

Exploring the City: The Urban Habitat of an Avian Apex Predator



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Summary

Ecosystems worldwide are undergoing unprecedented changes, with urbanization being a human-induced process with a significant effect on both environments and species. Birds, in particular, are one of the species groups severely affected by urbanization. Thus, understanding the consequences of urbanization on bird habitats and environments is crucial. This review examines the urban habitat of the Peregrine Falcon *Falco peregrinus* and its implications for population dynamics within the context of source-sink dynamics. The findings demonstrate that urban peregrines exhibit habitat and nest site selection similar to their natural counterparts, with similar effects on reproduction. Urban areas also provide abundant prey diversity, although the specific foraging locations during the breeding season remain uncertain. Limited knowledge exists regarding intraspecific competition in urban environments, yet ample food availability may reduce territorial conflicts. Additionally, the interactions with predatory species observed in nonurban habitats remain uncertain in urban settings. Immigration from nonurban habitats primarily sustains urban peregrine populations, indicating the role of urban areas as sink habitats. As urbanization advances and nonurban habitats transform, it becomes crucial to understand the duration for which nonurban peregrine populations can continue to provide immigrants. Investigating the adaptive capabilities of peregrines in urban breeding conditions seem to be essential for assessing the potential establishment of self-sustaining urban populations.

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Introduction

Earth's ecosystems are changing at unprecedented rates, emphasizing the need to understand how organisms cope with and adapt to environmental changes (Botero et al., 2015; Diffenbaugh & Field, 2013; Magurran, 2016). Over the past century, ecosystems worldwide have experienced widespread changes such as global mean temperature increases, sea level rises, changes in seasonality, and increasing extremes. These alterations are presumed to intensify in the upcoming decades at a rate of potentially multiple orders of magnitude more rapidly than that experienced in the past 65 million years (Diffenbaugh & Field, 2013). Current environmental changes are primarily caused by climate change and human-induced landscape alterations (Hautier et al., 2015) and affect the stability of ecosystems through the species living within them (Hautier et al., 2015). Therefore, organisms must find ways to cope with these changing environmental conditions. However, knowledge and understanding to predict the evolutionary ecological responses of organisms are currently lacking (Botero et al., 2015).

To predict how organisms will respond to future global changes, it is important to understand that adaptations evolve under different timescales and predictabilities of environmental change (Botero et al., 2015). Moreover, these adaptive response mechanisms are presumably subject to evolutionary tipping points, implying that a radical transition can be triggered by a very small disruption (Botero et al., 2015; Scheffer, 2010). Organisms can exhibit different forms of responses (also called 'response modes'), among which are types of bet-hedging, plasticity, and adaptive tracking, that may allow them to adapt to both natural and human-induced environmental variation (Botero et al., 2015; Lowry et al., 2013). However, the ability of organisms to successfully adapt to environmental change appears to rely more on the conditions and strategies they employ after the change rather than the conditions experienced during the transition toward the new environment (Botero et al., 2015).

Urbanization is among the most impactful human-induced processes affecting landscapes, ecosystems, and species globally (Grimm et al., 2008; Seto et al., 2010). Currently, over four billion people live in urban areas, and since 2007, it has been estimated that the urban population has overtaken the rural population (Ritchie & Roser, 2018). Urban populations and the accompanying urbanization process are most commonly defined by their relative population size per land area (Hussain & Imitiyaz, 2018; Ritchie & Roser, 2018). However, a general consensus on the definition of urbanization, which may also differ depending on the perspective one takes, is lacking. Perspectives on urbanization range from demographical to spatial or ecological mapping (Haase et al., 2018). Nonetheless, the current rate of global urbanization (Ritchie & Roser, 2018) drives and affects natural habitat loss, local and regional landscape environments, land cover, hydrological systems, and biogeochemistry, and increases the risk of current and predicted extinction of plant and animal species (Grimm et al., 2008). Spatial use, such as form and function, institutions, and governance structure, of urban areas is the main driver of environmental change (Seto et al., 2010).

Despite urbanization severely affecting natural areas, within urban landscapes, different types of habitats exist that are perceived as 'nature' and may provide refuge for non-human organisms (Niemelä, 1999). In general, 'nature' is a term that has many definitions depending on the perceiver and background looking at it (Hoyle et al., 2019; Keeler et al., 2019). Similar issues arise when discussing 'urban nature' (Hoyle et al., 2019), which may be received as a contradictory term, as urbanization alone has a strong negative effect on the natural landscape (Grimm et al., 2008; Niemelä, 1999; Seto et al., 2010). Urban nature can be defined as green infrastructure that is either natural or planted, in which case often planned and designed (Hoyle et al., 2019; Threlfall et al., 2016). Both types of urban natures can be managed (Hoyle et al., 2019). Examples of urban nature include gardens, city parks, cemeteries, green roofs, rivers, and street trees (Goddard et al., 2010; Hoyle et al., 2019; Morelli et al., 2018; Williams et al., 2019). Thus, the various types of green infrastructures cause gradient levels in terms of nature within urbanized environments (Threlfall et al., 2016).

The composition and diversity of avian species are severely affected by urbanization (Morelli et al., 2021); however, the mechanisms and intensity can be highly species-specific (Crooks et al., 2004). In general, both total and native numbers of bird species are negatively correlated with increased urban development (Reale & Blair, 2005). The diversity richness and nesting success of bird species can change along urbanization gradients (Crooks et al., 2004). As a result of nest site availability and the ability of some species to produce multiple broods in a season (Reale & Blair, 2005), urban fragments with high levels of urbanization show relatively high species diversity but relatively low abundance (Crooks et al., 2004). In contrast, with decreasing levels of urbanization, species diversity also decreased but species abundance increased (Crooks et al., 2004). Thus, areas with moderate urbanization levels may present the highest diversity and abundance of avian species (Crooks et al., 2004). Moreover, studies have shown that development and habitat fragmentation trigger species-dependent responses, which may be the drivers of overall avian assemblages throughout urban areas (Crooks et al., 2004; Patankar et al., 2021). Studying species-specific traits and responses to urbanization is essential to understand the dynamics of local species populations (Crooks et al., 2004).

