Journal of Field Ornithology

J. Field Ornithol. 83(2):203–211, 2012 DOI: 10.1111/j.1557-9263.2012.00370.x

Scavenging affects persistence of avian carcasses resulting from window collisions in an urban landscape

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Received 11 March 2011; accepted 8 December 2011

ABSTRACT. Collisions with windows remain an important human-related threat to bird survival in urban landscapes. Accurately estimating the magnitude of avian mortality at windows is difficult and may be influenced by many sources of error, such as scavenging of carcasses. Failure to account for removal of carcasses by scavengers can bias estimates of window mortality. We tested the hypothesis that carcass survival depends on local habitat factors known to influence scavenger behavior. Scavenger activity on bird carcasses was documented at 20 buildings in an urban landscape in northwestern Illinois for 1 week during each season of a year. Known-fate models were used to relate carcass survival to local habitat composition and to evaluate temporal variation in survival. We also documented species of scavengers and the timing of scavenging using motion-triggered cameras. Daily carcass survival was greater in winter than during spring, summer, and fall. Survival was related negatively to canopy cover (trees and shrubs within a 50-m buffer) and window area, and positively to pavement cover. Using an exponential model of survival time, estimated mean time of survival of carcasses ($t \pm$ SE) was 82.9 $\pm$ 11.7 d for winter and 11.8 $\pm$ 7.2 d for other seasons. Raccoons (*Procyon lotor*) scavenged more carcasses than other species. Our results suggest that (1) carcass survival times may be short at locations with preferred habitats of known scavengers and predictable sources of food, and (2) knowledge of scavenger distribution and activity can inform predictive models of persistence. In studies of bird-window collisions, the influence of scavenger bias can be minimized by maintaining short time intervals between carcass searches. Search intervals can be inferred by estimating the number of days that a carcass should persist at a site, which can be calculated using predicted daily survival probabilities of carcasses at study buildings.

RESUMEN. **Buscadores de cuerpos afectan la persistencia cadáveres de aves que son el resultado de la colisión con ventanas en un paisaje urbano**
La colisión con ventanas sigue siendo una amenaza importante sobre la sobrevivencia de las aves la cual está relacionada con los humanos en un paisaje urbano. Una estimación precisa sobre la magnitud de la mortalidad de aves en las ventanas es difícil y puede estar afectada por muchas fuentes de error, como los buscadores de de cuerpos. La incapacidad de tener en cuenta la remoción de cuerpos por los buscadores de cadáveres puede sesgar los estimativos de la mortalidad por ventanas. Pusimos a prueba la hipótesis que la permanencia de los cadáveres depende de factores conocidos en habitas locales que afectan el comportamiento de los buscadores de cuerpos. La actividad de los buscadores de cuerpos sobre los cadáveres de aves fue documentada en 20 edificios en un paisaje urbano al noreste de Illinois durante una semana en cada estación durante un año. Modelos deterministicos fueron usados para relacionar la permanencia de los cadáveres con la composición local del hábitat y evaluar la variación temporal en la permanencia. También documentamos las especies de los buscadores de cadáveres y cuando ocurrió el evento usando cámaras con sensores de movimiento. La permanencia diaria fue mayor en el invierno que durante la primavera, verano y otoño. La permanencia estuvo negativamente relacionada con la cobertura de dosel (árboles y arbustos dentro de un área de 50-m) y el área de las ventanas, y positivamente con la cobertura del pavimento. Mediante un modelo exponencial de supervivencia en el tiempo, estimamos el tiempo promedio de permanencia de los cadáveres ($t \pm$ SE) el cual fue 82.9 $\pm$ 11.7 días para el invierno y 11.8 $\pm$ 7.2 días para otras estaciones. Mapaches (*Procyon lotor*) buscaron mas cuerpos que otras especies. Nuestros resultados siguieren que (1) la permanencia de los cadáveres en el tiempo puede ser corta en lugares con hábitats conocidos y preferidos por los buscadores de cuerpos y con fuentes de alimentos predecibles y (2) conocimiento de la distribución de los buscadores de cadáveres y su actividad pueden proporcionar información para modelos predictivos de permanencia. En estudios de colisiones de aves con ventanas, el efecto de los sesgos de buscadores de cadáveres puede ser minimizado mediante el mantenimiento de intervalos cortos de tiempo entre las búsquedas de cadáveres. Los intervalos de búsquedas pueden inferirse estimando el número de días que un cadáver debería permanecer en un lugar, lo cual puede ser calculado usando probabilidades de supervivencia diaria predictiva de los cadáveres en edificios de estudio.

