# Behavioural ecology of urban Greylag Geese Anser anser – natural selection in the contemporary European city environment

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#### **Abstract**

The behavioural ecology of urban Greylag Geese Anser anser was reviewed in relation to selective forces or bottlenecks - such as habitat, food availability, predators, disturbance, hunting, diseases and parasites, nest sites and brood rearing areas, and competition with other species - which may act on geese in the contemporary European city environment. Special consideration was given to behavioural changes during winter and moult. Studies to date indicate that urban geese have developed survival and reproduction strategies which sometimes differ from those of geese in other habitats. For instance, they must adapt to a more built-up environment, as additional mortality may arise from collisions caused by flying within confined urban spaces. They are also exposed to urbanised native, introduced and "domestic" predators, such as dogs, to which they show size-related escape responses. Most urban geese adapt to human disturbances, adjusting the intensity of their behavioural response to the perceived danger. Like their rural counterparts, urban geese are also highly selective in their choice of food plants and feeding habitat, although supplementary feeding by people may induce a change in behaviour. There was no evidence that disease or parasite loads are higher for geese in urban than in rural areas. Urban Greylag Geese use a broader range of physical structures for nesting in urban than in rural areas, with some also adopting colonial nesting. Some families moved to new brood-rearing areas immediately post-hatching, elevating reproductive success. Competition with other species was evident at some sites, with Greylag Goose breeding success being inversely related to the local abundance of Egyptian Goose Alopochen aegyptiaca breeding pairs. Although wintry conditions with snow and ice cover may limit food availability and frozen lakes may hinder the ability of largely sedentary urban geese to escape from predators, they appear able to cope with prolonged periods of cold. Urban geese have also demonstrated resilience during their flightless wing moult period. It is unlikely that urban goose populations will grow indefinitely, as density-dependent processes will lead to a stabilisation of the numbers which occur within the boundaries of a given city, although the geese may disperse into surrounding rural areas.

**Key words:** availability of nest sites, competition with other species, diseases, disturbance, food, habitat fragmentation, hunting, parasites, predators, supplementary feeding.

Geese face countless dilemmas in their daily life (Black et al. 2007). Where and when to use particular sites (e.g. for feeding, roosting and nesting), how to avoid predators, which mate to select, and which flock to join for maximum benefit. Individual decisions may influence survival and the number of offspring produced. The sum of these individual decisions can be seen at the population level. For instance, changes in site use may result in goose populations colonising new sites or making major distributional shifts (Black et al. 2007). Compared to those of free-living wild birds, the underlying evolutionary selection pressures on urban avian populations have however received relatively little attention (Shochat 2004). When birds choose to live in new, previously unoccupied environments such as cities, they must adapt their behaviour if they are to thrive under the new selection pressures (Evans et al. 2011). Because these behavioural adaptations have not yet been described for urban geese, the idea of this review was born. In addition to providing a short overview of the history of geese in urban areas, this paper therefore aims to focus on their behavioural ecology, and to complement previous publications on the abundance, distribution, movements or management of urban geese (Adams et al. 2005; Baxter & Hart 2010; Fox 2019). Two sections towards the end of the review

provide evidence for some selective forces limiting urban geese and consider whether observed behavioural changes may be due to phenotypic plasticity or genetic change. Where research gaps exist, they are identified at the end of each section and, in a concluding paragraph, ideas for future research are developed.

#### Methods

Several approaches were adopted on searching the existing scientific literature for studies on the behavioural ecology of urban geese. Comprehensive searches were conducted in Google Scholar, and by consulting books and review articles on avian urban ecology and the behavioural ecology of geese in general. Relevant books on avian urban ecology and reviews on geese are included in the reference section, if applicable. The initial search on Google Scholar used the keywords "urban", "city", "cities", with "goose" and "geese". Subsequently, advanced Google Scholar searches were carried out using the above criteria in combination with the subject terms and their abbreviations: habitat, food, feeding, supplement, predat\*, disturb\*, hunt\*, disease, parasite\*, nest\*, breed\*, competit\*, Egyptian, winter\*, moult\*, population, behavio\*, blastici\* and genet\*. In instances where an excess of irrelevant articles was identified, certain subjects were excluded (e.g. subjects

such as "harassment" and "management"). The articles were then subjected to a thorough review, and only those that offered pertinent comparisons were included in the final compilation. It is acknowledged that non-English literature is likely to be underrepresented; however, where applicable, these sources were also included. When no information on geese was found, other wildfowl were included, especially Mute Swans Cygnus olor and Mallard Anas platyrhynchos.

Further searches were conducted within review articles on specific aspects of behavioural ecology of autochthonous geese (i.e. those native to the areas being considered) and potential bottlenecks which they may face, using the keywords "urban" to identify information "city" potentially missing from the Google Scholar searches. Notably, within Madsen (1991), Madsen et al. (1999) and Fox et al. (2010) for the status and distribution of goose populations western Palaearctic; Owen & Black (1990) for goose ecology; Platteeuw & Henkens (1997) for disturbance; Madsen & Fox (1995) for hunting; Elmberg et al. (2017) for disease transmission in geese and swans; Eichholz & Elmberg (2014) for nest site selection in Holarctic waterfowl; Davis et al. (2014) for habitat and resource use in autumn and winter; Fox et al. (2014) for moult; and Wood et al. (2017) for aggression.

Given the scarcity of articles on the behavioural ecology of urban geese and the bottlenecks they may face, books and reviews on avian urban ecology were also thoroughly searched, for mention of "goose", "geese", "swan", "duck" and "wildfowl" (Gaston 2010; Gil & Brumm 2014; Marzluff et al. 2001, 2008; Marzluff 2017; Møller 2009 for avian urban ecology; Gilbert 1989; Parris 2016 for urban habitat ecology; Bradley & Altizer 2007; Delgado-V & French 2012 for urban wildlife diseases: Koons et al. 2014 for population dynamics; and Møller & Ibáñez-Álamo 2012 for predation). This last search revealed that wildfowl are not usually included in urban bird ecology research.

# Occurrence of geese in urban areas

#### Urbanisation

More than 50% of all humans now live in cities (United Nations 2019) and urban areas are expanding (Colsaet et al. 2018), removing natural habitats for birds at an accelerating pace. The ecologically complex urban areas (Gaston 2010; Parris 2016) can be regarded as testbeds of evolutionary change (Beans 2019). An animal or a plant can either adapt to the new situation or die out (Candolin & Wong 2012), so populations may respond to urbanisation through dispersal away from urban areas or by adaptation to the changing environment through phenotypic plasticity, which may in turn result in genotypic change.

