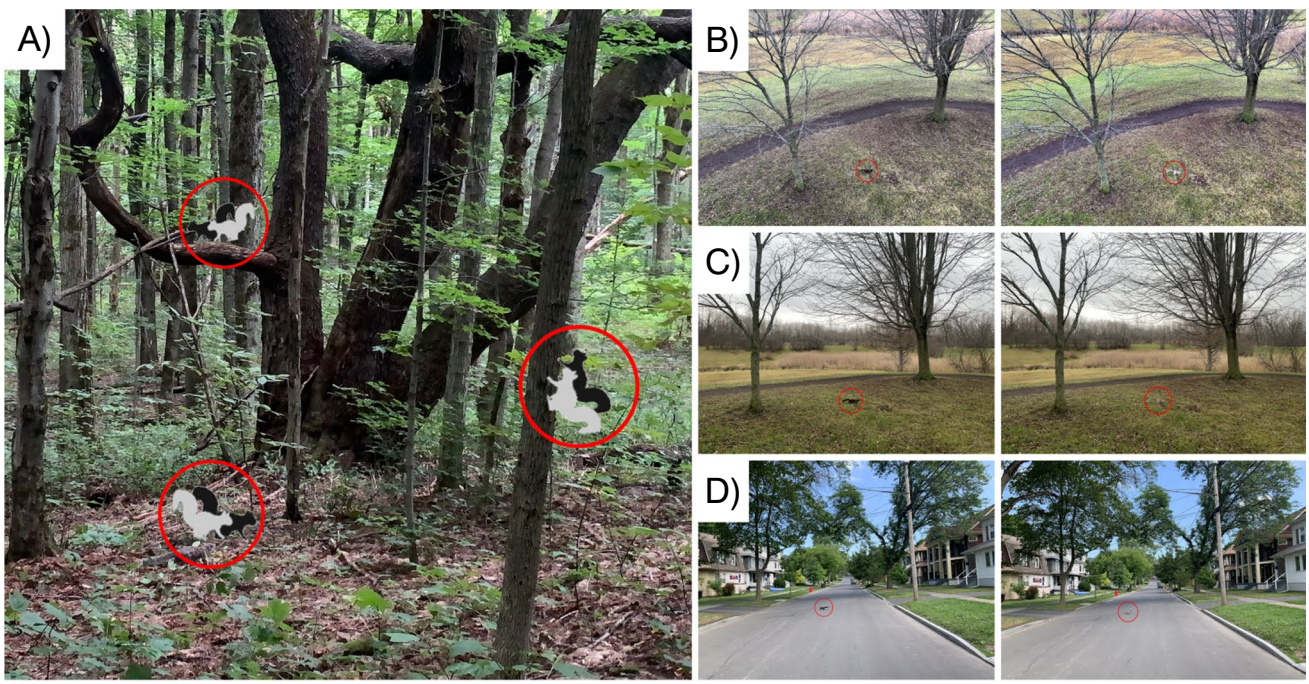

Fig. 2 Placement of taxidermy mounts of eastern gray squirrels within habitats. In non-road habitats, squirrels were placed in different postures (**A**; climbing, running on branch, running on ground) and photographed from aerial (**B**) and ground (**C**) viewpoints. Mounts on roads were photographed in running position from the ground viewpoint only (**D**)

canids) and aerial predators (e.g., raptors) (Fig. 2B-C). Ground-level images were taken at 1.6 m above ground, and aerial images were taken at 6 m above ground using an expandable tripod. A single squirrel model was included in each image, and each color morph was imaged in identical locations (Table 1). For the road environment, images were taken at 1.6 m above ground centered in a road lane. Only squirrels in a running posture were used on roads, oriented perpendicular to the road and randomly placed facing left or right (Fig. 2D). Gray squirrels are active year-round, so we repeated imaging in both leaf-on (spring/summer) and leaf-off seasons (fall/winter) to examine whether differential crypsis between color morphs varied between seasons.

Images were taken with an iPhone XR camera (Apple Inc., Cupertino, California, United States) using the ProCamera application (Cocologics GmbH, Manheim, Germany) controlled by a remote shutter trigger. Standard ISO was 100, and focus, white balance, and shutter speed were set to automatic. Each melanic-gray pair of taxidermy models was photographed at each posture location within a scene within a span of two minutes to control for lighting conditions. Model position within each image was randomized (left, center, right), as was focal distance to each model (5–20 m in non-road habitats, 10–40 m on roads). Imaging was replicated at each scene during leaf-off and leaf-on seasons using identical postures and locations (Table 1).

