Natural history models of bird–building collisions

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Abstract: Building collisions kill an estimated 1.28–5.19 billion birds annually in North America, making them the second leading cause of human-related avian mortality. Yet the behavioral and ecological drivers of collisions remain difficult to disentangle, as most knowledge derives from carcass surveys rather than direct observations. Here, we propose a conceptual framework that synthesizes four natural history models of bird–building collisions: a null model, a nocturnal collision model, a skyglow and stopover model, and a forest dispersal model. These models are hypotheses to be tested rather than mutually exclusive explanations, since multiple processes may operate simultaneously across species, landscapes, and time. We illustrate the models with published studies and limited observational data from a university campus in Houston, Texas, USA, emphasizing their potential to generate testable predictions and practical insights. Importantly, the framework highlights implications for survey design, the integration of structured monitoring with citizen science, and mitigation strategies. Specifically, while light reduction may help under some scenarios, reflective glass emerges as the most universal and tractable target for prevention. By framing collisions through alternative natural history models, we aim to stimulate more nuanced, place-specific investigations and accelerate the implementation of effective conservation strategies.

Resumo: Colisões de aves com edificações matam de 1,28 a 5,19 bilhões de aves anualmente na América do Norte, representando a segunda maior causa de mortalidade aviária associada a atividades humanas. Entretanto, os fatores comportamentais e ecológicos que levam às

colisões permanecem pouco compreendidos, já que a maior parte do conhecimento vem de levantamentos de carcaças e não de observações diretas. Neste artigo, propomos um arcabouço conceitual que sintetiza quatro modelos de história natural de colisões: um modelo nulo, um modelo de colisão noturna, um modelo de brilho do céu e parada migratória, e um modelo de dispersão entre florestas. Esses modelos devem ser vistos como hipóteses a serem testadas e não como explicações exclusivas, pois múltiplos processos podem atuar simultaneamente entre espécies, paisagens e períodos. Ilustramos os modelos com estudos publicados e nossas próprias limitadas observações em um campus universitário em Houston, Texas, EUA, destacando seu potencial de gerar previsões testáveis e insights práticos. O arcabouço também traz implicações para o desenho de levantamentos, para a integração entre monitoramento estruturado e ciência cidadã, e para estratégias de mitigação. Embora a redução de luz artificial possa ajudar em alguns contextos, o vidro reflexivo surge como alvo universal e viável de prevenção.

Bird-building collisions cause an estimated 1.28 billion to 5.19 billion bird deaths annually in North America alone (Kornreich et al. 2024; Klem et al. 2024), and represent one of the leading causes of anthropogenic avian mortality on the continent (Loss et al. 2015). And while overall mortality rates are less clear outside of North America, a growing number of studies, particularly from the Paleotropics (Tan et al. 2024; Hsieh et al. 2024; Li et al. 2025) and Neotropics (Piratelli et al. 2025; Rebolo-Ifrán et al. 2019; Ocampo-Peñuela et al. 2016; Menacho-Odio et al. 2019), similarly suggest that window collisions are responsible for a large number of bird deaths globally as well. Although the true impact of window collisions on bird populations remains unclear (Arnold and Zink 2011), this source of mortality nonetheless contributes to the broader global crisis of avian population declines (Butchart et al. 2010; Rosenberg et al. 2019; Johnston et al. 2025), and its impact is likely to grow as cities expand worldwide (Li et al. 2021).

Several factors operating at different spatial scales contribute towards the increased likelihood of bird-building collisions. At the finest spatial scales (i.e. individual building facades) bird-building collisions are stochastic local phenomena that occur at glass facades, when birds confuse reflections of sky, vegetation, or open space for continuous habitat (Klem 1989; Klem 2021; Klem et al. 2009; Rebolo-Ifrán et al. 2019; Schneider et al. 2018; Basilio et al. 2020). Transparent, non-reflective panes also pose risks, as birds may mistake them for unobstructed flight paths (Klem 1989; Klem 2021; Klem et al. 2009). At coarser spatial scales, however, other abiotic and biotic factors such as light pollution, the relative distribution of buildings and vegetation, geography, and taxonomy, have been shown to affect the patterns of bird-building collisions (Elmore et al. 2021b; Tan et al. 2024; Li et al. 2025; Hager et al. 2017). Although billions of collisions occur worldwide each year, each event unfolds in seconds, making direct observation exceedingly rare (but see Samuels et al. 2022 and Klem et al. 2024). Consequently, most knowledge of collisions comes indirectly from carcass surveys, often hours after the fact. This reliance on indirect evidence complicates efforts to infer behavioral and ecological drivers of collisions.

The goal of this perspective is to address those challenges by proposing a conceptual synthesis that unifies bird natural history and the environmental conditions under which bird-building collisions may occur. We propose four four natural history models of bird-building collisions: a null model, a nocturnal collision model, a skyglow and stopover model, and a rainforest dispersal model (Table 1). By "natural history", we mean the totality of organismal behavior, phenotype, and ecology apprehensible by observation (Moore et al. 2020; Jones et al. 2024), and by "natural history model," we mean a qualitative narrative describing the behavioral sequences and environmental conditions leading to collisions. Although elements of each model have appeared throughout the literature, they have rarely been considered side by side. Articulating them together highlights both their distinctions and their complementarities, and helps generate testable predictions about the timing, species composition, and ecological contexts of collisions and subsequent carcass encounters. These models should be viewed as hypotheses to be tested rather

than definitive explanations, and they are not mutually exclusive—multiple processes may operate simultaneously or vary across species, locations, and times.