On reviewing studies on avian urban ecology, it is striking that most have been carried out on songbirds (see Croci et al. 2008; Chamberlain et al. 2009; Ryder et al. 2010; Candolin & Wong 2012; Gil & Prumm 2014; Marzluff 2017); studies on non-passeriformes are rarer. They include Feral Pigeons Columba livia domestica (Carlen et al. 2021), Goshawks Accipiter gentilis (Merling de Chapa et al. 2020), Sparrowhawks Accipiter nisus (Thornton et al. 2017), Kestrels

Falco tinnunculus (Riegert et al. 2010), Peregrine Falcons Falco peregrinus (Carlen et al. 2021) and Burrowing Owls Athene cunicularia (Carrete & Tella 2013, 2017). Geese are notably missing from these studies.

# Origin and status of naturalised geese

When introduced animals form selfsustaining populations these are termed "naturalised" (Lever 2005). In Europe, naturalised goose populations are a relatively new phenomenon, starting to appear from the 1930s onwards (Kampe-Persson 2010). Some can be traced back to releases for ornamental purposes or hunting (Owen & Salmon 1988) or have escaped from captivity (Lever 2005; Bauer & Woog 2008). They can occur within or outside of their native (autochthonous) range, sometimes being actively introduced to their original or current range. Naturalised geese are largely missing from reviews of wintering goose populations in Europe (i.e. in Madsen 1991; Madsen et al. 1999; Fox et al. 2010) and no urban populations are mentioned. Kampe-Persson's (2010) review of 69 naturalised goose populations includes 15 Anser and Branta taxa from 13 European countries and reports some high numbers (e.g. the total for naturalised Greylag Geese in Europe was estimated at c. 315,000 individuals), including urban areas. Since that review, naturalised goose populations have expanded further and ring recoveries show that some individuals move from cities to rural areas and vice versa (F. Woog, unpubl. data). In contrast to autochthonous populations, naturalised populations are mostly sedentary and only rarely show long-distance migratory behaviour (Owen & Salmon 1988; Kampe-Perrson 2010); thus they are unable to avoid the severe winter conditions which generally occur in central Europe. In countries where both autochthonous and naturalised populations occur, these are often not differentiated by ornithologists (Clausen et al. 2023), although they behave differently regarding their tameness and migratory behaviour, and in most cases form separate populations. In Britain, some re-introduced Grevlag Geese have mixed with autochthonous ones and can no longer be distinguished from each other (Mitchell et al. 2012). A beginning of such mixing has been documented in Hamburg, northern Germany, where (albeit rarely), sedentary urban Greylag geese join birds passing through on migration (S. Hinrichs, pers. comm.).

This review is primarily of our current understanding of the behavioural ecology of naturalised urban geese, occurring outside their autochthonous range, that form self-sustaining populations (Sol *et al.* 2005).

# Origin of geese in cities

We all are familiar with ducks, geese and swans on park lakes. Some are native (autochthonous); others non-native (referred to as introduced, alien, exotic, adventive, immigrant, foreign or non-indigenous species). Urban waterfowl based on a few released exotic birds usually remain in small populations and never spread far, and thus generally are a more localised, temporary phenomenon (Lever 2005) which are not subject of this review. In contrast, some urban goose populations have increased

considerably and have spread from cities to rural areas, forming self-sustaining, naturalised populations. These may be in areas, where the species was formerly native such as northern Germany, or in areas, such as southern Germany south of the River Main (Kreuziger et al. 2004), that have lacked naturally occurring Greylag Geese since the Eem interglacial period 126,000-115,000 years ago (Hölzinger et al. 2018).

## Urban goose populations

Naturalised Greylag Goose populations are known from many large cities in Europe, for example in Germany from Hamburg (Kreutzkamp 2003), Stuttgart (Woog et al. 2008), Munich (Wüst 1973) and Zwickau (Hässler & Halbauer 2004) and are increasingly spreading to smaller cities. A self-sustaining population of domestic Swan Geese Anser cygnoides exists in Heidelberg, Germany (Randler 2003). Urban Greylag Geese in the Utterslev Mose, Copenhagen, Denmark are autochthonous and partially migratory (Kampp & Preuss 2005), as are urban Barnacle Geese Branta leucopsis in Helsinki, Finland (Väänänen et al. 2011) and in Malmö, Sweden (Bengtsson 2007). Urban Canada Goose Branta canadensis populations have been reported from the UK (in London, Baker & Coleman 2004), New Zealand (Caley 2020) and North America (in Anchorage, York et al. 2000; the Greater Chicago metropolitan area, Dorak et al. 2017; and Connecticut, Conover & Kania 1991). Sub-arctic Canada Goose subspecies have been reported to mix with more southerly urban Canada Goose populations during migration and in winter (see references in Dorak et al. 2017).

# Selective forces affecting urban geese

On considering why geese fare so well in cities, we can compare the different types of selective forces that act on them and how these may influence the survival and reproductive success of individuals, thereby shaping their fitness in evolutionary terms. It is however often difficult to measure these forces, and some considerations may be rather descriptive or even hypothetical, because selective forces not only influence each other, or are part of each other, but they may also act simultaneously. For example, the acquisition of food and selection of feeding sites in birds is related both to the perceived predation risk and the probability of disturbance at that site.

In this review, the following selective forces and factors are taken into account as possible bottlenecks affecting urban goose populations: (1) habitat, (2) food sources and feeding, (3) supplementary feeding, (4) predators, (5) disturbance, (6) hunting, (7) diseases and parasites, (8) nest sites and brood rearing areas, and (9) competition with other species. An overview of studies to date on the behavioural ecology of urban-living wildfowl in relation to the selective forces described above, and also two periods in the annual cycle - winter and moult - that are especially challenging and may change their behaviour considerably, is presented in Table 1. Winter is a strong selective force driving autochthonous goose populations to migrate to areas with milder climate, usually south, in order to avoid ice and snow cover, and the slowing or cessation of above ground primary

**Table 1.** Studies on the behavioural ecology of urban geese, swans and ducks in relation to selective forces. Species codes: GG = Greylag Goose, BG = Barnacle Goose, CG = Canada Goose, SG = Swan Goose, MS = Mute Swan, BS = Black Swan, MA = Mallard. Whether the study was carried out along an urban-rural gradient is indicated (yes, no). Type of population: n = naturalised, a = autochthonous.