Population dynamics and distribution of avian species can be strongly affected by source-sink dynamics (Brawn & Robinson, 1996; Dunning et al., 1992). Source-sink dynamics in an ecological context refer to the movement of individuals or populations between two types of habitats: source habitats and sink habitats (Dunning et al., 1992). Source habitats are environments that provide favorable conditions for population growth, such as abundant resources such as food, nesting sites, and suitable breeding conditions (Brawn & Robinson, 1996; Dunning et al., 1992). In contrast, a sink habitat lacks the resources necessary for sustainable population growth. As a result, bird populations residing in sink habitats experience low reproductive success and survival rates, which can lead to population decline or even local extinction if the habitat is not periodically replenished by individuals from the source habitats (Dunning et al., 1992). Birds from source habitats, where populations are thriving, may disperse to sink habitats in search of additional resources or because of high population density (Dunning et al., 1992). The population in the sink habitat is unlikely to be self-sustaining due to its inherent limitations and thus remains dependent on immigration (Brawn & Robinson, 1996; Dunning et al., 1992).

The Peregrine Falcon *Falco peregrinus* (hereafter peregrine) is a bird species that is strongly connected to urbanized habitats (Cade & Bird, 1990). The peregrine is a cosmopolitan species that can be found from the Arctic tundra to the tropics in a wide variety of both urban and nonurban habitats (Figure 1; White et al., 2020). Between the 1940s and the 1970s, peregrine populations crashed as a result of hunting pressure and pesticides, mainly toxic DDT (Padayachee et al., 2023). After the ban on DDT and through reintroduction programs, peregrine populations have successfully recovered and are now stable or even increasing (White et al., 2020). During the recovery period, peregrines reoccupied the old territories

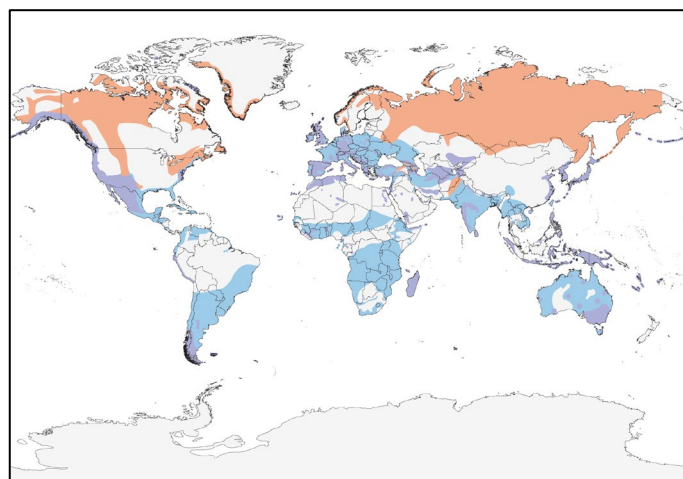


Figure 1: Map showing the global distribution of the Peregrine Falcon *Falco peregrinus*, the colours imply breeding grounds (orange), year-round presence (purple) or wintering grounds (blue). Directly copied from White et al., 2020.

(Leonardi, 2020) or occupied completely new territories (Geneijgen, 2014). Among the newly occupied territories are also urban areas; moreover, peregrines are considered a species that seemingly thrive

in human-dominated environments (Gahbauer et al., 2015; Kettel et al., 2018, 2019). However, populations that exclusively nest on buildings and other anthropogenic nesting sites are mostly found within lowland areas of Europe and North America (Cade & Bird, 1990; Lindner, 2018).

Following the successful settlement of peregrines in urban habitats, this study aims to answer the question: “How do urban habitat conditions affect the population dynamics of Peregrine Falcons *Falco peregrinus* in relation to source-sink populations?”. This study will assess the (1) nesting habitat, (2) diet and hunting methods, and (3) intra- and interspecific interactions of urban peregrines and compare these, where possible, with nonurban individuals. These subjects were chosen as they are considered prime selective forces that determine the nesting success of peregrines (Caballero et al., 2016; Reale & Blair, 2005). The population dynamics of urban peregrines are hypothesized to be significantly influenced by habitat conditions. It is expected that higher-quality habitats will support larger and more stable populations, whereas lower-quality habitats, specifically urban areas, will function as sinks, characterized by smaller and less sustainable populations. In particular, urban areas are considered lower-quality habitats because of various factors such as suboptimal nesting sites, limited prey availability, and increased competition. Consequently, the population in urban areas is expected to rely on immigration from nonurban populations. This hypothesis suggests that urban peregrines are unable to form self-sustaining populations and rely on external sources to compensate for the adverse conditions within urban habitats.

Methods

This study is presented as a literature review, where all published papers, found as described below, are used to assess the adaptive capabilities of peregrines to environmental change. To find relevant papers the following keywords were used: “peregrine falcon,” “*Falco peregrinus*,” “population,” “urbanization,” “urban,” “breeding,” “nesting,” “nesting site,” “reproduction,” “competition,” “intraspecific,” “interspecific,” “hunting,” “diet,” “innovation,” “habitat,” “predation,” “eagle-owl,” “evolution,” “adaptation”. Combinations of these keywords were entered in Web of Science, Google Scholar, and WorldCat, this resulted in over 75 papers that provided useful data to use in this study. The term ‘urban’ is widely used within the academic literature, however, defining urban is a complex matter. Most papers define an urban area as any populated area ranging from large cities to small towns. Other studies, such as Brambilla et al. (2010) and Kettel et al. (2019), used a minimum percentage of land with building development within a pre-defined km-radius to label an area as urban. Finally, the structure a peregrine uses for breeding can also be described as an anthropogenic or natural nesting site and may be unrelated to the type of habitat its located in (Kleinstäuber et al., 2018). This study defines an urban peregrine as an individual that uses an anthropogenic nesting site within a densely populated area such as an authority-recognized city. Existing literature will be assessed on a case-by-case basis to assess whether their definition of urban meets these requirements.

Results

Breeding Conditions

Nesting Sites

Peregrines use a variety of structures as nesting sites, such as cliffs, buildings, trees, and grid structures (Kleinstäuber et al., 2018). Depending on the structure, a peregrine nest can be just a small bowl of substrate scraped together or an old stick nest in a tree made by another species (Andreenkov et al., 2018; Kleinstäuber et al., 2018; White et al., 2020). Productivity in urban peregrines increases with height, as Gahbauer et al. (2015) showed that nest sites within the top quartile of productivity were, on average, located higher on buildings (96.2 ± 9.9 m, $n=21$) than those in the bottom quartile (63.6 ± 9.8 , $n=21$). Moreover, as the population increased over time from a mean of 9 nests (1980s) to 67 nests (2002 – 2006), the mean height of newly occupied urban nest sites declined by 39% from 93.6 ± 11.1 m (1983-1994, $n=21$) to 57.5 ± 11.5 (2004-2006, $n=21$) (Gahbauer et al., 2015). Additionally, nests with full overhead cover, meaning protection against meteorological influences such as rain, had a higher mean productivity (2.34 ± 0.2 , $n=30$) than those only partially covered or without any cover (1.69 ± 0.4 , $n=12$); however, the results were too variable for the differences to be significant (Gahbauer et al., 2015). Wightman and Fuller (2006) assessed 67 cliff-breeding attempts by peregrines between 1972 and 1999 and showed that the chance of occupation increased with both cliff height (3% per 1-meter increase) and cover (4% per 1-degree decrease in exposure). Wightman and Fuller (2006) found no significant associations between habitat features and productivity.

