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**Adapting to high life: morphological changes in the
recently urbanized, endangered nominate Lesser Black-
backed Gull (*Larus fuscus fuscus*)**

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Abstract

The rapid urbanization is referred to as the largest threat to wildlife besides climate change. As the urban areas continue to expand worldwide, animals are forced to move to other areas or adapt to the built-up habitats. The adaptation to new environment can sometimes lead to morphological changes between the urban and rural animal populations. Of all animal groups gulls, in particular, have been successful in colonizing urban areas and various gull species have started to nest in cities. In Finland this phenomenon has also occurred in the largest urban areas of the country and at present most of the Finnish gull species nest or feed in the cities. Among the urban gull species is the endangered nominate Lesser Black-backed Gull (*Larus fuscus fuscus*), which has declined in numbers throughout the species range since the 1970s. However, it seems that Lesser Black-backed Gull thrives in urban areas and contrary to this species' decline in its natural habitats, the Lesser Black-backed Gull has notably increased its numbers in cities. In this thesis I studied the morphological changes in urban Lesser Black-backed Gulls by measuring study skins and comparing the morphological measures and plumage patterns between urban and rural individuals. Based on the results, there were only slight differences between the size of urban and rural individuals and apparently no differences in plumage patterns. However, the sexual dimorphism in urban gulls seemed to have reduced and the two sexes were more difficult to distinguish from each other by morphological measures.

Key words: animal urbanization, nominate lesser black-backed gull, morphology, sexual dimorphism

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1. Introduction

1.1. Animal urbanization

Over half of the global human population today lives in towns and cities, and urban areas are the most rapidly expanding land cover type on Earth (Anderies et al. 2007; Evans et al. 2009; Johnson & Munshi-South 2017; Isaksson 2018). In general urbanization alters both biotic and abiotic factors present in the environment, but the magnitude of the impact differs depending on the size, density and age of the urban area (Johnson & Munshi-South 2017). Urbanization is often referred to as the largest threat to wildlife besides climate change (Isaksson 2018). However, more and more species have started to adapt to the built-up environment and to colonize urban areas successfully (Anderies et al. 2007; Evans et al. 2009; Isaksson 2018).

Habitat-wise urban areas differ greatly from other environments, even from adjacent rural areas (Anderies et al. 2007; Evans et al. 2009). The most obvious difference is the huge land transformation, in which most of the natural vegetation has been wiped out and replaced with different types of anthropogenic structures and the soil covered with impervious surface (Hooke et al. 2012; Shanahan et al. 2014; Johnson & Munshi-South 2017; Isaksson 2018). The few green areas appear in contrived and isolated patches, thus making urban areas heavily fragmented landscapes in general (Shanahan et al. 2014; Isaksson 2018).

In addition to land transformation, typical features of urban areas include extremely high food resource abundance, increased air, noise and light pollution, relatively lower predation pressure and warmer climate (Anderies et al. 2007; Rizwan et al. 2008; Johnson & Munshi-South 2017; Isaksson 2018). Since the total food abundance in urban areas can be up to four times greater than in rural areas, urban animal population are rarely bottom-up (resource) controlled (Rodewald & Shustack 2008; Shochat et al. 2010). Many studies suggest that urban animals are not top-down (predator) controlled either, as the number of predators is often lower in urban than in rural areas (Anderies et al. 2007; Shochat et al. 2010). The subject of predation pressure is, however, still under debate, as some studies claim that the abundance of domestic predators such as cats may in fact elevate the predation volume to match that of rural habitats (Anderies et al. 2007; Shanahan et al. 2014; Kauhala et al. 2015). The high

population densities of prey species seem to support the hypothesis that urban areas are safer environments, as do the manipulative experiments in which the removal of few predation species had only a minor effect on the abundance of prey populations (Shochat et al. 2010).

The warmer climate in urban areas is due to the effect known as Urban Heat Island, caused by the combination of low-albedo surfaces that absorb the heat and air pollution that traps the heat irradiation within the atmosphere (Rizwan et al. 2008; Isaksson 2018). Thus, urban areas experience higher temperatures and, especially in northern temperate regions, extended plant-growing season compared to adjacent natural habitats (Evans et al. 2009; Isaksson 2018).

The differences in the several ecological aspects result in urban environment having different selection pressures than other habitats (Liker et al. 2008; Lowry et al. 2012). Urban areas are legitimately novel ecosystems, since they are human-made habitats with species abundance and composition different to any other biome (Hobbs et al. 2006; Johnson & Munshi-South 2017). In fact, urban areas around the globe resemble each other more than they resemble any of their adjacent natural habitats (Shanahan et al. 2014). Animals face challenge, as they have to either adapt to the novel ecosystem, or abandon it and move to other areas (Johnson & Munshi-South 2017; Isaksson 2018).