Key words: bird-window collisions, carcass survival, known-fate models, program MARK, scavengers, urban ecology

Collisions with building windows are thought to be a significant source of mortality for urban birds (Erickson et al. 2005). Although monitoring programs are designed to identify

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the magnitude of window collisions, imperfect detection of carcasses can lead to biased estimates of total mortality (Smallwood et al. 2010, Huso 2011). One source of imperfect detection is the removal of carcasses by scavengers before surveys are completed. If scavenger activity and carcass survival (i.e., the time from carcass deposition to removal by a scavenger) exhibit spatiotemporal variation, then inferences regarding the proximate drivers of window collisions may also be biased.

Studies of bird-window collisions have assumed no prominent bias in persistence of carcasses (e.g., Arnold and Zink 2011), but scavenger bias has been demonstrated in numerous studies where mortality resulted from collisions with other structures (e.g., communication towers, wind turbines, power lines, fences, and vehicles on roadways), pesticide programs, and disease (Kostecke et al. 2001, Ward et al. 2006, Smallwood 2007, Gehring et al. 2009, Ponce et al. 2010, Santos et al. 2011, Stevens et al. 2011). One salient feature of the results of studies of scavenger bias is that the temporal aspects of carcass survival are site-specific. For example, Flint et al. (2010) reported low estimated carcass persistence (<50% of carcasses persisted for a day) at communication towers in Alaska, whereas persistence of carcasses at towers in Michigan was relatively high (mean time to removal was 7–8 d; Gehring et al. 2009). Estimating carcass persistence alone offers little insight into factors influencing persistence.

Studies of scavenger bias indicate that carcass size, carcass condition (partial vs. intact bodies), and ambient temperature explain variation in persistence (Bumann and Stauffer 2002, DeVault et al. 2004, Smallwood 2007, Flint et al. 2010). Equivocal results have been reported for the effect of local scale factors on carcass survival. Bumann and Stauffer (2002) found no correlation between local habitat variables and time to removal, yet persistence varied among land-cover attributes in other studies (Pain 1991, DeVault et al. 2004, Santos et al. 2011). Some authors have speculated that correlations between local habitat factors and survival are explained by the activity and habitat preferences of local scavenger populations (Pain 1991, Santos et al. 2011).

Stevens et al. (2011) hypothesized a priori that local features associated with predation of Greater Sage-Grouse (*Centrocercus urophasianus*) nests would also influence persistence of carcasses at fences. They found that variation in carcass survival was not explained by small-scale factors and reasoned that persistence was, instead, a function of landscape-level processes. We expanded upon the approach by Stevens et al. (2011) by examining how carcass survival varied in relation to local factors that affect the behavior of urban vertebrate scavengers. Urban mesopredators exhibit strong spatiotemporal variation in activity and distribution (Prange and Gehrt 2004, Prange et al. 2004, Gehrt et al. 2010), usually in response to the availability of food and suitable refugia (Hudenko et al. 2010). Mesopredator activity is also affected by weather conditions and is limited when temperatures are below freezing (Prange and Gehrt 2004, Prange et al. 2004). Together, these studies suggest that the survival of bird carcasses after window collisions should depend on forest cover, pavement cover, and ambient temperature.