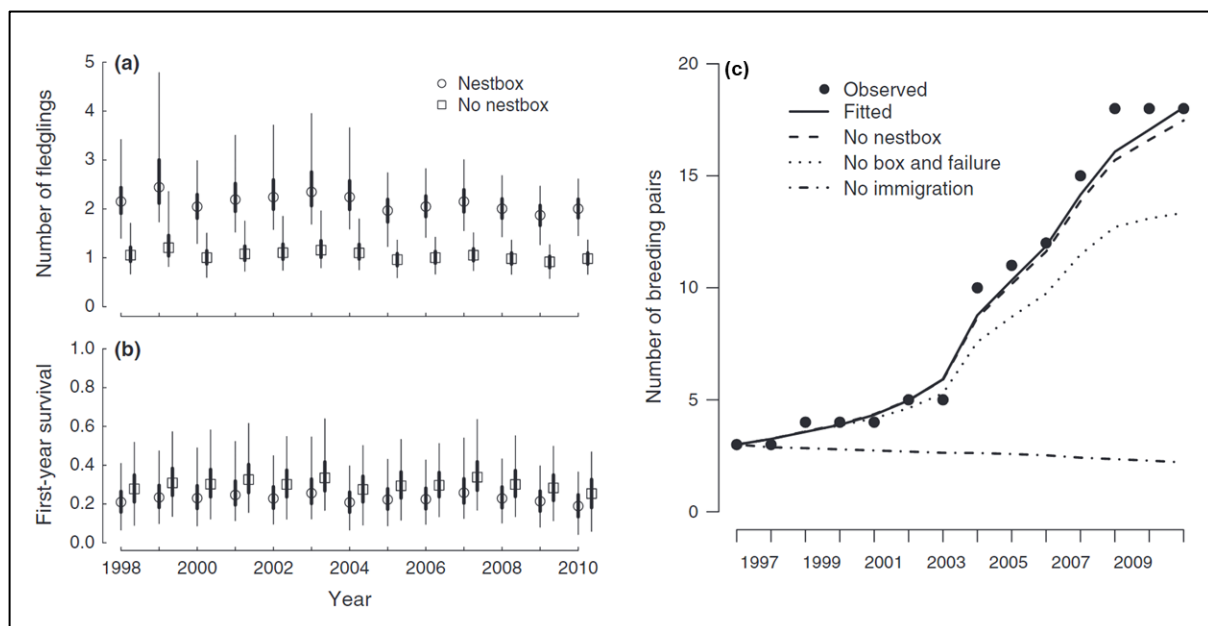


Figure 2: Here the analysis of an urban peregrine population in Cape Town is depicted. The median and the 95% confidence intervals (thin lines) of both the number of fledglings (a) and the probability of first-year survival (b) among peregrines are shown for buildings with (square) and without (circle) nest boxes. Below, are the observed and fitted lines of the total population (c) dependent on the absence and presence of nestboxes, immigration, and breeding success. Directly copied from Altwegg et al., 2014.

Over the past few decades, nest boxes have become a popular and widely used measure to support bird populations (Arlettaz et al., 2010; Newton, 1994). Gahbauer et al. (2015) showed that nest boxes or trays were used by 76% of breeding pairs within the top quartile of productivity ($n=21$). Only 23% of breeding pairs within the bottom quartile used a nest box or tray ($n=21$). Moreover, the combination of a nest box on a building produced the highest mean productivity compared to any other location (Mann-Whitney $U = 74.5$, $Z = 1.84$, $P = 0.066$). These results confirm the findings of Altwegg et al. (2014), who found that the number of fledglings and first-year survival were positively correlated with

nest boxes (figure 2a & 2b). However, these results cannot be explained without acknowledging immigration (figure 2c). Additionally, the fledgling success within urban areas also varies between nesting structures, such as quarries (2.83 ± 0.44 , $n=4$), buildings (2.10 ± 0.17 , $n=48$), and bridges (1.53 ± 0.19 , $n=35$) (Gahbauer et al., 2015). This also occurred when comparing nest boxes, as bridges had a low fledgling success (<1.7 , $n=35$) regardless of whether nest boxes or trays were provided (Gahbauer et al., 2015).

The nest site choice by peregrines might be driven by environmental cues, however, here we assess which internal processes may play a role. Firstly, imprinting on their nest site, described to take place during approximately the first two weeks of active orientation by nestlings and the first weeks after fledging, is suggested to make peregrines more likely to nest in a habitat similar to the one they were born in (Kleinstäuber et al., 2018; Olsen et al., 2006). Therefore, the reintroduction events of, for example, over 6,000 individuals that took place from the 1970s onward in the USA alone (National Park Service, 2021), may have affected where the future offspring settled to breed (Kleinstäuber et al., 2018). Secondly, once a nest site was chosen, Caballero et al. (2016) found that 95.1% of peregrines ($n=122$, 6-year period) returned close to ($<20m$) or to the exact same site in each breeding season. This is defined as nest site fidelity and is positively correlated to previous breeding success (Caballero et al., 2016).

Despite their strong attachment to nest sites, peregrines may still change their breeding sites over time. This gradual change is, for example, observed in an East German peregrine population that was studied by Kleinstäuber et al. (2018) between 1992 and 2014 ($n=600$). The population was divided into four categories according to the breeding structure (Figure 3). Over the years, the population has increased, and peregrines started to spontaneously settle on buildings, trees, and grid structures (Figure 3; Kleinstäuber et al., 2018). This shows that, despite imprinting and nest site fidelity, peregrines may still switch between nest sites later in life (Kleinstäuber et al., 2018). Moreover, Kleinstäuber et al. (2018) found that the probability of a peregrine fledged from a tree nest returning and breeding in a tree later in life (57%) was much lower than that of individuals for buildings (81%) and cliffs (95%). Additionally, individuals breeding in trees and on cliffs were also born on this type of nest site (95% and 91%, respectively). Peregrines breeding on buildings, however, were more often born from another nest type, as only 57% originated from a nest on a building; the remaining individuals came from trees (35%), cliffs (6%), or lattice towers (2%). The results of Kleinstäuber et al. (2018) show that tree breeders form a source population for peregrine populations breeding on anthropogenic structures.