We illustrate our models based on existing studies, as well as on our observations from our own work monitoring collisions on the campus of Rice University in Houston, Texas, USA, from the spring of 2023 to the spring of 2025. The Rice data (Fig. 1) are modest in scope and duration and admittedly not suitable for formal quantitative analysis. We caution readers not to interpret our Rice dataset as definitive evidence but rather simply as illustrative case material. We include it because it provides valuable anecdotal information that inspired us to think carefully about bird-building collisions and to write this paper. We hope that it will play the same role for other researchers and conservation practitioners, helping them design quantitative tests of the models we present here only qualitatively.

Beyond their conceptual utility, our models carry practical implications, which we discuss in depth. Because each model predicts distinct temporal, spatial and ecological patterns of collisions, they can guide survey design, including when and where to search for carcasses. They also underscore that bird-building collision mitigation must be multifaceted: while reducing nocturnal lighting may help in some contexts, we argue that reflective glass is the most universal and tractable target for preventing bird–building collisions.

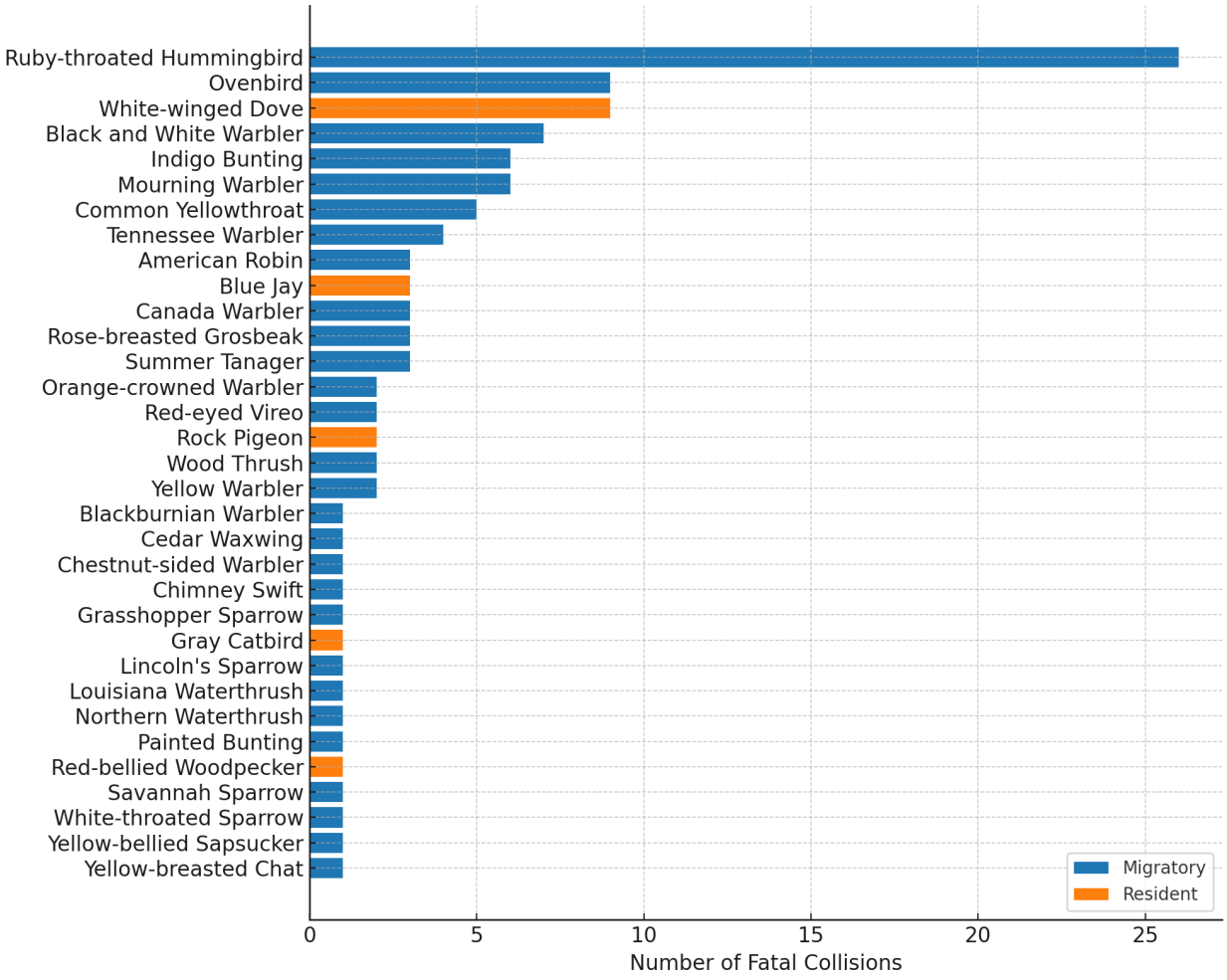


Figure 1. Fatal bird–building collisions by species documented on the Rice University campus, Houston, Texas, 2023–2025. Bars indicate the number of carcasses recorded for each definitively identified species. All carcasses listed have been deposited as research specimens in the Texas A&M University's Biodiversity Research and Teaching Collections. Color denotes migratory status (blue = migratory, orange = resident).