Variation in carcass survival may also depend on the relationship between the frequency of window collisions and vertebrate scavengers learning the locations of predictable sources of food. Scavengers may revisit buildings with many windows and predictable sources of food in the form of avian carcasses (Klem 1981, Evans Ogden 1996). Thus, scavenging of bird carcasses at buildings with many windows may occur as a learned response (Dalgish and Anderson 1979, Hadidian et al. 2010).

We tested the hypothesis that survival of carcasses resulting from bird-window collisions depends on factors related to spatiotemporal variation in scavenger distribution and activity. We replicated the availability of bird carcasses at multiple buildings, and evaluated how carcass survival depended on local habitat structure, building window area, and season. Based on spatial and temporal patterns of activity of mesopredators in our study area, we predicted that bird carcasses would survive longest during winter and at buildings with few windows in areas with limited forest cover. We also estimated mean carcass survival time using an exponential model to inform minimum sampling intervals for future window-monitoring studies.

METHODS

Study buildings. We studied habitat attributes and timing of scavenger activity at

20 buildings in Rock Island and Moline, Illinois. This 9330-ha urban area is bordered to the north and west by the Mississippi River and to the south by the Rock River. Using ArcGIS (2010), we used stratified random sampling to select 15 study points distributed as equally as possible within four urban land cover categories: (1) High Density (all or nearly all covered with structures), (2) Low/Medium Density (up to 50% covered with structures), (3) Urban Open Space (parks, golf courses, cemeteries, and other grassland-like cover within urban and built-up areas), and (4) Forested Land and Floodplain Forest (undeveloped land that occasionally includes buildings; Illinois Department of Agriculture 2009). A stratified design ensured selection of a sample of buildings with sufficient variation in land cover. We obtained permission to use the building closest to each point. Two property owners denied permission so we obtained permission to access the next closest building. Buildings ranged in size from small single-family residential (150 m^2 top-view area) to small commercial (680 m^2). Large commercial buildings were uncommon in our study area and were not represented in the initial sample of 15 points. Thus, we opportunistically selected five large buildings (880–12,140 m^2) within the same land cover categories as smaller buildings.

Habitat attributes around buildings were digitized from a Bing Map high-resolution aerial photograph taken during the growing season of 2010 (ArcGIS 2010). We characterized habitat attributes in a 50-m buffer zone around buildings by estimating the percent area of (1) canopy (canopy cover of trees and large shrubs), (2) exposed habitat (grass/lawn, landscaped ground cover, and open water), (3) structures (buildings, excluding the study building), and (4) pavement (roadways, sidewalks, and parking lots). A 50-m buffer captured detailed and ecologically relevant local scale attributes, which relate to movements and habitat use of urban scavengers (Crooks 2002, Prange and Gehrt 2004, Prange et al. 2004). Although scavengers may respond to habitat structure at larger spatial scales, land cover in our 50-m buffer zones was highly correlated with land cover at larger scales ($r > 0.80$ for all 50-m intervals up to 250 m; Illinois Department of Agriculture 2009). Building window area was estimated using a measuring tape.

Field study. We monitored carcass survival at buildings during each of four 7-d study periods during winter (28 December 2009 – 4 January 2010), spring (1–8 April 2010), summer (23–30 June 2010), and fall (2–9 October 2010). One of 80 bird carcasses representing 30 species was randomly assigned to each building-season combination (mean = 12.25 species/season).

We randomized the location of birds at buildings with respect to the cardinal direction of one of four walls. All bodies were placed below a window simulating the appearance and location of a bird following a window collision. Carcasses were placed on their backs and ~1 m from window edges. We also assumed that carcasses would most likely be found below the largest windows (Hager et al. 2008) and on the most common ground-cover type below windows. For example, if the ground cover adjacent to a wall consisted of decreasing amounts of grass (lawn), pavement (sidewalk), and tree mulch, we placed the carcass on grass below the largest windows. Carcass placement at five buildings was not randomized. In these cases, placement was selected to minimize the likelihood of theft of motion-sensitive cameras.