Only a small percentage of species have the prerequisites to thrive in the heavily human-influenced environment, and thus the species composition in urban areas differs strikingly from rural areas (Lowry et al. 2012; Isaksson 2018). The overall species richness of major taxonomic groups usually decreases with urbanization due to the loss of suitable habitat and resources (Marzluff 2001; Evans et al. 2009; Shochat et al. 2010; Isaksson 2018). At least in some urban areas the loss of species diversity is also linked to a relative high number of invasive native and introduced species, which dominate the resources and out-compete other species (Evans et al. 2009; Shochat et al. 2010; Johnson & Munshi-South 2017).

On the losing side are species with specialized habitat requirements and those in need of vast territories (Evans et al. 2009; Shanahan et al. 2014). Also, species inhabiting complex vegetation structures such as forest specialists are generally unable to settle in built-up environments (Evans et al. 2009; Shanahan et al. 2014). Even though there are vegetated

patches found within urban area, these habitats are usually surrounded by roads and buildings that act as barriers for animals making it difficult for many species to disperse between the green areas (Shanahan et al. 2014; Isaksson 2018). The increased habitat fragmentation in urban areas reduces the phylogenetic diversity within animal communities (Shanahan et al. 2014; Johnson & Munshi-South 2017), which in turn can make the urban animal populations more vulnerable for various threats or sudden changes.

The species that flourish in urban environment are usually characterized by high behavioural flexibility, tolerance for elevated stress and disturbance levels and overall versatility in foraging methods, diet and breeding (Lowry et al. 2012; Johnson & Munshi-South et al. 2017). A common pattern for urban environment is that the system is dominated by only a few species, but the species present show significantly high population densities (Liker et al. 2008, Shochat et al. 2010; Rodewald & Shustack 2008). The high population densities are explained by resource-matching rule, which means that the individuals distribute themselves in relation to resource availability, vast resources thus leading to a large number of animals (Rodewald & Shustack 2008).

Phenotypic plasticity, an ability of certain genotypes to produce various phenotypes in different environments, plays an essential part in the urbanization of animals (Lowry et al. 2012; Johnson & Munshi-South 2017). This ability becomes especially important in novel ecosystems, since it allows species to adjust their morphology and behaviour to environmental conditions different from those under which they have originally evolved (Lowry et al. 2012). Even individuals of the same species differ in how much they display phenotypic plasticity, which in part explains why some individuals have greater success in urban environment than others (Lowry et al. 2012). According to recent studies, urbanization does affect evolution because urban areas increase both random genetic drift and restricted gene flow, and thus contribute to the differentiation between urban and rural populations (Johnson & Munshi-South 2017).

1.2. Effects of urbanization on the morphology in birds

Because the evolution of populations can be rapid at times, evolutionary changes in the phenotypic traits of different animals species can be studied even on time scales of

urbanization (Shanahan et al. 2014; Johnson & Mushi-South 2017). The significant differences between rural and urban areas that lead to species facing novel selection pressures in built-up habitat, can ultimately lead to trait divergence in urban animal populations as an adaptive response to urbanization (Partecke 2014; Shanahan et al. 2014; Johnson & Mushi-South 2017).

The likelihood of evolutionary responses to urbanization depends on the rate of gene flow between urban and rural animal populations, as the genetic differentiation of urban population requires limited gene flow from the surrounding areas (Wandeler et al. 2002; Partecke 2014; Shanahan et al. 2014). Thus, the genetic differentiation is expected to be less common in mobile animals such as birds, which can usually maintain the high rate of gene flow between urban and rural populations despite the barriers (Partecke 2014; Shanahan et al. 2014). Notwithstanding the mechanisms against genetic differentiation, there is evidence that trait evolution and local differentiation occurs in urban bird populations also when the environmental conditions between the two areas are drastically different and the selection on phenotype is strong (Yeh 2004; Partecke 2014; Shanahan et al. 2014). The focus of this study is on the evolutionary changes in the morphological traits of birds.

Trait divergence has been noted in many studied urban bird populations relative to their rural counterparts (Yeh 2004; Liker et al. 2008; Evans et al. 2009; Jacquin et al. 2013; Potvin et al. 2014; Shanahan et al. 2014). The morphological changes in urban birds have been observed mainly in overall body size, body mass, wing length, bill ratio and plumage (Yeh 2004; Liker et al. 2008; Auman et al. 2011; Partecke 2014). In addition to the changes in morphological traits, intraspecific variation in urban and rural birds consists of changes in the intensity of carotenoid-based plumage pigmentation, in the strength and form of various signalling traits, in levels of stress indicators and migratory tendency (Evans et al. 2009; Partecke 2014; Potvin et al. 2014; Shanahan et al. 2014).