Selective force	Species	Species Country	Reference	Gradient	Gradient Population
Habitats & fragmentation	99	Germany	Käßmann & Woog 2007	ou	ü
Food sources and feeding	GG	Denmark	Kampp & Preuss 2005	no	В
	99	Germany	Schwarz 2010; Schwarz & Woog 2012; Woog et al. 2012; Ehret et al. 2020	no	ц
	S	USA	Conover & Kania 1991	yes	п
Supplementary food	GG	Germany	Käßmann & Woog 2008	no	п
	MS	UK	Sears 1989	yes	п
Predators	GG	Germany	Schwarz 2010; Woog & Schwarz 2024	no	п
	SG	Germany	Randler 2003	no	п
Disturbance	GG	Germany	Hohmann & Woog 2021a; Mai et al. 2023	no	ч
	SG	Germany	Randler 2003	no	П
	CG	Belgium	Deboelpaep et al. 2018	no	п
Diseases & parasites	GG	Germany	Woog et al. 2013	yes	и
	GG	Germany	Schmid et al. 2018	no	Ц
	S	USA	Charles-Smith et al. 2014	no	П
	SO	USA	Rutledge et al. 2013	no	п
Nest sites & rearing areas	BG	Finland	Väänänen et al. 2011	no	В
	S	USA	Gosser & Conover 1999	no	п
	SO	USA	Shearer et al. 2022	no	Я

Table 1 (continued).

Competition       GG       Germany       Hohmann &         Winter       GG       Germany       Käßmann &         GG       Germany       Kleinhenz &         MA       Finland       Pulliainen 19         CG       USA       Dorak et al.         MS       Ireland       Keane & O'         Moult       GG       Germany       Schwarz 201         Population limitations       GG       Germany       Mai et al. 20         CG       USA       Balkcom 20         CG       USA       Balkcom 20	Woog 2021b: Mai et al 2022		Gradient ropulation
GG Germany GG Germany MA Finland CG USA MS Ireland GG Germany GG Germany CG USA		no	п
GG Germany MA Finland CG USA MS Ireland GG Germany tion limitations GG Germany CG USA	y Käßmann & Woog 2007	no	п
MA Finland CG USA MS Ireland GG Germany tion limitations GG Germany CG USA	y Kleinhenz & Koenig 2018	no	п
CG USA MS Ireland GG Germany tion limitations GG Germany CG USA CG USA	Pulliainen 1963	no	В
MS Ireland GG Germany tion limitations GG Germany CG USA	Dorak et al. 2017		
GG Germany tion limitations GG Germany CG USA	Keane & O'Halloran 1992	no	п
GG Germany CG USA	y Schwarz 2010; Schwarz & Woog 2012	no	п
USA	y Mai et al. 2022	no	п
VSI1	Balkcom 2010	yes	п
	Guerena et al. 2016; Fontaine et al. 2018	yes/no	n
Genetic adaptation GG Germany Mai et al. 20	y Mai <i>et al.</i> 2023	yes	n
BS Australia Van Donger	ı Van Dongen et al. 2015	yes	В

production. Naturalised geese have not learned migration routes from their parents, and as a result may have to endure difficult winter conditions. Another annual event is moult, when geese replace all their remiges at the same time, which renders them flightless for several weeks and makes them more vulnerable to predation. Consequently, they may restrict feeding to areas near water to enable quick escape from predators. This review therefore considers how urban geese adapt their behaviour during this vulnerable and energy-demanding time.

#### Habitat

Like their rural counterparts, urban geese will congregate where food is plentiful and nutritious, and disturbance is low. In cities, preferred feeding habitats are usually in the larger, continuous parks, linked by water bodies such as lakes, rivers or streams. An important feature is an open grazing area such as short grass park lawns in proximity to the safety of open water, where the birds can retreat from disturbances (Conover & Kania 1991; Schwarz 2010).

In urban environments, large trees, bridges and buildings may hinder the movements of geese between their foraging and roosting habitats, and also their rapid escape flights when under threat. After a panic (e.g. through disturbance by low-flying helicopters, or a free-running dog; Schwarz & Woog 2012), fleeing birds are prone to collisions that can cause injury or mortality, and this may be exacerbated by the higher density of man-made structures in urban environments. In rural areas, collisions with powerlines and hunting mortality are the most frequently recorded causes of death

for swans and geese, respectively (e.g. see the species accounts in Wernham et al. 2002). In contrast, collisions with trees, bridges and houses have been the most important cause of death for adult urban geese in Stuttgart, southwest Germany (48°46'N, 9°10'E; F. Woog, unpubl. data).

In summary, whilst urban geese appear to adapt their behaviour (including use of feeding areas) to the built-up urban environment, some mortality resulting from collisions on flying in narrow urban spaces does occur.

## Food sources and feeding

Food availability affects the distribution of organisms in space and time. An individual's foraging decisions may have a direct effect on its survival and reproductive success (Alcock 2009. For example, arctic-nesting female geese that accumulate more fat lay larger clutches (Ankney & McInnes 1978) and rear more young (Ganter & Cooke 1996; Black et al. 2007). They select feeding sites where plants are high in energy and/or nutrients during the breeding season, with little disturbance or predation (Prop 1991; Black et al. 2007), and at autumn staging and wintering sites they often utilise agricultural crops (Davis et al. 2014; Fox & Abraham 2017; Strong et al. 2021). The same principles should apply for urban geese, but there are few detailed studies.

When looking at a frequently mown park meadow, one can assume that the table is richly laid for urban geese, with re-growth of young shoots high in protein being available almost all year round (Väänänen et al. 2011). Urban geese in Stuttgart are highly selective feeders, not only of plant species but also

the parts of plants ingested, with a study of their diet finding that it consisted of 20% grasses and sedges, 55% herbs, 10% fruit from shrubs and 15% fruit from trees (Hölzinger et al. 2018; Supporting Materials Table S1). Geese grazed most in areas with > 80% grass cover and < 40% herb cover, if in proximity to water (Schwarz & Woog 2012). The diet of urban geese varied seasonally, but also in relation to weather: in wet springs, urban park meadows offer protein-rich grazing areas that are further improved by regular mowing. In hot summers, meadows may dry up and turn brown (Schwarz 2010). As is the case for wild populations (Drent & Prins 1987), this was the time when geese switched from their leaf diet to feed on seeds, stolons, roots and fruit. While excavating subterranean roots is laborious, the energy content is higher than that of grass leaves, making such behaviour profitable (Owen 1972). Switching to roots during drought was also described by Amat (1986) for Greylag Geese wintering in Spain. Feeding on fruits such as cherries, apples, mulberries or plums often coincides with the period of severe drought, when only irrigated park lawns were visited (F. Woog, pers. obs.).