We checked bodies daily during each study period (~24-h interval between checks). Carcass survival was the probability of a carcass persisting one 24-h interval. We considered scavenging as a carrion-foraging event resulting in complete removal of a carcass or removal to an extent that detection of a whole body was compromised, such as feather piles. We collected carcasses not scavenged and carcass sign (i.e., feather piles) at the end of each study period.

Carcasses used in our study had been salvaged previously from below windows at Augustana College, Rock Island, Illinois, which is located in the same urban area. Species of carcasses ranged in size from a Ruby-crowned Kinglet (*Regulus calendula*; 7 g, Otis et al. 2008) to a Mourning Dove (*Zenaida macroura*; 130 g, Swanson et al. 2008) and corresponded to the same species found in the study area and potentially killed at study buildings. Bird carcasses were salvaged from July 2007 to September 2010, frozen immediately after collection, and allowed to thaw before placement at a building. Whole carcasses were used because window casualties rarely display external injuries, and this is what scavengers would naturally encounter. We handled carcasses with food-grade plastic bags to minimize any negative effects of human scent.

We used known-fate models in Program MARK (White and Burnham 1999) to assess how season, habitat cover, and window area influenced the probability of carcass survival (Ward et al. 2006, Flint et al. 2010). We used seven discrete intervals of a single day each to estimate the daily probability of carcass survival. A logit link function was used to model carcass survival as a linear function of covariates, and the Akaike Information Criterion corrected for small sample size (ΔAIC_C) was used to evaluate the support of 18 candidate models with different combinations of covariates (Burnham and Anderson 2002). All survival models included an intercept. We first built models to evaluate temporal variation in the probability of survival. Survival was modeled as either constant or variable over daily sampling intervals to evaluate whether there was strong daily variation in survival that was consistent across seasons. The most supported model of temporal variation was used in all subsequent models to evaluate the additive effects of up to two habitat factors on survival. Canopy cover and pavement cover were not included in the same model because they were correlated ($r = -0.88$; Graham 2003). Finally, we estimated mean survival times (t) for carcasses at each building using the exponential model $r = e^{-d/t}$, where r is the probability of survival for $d = 1$ d (Huso 2011). We specified r as the predicted probability of survival from the most-supported known-fate model to solve for t for each building.

Camera study. We monitored carcasses during each season using motion-triggered digital cameras (MFH-I-49, Moultrie, Alabaster, AL); one camera each was placed at buildings in Forest ($N = 2$), Urban Open Space ($N = 2$), and Low/medium Density ($N = 1$) land-cover categories. Buildings were selected based on the permission by landowners and camera security. No buildings in the High Density land-cover category fit these criteria. Cameras had quiet shutters and used infrared illumination at night to minimize disturbance of potential scavengers.

We programmed cameras to include time, temperature, and study building in each image. Upon motion activation, three pictures were taken at 13-s intervals. Following the third picture, default programming rendered the camera inoperable for 1 min, after which the camera could again detect movement and take additional pictures. Images were used to assist with scavenger identification. To avoid counting a single scavenger more than once, we classified a visit as unique if detected by a camera $\geq$10 min after a previous image. Cameras were mounted 2 m from and 1 m above carcasses on trees, posts, or tripods. We downloaded images daily to a computer after checking for the presence of carcasses. All cameras were removed from buildings either after a carcass was scavenged or at the end of a study period if carcasses were still present.

We recorded a scavenging event if an image depicted (1) a carcass being consumed by a scavenger in $\geq$1 consecutive photographs, (2) a carcass in the mouth of a scavenger in only one image and the disappearance of both scavenger and carcass in subsequent images, and (3) a carcass and scavenger in the same image and disappearance of both scavenger and carcass in subsequent images. Three scavenging events not recorded by cameras were labeled as either nocturnal or diurnal using images taken before and after an event.