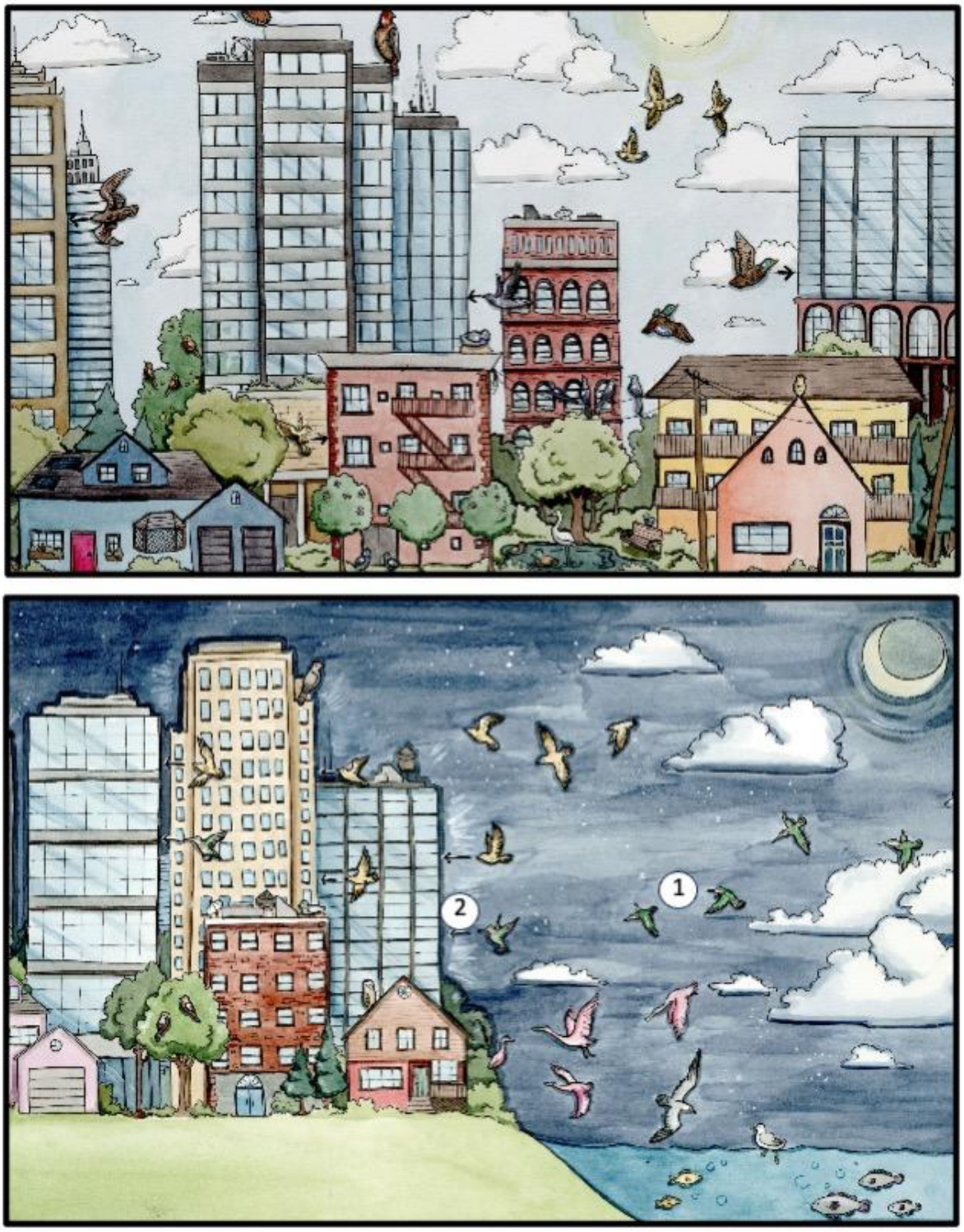
The models, their predictions, and examples

Null model. The first model we wish to articulate is a null model of bird-building collisions

(Fig. 2). This is necessary as a reference point to compare with more complex or specific collision models. This model assumes that the only architectural, landscape, temporal, or ecological features that affect the likelihood of collisions are bird abundance and area of reflective glass windows. The number of collisions per building will be proportional only to building glass area. All bird species–including residents and migrants–will be equally likely to be collision victims, and their rate of collisions will be roughly proportional to their abundance in the local area. Collisions will happen when birds are active: during daylight hours for the great majority of bird species. Carcasses will typically be located between mid-morning and early evening, assuming a lag of a few hours between collision/death and carcass detection.

Though much of the research on bird-building collisions focuses on migratory species (see below), with this model, we seek to direct researchers' attention to the growing evidence that some resident species are quite susceptible to collisions (e.g., Klem 1989; Klem 2021; Gelb and Delacretaz 2009; Loss et al. 2014; Kummer and Bayne 2015; Bracey et al. 2016; Brown et al. 2020; Riding et al 2021; Samuels et al 2022; Emerson et al. 2022; Ross et al. 2023; Hsieh et al. 2024; Tan, Freymueller et al. 2024). For example, in the "Lights Out Texas" project in the community science platform iNaturalist (https://www.inaturalist.org/observations?project_id=97415&place_id=any&verifiable=any&captive=any&view=species; accessed August 2025), which centralizes collision data from the entire state, the White-winged dove (*Zenaida asiatica*), a resident species, is the fourth most frequently colliding species, with 331 collisions out of 5,363, representing 142 species. At a more local scale, in our data from the Rice University campus (Fig. 1), *Z. asiatica* is the second top collider (tied with Ovenbird, *Seiurus aurocapilla*), with 9 out of a total 119 documented collisions representing 38 species since the Spring of 2023. *Z. asiatica* is also one of the most abundant species at Rice (pers. obs.), matching the abovementioned importance of abundance as a basic predictor of collisions at the species level.