Quantifying background matching as measured by human observers

We used an internet-based gamification approach (Karpestam et al. 2013; Troscianko et al. 2016; Troscianko et al. 2018a, b; Barnett et al. 2020) to engage human observers to measure morph-specific detection in each habitat: "Squirrel Spotter" (https://bcosentino.shinyapps.io/squirrelspotter/). The game presented each observer with a sequence of 36 images of taxidermy models of squirrels from three randomly chosen habitat types. Before playing, each observer was asked if they had played the game previously. To play the game, each observer was given 15 s to detect (by clicking) the squirrel model in each image. For each of the three habitat types chosen, six scenes were randomly selected and included paired images of each color morph in identical posture, viewpoint, and season. Images were presented to observers in a blocked fashion by habitat type, such that each sequence of three images included one scene of each habitat type for a total of 36 images (i.e., 3 habitats × 6 scenes × 2 morphs). Paired gray-melanic images never shown sequentially. The first six images were considered a "learning phase," allowing users to habituate to the game (Troscianko et al. 2018a, b), and the remaining 30 images (5 gray-melanic pairs from five scenes each of the three randomly selected habitats) were considered a "testing phase" and included in the analysis.

We used survival analysis to examine how detection of squirrel models was related to color morph and habitat with Cox proportional hazards models fit with the *coxme* package (Therneau 2024) in R 4.2.3 (R Core Team 2023). For non-road habitats, we modeled the hazard ratio (i.e., risk of being detected in an image) as a function of color morph, habitat, the morph × habitat interaction, distance of squirrel from the camera, and image order (i.e., order in which an image was presented during the game) with fixed effects. A separate model was fit for the road habitat, which included fixed effects of morph, distance, and image order. Scene and user were included as random intercept terms in both models. We only used the initial game play of users who had played multiple times. Images for which squirrel models were not detected within 15 s after presentation were right censored. Exploratory analyses revealed a strong carry-over effect such that users tended to find the second of each pair of squirrel morphs faster than the first squirrel encountered within scenes; to address this bias, we limited our analyses to detection data from only the first morph presented in each scene to a user (i.e., a two-sample design with $n = 15$ scenes for each game play).

Tests of significance of fixed effects were made with Wald Chi-square tests using the *car* package (Fox and Weisberg 2019). Separate models were fit for each combination of levels of squirrel posture, viewpoint, and season, resulting in 66 hypothesis tests. We applied a Bonferroni correction to maintain a familywise Type I error rate of 0.05. To do so, we quantified adjusted *P*-values by multiplying raw *P*-values by the number of tests (Jafari and Ansari-Pour 2019).

Quantifying background matching with machine learning

We also measured background matching via pixel classification (e.g., Stevens et al. 2015; Barnett et al. 2020; Nokelainen et al. 2021). We used the Waikato Environment for Knowledge Analysis (Weka Machine Learning) toolkit (Arganda-Carreras et al. 2017) as implemented in Fiji ImageJ (Schindelin et al. 2012) to create unique FastRandomForest classifiers for each melanic-gray image pair (880 pairs from 1,760 total images, Table 1). For each pair, we trained classifiers on an equal proportion of pixels on the dorsal surface of each color morph (Fig. 3) based on Red, Green, and Blue (RGB) intensity scores, using the mean and variance of RGB intensity scores in a 1-, 2-, 4-, and 8-pixel radius from each target pixel. The classification model was then used to predict all remaining non-squirrel pixels in the image (i.e., the background of the squirrel) as melanic or gray (Fig. 3), and we quantified the proportion of background pixels that matched each morph. Deviations in