Photos allowed us to identify scavenger species, potential scavenger species (photos of a known or potential scavenger that did not remove a carcass), and the timing of scavenging behaviors. We excluded from our analysis images of nonscavengers, e.g., songbirds.

RESULTS

We monitored 20 bird carcasses in each season. Scavengers removed two (10%) bodies in winter, 11 (55%) in spring, eight (40%) in summer, and 13 (65%) in the fall. Overall, the most supported model of carcass survival included effects of season, canopy cover, and window area (Table 1). Carcasses survived longer in winter than other seasons, and survival was negatively related to canopy cover and window area (Fig. 1; $\hat{\beta}$ for the top model: canopy cover $= -0.53$, SE $= 0.22$; window area $= -0.42$, SE $= 0.16$). A competing model ($\Delta AIC_C \leq 2$) included the effect of pavement cover in addition to season and window area, and survival increased with pavement cover (Fig. 1; $\hat{\beta}$: pavement cover $=$ 0.53, SE $= 0.24$). Models with structures or exposed cover were not supported (Table 1). Using predicted survival probabilities from the most-supported model, estimated mean carcass survival times ranged from 22.7 to 212.0 d in winter, and 3.5 to 29.6 d in other seasons (Table S1).

Scavengers visited carcasses monitored by cameras on 60 occasions, but only 11 (18%) visits resulted in carcass removal (Table 2). Photos revealed that raccoons scavenged more carcasses than other species and decomposers removed one carcass. Six of 11 carcasses (55%) were removed at night by raccoons ($N = 3$ carcasses), an opossum ($N = 1$), a domestic cat ($N = 1$), and an unknown scavenger ($N = 1$). A domestic cat and eastern gray squirrel (*Sciurus carolinensis*) each removed one carcass during the day. The time of removal of the remaining carcasses ($N = 3$) could not be determined. In winter, only domestic cats visited carcasses at one building.

Of carcasses removed by scavengers ($N = 34$), feather piles remained for 18 (53%) carcasses. Feather piles (mean $\pm$ SD) contained 17.3 $\pm$ 13.5 (range = 2–40) pennaceous feathers from wings and other parts of the body and 4.1 $\pm$ 3.5 (range = 0–11) bundles of pennaceous feathers.

Table 1. Most-supported models of carcass survival probability at 20 buildings in an urban landscape in northwestern Illinois, 2010. Summary includes the relative difference between model AIC_C and the best model (ΔAIC_C), Akaike weights (ω_i), number of parameters (K), and deviance. Only models with $\Delta AIC_C \leq 5$ are included.

Model[a]	ΔAIC_C	ω_i	K	Deviance
$Season_{Winter}$[b] + Canopy + Window	0.00	0.41	4	218.15
$Season_{Winter}$ + Pavement + Window	0.61	0.31	4	218.76
$Season_{Winter}$ + Canopy	4.26	0.05	3	224.44
$Season_{Winter}$ + Window	4.41	0.05	3	224.60
$Season_{Winter}$ + Pavement	4.80	0.04	3	224.98

[a]Main effects include time (Season), percent canopy cover (Canopy), percent pavement cover (Pavement), and window area (Window).
[b]Subscript for Season indicates that survival probability varied between winter and nonwinter (Winter).

Table 2. Urban scavenger species, number of carcass visits, and number of carcasses removed at study buildings monitored by motion-sensitive cameras in northwestern Illinois, 2010. Cameras monitored one carcass at each of five buildings in winter and nonwinter seasons (spring, summer, fall).