Urban Greylag Geese in Stuttgart exhibited diurnal feeding patterns similar to wild birds, which typically graze in the mornings, rest during midday and feed again in the afternoon (Amat 1986; Owen 1972). This pattern was disrupted when given supplementary food (Käßmann & Woog 2008) or in winter (Käßmann & Woog 2007). They adapted their feeding behaviour (measured as peck rates) to grass height, a pattern commonly found in wild geese (White-fronted Geese: Owen 1972; Barnacle Geese: Ebbinge et al. 1975; Black et al. 1991; Brent Geese Branta bernicla: Bos et al. 2005). Urban Greylag Geese in Stuttgart pecked most quickly in short vegetation (< 4 cm) and more slowly in long vegetation (> 8 cm). Goslings increased their peck rates with age, and parental geese (of both sexes) pecked faster than other adults and juveniles, maybe having to compensate for lost body weight during incubation and associated defence of the nest site during incubation and after hatching. They spend much of their time guarding the goslings (Kotrschal et al. 1993), and may therefore have tocompensate for their lack of foraging time by increasing their food intake rates (Woog et al. 2012).

In summary, urban geese are highly selective in the choice of feeding habitat and their food plants. Their diet varies with seasons. They show similar feeding behaviour to wild birds, regarding their diurnal feeding pattern and their rates of food intake, except when being interrupted by people disturbing them, e.g. by feeding them bread or grain (see below).

# Supplementary feeding

Large scale feeding of grain to wildfowl is practised in some countries to lure birds to safe roosting sites for conservation and education purposes (e.g. Ryley & Bowler 1994) and may increase survival rates, for instance in Whooper Swans Cygnus cygnus (Soriano-Redondo et al. 2023). Baiting for hunting is now restricted or prohibited in many countries (e.g. Sonant & Maestro 2006). Some of the supplementary feeding activities may have brought wildfowl into

cities in the first place. For example, in Finland, overwintering Mallard Anas platyrhynchos rely on food given by man, to the extent that some birds have even stopped taking natural food (Pullianen 1963), and in the UK urban Mute Swans Cygnus olor may also rely on the food provided by humans (Davis et al. 2014). People feeding waterbirds in urban parks probably assume that they are helping the birds to meet their daily energy needs; however, this may not be the case. In Finland, losses of young Mallard have been attributed to people feeding them with grain or bread which cause swelling in their stomachs (Pullianen 1963). Ecologically, bread and grain rotting in the lakes can cause eutrophication and a lake may tip over into a turbid eutrophic state, causing fish deaths. Supplementary feeding also makes waterfowl tame and thus vulnerable to being caught or predated (Sears 1989). It can increase competition for food (Shochat 2004) and may alter the birds' behaviour.

In an urban versus rural comparison of feeding behaviour of Mute Swans, the average percentage of time spent feeding was considerably reduced in areas where people fed bread to the swans (Sears 1989). They even gave up taking natural food, suggesting a behavioural change to prefer bread over all other food sources. Hence, although unlimited grazing on park lawns is available to urban Mute Swans, and they should be able to subsist by grazing with no need of provisions from humans, they preferred bread. Greylag Geese in Munich have likewise been reported as benefitting from supplementary feeding (Kleinhenz & König 2018). Käßmann & Woog (2008)

found that supplementary feeding of bread was a rare event during the average course of a day (during only 3% of behavioural scans) but it was enough to change the daily activity budgets of urban Greylag Geese considerably. When being fed, birds grazed much less (feeding on grass for 40% instead of 67% of the day) but vigilance behaviour doubled (16% versus 8%) and locomotion and agonistic encounters increased. Energetically, deriving food from human supplementary feeding may not pay off for all individuals, because dominant birds are more likely to be successful in accessing food whereas, depending on how the food is distributed, subordinate birds may lose energy by moving around without obtaining any food. This can be especially disadvantageous in winter, when the birds' body reserves are low. Feeding bread also disrupts the natural diurnal feeding pattern of the geese. It was found to change the timing of feeding activity during the day for Greylag Geese in Stuttgart (Käßmann & Woog 2008), and also for Mute Swans in the Republic of Ireland (Keane & Halloran 1992).

In summary, supplementary feeding in an urban setting may change the behaviour of geese and other wildfowl considerably, and be energetically unfavourable to low-ranking birds especially in winter.

#### **Predators**

Predators may take eggs, young or adult geese. It is difficult to study anti-predator behaviour in wild geese because most predator-prey interactions are reported anecdotally rather than being systematically recorded, and actual predation is rarely witnessed. In urban areas goslings are

known to have been taken by large gull species Larus sp., crows Corvus sp., Northern Pike Esox lucius and catfish (Order: Siluriformes) (S. Sorge, pers. comm.), but the annual proportion of the population depredated again is usually unknown. It is often claimed that the main advantage of cities is their lower predator density, which leads to higher reproduction rates and survival (Shochat 2004; Fox 2019; Møller & Ibáñez-Álamo 2012). The situation, however, is more complicated. For example, in the Neotropics, native bird species often decline because predation is higher in urban areas (Friesen et al. 1995). In Europe, predatory Red Foxes Vulpes vulpes (Wandeler 2003) and introduced Racoons Procyon lotor (Stope 2023) have themselves become urbanised. Sorace (2002) reported that the density of predators such as foxes and dogs was higher in urban parks than at rural sites. Whereas night-active foxes are difficult to study, dogs are a good species to investigate responses of geese towards this potential predator. Dogs caused the most pronounced flight reaction in Greylag Geese at Lake Neusiedl, Austria, compared to people without dogs (Steiner & Parz-Gollner 2003). Based on their responses, urban Greylag Geese in Stuttgart were able to distinguish between different sizes of dogs and whether dogs were on a lead (Woog & Schwarz 2024). The Stuttgart geese reacted to larger dogs at larger distances, as did urban Swan Geese in Heidelberg, southwest Germany (Randler 2003), which is perhaps not surprising because large dogs resemble foxes or Grey Wolves Canis lupus which are natural predators of geese. Dogs show a wide

variety of behaviours towards the geese including barking, chasing or killing of geese. Such unpredictable behaviour may also prevent habituation.