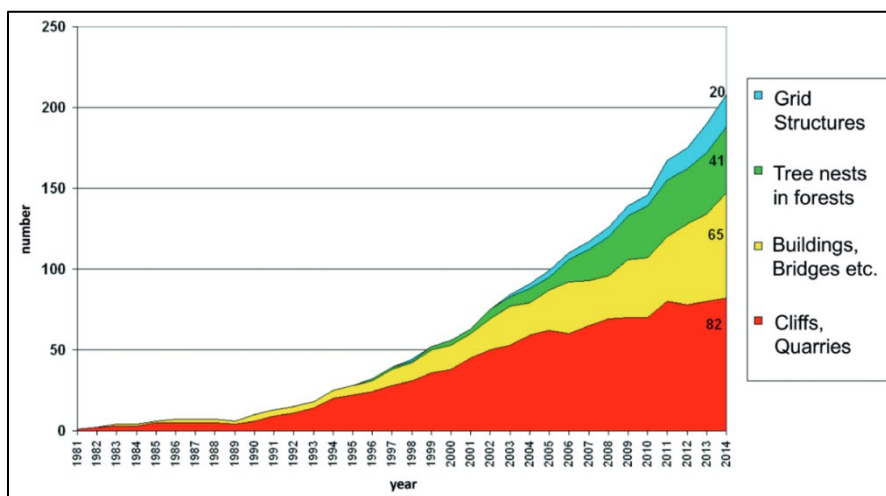


Figure 3: Graph showing the East German peregrine population ($n=600$) that has been studied between 1992 and 2014. The number of individuals subdivided with respect to the structure or habitat that used to breed on. Directly copied from Kleinstäuber et al., 2019.

Breeding Habitat

The territories of urban peregrines are, according to a study in London, England, spaced in a way that the mean distance between nests is approximately 2 km (range 314,5m – 7666,6m; Mak et al., 2021). Within urban landscapes, peregrines preferably nest in built-up areas with tall buildings or church towers, which are considered analogous to nesting cliffs in natural environments (Mak et al., 2021). Moreover, Mak et al. (2021) analyzed the breeding habitat selection of urban peregrine pairs in the Greater London area (1600 km²), England, relative to the habitats available using locations of nesting sites obtained through sightings submitted by the public between 2003 and 2018. They found that urban peregrines, when combining the 500- and 2000-meter buffers around the nests (n=30), favored water, public parks, gardens, and built-up areas (Figure 4; Mak et al., 2021). When comparing figure 4 with the results of Gahbauer et al. (2015), the latter found no correlation between the distance to water and productivity. However, between the first (1983 – 1994; n=21) and most recent colonized nests (2004 – 2006; n=21), Gahbauer et al. (2015) found that the mean distance of nests from water increased from 0.3 ± 0.1 km to 2.1 ± 1.0 km. Aside from preferences exhibited by peregrines, the habitat in which an individual nests, may also present threats that cannot be accounted for. For example, urban areas have been reported to have relatively high mortality rates among young peregrines due to collisions with buildings, vehicles, and power lines (Table 1, Hager, 2009; Gahbauer et al., 2015). With potentially harmful infrastructure networks also increasing outside urban areas (Travers, 2023), further research is necessary to compare urban and nonurban mortality rates.

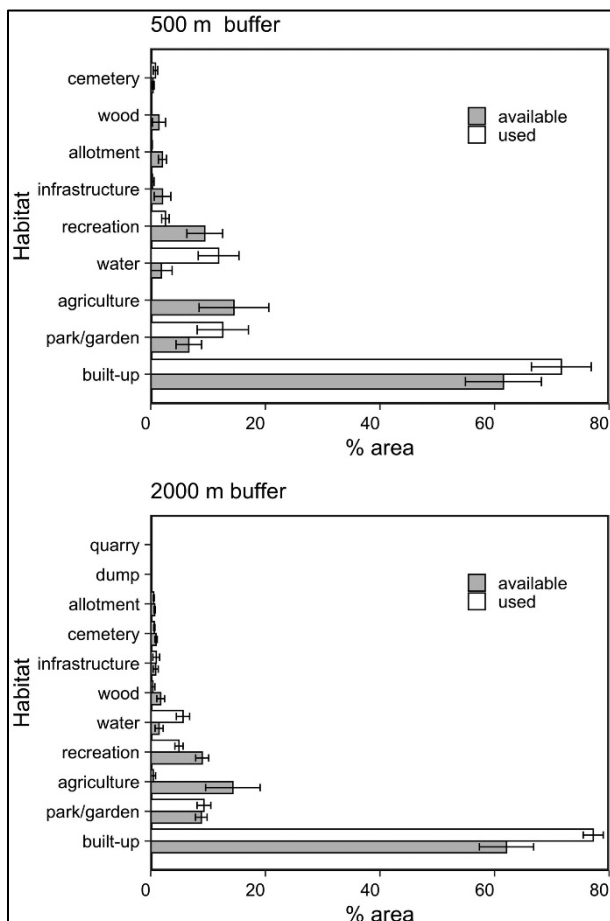


Table 1: The percentages of known causes of death for peregrines recorded between 1988 and 2006 in North America (Ontario, Massachusetts, and Pennsylvania). The study included a total of 1,613 young from 801 nesting attempts at 152 nest sites. Directly copied from Gahbauer et al., 2015.

	Fledgling (<1 month)	Juvenile (>1 month)	Adult (>1 year)
Collision: building	38 (61%)	2 (8%)	3 (16%)
Collision: vehicle	4 (6%)	5 (19%)	2 (11%)
Collision: aircraft	1 (2%)	8 (31%)	1 (5%)
Collision: power lines	4 (6%)	4 (15%)	1 (5%)
Territorial battle			7 (39%)
Other raptor/predation	5 (8%)	1 (4%)	
Drowning	4 (6%)		
Other	6 (10%)	6 (23%)	5 (26%)
Unknown	18	12	12
Total	80	38	31

Figure 4: Barplot showing the habitat use of urban peregrines in London over the period of 2003-2018. Both a 500- and 2000-meter buffer were used to record the type of habitat surrounding each nest site, here given in mean percentage of the total area. Directly copied from Mak et al., 2021.