	Winter[a]		Nonwinter		
Scavenger species	Number of visits[b]	Number removed	Number of visits	Number removed	Number of feather piles
Raccoon (*Procyon lotor*)	0	0	17	3	3
Domestic cat (*Felis domesticus*)	23	0	9	2	0
Virginia opossum (*Didelphis virginiana*)	0	0	1	1	1
Eastern gray squirrel (*Sciurus carolinensis*)	0	0	6	1	0
Eastern chipmunk (*Tamias striatus*)	0	0	1	0	-
Eastern cottontail (*Sylvilagus floridanus*)	0	0	3	0	-
Invertebrate decomposers	–	0	–	1[c]	1
Unknown	–	0	–	3[d]	2
Total	23	0	37	11	7

[a]Seasons were grouped by "winter" and "nonwinter" because the probability of carcass survival was significantly higher in winter than the other seasons.
[b]Identifies the number of images of scavengers and potential scavengers inspecting a carcass, which included active inspection (i.e., image of animal staring at or appearing to sniff the carcass) or passive inspection (i.e., quickly walking past a carcass).
[c]Invertebrate decomposers were observed within and on the surface of the carcass for the first 3 d of exposure; by day 4, all soft and bony tissue was removed and only feathers remained; thus, carcass removal was not captured by the camera and the carcass gradually decomposed in 4 d during the summer trial period, which precluded classification of nocturnal or diurnal removal.
[d]Cameras failed to respond to scavenging events in the spring ($N = 2$) and fall ($N = 1$).

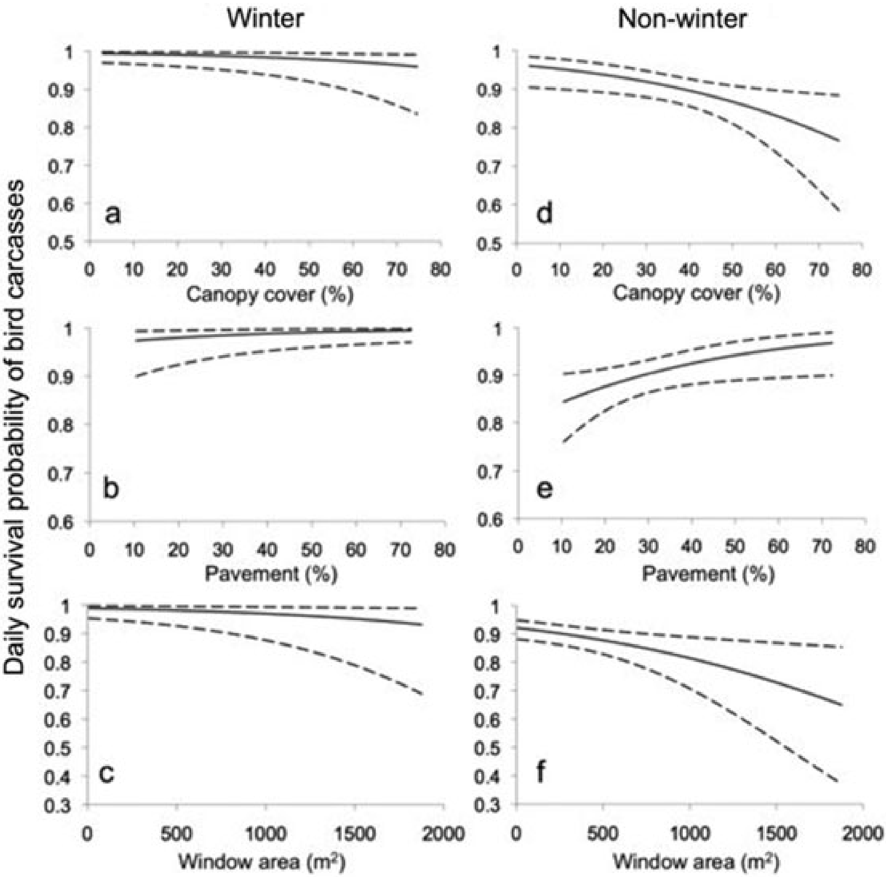

Fig. 1. Relationships between predicted daily survival probability of bird carcasses at study buildings and canopy cover, pavement cover, and window area in northwestern Illinois in winter (a–c) and nonwinter (d–f). Predicted survival probabilities for canopy cover and window area were based on the most-supported model, whereas predicted persistence probabilities for pavement cover were based on the second-best model (Table 1). Dashed lines represent upper and lower 95% confidence intervals.