139



140 *Figure 2. The null model (top) and the nocturnal collision model (bottom) of bird-building collisions. In the null model,*

141 *bird collisions occur during the normal course of all bird daily activities, and the only ecological, landscape or*

architectural features that play a role in causing collisions are reflective glass and adjacent vegetation. In the nocturnal collision model, nocturnally migrating birds (1) become disoriented by skyglow, which causes them to collide with buildings, usually high-rises with bright lighting and glass windows. Watercolors by Caroline Pollan.

The nocturnal collision model (Fig. 2). Most migratory birds–even those normally active during the day–perform their migratory endurance flights at night (Gill 1995). Thus, much of the literature on bird-building collision has rightly emphasized the role of Artificial Light At Night (ALAN), which causes nocturnally migrating birds to become disoriented, leading them to fly directly into large, glassy, illuminated buildings (Gauthreaux et al. 2006; Van Doren et al. 2021; Klem 2021). Particular single-night mass casualty events caused by ALAN and large buildings have often received considerable attention in mass media, such as when almost 1,000 migrating birds died on the night of 4-5 October, 2023 at McCormick Place Lakeside Center on the shore of Lake Michigan in Chicago (Farnsworth et al. 2024; https://www.npr.org/2023/10/09/1204641722/nearly-1-000-migrating-birds-died-after-crashing-into-chicago-building). Consequently, and justifiably, collision mitigation and outreach initiatives in North America have focused on reducing ALAN, often under the umbrella of the Audubon Society's "Lights Out" program in the US and FLAP (Fatal Light Awareness Program) in Canada.

This model predicts resident species will be little affected by building collisions. Most collisions will happen during peak migration season in the local area (March-May and September-October for Nearctic-Neotropical migrants in North America), and carcasses will mainly be found early in the morning, when daylight and increased human foot traffic will allow detection of birds that died overnight. At the individual building level, ALAN will be a good predictor of collision rate. Features of the landscape at or near ground level, such as vegetation, are unlikely to be relevant. Cardinal orientation of building facades will predict collision rates: in the Northern hemisphere, north-facing facades will see more collisions during post-breeding (Fall) migration, when birds are flying southwards, and south-facing facades during pre-breeding migration (Spring), when birds are flying northwards. Finally, this model predicts that carcass detection rates will peak in mornings

immediately following nights with high migrant passage, as was indeed the case in Stillwater, Oklahoma, USA (Elmore et al. 2021a).

As a putative and anecdotal example of the nocturnal collision model, during post-breeding migration we have frequently found dead Ruby-throated hummingbirds (*Archilochus colubris*)–a nocturnally-migrating species–in the morning at the foot of the north-facing facade of Memorial Hermann Medical Plaza (6400 Fannin St.) in Houston TX, a glassy, illuminated, 28-story building. Just between September 4 and October 2, 2024–peak post-breeding migration–we found 9 *A. colubris* carcasses (data and photographs on iNaturalist: https://www.inaturalist.org/observations?subview=table&taxon_id=6432&user_id=rafael_marcondes). In contrast, we never found a single *A. colubris* carcass at that location during pre-breeding migration, when birds are flying northwards. We believe the nocturnal migration model is the best explanation for the spatial and temporal pattern of carcass detection for this particular species at this particular location, though we have never directly observed a collision at this location, nor have we systematically surveyed it. Support for this model also comes from studies showing that nocturnal migrants are more susceptible to collisions than diurnal migrants or non-migrants (Arnold and Zink 2011), although this does not necessarily imply that the collisions are happening at night.

Table 1. Predicted drivers and collision patterns under each conceptual model of bird–building collisions. For each model, we indicate the expected influence of artificial light at night (ALAN) and glass windows, as well as predicted variation in seasonality, time of peak collision risk, collision height relative to the building façade, and alignment with migratory flight direction.

	Drivers of collisions		**Temporal and spatial predictors of collisions**			
Model	**ALAN**	**Glass**	**Seasonality**	**Timing**	**Building height**	**Cardinal direction**
Null	None	Direct	No prediction	Daytime	Matching adjacent foraging vegetation	No prediction
Nocturnal collision	Direct & indirect	Indirect	Migration season	Nighttime	Matching migratory flight height	Matching migratory flight direction
Skyglow & stopover	Indirect	Direct	Migration season	Daytime	Matching adjacent foraging vegetation	No prediction
Forest dispersal	None	Direct	No prediction	Daytime	Matching adjacent foraging vegetation	No prediction