Diet and Hunting

Diet and Prey availability

Peregrines primarily consume a wide range of avian species, occasionally complemented by mammals (such as squirrels, rats, and microtines), bats, amphibians, fish, and insects (White et al., 2020). Bird species caught by peregrines can be generalized by subdividing them into species groups, mostly corvids, pigeons, starlings, wildfowl, waders, and other passerines (Forsman, 2006; White et al., 2020). However, prey composition, even when only considering species at the group level, can differ between regions, habitats, and seasons (Dixon & Drewitt, 2018; Drewitt & Dixon, 2008; Rejt, 2001). An example of prey composition is given in figure 5. The figure, based on 5,275 prey remains collected over three cities in England between 1998 and 2007, shows both urban residents, such as pigeons, and nonurban species, such as waders, as prey caught by urban peregrines (Drewitt & Dixon, 2008). When considering seasonal variation (figure 6), it is clear that certain species are primarily caught during periods of migration in spring or autumn (Drewitt & Dixon, 2008; Rejt, 2001). Most of these season-dependent species are nocturnal migrants that may have been caught by peregrines at night (DeCandido & Allen, 2006; Dixon & Drewitt, 2018; Drewitt & Dixon, 2008; Kettel et al., 2016; Time, 2016).

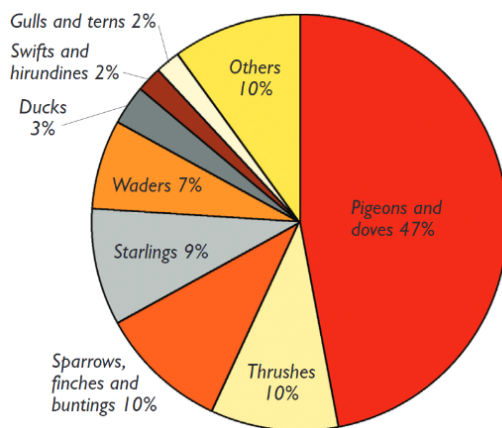


Figure 5: The percentages for each prey type (species group) caught by urban peregrine pairs in Exeter, Bristol, and Bath (n=5,275) collected between 1998 and 2007. Directly copied from Drewitt and Dixon, 2008.

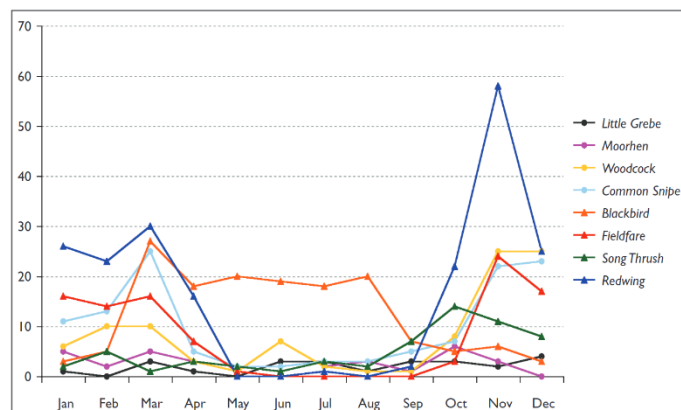


Figure 6: Seasonal variation of prey caught by peregrines in Exeter, Bristol, and Bath (n=5,275) collected between 1998 and 2007. Note that common, mostly non-migratory, species are excluded to emphasize the seasonal variation of other species. Directly copied from Drewitt and Dixon, 2008.

In a study conducted by Kettel et al. (2019) in the United Kingdom between 2006 and 2016, it was discovered that landscape type had a notable effect on the prey characteristics of peregrines. They used the prey component as a measure of prey availability, which included the related variables of prey density, biomass, and diversity. In their study area, urban sites (n=22) exhibited a higher prey component than rural areas (n=58) (Figure 7a). The higher prey component was characterized by increased prey density and biomass, with decreased prey diversity per 1 km² (Kettel et al., 2019). The prey component was positively correlated with both nesting success and number of fledglings (Figure 7b; Kettel et al., 2019). Additionally, other factors, such as human presence, should be considered to have a potential influence on food availability in urban areas. Mak et al. (2023) studied the diet of 31 peregrine breeding pairs across cities in the United Kingdom between 2020 and 2022. During these periods of COVID-19 lockdowns, Mak et al. (2023) showed that the diet composition of peregrines changed between years, with, for example, reduced pigeon consumption of peregrines as a result of decreased human activity. However, no evidence was found to suggest a correlation between human activity and total food availability for peregrines (Mak et al., 2023).

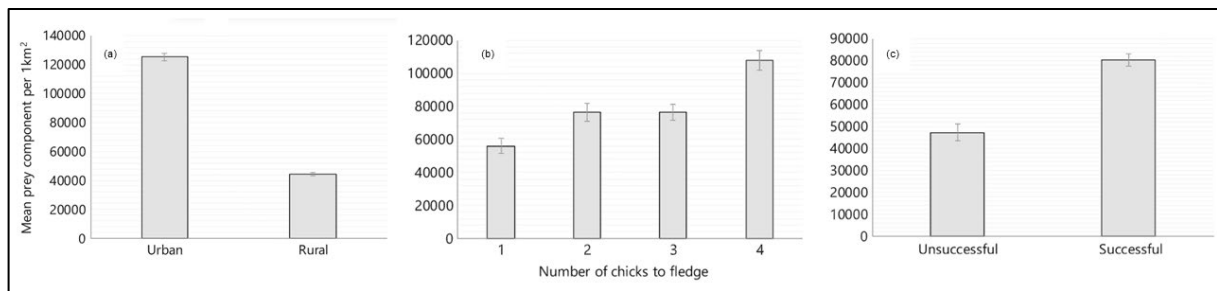


Figure 7: Bar plots showing the mean (± 1 SE) prey component (1-km^{-2} in $<2\text{km}$ radius) within urban and rural habitats (a), relative to the number of chicks fledged (b), and the nesting success of urban and rural areas combined (c) ($n=49$). Directly copied from Kettel et al., 2019.