One prevailing hypothesis is that the urban birds would be smaller in size than their rural counterparts (Liker et al 2008; Evans et al 2009; Partecke 2014). At higher latitudes the smaller body size in urban birds is expected to result from urban environments experiencing warmer climate than their adjacent environments (Evans et al. 2009). This hypothesis is largely based on Bergmann's rule, which states that there is a tendency for animals, especially

birds and mammals, to evolve larger body size at the colder environments of higher latitudes than at the warmer climate of lower latitudes (Bergmann 1847; Meiri & Dayan 2003). This rule is applied frequently both in interspecific and intraspecific comparisons (Evans et al. 2009). However, the studies on urban and rural European Blackbirds *Turdus merula* did not show any significant difference in the body size between the two groups (Evans et al. 2009).

The smaller body size in urban birds has gained support from studies on House Sparrows *Passer domesticus* that revealed that the urban individuals were consistently smaller and in worse condition than their rural counterparts (Liker et al. 2008). The study suggested that because urban habitats are characterized by high food predictability and low mortality, urban bird populations would respond to these conditions by increasing their abundance over the carrying capacity of the environment (Liker et al. 2008; Partecke 2014). The over-exploitation would thus lead to the worse body condition of urban birds and in addition result in urban birds producing lower quality offspring than their rural counterparts (Liker et al. 2008; Shochat et al. 2010; Partecke 2014). The urban House Sparrows had also smaller tarsi than their rural counterparts, which may be linked to the production of lower quality offspring as the tarsus develops to its full length already in the early life of individual (Smith 1993; Liker et al. 2008; Partecke 2014). In addition, the smaller tarsus length was discovered in studies on urban Carrion Crows *Corvus corone* (Richner 1989).

On the other hand some studies have suggested, conversely, that certain urban birds species would have larger body size than their rural conspecifics. This alternative hypothesis is supported by one of the few studies on morphological differences between urban and rural gulls (Auman et al. 2008). According to the study, the urban Silver Gulls *Larus novaehollandiae* males had larger body size than the rural Silver Gulls males (Auman et al. 2008). Urban male gulls had also overall greater body condition than their rural counterparts (Auman et al. 2008). However, there was no difference between the female Silver Gulls in the two habitats (Auman et al. 2008).

Recent studies have also reported differences in coloration between urban and rural birds (Jacquin et al. 2011, 2013). For instance, the yellow plumage of Great Tits *Parus major* is less bright in urban individuals than in their rural counterparts (Jacquin et al. 2013). Also the North American passerine the Dark-eyed Junco *Junco hyemalis* have reduced ornamental

coloration in urban areas compared to its natural habitats (Yeh 2004). Studies on Domestic Pigeons *Columba livia domestica* have suggested that the urban birds have an increased amount of melanin pigment in feathers, which may be linked to the higher parasite amounts in urban environment (Jacquin et al. 2011, 2013).

It is also assumed that as a result of various factors from chemical contaminants to elevated noise pollution, animals in urban environment would experience higher stress levels than their rural counterparts (Anderies et al. 2007; Shanahan et al. 2014). The higher stress levels and different chemical pollutants could in turn effect on the normal development of the individuals and possibly cause feather asymmetry and increase feather abnormalities (Eeva et al. 2000; Bustness et al. 2002, 2007).

Although morphological traits are heritable in birds (Richner 1989; Smith 1993; Yeh 2004; Liker et al. 2008; Evans et al. 2009), the body size and plumage are also affected by the growth conditions of the individuals (Richner 1989; Smith 1993; Partecke 2014). Thus, as regards the body size and other morphological traits, it may be difficult to argue to what extent the changes in body size are adaptive responses to the urbanization and to what extent they are just consequences of the nutrition quality during ontogeny (Partecke 2014). For instance, the reduced body size and plumage abnormalities in larger birds as crows and gulls are more often considered as direct consequences of malnutrition than as evolutionary changes in morphology (Richner 1989; Auman et al. 2008; Partecke 2014).

1.3. Gulls in urban areas

The focus of this study is on gulls, which have been at the forefront of animal urbanization since the beginning of the 20th century. Gulls, in particular, have benefitted from increased availability of human-derived food, which has led to remarkable increases in many gull populations worldwide (Cramp 1971; Auman et al. 2008; Kosonen 2008). In many built-up areas people consider gulls to be pests nowadays and try to manage the urban gull populations with various ways (Calladine et al. 2006; Pienmunne et al. 2008; Pakarinen 2013). Although gulls are so prominent in urban areas, relatively few studies have focused on their urbanization.

The success of gulls in urban areas is much related to their behavioural flexibility and overall adaptability that is typical for this taxon of birds (Pienmunne et al. 2008; Pakarinen 2013; Shanahan et al. 2014). Compared to other seabirds, gulls are the least specialized to any particular foraging method, prey item or nesting habitat (Burger & Gochfeld 1996). They are social birds in general, capable of learning to exploit novel food sources and modify their behaviour by, for instance, observing their conspecifics (Pienmunne et al. 2008; Obozova et al. 2011). There seems to be a lot of variation in behaviour and foraging between individual gulls regardless of species (Pienmunne et al. 2008; Juvaste et al. 2017). Thus, individuals can be highly specialised in their foraging even to the extent that some of them utilize waste dumps or other anthropogenic food sources exclusively, while others exploit them rarely if ever (Pienmunne et al. 2008; Juvaste et al. 2017). Last but not least, gulls are also characterized by a relatively big brain size and an excellent memory as well as long life spans of up to 32–34 years in the wild (Kuitunen 2006; Pienmunne et al. 2008).