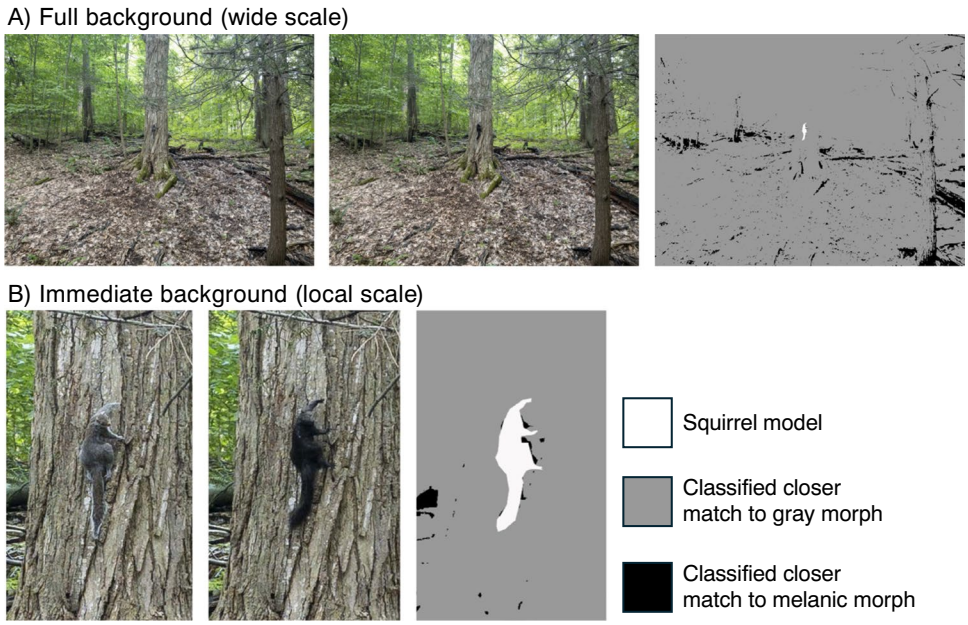

Fig. 3 Example set of images used for background matching analysis at wide (**A**) and local (**B**) scales. Panels include image of gray morph (left), melanic morph (middle), and the classified output (right). Classifiers were trained to pixels on the torso of each squirrel model to create a binary classification of the entire scene indicating a better match to the gray or melanic morph. Pixels associated with the model were excluded from the analysis

the proportion of pixels classified as melanic from 0.5 would indicate a better match to melanic (> 0.5) or gray (< 0.5). Because the image background for each melanic-gray pair was virtually identical (see Fig. 3), we only applied the classification model to the image with the melanic morph to quantify background matching. Moreover, because crypsis can be a scale-dependent phenomenon (more complex backgrounds can reduce detection; Merilaita 2003), we analyzed background matching for each image at two scales: every pixel in the image ("wide scale") and within a rectangular region of interest surrounding the squirrel ("local scale"). The local scale was defined as a region of interest with dimensions double the length and width of the squirrel in each given image (Fig. 3).

We used generalized linear mixed models to examine variation in the proportion of background pixels classified as melanic. For images in non-road habitats, we specified fixed effects of habitat, posture, perspective, and season. Two-way interaction terms were included between habitat and each of the other fixed effects to test whether variation in background matching among habitats depended on posture, perspective, and season. Random intercept terms were included for scene. We specified a beta distribution for the response variable because it was a proportion bounded between 0 and 1. The beta distribution is not inclusive of the values 0 and 1, so we added a trace value of 0.0001 to five instances of zero values in our dataset (Damgaard and Irvine 2019). Separate models were fit for wide and local background scales. For images on roads, we fit separate models with a fixed effect of season, as there was no variation in posture or viewpoint in the road scenes. All models were fit with the *glmmTMB* package (Brooks et al. 2017) in R 4.2.3, with Wald Chi-square tests to examine the significance of each fixed effect. Fitting four models (full and immediate backgrounds for road and non-road habitats) resulted in 16 hypothesis tests, to which we applied a Bonferroni correction to *P*-values to maintain a familywise Type I error rate of 0.05.

Results

A total of 1,765 unique participants generated 24,050 observations that were included in our detection analysis from the online game. Detection probability was greater for the melanic morph than the gray morph in virtually all cases (Fig. 4, Supplemental Table S2). The difference in detection probability between morphs varied among habitats in some postures (morph × habitat interaction effects, Supplemental Table S2). For example, the difference in detection probability between color morphs was weaker in urban than forest habitats when placed in the branch posture (Fig. 4). For squirrels in running position on the ground, detection probability was generally greater in urban than forested habitats for both morphs (Fig. 4, Supplemental Table S2). Squirrels were more detectable from the ground than aerial viewpoint in forests, whereas the effect of viewpoint was less consistent and pronounced in urban habitats (Fig. 4). Squirrels tended to be more readily detected in ground and climbing positions than in the branch position, particularly in urban habitats (Fig. 4). Squirrel detection was similar between seasons, although detection differences between morphs were greatest during the leaf-off season in forested habitats (Fig. 4).