Hunting Methods

Peregrines are skilled hunters able to swoop up their prey mid-air while diving down at speeds of up to 250+ kilometers per hour (J. Ferguson-Lees & Christie, 2005; White et al., 2020). The general sequence of actions peregrines follow when hunting can best be described in the order of searching, attacking, capturing, killing, and eating. Peregrines most often search for their prey from a high vantage point, this can be either an elevated position or flying, often circling, high in the sky; occasionally, peregrines may hunt or sit on the ground (White et al., 2020). Peregrines engage in hunting across a wide range of habitats. During the breeding season, they primarily hunt from elevated positions, targeting flying birds in the airspace. However, during the non-breeding season, they can also be found perched on lower vantage points in environments such as wetlands, mudflats, and other open terrains (White et al., 2020). Overall, peregrines employ various hunting methods and generally exhibit a consistent sequence of behaviors. Nevertheless, over the years, several instances of peregrines displaying novel hunting behaviors have been observed (Lefebvre, 2021).

‘Innovation’ is a term used to describe animal behavior that arises as a solution to a novel problem (Kummer & Goodall, 1985). When this behavior is aimed at obtaining resources, it is referred to as a feeding innovation (Kummer & Goodall, 1985; Lefebvre, 2021). In a study by Lefebvre (2021), 4,455 papers describing feeding innovations were collected, of which 35 were specific to peregrines. Among the papers focusing on peregrines, 10 observed behaviors were directly associated with urban landscapes or human activities. These include, for example, using buildings for cover during hunting and attempts to steal food from carrion crows *Corvus corone* at a garbage dump (Lefebvre, 2021). One of the most notorious and well-known adaptations, however, is hunting at night using artificial light at night (ALAN; DeCandido & Allen, 2006; Kettel et al., 2016; Lefebvre, 2021; Time, 2016). Studies suggest that hunting by peregrines at night is strongly connected to the autumn period and the occurrence of migratory birds flying at night (DeCandido & Allen, 2006). Prey caught between dusk and dawn, in which peregrines have been seen (DeCandido & Allen, 2006) or suggested (Kettel et al., 2016; Lefebvre, 2021; Time, 2016) to use ALAN, include passerines, waders woodcocks, nightjars, and rails.

Different studies have described the diet of urban peregrines; however, care should be taken when assigning prey remains to hunting methods. While some studies have visually observed nocturnal hunting by peregrines (DeCandido & Allen, 2006; Time, 2016) or feeding of young at night (Kettel et al., 2016; Rejt, 2001), others have only described the diet based on prey remains, suggesting nocturnal hunting (Bondi et al., 2016; Drewitt, 2010; Drewitt & Dixon, 2008; Leonardi & Mannino, 2007; Mak et al., 2023). Nonetheless, studies have shown that the peregrine foraging flights can range from direct vicinity to the nest to over 43 km, with extremes of up to 79 km in one-way flight (Enderson & Craig, 1997; Ratcliffe, 1993; The Canadian Peregrine Foundation, n.d.). Additionally, urban peregrines are suggested to hunt primarily 1-5 km away from their nest site, and thus do not hunt in the direct vicinity of their nest (Taranto, 2007). Depending on the city and location of an urban nesting site, the foraging flight distances of urban peregrines may bring them outside of urban areas. Peregrines are well-known

predators of waders at, for example, tidal mudflats, during the non-breeding season (J. Ferguson-Lees & Christie, 2005; Piersma et al., 1993; White et al., 2020). Therefore, specifically because of the partial lack of knowledge as to where urban peregrines hunt, the possibility that urban peregrines may also hunt in nonurban areas during the breeding season should be taken into consideration in future studies.

Competition and Predators

Intraspecific Competition

The establishment of nesting territories is the main cause of intraspecific competition among peregrines (Leonardi, 2020). In some studies, territorial conflicts were even the primary cause of death for adult urban peregrines (Table X; Gahbauer et al., 2015). While other studies also report mortalities as a result of territorial conflicts (Herbert & Herbert, 1965; White et al., 2020), it remains unknown how mortality rates in urban areas stand out from those in rural areas. Nonetheless, the intensity of and motivation for competition within peregrine populations may change gradually throughout the breeding season (Leonardi, 2020). Competition for nesting territories is most intense at the beginning of the breeding season in early spring but gradually decreases in intensity as the season progresses (Caballero et al., 2016; Leonardi, 2020). Caballero et al. (2016), who assessed 6-year data from the Chicago area, USA, involving 122 nesting attempts, found no correlation between nest site fidelity and breeding density, the distance between nests, or the number of active nests. Given the absence of a correlation between nest site fidelity and breeding density, Caballero et al. (2016) suggested that the interference between urban peregrines had no significant effect on breeding success.

Competition between peregrines when choosing a nest site is a rather complicated process. Peregrines are selective when choosing natural breeding sites on cliffs (Leonardi, 2020). Spacing, habitat quality, and the presence of other peregrine nest sites are the most important selective forces (Wightman & Fuller, 2005, 2006). This can be further explained using the *Nearest Neighbour Distance*. Food sources generally determine the spacing of nest sites, where the distance between nests decreases with increasing prey availability (Newton, 1980). The same spacing provides a mechanism to reduce intraspecific competition for food or nesting sites (Leonardi, 2020). Additionally, high food abundance means less territorial behavior between individuals, whereas less food means more territorial behavior (Cavé, 1967). If urban areas indeed offer a higher food abundance than rural areas (Figure 7a; Kettel et al., 2019), this would eventually lead to relatively smaller territories, fewer territorial battles, and thus, a higher density of peregrines in urban areas. However, studies that directly compare these two are lacking.

Interspecific Interactions

Interspecific interactions are often dominated by predator-prey interactions (Leonardi, 2020; White et al., 2020). While predation is often considered to mainly act on lower trophic levels, competition is expected to be more influential at higher trophic levels (Sergio & Hiraldo, 2008). Although, this does not seem to be the case for each species, as apex predators such as peregrines may be subject to predation (Brambilla et al., 2010; Lindner, 2018; White et al., 2020). Interactions between different predator and prey species are intricate within peregrines and are highly influenced by the local habitat and ecoregion. Within the predator-prey complex, peregrines tend to be the prey or subordinate party (Brambilla et al., 2010).