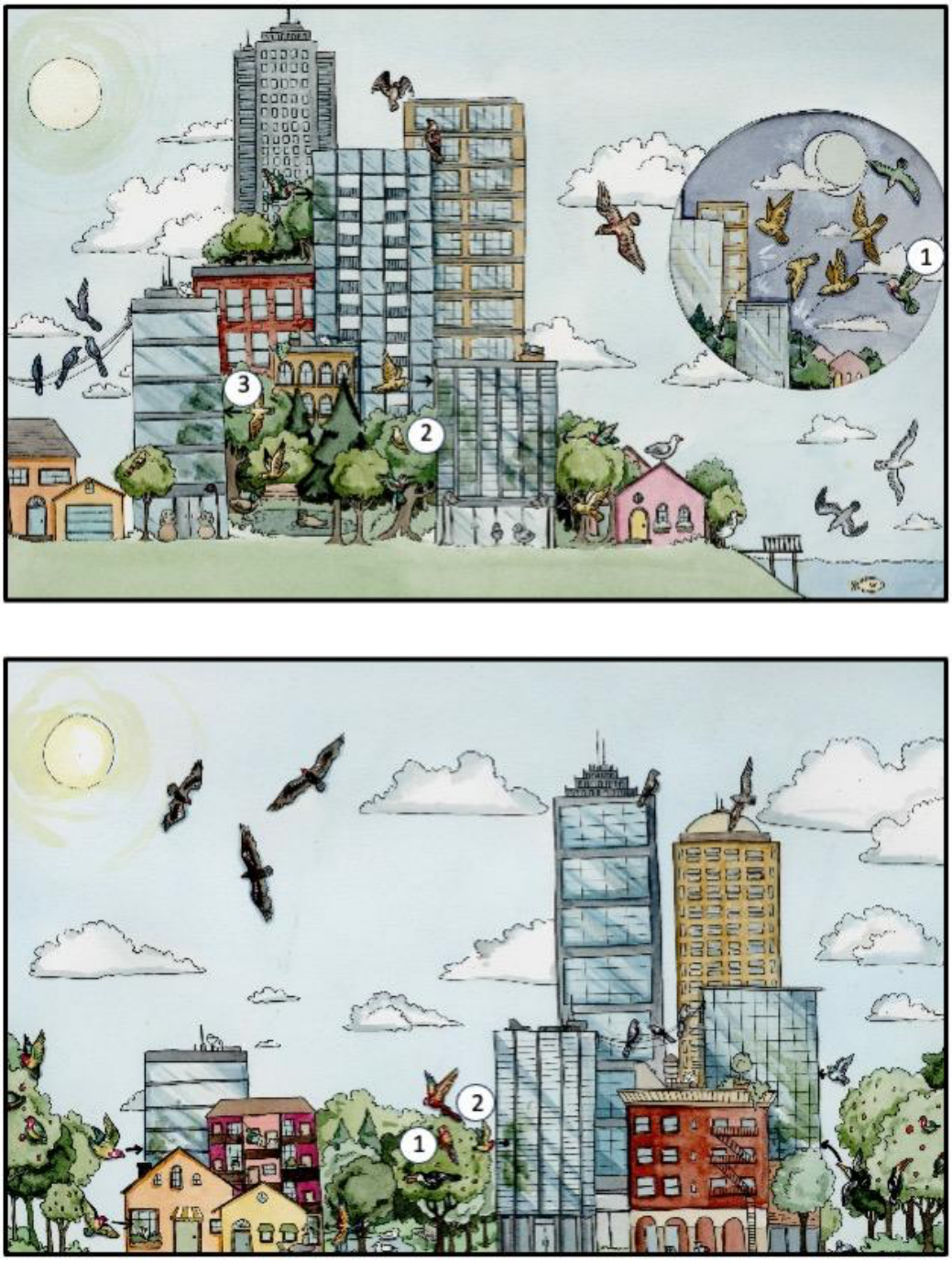


Figure 3. The skyglow and stopover model (top) and the rainforest dispersal (bottom) model of bird–building collisions. In the skyglow and stopover model, nocturnally migrating birds (1) become disoriented by skyglow, which causes them

to alight for stopover (2) in suboptimal habitat in an urban matrix. Birds then collide (3) with reflective windows at vegetation height during the course of daytime foraging. In the rainforest dispersal model, birds adapted to forest edge habitat (1) collide with reflective windows (2) when they attempt to traverse the urban matrix. Watercolors by Caroline Pollan.

The skyglow and stopover model. With this model, we posit that some bird-building collisions result from a three-step process (Fig. 3): first, birds are drawn into urban areas by skyglow—broad, diffuse light pollution that emanates from entire cities, which we distinguish from the more localized light emanating from individual buildings. Unlike direct light sources, skyglow affects large areas of the night sky and is visible from up to 300 km away (Olsen et al. 2014), creating a glowing horizon that disorients nocturnally migrating birds (Gauthreaux et al. 2006; McLaren et al. 2018). But many collisions might not happen by flying into illuminated buildings at this stage (Klem 2021). Instead, we posit that, in a second step, disoriented birds alight in urban areas to use them as stopover sites (Klem 2021, Horton et al. 2024). Then, in a third and final step, they collide with glass windows as they engage in daytime foraging.

Though we have not conducted any formal tests, we believe this model is the best explanation for our carcass detection patterns at the Rice campus, a forested area with abundant food resources in central Houston. At Rice, we conducted careful surveys at the foot of buildings with reflective windows every morning at sunrise during migration season, but we rarely encountered carcasses then. Instead, we found (or, more frequently, members of the university community reported to us) carcasses at all times of the day, often at the very same facades we had carefully surveyed at sunrise finding no birds.