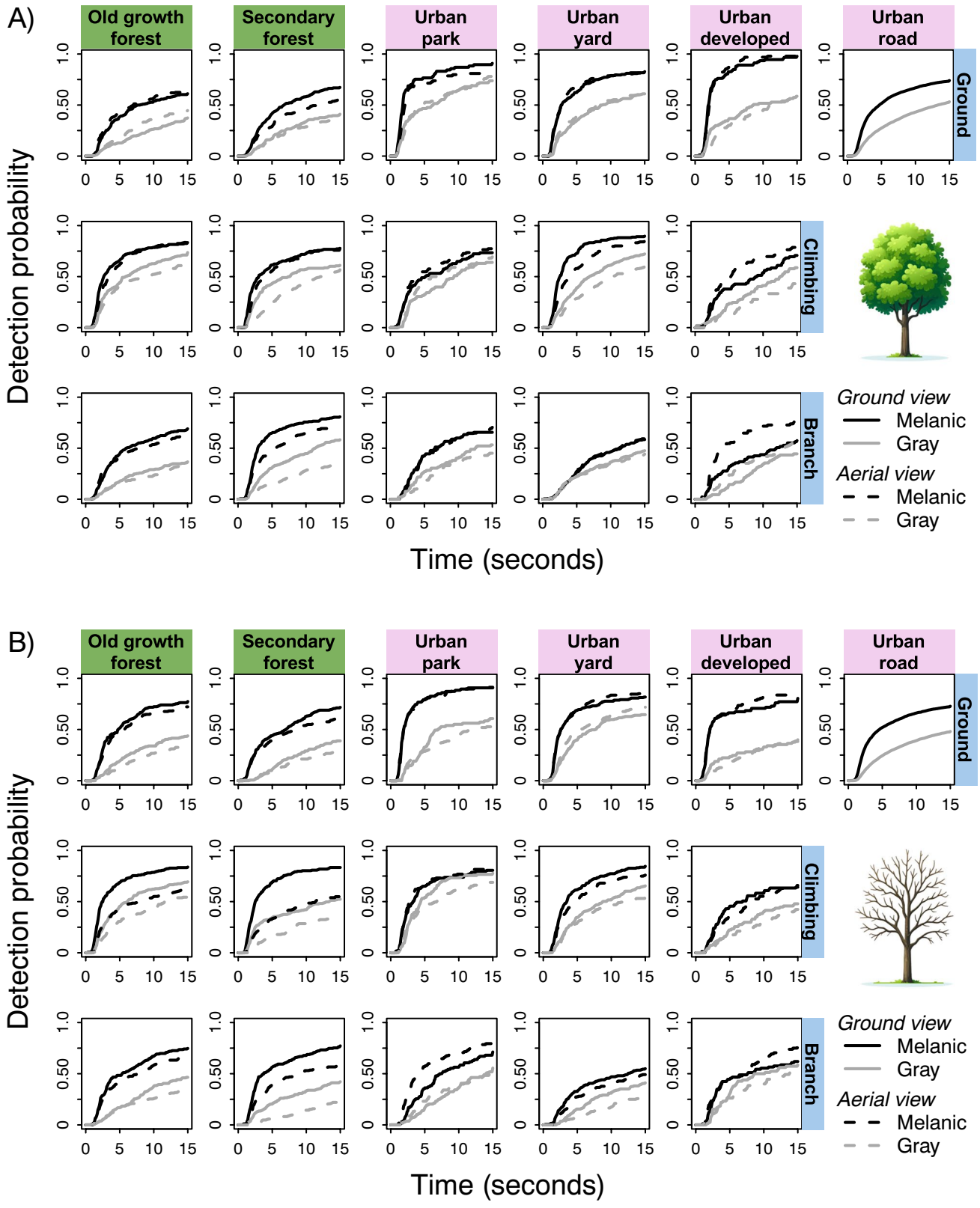

Fig. 4 Predicted detection probability for melanic and gray color morphs of eastern gray squirrels during leaf-on (**A**) and leaf-off (**B**) seasons and from ground (solid line) and aerial (dotted line) perspectives and among habitats (columns) and squirrel model position (rows)

Scene order had a positive effect on detection in the road habitat (i.e., greater detection probability for images presented later in the game), whereas there was no effect of scene order on detection in non-road habitats (Supplemental Table S2). Squirrel detection was negatively related to distance from the camera when squirrels were imaged from the ground perspective in climbing and branch postures in non-road habitats (Supplemental Table S2). Detection decreased with increasing distance in the leaf-off season when imaged on roads, and was lower in non-road habitats when imaged from the aerial viewpoint in branch posture (Supplemental Table S2).