Peregrines experience interspecific competition for food and nesting sites almost exclusively with sympatric falcons, particularly the hierofalcons Lanner Falcon *Falco biarmicus*, Gyrfalcon *Falco rusticolus*, and Saker Falcon *Falco cherrug*, which overlap in range (Booms et al., 2020; Kemp & Marks, 2020; Leonardi, 2020; Orta et al., 2020; White et al., 2020). Firstly, lanner falcons and peregrines show a 99% overlap in diet, but differences in their breeding habitat preferences allow them to coexist (De Rosa et al., 2019; Sara et al., 2016). Secondly, gyrfalcons and peregrines also have limited overlap in

their distribution in the Nearctic (30%) and Palearctic (10%) (Pokrovsky & Lecomte, 2011). Nonetheless, where they overlap, gyrfalcons are known to occasionally kill adult peregrines or predate their chicks (White et al., 2020). Finally, while information is limited, saker falcons and peregrines compete for nesting sites in regions where their ranges overlap (I. J. Ferguson-Lees, 1963; Prommer & Bagyura, 2018). Sympatric competition thus clearly exists between peregrines and other sympatric falcons; however, the interactions described concern populations in nonurban habitats. Because hierofalcons generally do not occupy urban habitats (Booms et al., 2020; Kemp & Marks, 2020; Leonardi, 2020; Orta et al., 2020), peregrines might be able to avoid competition with these species by moving toward cities.

Competition for nest sites within urban environments may also exist between peregrines and non-raptor species. For example, Egyptian Geese *Aloochen aegyptiaca*, native to the African continent but widespread in Northwestern Europe (Callaghan et al., 2020), have been observed to displace peregrines in Germany by taking over their nest boxes and natural nesting sites (Lindner, 2018). Although Lindner (2019) only mentioned eight displacement events in Germany up to 2017, they acknowledged that their database was incomplete. Thus it remains unclear what the effect of Egyptian geese will be, especially considering their range expansion within Europe (Callaghan et al., 2020), in terms of nest site competition with peregrines.

When considering predation, adult peregrines may be targeted by a variety of larger avian predators, such as owls, eagles, or even gyrfalcons. Specific avian predator species vary depending on the geographical region; for example, Great Horned Owls *Bubo virginianus* is the primary predator in North America, while Eurasian Eagle-owls *Bubo bubo* (hereafter eagle owl) fulfill this role in Europe (Lindner, 2019; White et al., 2020). While nestlings and fledglings of peregrine falcons are susceptible to predation by a wide range of species, the type of predator depends on whether the peregrines nest on the ground. Peregrines nesting on the ground, primarily in the Arctic region, face a high risk of predation by mammals (White et al., 2020). In urban environments, on the other hand, peregrines are typically observed breeding in elevated locations, ruling out mammalian predators as a threat.

A well-studied example of an interspecific interaction is the predation of peregrine nestlings by eagle owls. Since the 1970s, the populations of both eagle owls and peregrines have significantly increased in Europe, leading to an increased likelihood of their encounters owing to overlapping ranges and rising abundances (Lindner, 2019). Lindner (2019) studied a peregrine population in natural habitats in North Rhine-Westphalia, Germany, between 1989 and 2017. Until 1994, there were no eagle owls present; however, from 1995 onward eagle owls started breeding in the area. Between these periods, Lindner (2019) recorded a drop in clutch size from 2.83 to 1.10. Moreover, in Baden-Württemberg, Lindner (2019) reported an increase in peregrine nests on anthropogenic structures (0 - 38%) between 1988 and 2015 and a decrease in nests on rock faces (100 - 62%) during the same period. Lindner (2019) attributed these changes to the increase in the eagle owl population within the same region; unfortunately, no exact numbers were presented. On the other hand, Brambilla et al. (2006) found no effect of eagle owl presence on the productivity of peregrines. Only in areas where both species were found at high density (figure 8) did eagle owls negatively affect the productivity of peregrines (-1.25 ± 0.50 peregrine productivity, $P = 0.026$; Brambilla et al., 2006). Recently, there has been an increase in

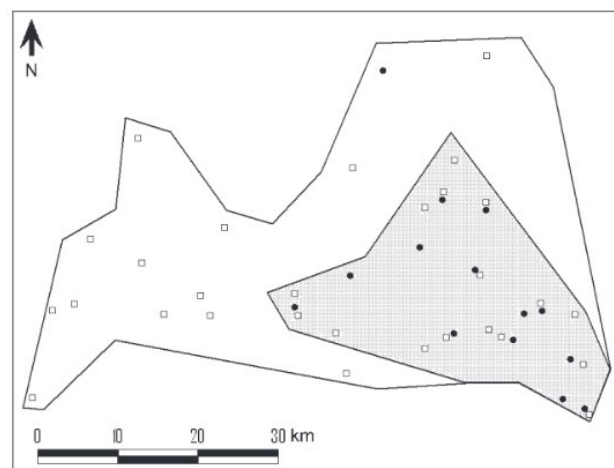


Figure 8: The study area of Brambilla et al. (2006) showing the nests of peregrine (open squares) and the nests of eagle owls (black dots). The shaded polygon is a high-density area. Directly copied from Brambilla et al.,

the eagle owl population and the trend of the species occupying anthropogenic nesting sites, particularly nest boxes, which have been observed across Europe, including Spain, Sweden, Belarus, Austria, Italy, Finland, France, and Russia (Lindner, 2019). How this affects the breeding success and distribution of urban peregrines is yet to be revealed (Kettel et al., 2019; Lindner, 2018). Finally, interspecific interactions do not always have a negative effect on one of the two species. For example, peregrine population density is positively correlated with raven population density (Sergio et al., 2014). Although ravens may predate peregrine nestlings when the parents are not nearby, they do not push back peregrine populations or affect their breeding success in any way (Leonardi, 2020).

Discussion

Habitat selection and the effects of nest sites on the productivity of urban peregrines are in great lines similar to those of peregrines breeding in natural environments. Urban nest sites seem to be mostly selected based on the surrounding habitat, such as water, public parks, gardens, height of buildings, and the height and cover of the nest itself. The latter is similar to the preferred nest site under natural conditions. The diet of urban peregrines includes a wide variety of urban and nonurban species. Peregrines can travel tens of kilometers during foraging flight. Nonetheless, the exact environments where urban peregrines find food remain largely unknown, regardless, prey availability seems higher within urban environments. Additionally, within cities, peregrines may hunt and feed their young at night, presumably assisted by ALAN. Intraspecific competition within urban environments is not yet fully understood. However, the presumed abundance of food may decrease territory size and the number of territorial battles in urban peregrine populations. Finally, in nonurban habitats, strong interspecific interactions exist between peregrines and predatory species such as eagle owls, and how this will evolve in urban habitats is yet to be determined.