Of all piles, 77% contained bundles of remiges, 65% contained bundles of nonflight feathers, and 18% contained bundles of rectrices; only three piles contained body parts (wing, tail, and legs) and uneaten soft tissue (e.g., viscera). Feather piles were confined to a roughly circular area with a diameter of 23.1 ± 10.6 cm (range = 5–45 cm) and persisted in the same spots ≤24 h, after which monitoring ceased. Cameras recorded all raccoons and opossum consuming carcasses at the site of initial placement and leaving feather piles; domestic cats and an eastern gray squirrel carried carcasses from their original locations.

DISCUSSION

Carcass survival and local habitat structure. Longer carcass survival in winter may be explained by the response of raccoons to unpredictable food sources (DeVault et al. 2003, Prange and Gehrt 2004). In winter, few carcasses may be available at buildings because mortality due to window strikes is low relative to nonwinter seasons (Hager et al. 2008). As a result, raccoons would be expected to focus foraging activities away from buildings. Carcass persistence in winter may also be affected by reduced activity by vertebrate scavengers when temperatures are below freezing (Hoffmeister 2002, Prange and Gehrt 2004, Prange et al. 2004).

Prolonged carcass survival was observed at buildings surrounded by a high percentage of pavement and little canopy cover. Vertebrate scavengers avoid busy roadways and parking lots (Prange et al. 2004, Santos et al. 2011). For example, raccoons avoided roadways in urban Illinois even though busy streets tend to provide substantial amounts of food from vehicle-killed animals (Prange and Gehrt 2004, Ditchkoff et al. 2006). Other investigators have found that reduced scavenger activity along roadways with heavy traffic significantly increased survival of small bird carcasses (Slater 2002, Santos et al. 2011).

Carcasses survived for shorter periods at buildings with little pavement and high canopy cover, suggesting higher levels of scavenger activity at these sites, especially in nonwinter seasons. Scavengers in our study area prefer wooded habitat for daily and seasonal refugia and reproduction (Hoffmeister 2002, Gehrt et al. 2010). In addition, avian mortality rates due to window strikes are higher in areas with high canopy cover and large window area (O'Connell 2001, Hager et al. 2008, Klem et al. 2009). Raccoons would be expected to capitalize on this consistent source of food, and other scavengers (e.g., domestic cats and opossums) should occasionally exploit this resource during foraging bouts.

Our estimates of carcass survival could have been influenced by carcass condition. Carcasses placed at buildings were whole and intact, which may have increased persistence rates (Bumann and Stauffer 2002, Smallwood 2007). In addition, carcasses were frozen prior to use in scavenger trials, and freezing may decrease carcass detection and attractiveness by altering olfactory signals and extending survival rates (Bumann and Stauffer 2002, Smallwood 2007, Smallwood et al. 2010). Conversely, small carcasses persist for shorter periods of time than large carcasses (e.g., raptors; Ward et al. 2006, Flint et al. 2010, Smallwood et al. 2010, Santos et al. 2011) because a wider range of potential scavengers is capable of removing small carcasses (Santos et al. 2011). However, carcasses used in our study were salvaged from window collisions in our study area, and carcasses were randomly assigned to buildings. Thus, we have no reason to believe that our model selection results were affected by carcass condition, freezing, or size.

Importance to future studies. Scavengers at other urban locations would be expected to exhibit patterns of distribution and activity correlated with local conditions, which may be used to model carcass persistence. An understanding of local predator populations would facilitate formation of predictions about how carcass survival should vary in an urban landscape. Urban predators have generalist diets and the location of food is a strong proximate driver of foraging behavior (Prange et al. 2004, Gehrt et al. 2010, Hudenko et al. 2010). Scavenging pressure on bird carcasses from window collisions likely varies among species, but would be (1) primarily influenced by predators, such as raccoons and Common Ravens (*Corvus corax*), capable of learning the locations and timing of predictable sources of food, and (2) secondarily affected by other predators, such as opossums and various rodents, that are opportunistic foragers (Dalgish and Anderson 1979, Prange and Gehrt 2004, Ditchkoff et al. 2006, Webb et al. 2011).