Pixel matching analyses indicated that the gray morph always matched more closely the wide-scale and local-scale background than did the melanic morph (i.e., < 50% background classified as melanic; Fig. 5). The gray morph's matching advantage at wide scale tended to be weakest in urban habitats, particularly urban yards, urban developed, and roads (Fig. 5). There was little variation in the degree of local-scale background matching among habitats (Supplemental Table S3), except for the gray morph's matching advantage being weakest in urban yards and developed areas when in the branch posture (Fig. 5). The gray morph showed greater background matching in the leaf-off season, especially at the full background in urban yard, urban developed areas, and old growth forests (Fig. 5). Patterns of background matching were generally consistent between imaging viewpoints (Fig. 5, Supplemental Table S3).

Discussion

The melanic morph of the eastern gray squirrel was more conspicuous than the gray morph among all habitats assessed across the urban–rural gradient, a conclusion supported by two measurements of crypsis. First, melanic squirrels had greater probabilities of detection and were detected faster by human observers compared to the gray morph. Second, the melanic morph was a weaker match to its background than the gray morph when using quantitative image analysis. These results highlight a clear effect of color polymorphism on conspicuity of squirrels across the urbanization gradient, the consequences of which may play an important role in contributing to the maintenance of urban–rural clines in pigmentation.

Our results clearly show that the melanic morph was more detectable than the gray morph in forested habitats, including the secondary forests that dominate rural areas and the urban greenspaces where squirrels commonly occur in the city. Visual conspicuity is an important driver of individual predation risk. Previous experimental studies of small mammal species have found melanic morphs are attacked by predators more than other morphs when on mismatched backgrounds (e.g., Hoekstra et al. 2004; Vignieri et al. 2010; Linnen et al. 2013). Given that predation is a significant source of mortality for tree squirrels in rural woodlands (Bowers and Breland 1996; McCleery et al. 2008), predators may play an important role in causing selection against the melanic morph where secondary forests dominate the landscape.

The difference in camouflage between color morphs may also help explain historical trends in the prevalence of melanism in eastern gray squirrels in rural forests. The melanic morph was the prevailing color morph in forests of the northeastern U.S. prior to European settlement (Schorger 1949; Robertson 1973). However, as forests were cleared for agriculture, gray squirrels were viewed as agricultural pests, leading to bounties and a period of intensive hunting (Benson 2013). The greater visual conspicuity of the melanic morph to squirrel hunters may have contributed to their decline. Notably, we did not find that the melanic morph was more cryptic in old growth forests where it was once common. Old growth forests have structural features that should provide greater concealment to melanic individuals, including vertical stratification of vegetation that creates deep patches of shade and greater prevalence of coniferous species with dark bark and foliage (Franklin and Van Pelt 2004; Bauhus et al. 2009). However, our study sites may not have provided a valid representation of old growth forest conditions, given that old growth forests remaining today are rare (< 1% of forest cover; Foster et al. 2010) and differ in structure and composition from historical old growth stands (White 2012; Elliott and Swank 2008).

Notably, the melanic morph was far more conspicuous on roads than the gray morph. In contrast to rural woodlands where conspicuity is likely deleterious in the context of predation, conspicuity may be advantageous in the context of road mortality risk in cities. The median detection time on roads was more than three times greater for the gray morph than the melanic morph (Fig. 4). By detecting the melanic morph faster, motorists should have more time to react and avoid striking melanic than gray morphs. Indeed, standardized road cruise surveys in Syracuse and citizen science observations worldwide show the melanic morph is underrepresented among roadkill proportional to its frequency in live squirrel populations (Gibbs et al. 2019; Parlin et al. 2025). Roadways can cause intense selection pressures on trait variation in wildlife (Brady and Richardson 2017), and high density of roadways associated with urban areas may introduce a novel pressure on visual conspicuity. Roadways are a leading cause of mortality in urban squirrel populations (McCleery et al. 2008), however, when possible, most motorists attempt to avoid striking animals on roads (Beckmann and Shine 2012).