The underlying reasons for gull urbanization are still under debate, although the easily accessible, abundant food obviously plays a major part in attracting gulls to urban areas (Cramp 1971; Pienmunne et al. 2008; Kosonen 2014). However, as gulls are able to perform foraging flights of up to 50 kilometres away from their breeding sites, they are certainly not forced to nest in urban areas in order to feed there (Vuorisalo & Tiainen 1993; Pienmunne *et al.* 2008; Juvaste et al. 2017). Therefore, it is reasonable to presume that there are other advantages of urban living as well. Among these benefits of urban areas are presumably lower predation pressure, safer nesting sites in the form of predator-free roofs, and the artificial light that enables gulls to search for food even after sundown (Kosonen 2008; Pienmunne et al. 2008; Kosonen 2014). Moreover, the intra and interspecific competition for nesting sites seems to be lower in urban areas, which may be one of the main factors that drive gulls from rural areas to built-up environments (Pienmunne et al. 2008).

On the other hand, some studies have suggested instead that gull urbanization is due to individuals forced to move from their overpopulated natural breeding areas to built-up areas (Cramp 1971; Raven & Coulson 1997; Pienmunne et al. 2008). These studies claim that urban areas are actually viewed as secondary nesting sites by gulls, and thus individuals that breed in urban areas are those that have been unsuccessful to claim a nesting site from the

traditional breeding areas due to the increased competition (Cramp 1971; Raven & Coulson 1997; Pienmunne et al. 2008).

The timeline of gull urbanization is unknown but the most reliable sources trace this phenomenon back to the coastal towns of Britain and Ireland in the 1940s (Cramp 1971; Rock 2005). Having begun as a small-scale habit in a few built-up areas, the urban nesting of various gull species became widely distributed in the 70s (Cramp 1971; Raven & Coulson 1997). The numbers of urban gulls have since increased rapidly and in 2004 the urban gull population of Britain and Ireland already consisted of more than 120 000 pairs (Rock 2005). A process of similar nature was taking place in other parts of Europe as well, as gulls started to nest in coastal urban areas in France, Italy and Belgium in the 1970s, 1980s and late 1990s, respectively (Pienmunne et al. 2008).

In Finland the urban nesting of gulls started in the 1970s (Kosonen 2008; Vuorisalo & Tiainen 1993). The Herring Gull *Larus argentatus* was the first species to start nest on buildings in both Helsinki and Tampere (Kosonen 2008; Rapp 2018). The Common Gull *Larus canus* was quick to follow in the late 1970s and since it has quickly become the most numerous urban gull species both in Helsinki and Tampere (Kosonen 2008). Because relatively little research has been done on Finnish urban gulls, the exact numbers and the status of many urban gull populations are poorly known. The main cities inhabited by gulls are Helsinki, Tampere and Turku while other cities, such as Espoo, Jyväskylä and Joensuu, host significantly smaller gull populations and fewer species (Kosonen 2008, 2014). All in all, the urban nesting of gulls is a lot more common and widespread elsewhere in Europe than in Finland (Pienmunne et al. 2008).

1.4. Urbanization of the nominate Lesser Black-backed Gull *Larus fuscus fuscus*

Although the Herring Gull and Common Gull have thrived in Finnish towns for decades, the Lesser Black-backed Gull *Larus fuscus fuscus* was absent for long. The nominate Lesser Black-backed Gull (hereafter LBBG), also known as the Baltic LBBG (Jonsson 1998), inhabits the Baltic Sea area, northern Norway, Estonia and Russian Karelia (Jonsson 1998; Lif et al. 2005). Around 45% of the population breeds in Finland (Hario 2013, 2014). Even though the global population of LBBG, all subspecies included, is around 650 000–700 000 pairs, the nominate LBBG population holds only 18 000–19 000 pairs (Hario 2014; Juvaste et al. 2017).

The nominate LBBG is known for being one of the few gull species that has not become more abundant and widespread during the past decades but instead has shown decreasing population trends throughout its distribution, and has even disappeared from most of its peripheral breeding areas, such as the Kola Peninsula and the south-western Baltic (Hildén & Hario 1993; Jonsson 1998; Juvaste et al. 2017). The dramatic decline has continued since the late 1960s, and has been particularly drastic in Finland, northern Norway and Sweden (Strann & Vader 1992; Hildén & Hario 1993; Lif et al. 2005; Juvaste et al. 2017). In Sweden the nominate LBBG population decreased from 17 000 to less than 5 000 pairs in only 20 years, although the population has slightly recovered in the last couple of decades to around 10 000 pairs in 2013 (Lif et al. 2005; HELCOM 2013).