This model highlights the crucial role of stopover sites in bird migration (Schmaljohann et al. 2022; Horton et al. 2024) and in the natural history of bird-building collisions (Horton et al. 2024). Stopover sites are locations where migrating birds temporarily stop for a period to use resources like food, water, and shelter, replenishing energy reserves before continuing their journey (Schmaljohann et al. 2022; Horton et al. 2024). These sites are particularly important just before and just after

transoceanic migratory flights: for example, the Texas coast, where Houston is located, is a well-known stopover area for Neartic-Neotropical migrants that just crossed, or are about to cross, the Gulf of Mexico (Rappole and Ramos 1994; Cohen et al 2021). Birds may lose up to 8% of their body mass after a long migratory flight (Gerson et al. 2020), so during stopovers they are likely in poor physical and cognitive conditions (Fuchs et al. 2006) which, along with the need to consume a lot of food quickly, may make them less likely to perceive and avoid reflective windows. Forest cover is among the most important predictors of bird stopover in the Eastern United States (Cohen et al. 2021; Guo et al. 2023; Horton et al. 2024); indeed, much of the Rice campus and adjoining neighborhoods in Houston are covered a forest-like continuous canopy of Southern live oaks (*Quercus virginiana*).

Similar to the nocturnal collision model, the skyglow and stopover model predicts that collision rates will peak during migration seasons. But the latter also makes some predictions that crucially differ from the former. First, there may not be a concentration of collisions at tall, illuminated buildings. Since most collisions will occur as birds forage during the day, they will be concentrated in low- to mid-rise buildings matching the height of species-specific foraging strata and with windows reflecting foraging microhabitats. This has been observed in the campus of Duke University (Ocampo-Peñuela et al. 2016a), and also matches our observation at Rice University, where the aforementioned Live oak canopy provides good foraging habitat for insectivorous Parulid warblers during migratory stopovers.

Under the skyglow and stopover model, the timing of collisions and of carcass encounters will also differ from the nocturnal collision model. Because birds typically spend at least two days at a stopover site (Schmaljohann et al. 2022), we predict there may be a lag of a few days after high nocturnal migration intensity overhead and before bird collisions and carcass detections on the ground. And because collisions will occur throughout the day, this model also explains the rarity of our encountering carcasses during our sunrise surveys at Rice.

The forest dispersal model (Fig. 3). While both the nocturnal collision and stopover

models focus primarily on migratory species, emerging research from the tropics suggest that non-migratory species are equally, if not more, susceptible to window collisions (Fornazari et al. 2021; Gómez-Martínez et al. 2019; Ocampo-Peñuela et al. 2016b; Rebolo-Ifrán et al. 2019; Tan, Freymuller et al. 2024). Indeed, studies of bird-building collisions outside of North America, especially in the tropics, are scarce in the literature (though see citations herein). This is problematic because temperate and tropical birds tend to differ widely in their ecology and life history, and thus likely also in the circumstances and causes of building collisions.

In tropical Asia, collision reports are dominated by frugivorous and granivorous non-migratory forest edge-dwelling species such as pigeons, barbets, bulbuls, and starlings, although the exact species compositions vary depending on the city (Tan, Freymuller et al. 2024). In particular, the Asian Emerald Dove (*Chalcophaps indica*), a ground-dwelling granivore and frugivore that inhabits forest edge habitats across south and southeast Asia, appears to be a major "super collider" (Arnold and Zink 2011) across multiple Asian cities (Tan, Freymuller et al. 2024; Hsieh et al. 2024). In the Neotropics, forest edge-dwelling thrushes such as the Rufous-bellied (*Turdus rufiventris*), Black-billed (*T. ignobilis*), and Clay-coloured Thrushes (*T. grayi*) are among the species most susceptible to collisions (Ocampo-Peñuela et al. 2016b; Gómez-Martínez et al. 2019; Fornazari et al. 2021)--although on the campus of the Pontificia Universidad Javeriana de Bogota in Colombia, the top collider, with 35 out of 119 collisions was the migratory Red-eyed vireo (*Vireo olivaceus*) (Agudelo-Álvarez et al 2010).

The preponderance of forest edge-dwelling species in tropical colliding assemblages suggests that movements at the interface of forests and urban areas are likely to be a key driver of window collisions in the tropics. Under this model, collisions are therefore most likely to occur at the edges of forested areas, especially where the forest-urban ecotone is narrow. In addition, because collisions are likely driven by the reflections of forest vegetation in glass facades, we expect that collision heights will rarely exceed the maximum canopy height of the adjacent woodland. The exact distribution of collision heights, however, will likely depend on the assemblage of collision-susceptible species in the area and the relative height of maximum resource availability. In

Singapore, for example, *C. indica* was found to collide more frequently with lower buildings owing to its ground-foraging behaviour (Tan, Freymuller et al. 2024), which restricts vertical activity to lower forest strata. In contrast, collisions involving canopy-foraging species such as barbets and green pigeons occurred at more variable heights, often coinciding with the vertical position of mass fruiting events (Tan, Freymuller et al. 2024). We further expect that collisions based on the forest dispersal model will likely occur diurnally, with peaks in the morning and evening consistent with the diel activity patterns of most tropical bird species.

It should be noted, however, that the forest dispersal model does not preclude a role for migration-associated models in the tropics, and they may in fact not be completely separable. In the Singapore dataset (Tan, Freymuller et al. 2024), for instance, nocturnally migranting species such as Yellow-rumped (*Ficedula zanthopygia*) and Mugimaki Flycatchers (*Ficedula mugimaki*) were found to have collision patterns similar to the non-migratory green pigeons and the dove *C. indica*. The forested sites where pigeons and doves reside year-round are also likely serving as stopover sites for the *Ficedula* flycatchers, though the role of light pollution in attracting birds to urban stopover sites in the tropics remains to be studied.