We found a modest effect of viewpoint on the detection of squirrel models, particularly in secondary and old

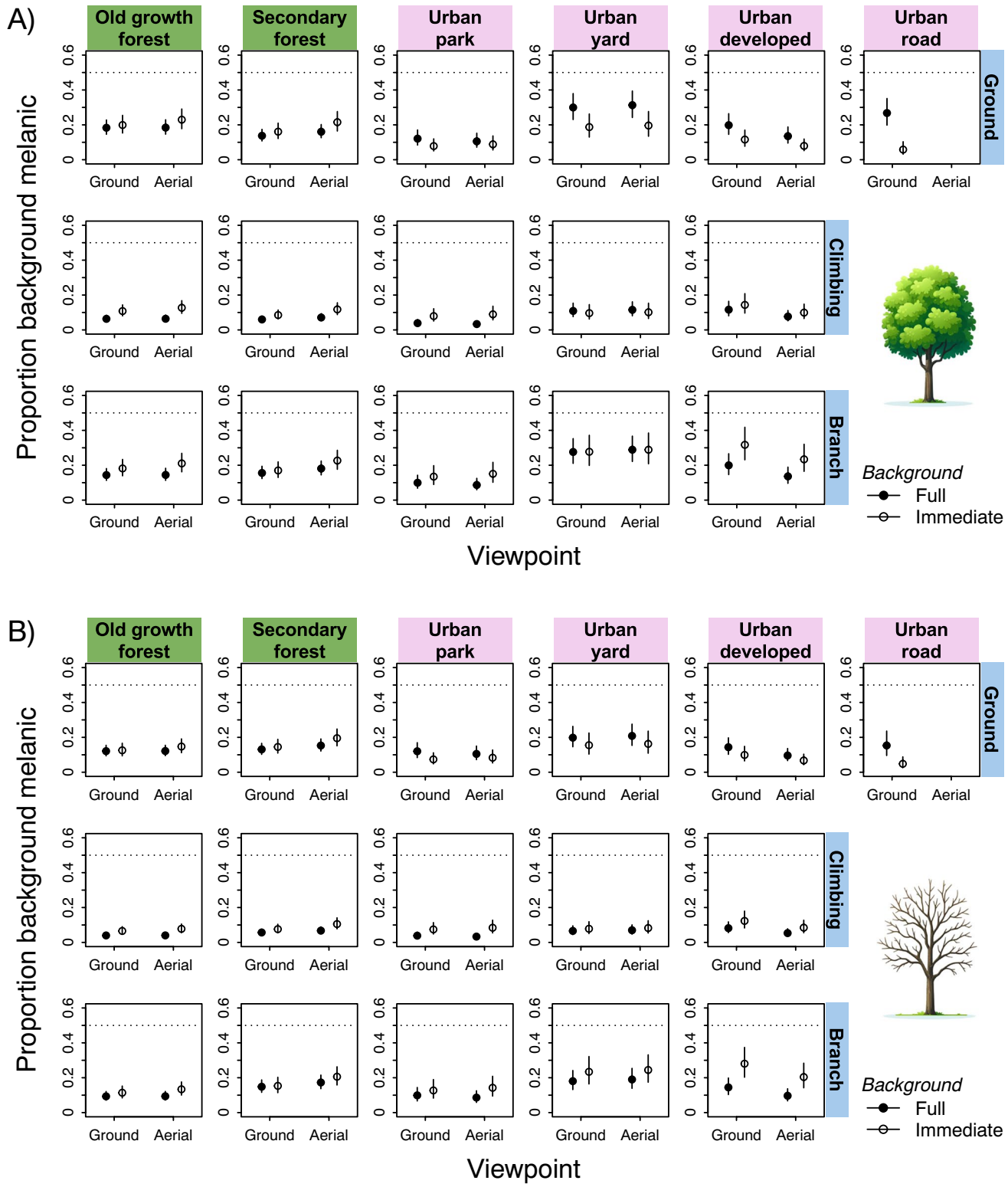

Fig. 5 Predicted proportion of background pixels classified as matching the melanic morph of eastern gray squirrel during leaf-on (**A**) and leaf-off (**B**) seasons and from ground and aerial perspectives among habitats (columns) and squirrel model position (rows). Values less than 0.5 (dotted line) indicate greater matching of the gray morph to the background than the melanic morph. Error bars represent 95% confidence intervals