In summary, urban geese are confronted with urbanised native and introduced predators and a high density of domestic predators such as dogs. We can rarely witness direct interactions between predators and geese, but they seem to be able to adapt their flight distance to the risk level exhibited by the disturbance, such as being able to distinguish between dogs of different sizes. Humans without dogs are not seen as a threat (Woog & Schwarz 2024).

#### Disturbance

When disturbed by humans, waterbirds may stop feeding, spend more time alert, or eventually leave an area by walking or flying away, all of which are energetically costly. To compensate for these different levels of energy loss birds have to feed more, which may reduce the carrying capacity of their feeding habitat if disturbance levels are elevated (Platteeuw & Henkens 1997). Many studies of disturbance to wildfowl have been carried out in the wild (e.g. Béchet et al. 2004; Laursen et al. 2005; Wang et al. 2022), but only a few in urban settings.

When settling in the city, animals may perceive humans, their dogs, lawn mowers or other traffic as a new form of predation risk (Fernandez-Juricic & Jokimäki 2001; Blumstein 2014). On comparing disturbance tolerances at urban versus rural sites for different waterfowl species, Donaldson et al. (2007) however found that ducks, geese and swans in rural areas reacted more often and more strongly towards humans, while at the

urban sites they reacted less frequently, probably because they were more habituated to them. Indeed, a higher tolerance for anthropogenic disturbance may be necessary for animals living in cities to thrive (Møller 2009). Human disturbance can reduce breeding success in Greylag Geese (Giles 1992 in Allan *et al.* 1995); *e.g.* by frequently preventing females from brooding small goslings, which could elevate gosling mortality (Sorge 2022) and can therefore be regarded as an important selective force.

Naturalised geese are not tame per se, but some urban geese completely lose their fear of people. Not all individuals show the same degree of tameness and there is a large variation in individual responses (e.g. C. Wittor, unpubl. data on individual flight distances in relation to age, sex and condition). Studies of urban goose behaviour in relation to human disturbance, conducted on several species illustrate this point (e.g. Schwarz 2010 on Greylag Geese; Hohmann & Woog 2021a,b on Greylag and Egyptian Geese; Randler 2003 on domesticated Swan Geese: Deboelpaep et al. 2018 on Canada Geese). Newly-established urban Egyptian Geese reacted at much greater distances and more intensively to almost all disturbance stimuli (i.e. pedestrians, joggers, bicycles, Nordic walkers, people with buggy, children, cars, supplementary feeding and dogs) than Greylag Geese. Both species exhibited the greatest response (i.e. were alerted or displaced at greater distances) when disturbed by dogs (Hohmann & Woog 2021a).

There is a large body of standardised research on alert and flight initiation distances (ADs and FIDs) comparing escape behaviour along rural-urban gradients or between rural and urban areas (Blumstein 2014; Møller & Ibáñez-Álamo 2012). Among waterfowl, only Black Swans Cygnus atratus and Greylag Geese have been investigated on an individual level (Van Dongen et al. 2015; Mai et al. 2023). Both species showed a much higher AD and FID in rural areas than in urban areas, indicating that they have adapted the intensity of their behavioural response to the perceived danger. More data are needed to better understand how individual geese change their alert behaviour in relation to urban habitat, and if the observed differences may be related to other factors such as their personality traits.

In summary, urban geese are exposed to a great number of disturbances caused by humans but most individuals can adjust the intensity of their behavioural response to the perceived danger. Standardised tests of escape responses show much higher escape distances among rural compared to urban geese. Species-specific escape responses need further study, especially for a comparison of urban and rural sites.

# Hunting

Hunting affects goose populations directly through killing and indirectly through shooting disturbance up to the flyway scale (Madsen & Fox 1995; Adam et al. 2016). In addition to hunting mortality, movements of individuals in response to hunting may lead to a reduction in the time spent feeding as well as displacement from good quality and safe feeding sites, which in turn may result in poorer body condition and higher predation risk, which can have an effect at the

population level. In naturalised Greylag Geese in the UK, hunting reduced the number of pairs which bred the following year (Giles & Street 1990 in Allan et al. 1995).

Geese are known to concentrate in areas with low shooting intensities (Madsen 1986). The hunting season for most wildfowl is autumn and winter, so urban areas may become especially attractive to wildfowl during this time, as hunting is usually prohibited in public parks because of human safety issues. Although much is known about the redistribution of waterbirds after hunting in agricultural areas (reviewed by Madsen & Fox 1995), studies of the effects of hunting on geese using urban areas are missing, although there are indications for shifts. For instance, after goose hunts at the private Schloss Monrepos golf course in Ludwigsburg, near Stuttgart, the geese flew to a nature reserve and did not return before the next breeding season (U. Rühl, pers. comm.), and Greylag Geese in Bavaria flew from Lake Altmühl to the city of Munich at the beginning of August, which coincides with the start of the hunting season (Kleinhenz & König 2018).

In summary, hunting disturbance is absent or very low in cities. Cities may serve as a refuge for rural geese during the hunting season, but this needs further study.

# Diseases and parasites

Environmental change due to urbanisation influences the complicated interplay between bird hosts, parasite vectors and pathogens (reviewed by Bradley & Altizer 2006). Some disease outbreaks in wildfowl cause high mortality in the affected populations (Wobeser 2007). Parasites rarely kill birds but may lower their reproductive success and survival (Barber & Dingemanse 2010), and birds may infect each other through droplet infection or faeces if they contain pathogenic bacteria or parasites (Elmberg et al. 2017). In addition to the effects of these pathogens on wildlife, infection through goose droppings has been of human health concern, especially in urban areas (Fallacara et al. 2001). Whereas parasites are often very host-specific and thus unlikely to harm humans (Elmberg et al. 2017; Fischer et al. 2023), some bacteria may, in rare cases, be harmful to humans and poultry (Feare et al. 1999). Out of 169 citations in a review on wildlife diseases (Elmberg et al. 2017) only two considered urban or suburban geese (1.2%), which concerned Canada Geese in the USA (Rutledge et al. 2013; Charles-Smith et al. 2014). In their reviews of urbanisation and the ecology of wildlife diseases, neither Bradley & Altizer (2007) nor Delgado-V & French (2012) mentioned ducks, geese or swans. Hence, except for a few exceptions described below, our knowledge of disease and parasites in urban wildfowl is limited.