A similar decline has taken place in Finland where the LBBG was once the most abundant gull species (Pienmunne et al. 2008; Hario 2014). During the heyday of the LBBG in the 1950s and 60s, the LBBG population reached its peak at 20 000 pairs, benefitting from the coastal fisheries and the abundance of Baltic Herring *Clupea harengus* (Hildén & Hario 1993; Hario 2014). Thereafter the population has decreased steeply to only 7 300 pairs in 2013 (Hildén & Hario 1993; HELCOM 2013; Hario 2014; Juvaste et al. 2017). The decline of the LBBG has continued seemingly unstoppably throughout the 2000s with only small glimpses of recovery in some coastal populations (Hario & Nuutinen 2011; Hario 2014). In the 2019 Red List of Finnish Species the nominate LBBG was classified as endangered, being the only gull species in Finland in that category (Hyvärinen et al. 2019).

The ultimate reason for the decline of the LBBG remains unclear but recent studies have suggested a combination of several different factors, the most important ones being environmental toxins (mainly organochlorine pollutants), inflammatory disease in chicks and severe interspecific competition with the Herring Gull (Hildén & Hario 1993; Hario 1994; Lif et al. 2005; Bustnes et al. 2006, Hario & Nuutinen 2011; Juvaste et al. 2017). There is evidence for all of the listed factors playing a role in the decline, in addition to the scarcity of food in the breeding area, human hunting on fur farms and predation by both White-Tailed Sea Eagle *Haliaeetus albicilla* and Herring Gull, the latter focusing solely on the chicks and thus diminishing the reproduction performance of the LBBG (Strann & Vader 1992; Hario 1994; Lif et al. 2005; Juvaste et al. 2017).

Interestingly, while many studies have focused on documenting the decline of LBBG as well as on the possible factors contributing to it, little research has been carried out on the relationship between the LBBG and humans, or more precisely on the LBBG and heavily human-influenced environments as urban areas. According to previous studies, the LBBG has been shyer towards humans than many other gull species and as a result the LBBGs avoided the urban areas before the late 1970s (Hildén & Hario 1993; Vuorisalo & Tiainen 1993; Kunttu & Laine 2002). It is worth noting that one key characteristic for almost all gull species whose global populations have increased considerably in the past decades has been their success in adapting to live alongside humans and, moreover, their ability to embrace new habits as scavenging on human-derived food and breed in a built-up environment. This ongoing adaptation to a novel and heavily human-influenced environment, so obvious in species as the Common Gull or the Herring Gull, has occurred slower and in more cautious manner in the LBBG (Vuorisalo & Tiainen 1993; Kosonen 2008; Pienmunne et al. 2008).

The urbanization of Finnish LBBG started in the 1990s, when the first nesting was recorded in Helsinki in 1996 (Laaksonen et al. 1996), in Turku in 1999 (Kunttu & Laine 2002) and in Tampere in 2007 (Kosonen 2008). During the following decades, the LBBG has become more and more numerous in cities. In Turku this species already outnumbered the Herring Gull despite the latter being one of the first gull species to inhabit the area (Rapp 2018; Vuorisalo, personal communication January 2019). At present the LBBG is known to breed in at least three cities in Finland, shown in the Figure 1. The urban areas inhabited by the LBBG are Helsinki, Turku and Tampere with urban populations of approximately 40, 20, and four pairs, respectively (Kosonen 2014; Rapp 2018; Pakarinen R, personal communication March, 2019).

There is a lack of studies that focus on the urbanization of the LBBG, and thus it is currently unknown why the LBBG has been later in the game to colonize the urban environment. The absence of LBBG in the anthropogenic environment has been pointed out in many studies from early on (Hildén & Hario 1993; Vuorisalo & Tiainen 1993; Kunttu & Laine 2002). Apparently the LBBG has also been among the last gull species in Finland to start to utilize waste dumps (Juvaste et al. 2017).