Implications for surveying

Expedient detection of birds killed by collisions is crucial, because carcass persistence time is quite low, due to animal scavengers and to removal by humans. For example, in Stillwater, Oklahoma, USA, the mean time from experimental carcass placement to the first interaction with a vertebrate scavenger was 38 minutes, and on average, carcasses disappeared or became undetectable after 3.1 days (Riding and Loss 2018). In our own anecdotal experience at Rice, carcasses left in place in the late afternoon or evening almost always disappeared by the morning. Loss of carcass to scavengers or human removal can lead to an underestimation of collision rates. Moreover, any additional time elapsed between death and salvaging results in loss of value of the dead animal as a research specimen, as decomposition and partial scavenging (such as by ants and insect larvae) degrade formerly living tissues.

Typically, and including in our own work at Rice, bird-building collision surveys are conducted shortly after sunrise by researchers and volunteers who walk the perimeters of target buildings to search for bird carcasses (e.g., Klem et al. 2009; Ocampo-Peñuela et al. 2016a; Nichols et al. 2018; Winger et al. 2019). This timing is informed by the nocturnal collision model, in which most deaths occur overnight as migrants strike illuminated buildings, and carcasses accumulate before most human activity increases in the early morning. However, this standard approach reflects assumptions specific to only one collision model and may not capture the full scope of collision events.

If the nocturnal collision model is not the prevalent one, then a sunrise-only survey protocol may miss a substantial proportion of collisions, which is consistent with our experience on the Rice campus. Under the skyglow and stopover model, for instance, collisions may occur at any time during the day as birds forage during migratory stopovers. Similarly, in the forest dispersal model, collisions can occur across a broader daily activity window. The focus on sunrise searches also presents logistical and human challenges. Because surveys are often conducted by volunteers, sustaining consistent effort at dawn can be difficult without institutional support. Whereas securing dedicated funding to compensate surveyors can be challenging, we suggest that must be a top priority for any monitoring effort. That would help ensure survey consistency, improve data quality, and ensure long-term monitoring capacity.

Thus, we suggest work on bird-building collisions might benefit from a holistic approach to carcass detection, including late morning or afternoon surveys (Hager and Cosentino 2014; Brown et al. 2020) by dedicated researchers and volunteers, as well as engagement of the general public. For example, at Rice we have conducted an outreach campaign including talks and bilingual (English and Spanish) informative flyers. In these talks and flyers, we inform all members of the university community (students, academic staff, and nonacademic staff) about the existence and magnitude of the bird collision problem and ask them to email us if they observe a dead bird on campus. We ask them to not touch or move dead birds and to include a photo and a detailed description of the location in their email. This campaign has clearly had the desired effect, as we started frequently

receiving emails from members of the university community alerting us to bird carcasses on campus–sometimes multiple times a day during peak migration. Indeed, 75% of our dataset of 142 collisions have been reported to us in that manner, rather than found by us during our dedicated early morning searches.

We also wish to highlight the tremendous potential of community science (also called citizen science) to collect and centralize data on bird-building collisions (Loss et al. 2023). There have been small-scale attempts to leverage the public in general to gather information on bird-building collisions (e.g., Ogden 1996, Rebolo-Ifrán et al. 2019; Brown et al. 20120, Tan, Freymuller et al. 2024). However, the platform iNaturalist (www.inaturalist.org) provides a largely untapped tool for documenting bird-building collisions through opportunistic, georeferenced photographs contributed by the public at a massive scale. Unlike structured surveys, which are constrained by time, location, and personnel, iNaturalist allows anyone with a smartphone to report carcasses anytime and anywhere, greatly expanding spatial and temporal coverage. Each observation includes metadata such as date, time, and location, and can be verified by the community, ensuring data quality. For example, the "Lights Out Texas" project (reviewed in Loss et al. 2023) on iNaturalist currently (August 2025) includes 4,838 photography-documented collision events representing 136 species. A dataset of this size–ripe for much-needed macroecological analyses of the drivers of bird-building collisions–would be well-nigh impossible to generate based only on structured local surveys directly coordinated by professional researchers. To potentialize the use of iNaturalist even more, we suggest researchers should conduct outreach campaigns informing the public about bird-building collisions and how to report them on iNaturalist. These campaigns will have to be regional or even national in scope-- much wider than the one we have conducted with the Rice University community. Most universities have dedicated public relations teams who could help run well-designed and successful campaigns, potentially by engaging relevant mass media outlets (e.g., Ocampo-Peñuela et al. 2016; Brown et al. 2020).

A success story along these lines is that of the China Anti-Bird Window Collision Action Alliance (Shi et al. 2022; Loss et al. 2023; Li et al. 2025), which emerged from the combined efforts

of Duke Kunshan University, the Chengdu Bird Watching Society, and multiple nonprofit partners. This initiative is semi-structured: it relies on community participants distributed nation-wide, but their surveys are coordinated around standardized protocols, defined periods during migration, and centralized reporting through a dedicated portal on WeChat, China's most popular social media platform. By combining the flexibility of citizen engagement with some of the rigor of structured surveys, the alliance has demonstrated how community science can rapidly generate large-scale, policy-relevant datasets while simultaneously raising awareness and driving practical mitigation actions. Similar initiatives leveraging iNaturalist as a unifying global platform could provide even greater benefits.