In Munich, ectoparasites such as ticks often infect introduced Canada and Barnacle Goose goslings (S. Sorge, pers. comm.). In Stuttgart, Woog et al. (2013) found seven endoparasite taxa in Greylag Goose droppings (Nematoda: Amidostomum anseris, Cyathostoma, Trichostrongylus, Capillaria, Syngamus trachea; Cestoda: Cestodea; Protozoa: Eimeria). Endoparasite prevalence was low in the inner city but was most pronounced at a suburban lake where geese aggregate during moult and varied seasonally, being highest in winter (Woog et al. 2013).

Prevalence of low pathogenic avian influenza was low; only 60 out of 8,224 faecal swabs of ringed individuals tested positive (2007-2023; F. Woog, unpubl. data). Although Greylag Geese are very much associated with water, where avian malaria vectors such as mosquitoes Culicidae sp. or Black Flies Simuliidae sp. occur, out of 143 blood samples only one female was tested positive for avian malaria (Schmid et al. 2018). Similarly, only 3% of nonmigratory Canada Geese in North Carolina, USA showed an infection with Haemoproteus sp. (Charles-Smith et al. 2014). Low avian malaria prevalence was also found in a whole array of other bird species associated with water (waders: Yohannes et al. 2009; Soares et al. 2016; gulls: Krams et al. 2012) and this may be an adaptation to an aquatic lifestyle.

In summary, we know surprisingly little about the incidence of diseases and parasites of wildfowl in the city, or how they vary between individuals. So far there is no evidence that diseases are more frequent in the city compared to rural sites or that parasite loads would be higher in city environments. Given their close proximity to people, however, obtaining a greater understanding of the diseases of birds in urban environments is important for ensuring, with the highly pathogenic avian influenza (HPAI) epidemics in mind, that any risk of transmission to other birds and humans can be addressed and does not become of concern.

#### Nest sites and brood rearing areas

In their review on nest site selection in waterfowl, Eichholz & Elmberg (2014) do

not consider urban nest site selection. To avoid predation, most urban geese do well by nesting on islands, with some nesting in reed-beds or on elevated structures (Hölzinger et al. 2018; Väänänen et al. 2011). In resident Canada Geese, production of young was limited by the availability of insular nesting sites: although hatching rates were similar, mainland nesting geese had fewer young on average (Gosser & Conover 1999).

When population density increases and nest sites become rare, urban geese become rather inventive in their choice of nesting site. Firstly, they may lose aggressiveness and adopt a more colonial nesting style (Mai et al. 2022). Secondly, birds that do not find their own nest site may possibly dump eggs in other Greylag Goose nests, as shown by Kruckenberg (2019) for rural Greylag Geese, although no data on this behaviour or its frequency was found for cities. Thirdly geese may use unusual nest sites such as heron nests, tree stumps, garbage bins or rooftops of small houses (H. Haag & F. Woog, unpubl. data). In Hamburg, they even nest on high roof terraces, > 25 m above ground, from which the goslings cannot disperse without human help (Hinrichs et al. 2025), and in Indiana USA Canada Geese also used rooftops for nesting (Shearer et al. 2022). In Stuttgart, when the density of nests increased on the suburban breeding islands, a proportion of parental birds left the nesting areas with their day-old goslings to move to brood rearing areas in the inner-city parks 4 km away (Mai et al. 2022). Dropping densities (Schwarz & Woog 2012) and disturbances (Hohmann & Woog 2021a) were higher at

the suburban site, so dispersing families may have avoided grazing competition and disturbance. Changing sites to a less disturbed area for brood rearing increased hatchling survival (Mai et al. 2022). Such dispersal behaviour between nest sites and brood rearing areas is known for other urban Greylag Geese - in Munich (S. Sorge, pers. comm.) and Hamburg (S. Hinrichs, pers. comm.) - and also for several goose species in the wild. For example, Lesser Snow Geese Anser caerulescens caerulescens moved up to 50 km from their nests to brood rearing areas after overcrowding at the nest sites created poor local feeding conditions. Dispersing pairs had higher reproductive success (Cooch et al. 1993), just as in the case of the urban Greylag Geese.

The timing of nesting by urban geese was related to the severity of winter: after a cold winter breeding was delayed by about a month (Stuttgart: Käßmann & Woog 2007), whereas after a mild winter it advanced to January (Hamburg: Kreutzkamp 2003).

In summary, urban Greylag Geese use a wider spectrum of physical structures for nesting compared to their rural counterparts. At high nesting densities, they become more colonial in their nesting behaviour. Some families disperse to more distant brood-rearing areas once the goslings have hatched, which enhances their reproductive success.

# Competition with other wildfowl

Sharing similar habitats may result in interspecific competition between waterbird species for food and/or nest sites. In cities, bird species may interact that: a) would never have met under "natural" circumstances,

and b) coexist under very different conditions than would occur in the wild. Urban geese, swans and shelducks Tadorna sp. all feed on grasslands and may compete for this resource, but studies are lacking. In Stuttgart, some degree of spatial separation was observed, where Greylag and Egyptian Geese often form separate feeding and roosting flocks (F. Woog, unpubl. data).

Invasive Egyptian Geese could be potential competitors of urban Greylag Geese for nest sites, although Greylag Geese are usually dominant over Egyptian Geese and exclude them vigorously from their nesting areas (Hohmann & Woog 2021b). Because Egyptian Geese are mainly treenesting in Stuttgart, and Greylags rarely do so, Egyptian Geese evade competition by their more flexible nest site selection. Over a 17-year period, however, there's been a negative association between number of breeding pairs of Egyptian Goose in Stuttgart and the number of goslings fledged per Greylag Goose pair, indicative of density dependence (Mai et al. 2022).

In summary, studies on the competition for urban feeding and nest sites between similarly sized wildfowl are lacking. Some spatial separation can be observed, which may reduce competition, but adverse density effects of Egyptian Geese on Greylag Geese fitness suggest that fitness consequences can occur. The processes involved require further study.