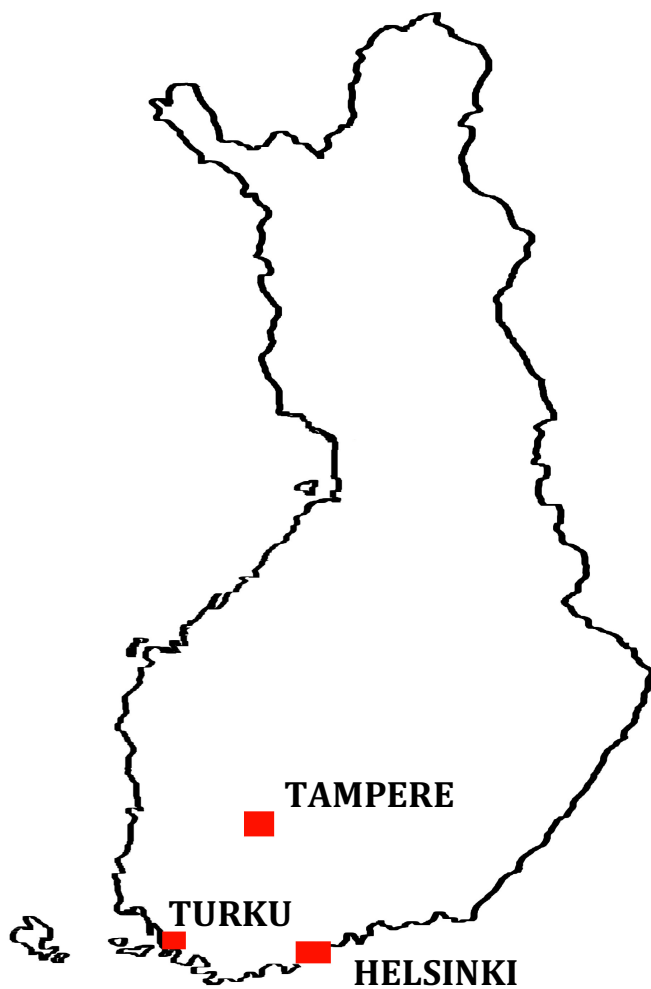


Figure 1. Map of Finland that shows the urban areas where the Lesser Black-backed Gull was known to breed prior to the year 2019.

1.5. This study

This study focuses on the consequences of a recent urbanization on the morphology of endangered nominate LBBG. In order to study the changes in morphology between urban and rural LBBG, I relied on the extensive skin collection of The Finnish Museum of Natural History LUOMUS in Helsinki. This collection consisted of LBBG individuals from year 1879 to 2017, thus covering over 130 years and more than ten generations of LBBGs. As the data also covered the entire time period from the late 1970s to 2017, in which LBBG first started to

feed in urban areas and later breed there, I could observe the morphological changes in more than two generations of urbanized LBBGs.

The aim of this study was to observe the changes in morphological traits in urban LBBGs by conducting careful measurements of various anatomical structures of urban and rural birds. Based on the previous studies on the morphological changes in urban birds, I presumed that the changed feeding behaviour of urban LBBGs would affect the morphological traits as the urban gulls would be feeding on less-protein rich anthropogenic food waste compared to the fish diet of their rural counterparts (Richner 1989; Auman et al. 2008). On the other hand, I presumed that urban LBBGs would benefit from the high resource abundance of the urban areas, and thus the offspring quality of urban LBBGs would be better. The tarsus length is often associated with the quality of offspring (Richner 1989; Smith 1993; Liker et al. 2008). I also suggested that there would be differences in the plumage patterns of urban and rural LBBGs as a result of the different chemical contaminants and nutrition quality between the two habitats.

My hypotheses for this study were:

- 1) Urban adult LBBG males have longer wings and bills than their rural male counterparts.
- 2) Both sexes of urban LBBGs have longer tarsi than their rural counterparts.
- 3) There is a difference in plumage patterns between urban and rural LBBGs.

To my knowledge, this is the first time that the museum collection of LBBGs, or any Finnish gull species for that matter, is examined at this scale. Furthermore, this is the first study to my knowledge that focuses on the morphological changes in LBBG, or any Finnish urban gull species. This study is also among the few that highlights the morphological differences between urban and rural gulls.

2. Material and methods

2.1. Data

I measured 101 LBBG study skins for the purposes of this study, approximately 60 percent of the whole collection of LBBGs in the museum. All study skins of nominate LBBGs were

included, whereas different subspecies of LBBG and damaged study skins were excluded from this study.

The included individuals were all in well-preserved state and had properly done labels with information related to the given specimen. This information consisted of the municipality and area where the individual had been encountered, the found date and year, the name of the collector and the ring number combined with the ringing date and place. However, only 12 individuals were ringed in the first place. In addition, most museum skins had information about the sex and the age of the individual. I divided the data into adults and juveniles according to the age-specific plumage characteristics of the individuals. I also divided both groups according to their sex into females and males.

2.2. Urban and rural individuals

In order to compare the urban and rural LBBG individuals, it was essential to make a difference between the two. I gave specific requirements for these classes. I based the classification on two reliable pieces of information tagged to the museum specimens, the collection location and the collection time.

In this study urban areas refer to the built-up areas, which meet the criteria for urban areas as defined by the Finnish Environment Institute SYKE. Thus, urban area is an inhabited locality whose population exceeds 15 000 people, and which consists of the core urban area and its neighboring localities (Helminen & Nurmio 2013).

Gulls are usually very loyal to the area where they have been born in, especially if they have been born in urban areas (Pienmunne et al. 2008; Juvaste et al. 2017). Thus, individuals born in urban areas are expected to continue living and nesting in those areas. This was supported by the ringing information attached to 12 individuals of my data. The ringing information revealed that the collection location of both adults and juveniles matched 100 percent to the ringing location when the maximum difference between the two locations was ± 20 km. Even if the maximum difference between the two locations was set to ± 10 km, the locations still matched 83 percent. The time between the ringing date and collection date varied from 1–27 years.