The results of this study support the hypothesis that urban habitat conditions significantly influence the population dynamics of Peregrine Falcons *Falco peregrinus* in relation to source-sink populations. The findings show that habitat selection and the effects of nest site on productivity of urban peregrines closely resemble those of peregrines breeding in natural environments. However, urban areas were found to provide higher food availability than nonurban areas, potentially leading to reduced territory sizes and fewer territorial battles among urban peregrines. Despite this, multiple studies have consistently shown that urban peregrine populations rely on immigration from peregrines in natural habitats. Consequently, urban peregrines may be classified as sink populations that cannot sustain themselves without the continuous influx of individuals from source populations in natural habitats.

When comparing the breeding performance of different raptor species in urban landscapes, peregrines do not seem to stand out (Kettel et al., 2018). Falcons as a family (*Falconidae*) have a relatively low probability of a positive response to urbanization (figure 9a), meanwhile, peregrines as a species, based on their bird-dominated diet, should, according to figure 9b, have an increased probability of a positive response to urbanization (Kettel et al., 2018). Meaning that if the general response of peregrines to urbanization can be quantified, this may be used as a model to use the study by Kettel et al. (2018) to predict other raptor species' reactions to urbanization. In future models, the breeding modes, single- or multiple-brooding, and migratory nature of certain subpopulations should be taken into consideration as they may also affect a peregrines' ability to adjust to urbanization (Gahbauer, 2008; Reale & Blair, 2005).

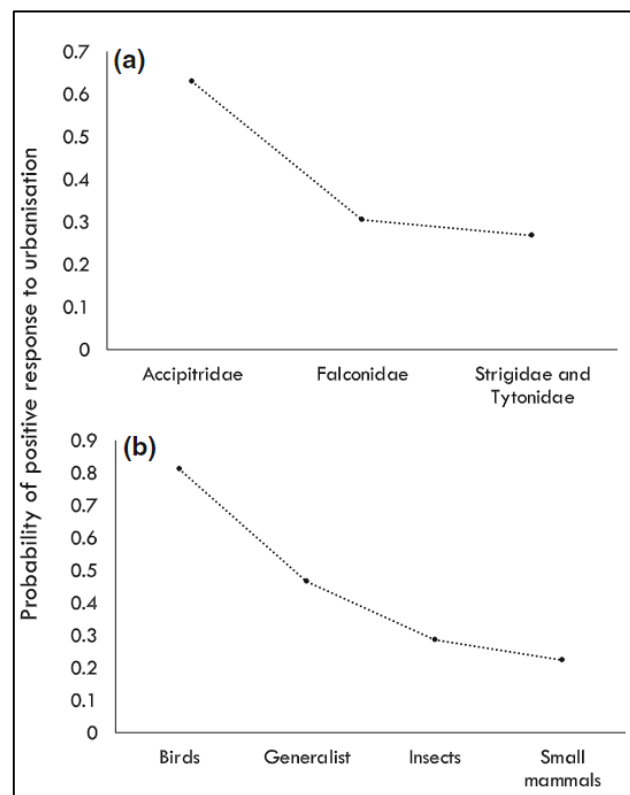


Figure 9: The probabilities of different raptor families (a) and diet-based raptor groups (b) on a positive reproductive response towards urbanization. Based on a meta-analysis of 23 paired-comparison studies of a variety of raptor species from the USA (54%) and Europe (35%). Directly copied from Kettel et al., 2018.

Aside from raptor species, peregrines may also be compared to other species, such as common swifts *Apus apus*, that also once nested mostly in tree holes but nowadays switched in much of its range to breeding in buildings within urban environments (Keller et al., 2020). This could open the doors to more interspecific comparisons of birds and urbanization. The majority of urban bird species are generalist species leading to a loss of functional avian diversity within urbanized habitats (Morelli et al., 2021). Nonetheless, because high buildings and grid structures are homologous to rock faces trees, this may still provide alternative habitats to a wider range of species than previously anticipated. Although some species may benefit from human assistance for nesting sites, such as storks *Ciconia spec* (Kopij, 2017; Yang et al., 2007), others, such as vultures (already urban breeding species on the American and African continents; (Bildstein & Therrien, 2018; Mullié et al., 2017) and smaller species such as rock face breeding rock nuthatches and wallcreepers, may be able to settle within certain gradients of urbanization as well. However, for each of these species, food availability and predation remain crucial elements (Seress & Liker, 2015). Finally, following the strong urbanization nowadays, all species should be thought of when attempting to predict future habitat and distribution.

The peregrine is a well-studied species when it comes to urbanization, nonetheless, knowledge gaps remain, especially when attempting to understand adaptive capabilities. The main shortcomings when it comes to urban peregrines are the understanding of their hunting methods, the degree of interspecific interactions, and finally general understanding of how peregrines would fare if urbanization did not exist. Firstly, understanding where urban peregrines go hunting is a primary knowledge requirement. Currently, it is mostly assumed that all hunting is done within their urban habitat, however, without tracing individuals through for example GPS tags, one can never be certain. This knowledge may be used to understand the absolute importance of urban habitats as hunting grounds. Moreover, within urban areas, more effort should be invested in the effect of urbanization gradients, which strongly affect the abundance of avian species functioning as prey (Crooks et al., 2004; Reale & Blair, 2005), on peregrines. This may also allow for an easier comparison of different urban areas worldwide. Competition and predation-wise, future studies should consider the relative densities of predators of peregrines in urban environments, as seen with eagle owls (Gainzarain et al., 2010), density may strongly influence the interactions with peregrines. Moreover, while these types of predator-prey interactions with peregrines are extensively studied within Europe, it is only sparsely described in North America. Therefore, the European data may be used as a basis to assess the predator-prey situation in North American urban territories. Finally, to understand the plasticity and adaptive capabilities of peregrines, future studies may profit from focusing on more experimental and manipulative approaches (Seress & Liker, 2015), for example by replacing eggs between urban and nonurban environments and following their fates afterward.

The dynamics of sink-source interactions significantly affect avian population dynamics and species distribution by determining the movement of individuals or populations between different habitats. Several studies focusing on urban peregrine populations have observed relatively high clutch sizes and population densities. However, it has been proposed that immigration is the primary driver of urban peregrine populations. This implies that urban areas serve as sink habitats, sustained by the influx of individuals from nonurban source habitats. Given the ongoing process of urbanization and the alterations occurring in nonurban habitats, the important question arises as for how long can nonurban peregrine populations can continue to grow and provide sufficient immigrants to sustain urban populations. Therefore, comprehending the adaptive capabilities of peregrines in relation to the breeding conditions in urban habitats, as described in this study, is crucial. Such understanding may shed light on whether peregrines can establish independent and self-sustaining populations in urban environments.

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Afterword

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