#### Seasonal limitations

#### Winter

Deep snow and sub-zero temperatures deny many waterbird species of food and cause

depletion of body fat stores as they attempt to meet thermoregulatory demands (Canada Geese: Lefebre & Raveling 1967; Barnacle Geese: Owen et al. 1992; diving ducks: Kestenholz 1994; Madsen & Fox 1995). Prolonged sub-zero temperatures cause cessation of vegetation growth, and the digestibility of food plants and their energy content are typically lower than in other seasons. Reduced food availability influences the foraging behaviour and movements of geese (Owen 1972). While studies on the winter ecology of various Arctic goose species in Europe are plentiful (e.g. Bergmann 1999; Stahl 2001; Borbach-Jaene & Kruckenberg 2002; Black et al. 2007; Harrison et al. 2018), little is known how sedentary, urban goose species deal with winter (Käßmann & Woog 2007; Dorak et al. 2017). Many native goose populations are doing well in winter, as they increasingly utilise agricultural crops which are high in energy for feeding (Fox & Abraham 2017), and climate warming is enabling them to reduce their migration distances (Ramo et al. 2015), but how urban geese respond to winter conditions is relatively poorly understood.

As naturalised goose populations in Europe are usually residential and do not show long-distance migration (Kampe-Persson 2010), naturalised urban geese could find themselves in an ecological trap, where winter conditions impose severe fitness costs. On the other hand, by not migrating, urban geese avoid energy expenditure and mortality. During wintry conditions, urban Greylag Geese in Stuttgart changed their activity budgets, feeding behaviour and abdominal fat stores (Käßmann & Woog 2007). Here frequent

snowfall resulted in a persistent snow cover and frozen lakes, but the limited food availability did not result in Grevlag Geese moving further south to snow- or ice-free locations. Instead, the birds changed their daily feeding patterns, reducing their feeding time from 66% to 42% with an increase in loafing from 14% to 41%, probably resulting in a lower food intake and a subsequent loss of abdominal fat stores. In overwintering Canada Geese in the Greater Chicago Metropolitan Area (GCMA), both snow depth and minimum daily temperatures were similarly associated with decreased movement distances within habitats and an increase in loafing (Dorak et al. 2017). When park lakes freeze, the geese in Stuttgart relocate to an ice-free river for roosting. Wintering Canada Geese likewise stayed in the GCMA, seeking warmer places within the city such as roofs of industrial buildings or yards and warm water discharge areas along a canal to aid thermoregulation; they sought thermal refuge especially on black rooftops, with as many as 450 individuals occupying a rooftop at one time (Dorak et al. 2017). In Stuttgart, diurnal feeding routines of Greylag Geese changed completely during cold spells. Like Greylag Geese wintering in Spain (Amat 1986), urban geese grazed in the mornings and in the evenings. In Stuttgart, when it was cold, geese loafed until midday and only started feeding when higher temperatures made the snow more penetrable. They dug holes into the snow and fed on the grass underneath, sometimes right underneath their bodies where they had been roosting. On average, peck rates were much slower when snow was present (Käßmann & Woog

2007). Birds lost weight (as measured by their abdominal profile indices; Zillich & Black 2002) during wintry conditions, and this was visible within a few weeks after snowfall or freezing of the lakes. Such quick changes have been reported for other goose species (Zillich & Black 2002). Although there was hardly any food towards the end of winter, females managed to gain weight, presumably to accumulate energy for egg formation. A very similar weight gain was observed in a spring study even in unpaired females and appears to be endogenously driven (Ehret et al. 2020). In a semi-tame flock in Grünau, Austria, reproductive success increased with average annual temperature, and laying dates were advanced when winters were milder (Frigerio et al. 2021). This needs further studies in urban areas.

Mortality attributable to severe wintry conditions was not reported for Greylag and Canada Geese remaining in the urban areas (F. Woog, unpubl. data; Dorak et al. 2017) but only 48% Canada Geese that left the urban area survived, with all mortality due to hunting (Dorak et al. 2017).

In summary, it appears that sedentary geese can deal with wintry conditions well, and females may even put on weight towards the end of winter, at a time when there is still very little plant growth. It appears that geese have found mechanisms to overcome even prolonged cold periods without obvious fitness costs.

#### Moult

Most wildfowl species become flightless for several weeks each year, on shedding their primary and secondary flight feathers, with

moult by parent geese scheduled so that the adults can fly by the time that their young become fledged (Owen & Black 1990). In Greylag Geese the flightless period lasts up to five weeks (Lebret & Timmerman 1968), during which period the behaviour and ecology of geese changes (Kahlert 2006). For example, Greylag Geese moulting on the island of Saltholm in Denmark foraged closer to water than when able to fly, which enabled them to escape quickly from predators (Fox & Kahlert 2000; Kahlert 2006). This adaptability of the geese may be a reason why mortality was not elevated during moult (Fox et al. 2014). During moult, urban geese similarly foraged closer to the water's edge than outside the moulting season (Schwarz & Woog 2012), which reduced the height of vegetation close to the water, potentially causing the birds nutritional stress during an energy demanding process. During moult, the geese in Stuttgart rarely ventured more than 30 m from the water's edge (Schwarz & Woog 2012). In comparison, moulting Pink-footed Geese in Greenland ventured 200-220 m (Madsen & Mortensen 1987) and the Greylags moulting on Saltholm up to 150 m from water (Fox & Kahlert 2000). Stuttgart's city parks are laid out as English gardens with large trees in meadows, making them more enclosed by vegetation compared to open Arctic habitats, so the geese cannot see far. This, combined with more disturbances from a range of different sources, may explain why urban geese use a much smaller feeding area during moult.

Little is known about the criteria that geese use to choose moulting habitats but presumably most waterfowl species moult in relatively undisturbed locations (Fox et al. 2014). This does obviously not apply to geese moulting in urban areas because disturbances are frequent and diverse.

In summary, urban geese adapted well during their flightless time. They may be under more nutritional stress as their foraging area is much reduced compared to the non-moulting season. Whether urban geese show behavioural or physiological adaptations to compensate for this lack of access to food needs further study.