The nominate LBBG was rare in urban areas and even in waste dumps prior to 1970s (Vuorisalo & Tiainen 1993; Kunttu & Laine 2002; Juvaste et al. 2017). In other words, it can be assumed that prior the early 1970s the nominate LBBG rarely if ever fed on anthropogenic food and in contrast relied extensively on its natural prey fish and earthworms (Strann & Vader 1992; Vuorisalo & Tiainen 1993; Coulson & Coulson 2010). Almost all LBBG individuals from late 1970s were from areas within 50 kilometres of nearest urban areas, meaning that in theory they could have foraged in those areas and thus potentially fed on anthropogenic food. Especially during the breeding the LBBGs may use easily accessible food sources as urban areas, waste dumps and fur farms even if they have to perform long foraging trips (Juvaste et al. 2017). Based on this study, even the gulls collected from seemingly rural areas could have fed in urban areas if only these areas were not too far away.

I classified an individual as "urban" if it fulfilled two specific criteria. First, the individual had been collected directly in an urban area or maximum 50 km away from an urban area. Urban areas refer mainly those towns where the LBBG is known to have bred and visit regularly as Helsinki, Turku and Tampere, but also to other notable urban areas as Jyväskylä and Lappeenranta (Figure 1). Second, the individual was from the time period of 1979–2017, as in this period the LBBGs had most likely started to feed in urban areas and waste dumps and later (from mid-1990s on) breed in urban areas. Thus, I classified all individuals that had been collected between year 1879 and year 1971 as rural individuals, regardless the area.

Following these criteria, I identified 27 individuals as urban LBBGs and 68 individuals as rural LBBGs. I excluded six individuals from the study, as I could not confirm whether they were rural or urban individuals. As these six individuals were found in the period of 1973–2005, when the LBBG had already started to feed in urban areas and waste dumps, I could not classify them as rural individuals. However, as they were found over 50 km away from nearest urban areas, I could not classify them as urban gulls either. The six excluded individuals were from Åland Islands (2), Uusimaa (1), Pirkanmaa (1) and Southern Savonia (2).

In my data the urban individuals were mainly from Helsinki and its neighboring areas (17) or from Tampere and its neighboring areas (8). One urban individual was from Jyväskylä and one from Lappeenranta (Figure 2).