In addition to foraging behavior, carcass survival would be expected to vary among patchily distributed urban habitats, which are differentially occupied by urban scavengers in time and space (Riley et al. 2010). Carcass survival times should be short at buildings located near preferred habitat, e.g., nature preserves and manicured green space (golf courses, parks, and cemeteries; Prange and Gehrt 2004, Chace and Walsh 2006, Gehrt et al. 2010). Carcasses should persist longer at buildings in habitats less preferred by urban scavengers, such as industrial areas, linear rights of way (roadways and train tracks), and undeveloped lots (Prange and Gehrt 2004, Gehrt et al. 2010). Predictions about variation in carcass persistence follow from an understanding of the behavioral ecology of local predator populations, and survival models can be constructed based on local conditions predicted to affect persistence.

Our results suggest that the influence of scavenging bias in studies of bird mortality due to window collisions can be minimized by maintaining short time intervals between carcass searches. Search rate may be inferred by estimating the number of days that a carcass should persist at a site, which can be calculated using predicted daily survival probabilities (Huso 2011). For example, we estimated that carcasses at Building 23 persisted for an average of 23.7 d in the winter and 3.5 d during other seasons (Table S1). Therefore, search intervals can be matched to each site's estimated persistence times. Alternatively, investigators could maintain constant search intervals at all buildings based on the site with the lowest estimated persistence time, which was ≤3 d at Building 23 in our study.

Scavenger bias could also be minimized by including carcass sign (i.e., feather piles) as well as whole carcasses in fatality estimates. Most carcasses in our study were consumed at the site of initial placement and feather remains were present for >50% of the carcasses scavenged. Carcass sign has also been reported in numerous other studies and habitats (Balcomb 1986, Tobin and Dolbeer 1990, Pain 1991, Wobeser and Wobeser 1992, Smallwood et al. 2010, Stevens et al. 2011). The probability of detecting carcass sign is likely high if search intervals are short (Rosene and Lay 1963, Wobeser and Wobeser 1992, Stevens et al. 2011), but further study is needed to evaluate how persistence of carcass sign might vary among sites.

In summary, our study adds to a growing body of evidence that scavenger bias is an important source of imperfect detection in studies assessing anthropogenic threats to birds (Ward et al. 2006, Gehring et al. 2009, Ponce et al. 2010, Smallwood et al. 2010, Huso 2011, Santos et al. 2011, Stevens et al. 2011). As predicted, we found that carcasses persisted longer in winter and at buildings with low window area in areas dominated by impervious surfaces and little woody vegetation. Our results suggest that carcasses survive for shorter periods at locations with predictable sources of food and preferred habitats of known scavengers, and that knowledge of scavenger distribution and activity can inform predictive models of persistence.

ACKNOWLEDGMENTS

We are deeply grateful to all landowners for granting us permission to conduct this research on their property. Financial support was generously provided by the Quad City Audubon Society and by an Augustana College Presidential Research Fellowship awarded to SBH. The helpful comments of G. Ritchison, P. Flint, M. Craig, and several anonymous reviewers greatly improved the quality of an earlier draft of the paper. We appreciate the assistance of R. Heine and M. Craig with Bing Maps and ArcGIS. Bird carcasses used in this study were salvaged via state Scientific Permit (#NH11.0313), Illinois Department of Natural Resources, and federal Salvage Permit (#MB08907A-0), U.S. Fish and Wildlife Service.

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Supporting Information

The following supporting information is available for this article online:

Table S1. Study building characteristics, persistence probability (*r*), and estimated persistence time (*t*) for carcasses in winter and nonwinter.

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