growth forests. Images of squirrel models from an aerial perspective yielded slower detection times than those from the ground view in forests. This could be the result of human observers being inexperienced at searching for squirrels from an aerial angle. We also found that observer distance can affect detection times, which may also explain the viewpoint effect. Aerial perspectives created greater distances between the camera and squirrel models than ground perspectives, an effect on detection that may be compounded in the more visually complex forested habitats than urban greenspaces. Overall, detection probability was similar between seasons, with a weak seasonal effect detectable in secondary forests (e.g., greater difference in detection between morphs in leaf-off season), where the primarily deciduous tree canopies create stronger visual variation between seasons.

It is important to note that while our detection methods are an accurate model for detection by human hunters and motorists, they assume human detection is also representative of detection by avian and mammalian predators. Although detection efficiency can vary among organisms with different color vision systems (e.g., Saito et al. 2005; Troscianko et al. 2018a), we suspect the largely achromatic differences between squirrel color morphs mitigates the potential for bias. Indeed, previous studies have shown human detection experiments can reliably predict natural detection, including that of birds (Karpestam et al. 2013). However, using humans as proxies for detection still has shortcomings because doing so does not account for the cognitive processing associated with color perception (Cuthill et al. 2017). The quantitative background matching analysis removes some of this human bias to support our results, but future research should focus on using visual models specific to different types of predators and quantifying actual predation rates between morphs.

Our study focused on the direct visual consequences of animal color, but it is important to note that the fitness consequences of color may include both direct and indirect mechanisms. Melanism in a variety of animals has been linked to physiological and behavioral variation, due in part to pleiotropy in the melanocortin system (Ducrest et al. 2008). Internal melanin can also confer direct benefits in the context of a variety of stressors, such as toxins, parasites, and low temperature (Dubey and Roulin 2014). Indeed, melanic squirrels have greater potential for non-shivering thermogenesis at low temperature (Ducharme et al. 1989), which is thought to contribute to their high prevalence at cold, northern latitudes in North America. Further studies are needed to tease apart the direct and indirect mechanisms by which melanism mediates fitness in gray squirrels living in urban and rural environments.

This study builds upon previous work on gray squirrel color morph frequencies and urban coloration in general. Previous work has shown that the gray morph has a greater survival rate in rural woodlands than the melanic morph, but urban survival rates are comparable between morphs (Cosentino et al. 2023). Our study showed the melanic morph is more visible than the gray morph in all habitats. This conspicuousness may contribute to selection against the melanic morph in rural forests, likely from predators and human hunters. In contrast, the greater visual conspicuity of the melanic morph on roads may be to its benefit, particularly in cities where road densities and traffic volume are greatest. It is notable that squirrels in general tended to be more detectable in urban parks and yards than in forests when running on the ground (Fig. 4), likely due to the predominance of open turf grass in parks and yards. The melanic morph may be at particularly high predation risk in these open urban habitats, and the conflicting selection pressures of roads and predation in cities may offset, explaining the comparable survival rates between color morphs in the city. Additional studies that quantify morph-specific predation and road-mortality rates are needed to provide insight into the spatial variation of these selection pressures along the urbanization gradient. Overall, this study highlights how visual landscape changes across urban–rural gradients may cause shifts in evolutionary pressures and novel interactions among those pressures, leading to opportunities for evolution of novel animal coloration in cities. While urbanization is often viewed as detrimental, our study highlights the possibility that cities may provide novel habitats and create points of refuge for unique morphologies to thrive.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11252-025-01708-4.

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Author contribution J.P., A.B., B.J.C., and J.P.G designed the study. J.P. and A.B. collected the data. J.P. and B.J.C. analyzed the data. J.P. wrote the first draft of the manuscript. A.B., B.J.C., and J.P.G. reviewed and edited the manuscript. B.J.C. and J.P.G. acquired financial support for the study.

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Data availability Data and code used for analyses in this manuscript are available at https://github.com/bcosentino/urban-squirrel-crypsis/.

Declarations

Competing interests The authors declare no competing interests.

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