Implications for mitigation

Current mitigation strategies have largely been shaped by the nocturnal collision model, emphasizing "Lights Out" campaigns aimed at reducing ALAN during peak migration periods. This is supported by retrospective, non-interventional studies showing a correlation between ALAN and collisions at the building level: based on almost 20 years of daily collision and ALAN monitoring at McCormick Place Lakeside Center in Chicago, van Doren et al. (2021) showed that lighting was a top predictor of number of collisions. Similar results were found by Lao et al. (2020) in Minneapolis, Minnesota, USA, but in contrast, Li et al. (2025) found that ALAN within 10 m of a building was only a marginally significant predictor of collisions in China–potentially contradicting the nocturnal collision model–, and that ALAN within 10 km was not a significant predictor of collisions at all–contradicting also the skyglow and stopover model.

However, there is a dearth of studies looking at the effectiveness of ALAN reduction as a mitigation strategy–that is, monitoring collisions before and after deliberate interventions to reduce ALAN. In fact, the single piece of such evidence we are aware of is a reduction in collisions at McCormick Place after it shifted from fully to only partial overnight illumination in 1999 (van Doren et al. 2021), though a role for overall migratory bird population declines cannot be ruled out (van Doren et al. 2021).

In any case, ALAN is only a direct factor leading to collisions in one of our four models (the nocturnal collision model), and an indirect factor in a second model (the skyglow and stopover model). And even under those models, while turning off lights at specific buildings might lead to a local reduction in collisions (van Doren et al. 2021), that is unlikely to have ecologically significant effects. If, as we argue, collisions are caused in part by skyglow–broad, diffuse light pollution,– "Lights Out" efforts can only be truly effective if they succeed in dimming the lights not only of single buildings, but across entire metropolitan areas often spanning hundreds of kilometers and including lights from high rises, street lighting, airports, motor vehicles, industry, and many others sources. This seems impractical.

Instead, we suggest a better and more practical target for mitigation efforts may be not so much ALAN but rather glass windows, which are the immediate physical cause of bird-building collisions under all our models. Bird-friendly window treatments aim to make glass visible to birds and reduce collisions. External patterns, such as dots spaced no more than 5 cm apart horizontally or 10 cm vertically, help birds perceive glass as a barrier (American Bird Conservancy 2011) and have been demonstrated effective in the field (e.g., Ribeiro and Donatelli 2020, Koh and Eo 2025) and in wind tunnels (reviewed in Sheppard 2019).

The American Bird Conservancy has detailed guidelines on bird-safe glass (American Bird Conservancy 2011, Sheppard 2021). For existing buildings, bird-safe decals can be easily applied to glass windows, and for new construction, fritted glass should be used (American Bird Conservancy 2011, Sheppard 2021; Klem 2021). A persistent challenge, however, is cost: retrofitting existing buildings or specifying bird-safe glass in new construction can be more expensive than conventional materials, which may limit widespread adoption despite the clear conservation benefits.

We suggest including information about these simple mitigative actions in the aforementioned outreach campaigns to inform the public about bird-building collisions. We have done so at Rice University, which elicited support from students and administrators. This support has led to a pilot application of bird-safe decals to a window bank we detected as particularly problematic, and to the fitting of two major new buildings currently under construction on campus

413 with fritted glass. Additional success stories of paired research and advocacy campaigns leading to
414 the application of bird-safe decals include the campuses of Duke University (Ocampo-Peñuela et al.
415 2016), the University of Utah (Brown et al. 2020) and Duke Kunshan University in China (Loss et al.
416 2023), among others. Pardew (2024) provides a large list of university campuses that are monitoring
417 and/or taking action to mitigate bird-building collisions.
418

419 **Conclusion**

420 Bird–building collisions represent one of the largest human-caused sources of avian
421 mortality, yet their underlying causes remain difficult to disentangle. By framing collisions through
422 four natural history models, we highlight the value of developing testable hypotheses grounded in
423 natural history about when, where, and why collisions occur. These models are best viewed as
424 hypotheses rather than definitive explanations, and they are not mutually exclusive: multiple
425 processes may act simultaneously, or vary across species, locations, and times. Importantly, the
426 drivers of collisions are likely idiosyncratic. We highlight differences between migratory and
427 nonmigratory species, and between temperate and tropical species, but these are just two aspects
428 among many that may influence collisions. The drivers of collisions are certainly myriad, shaped by
429 organismal, landscape, and architectural features. This means no single model, explanation, or
430 mitigation measure will be universally applicable. Instead, effective solutions will require context-
431 specific approaches informed by both structured surveys and community science contributions. By
432 encouraging the articulation and testing of natural history models, we hope to stimulate such
433 nuanced, place-based investigations that improve our understanding of bird–building collisions and
434 accelerate the implementation of effective conservation strategies.

435

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Ethics statement

We followed the Ornithological Council's *Guidelines for the Use of Wild Birds in Research*. Bird carcasses on the campus of Rice University were salvaged under United States Fish and Wildlife Service Migratory Bird Permit MB89966C-0 and Texas Parks & Wildlife Department Scientific Permit Number SPR-0720-091 and are deposited as research specimens in the Texas A&M University Biodiversity Research and Teaching Collections.

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