# Population limitations

In wild and urban populations alike, a high population density can give rise to competition for territories and mates, as well as for limited and increasingly depleted food sources (Sutherland & Parker 1985). It can also affect the rates of pathogen transmission and the functional responses of interspecific competitors or predators (Koons et al. 2014). To identify how successful birds are in the city, we should evaluate their individual reproductive success and survival in relation to the selective pressures mentioned in this article. This requires long-term data on individually marked geese measured in combination with the selective factors, which are rarely available. To identify such factors that may limit reproductive success of urban geese, Mai et al. (2022) found that in Stuttgart, over a 17-year period, the number of surviving goslings per brood decreased with increased population size and an increasing number of breeding pairs of both Greylag and Egyptian Geese. More goslings survived from broods that dispersed from their initial nesting area to rear their young somewhere

else. Larger broods had higher survival rates fledging and reproductive success increased with the number of times a pair had bred together but decreased with age in this resident population. However, the authors were unable to show if the observed patterns were due to urbanisation, because comparisons with rural sites were not undertaken. Elsewhere, in Hamburg, the reproductive success of urban Greylag Geese similarly decreased with an increasing population size (Mendel 2018). Mean Canada Goose reproductive success (Guerena et al. 2016) and survival rates were higher among birds living in urban areas than those in rural areas, the latter largely attributable to lower shooting pressure (Balkcom 2010; Dorak et al. 2017). Such comparisons are largely missing for urban goose populations in Europe.

In summary, urban goose populations do not grow indefinitely but density dependent processes will lead to a stabilisation of the population at a certain level. Competing species may interact regarding their reproductive success, but more data are needed on this.

# Behavioural changes due to phenotypic plasticity or genetic change?

In cities, behavioural changes cannot always be explained by phenotypic plasticity alone (i.e. an individual changing its behaviour in relation to its environment, for instance by habituation), but may also be an adaptation through micro-evolutionary processes (Vincze et al. 2016; Miranda et al. 2013; Møller 2014) or site selection (Carrete &

Tella 2010). This would mean that natural selection should favour tamer individuals in cities with a lower fear threshold (Samia et al. 2017). In Burrowing Owls it has been hypothesised that birds may distribute across breeding sites depending on their individual susceptibility to human disturbance (with tolerant birds using urban areas and less tolerant birds preferring rural sites; Carrete & Tella 2017) and that this may be heritable (Carrete et al. 2016). Genetic differences have been shown to influence behavioural variation and there is evidence for a genetic inheritance of personality traits (Van Oers & Sinn 2013). Personality differences in captive Barnacle Geese were revealed in novel object tests: some birds were more shy, others more exploratory, and this correlated with their leadership scores (Kurvers et al. 2009).

Regarding wildfowl, only two studies have so far tried to resolve whether the changes in behaviour we see in urban birds are due to phenotypic changes or have a genetic component maybe in the form of personality traits (Van Dongen et al. 2015; Mai et al. 2023). A good candidate gene to study tameness is the dopamine 4 receptor gene (DRD4) as the dopaminergic system controls fear among other functions. In Great Tits Parus major, it was related to novelty seeking and explorative behaviour (Fidler et al. 2007; Timm et al. 2019) and in Blue Tits Cyanistes caeruleus to escape behaviour (Kluen et al. 2012). Van Dongen et al. 2015 showed polymorphisms of this gene along a rural-urban gradient in relation to escape behaviour (FIDs) of Black Swans. Birds with the most common genotype were tamer and occurred at the more urban sites.

whereas more wary birds in rural areas showed the less common genotypes. Similarly, in urban Greylag Geese, DRD4 allele frequencies varied between urban and rural sites and autochthonous populations (Mai et al. 2023).

In summary, it appears that geese and swans may show some genetic predisposition where they occur along an urban-rural gradient, and that this may be linked to their tolerance toward human disturbance. More studies are however needed to be able to distinguish personality effects from habituation.

# Research gaps

Our knowledge of Arctic migratory geese is far greater than that of naturalised populations, and there are even fewer studies of urban geese. Considering that most people live in cities, this bias may be due to a lack of interest by goose researchers rather than to their societal relevance. On the other hand, the field of avian urban ecology has so far not considered wildfowl, albeit that they might provide a rather useful system to study. For example, individual differences in stress levels may be of key importance which may become visible in the endocrine system (Buchanan & Partecke 2012), haematology (Frigerio et al. 2017) or physiological metrics, such as heart rates (Wascher 2022). In songbirds, there was a corticosterone gradient between urban and rural sites (Zhang et al. 2011), with urban birds having higher stress levels. In geese, this could easily be investigated using a non-invasive method to study hormone levels in goose droppings (Kotrschal et al. 2000). For

instance, more innovative Greylag Geese excreted more corticosterone than less innovative individuals (Pfeffer et al. 2002). Could it be that more innovative geese survive and reproduce better in urban environments? Urban geese had lower alert and flight initiation distances as their rural counterparts (Mai et al. 2023) which may be an indication that physiologically, they are more resilient towards human disturbance and as a result allocate more time for feeding than geese not showing similar responses. As a result, their energy deposits should be higher, for subsequent investment in breeding, as has been shown for songbirds (Møller 2014). More studies are needed on this topic in non-passerine birds such as geese.

Chamberlain et al. (2009) reviewed avian productivity in urban landscapes. They found that urban passeriform birds lay earlier than rural ones, have a lower clutch size, a lower nestling weight and lower fledging success. Early nesting in Canada Geese correlated positively with both hatching and fledging success (Johnson & Sibly 1993) and pre-fledging survival (Fontaine et al. 2018), and a similar pattern was found for urban Greylag Geese in Hamburg (Mendel 2018). It would be interesting to compare several urban goose populations and their rural counterparts regarding the timing of nesting along climatic and latitudinal gradients.

On a more applied level, we need more published information on urban wildfowl populations, so that they can be included in a much-needed follow-up to the Kampe-Persson (2010) review of naturalised and urban goose populations in Europe. Regular monitoring of population sizes and reproductive success is of course the basis for further research, but it is only through ringing that we can understand the decisions made by individuals. The re-sightings of geese ringed in and around urban areas provide valuable information about the exchange of urban populations with the surrounding countryside and also refine data on reproductive success and survival. For ring reading and coordinated data collection by volunteers, it should be possible to enter ring readings and associations data (such as pair status, age) directly into E-bird or the national online databases. Finally, existing data on urban geese needs to be published and could be combined from different cities enabling the analysis of larger data sets, with the prerequisite that standardised data collection methods are in place.

#### Conclusion

Urban geese do interesting things. This review provides evidence that they readily adapt to urban conditions and deal with differences in selective pressures or bottlenecks. By applying some of the methodology used in urban avian ecology, many more questions on these versatile birds could be answered. So far, few goose researchers have paid attention to urban geese, whilst the ever-growing field of avian urban ecology has so far not considered wildfowl. It would be very fruitful to combine these two fields of research.

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