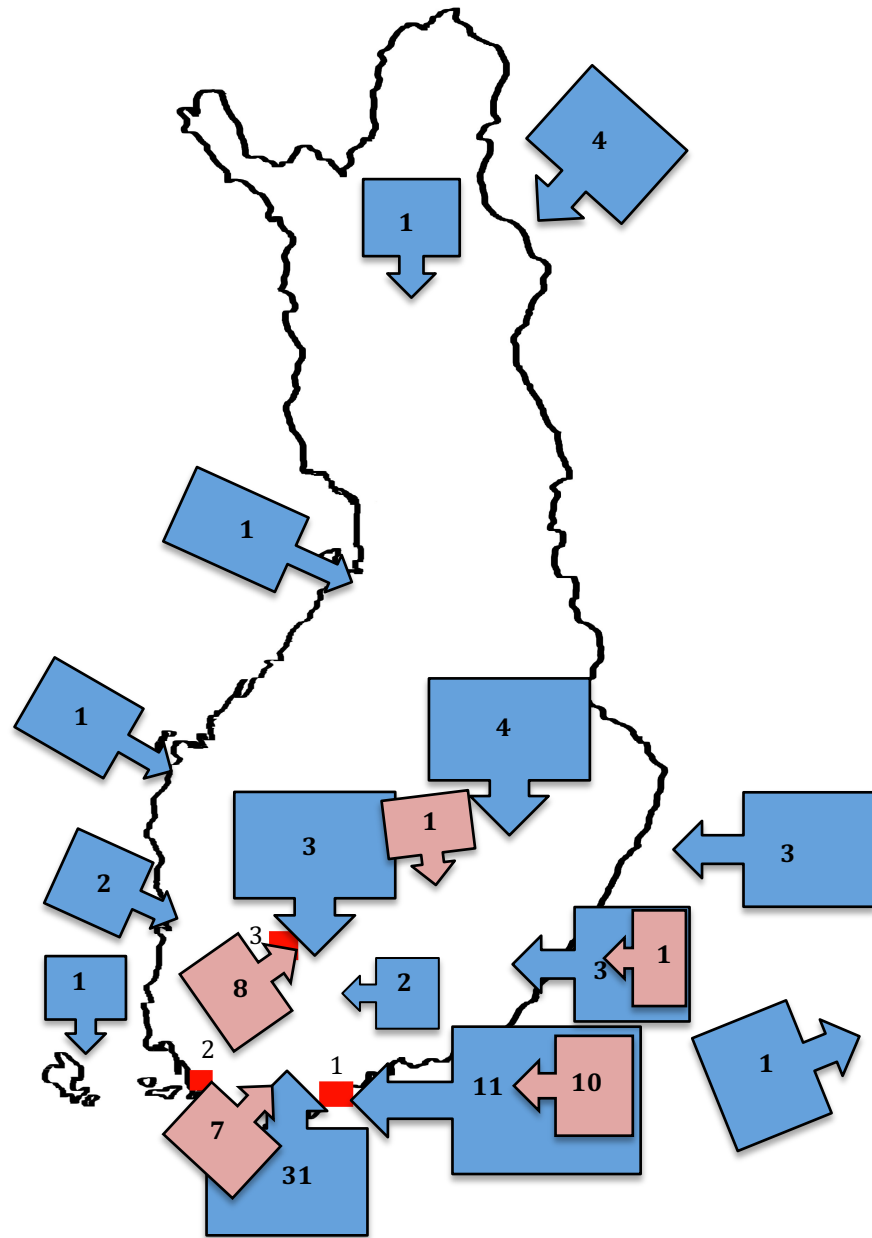


Figure 2. Map of Finland where the arrowed boxes show from which areas the total 95 of Lesser-Black-backed Gull individuals included in study were originally collected in the data. The blue boxes show the number of rural individuals collected from the pointed area. The red boxes show the number of urban individuals collected from the pointed area. The red squares display the urban areas inhabited by LBBG in 2018: 1. Helsinki 2. Turku 3. Tampere.

The rural individuals were from various areas around the country, although the majority was from southern and eastern Finland (Figure 2). A total of 31 individual were from the Uusimaa region, the municipality of Helsinki excluded. 11 rural individuals were from Helsinki, while only one individual was from the Åland Islands. Two individuals were from central and northern Finland, one from North Ostrobothnia and the other from Lapland. A total of eight individuals were from the areas outside the present borders of Finland (Figure 2). They were from Karelia (3), Kola Peninsula (1), White Sea (1) and Pechengsky District (3) as shown in Figure 2.

2.3. Age determination

As adults are larger in size and have longer and thicker bills than juveniles, the two groups had to be separated from each other. Age determination was also required in order to determine the sex of the LBBGs from morphometrics (Hallgrímsson et al. 2016). Age determination was based on two pivotal pieces of literature that are focusing on the age determination in family Laridae (Grant 1982; Hario 1986). I relied mostly on the handbook by Hario (1986) that focused on the Baltic gull species, and hence emphasized the different age characteristics of the nominate LBBG.

Based on the distinctive plumage features, the LBBG can be divided into six age classes: juvenile, first calendar year, second calendar year, third calendar year, fourth calendar year and adult (Grant 1982; Hario 1986). However, as the first calendar year individuals are usually treated as juveniles and the fourth calendar year individuals as adults (Hario 1986, Hallgrímsson et al. 2016), I did not separate them on this study either. The juvenile LBBG is characterized by dark bill, darkish brown wings, spotted chest and abdomen and black legs. The adult, on the other hand, has typically yellow bill, black wings, pale white chest and abdomen and yellow legs. The second calendar year individuals resemble the juveniles but have yellowish legs, while the third calendar year individuals are more similar to adults in their appearance. The second and third calendar year individuals are often referred to as sub-adults (Grant 1982; Hario 1986).

The majority of the individuals in my sample, 73 out of 95 studied individuals, were adult or third-year birds. As there were only eight third calendar year individuals and they did not

differ from adults in any morphological measurements, I hereafter refer to them as adults as well. The numbers of juveniles and second calendar year individuals were 20 and two, respectively. As the second calendar year individuals did not differ much from juveniles in their morphological measures I grouped them together with other juveniles. The exact number of adults and juveniles of both urban and rural individuals are presented in the Table 1.

Table 1. The number of urban and rural Lesser Black-backed Gulls separated by age.

	Adults	Juveniles	Total
URBAN individuals	20	7	27
RURAL individuals	53	15	68
Total	73	22	95

2.4. Sexing

The LBBG, similarly to other gull species under family Laridae, is monomorphic in plumage characteristics but the size between males and females differs (Hario 1986; Hallgrimsson et al. 2016). Males are larger and have longer wings, head, bill and tarsi than females (Grant 1982; Hario 1986; Hallgrimsson et al. 2016). Male gulls also have larger bill depth than females (Hallgrimsson et al. 2016).

Since I wanted to do female–female and male–male comparisons in rural and urban gulls as well as in different generations, the identification of the sex was necessary. Of the 95 gull individuals examined in the study majority had been sexed beforehand by the museum conservators (Table 2). However, the only way to confirm the sex with 100% probability is by dissection and the reliability of sexing by other ways depends largely on the given method (Hallgrimsson et al 2016). Based on the LUOMUS database only ten individuals had been sexed by dissection (Table 2). Thus, I determined the sex of those individuals with unknown sex, as well as the sex of those individuals that had been sexed beforehand with no documentation of the method used (Table 2).

Table 2. Number of pre-sexed Lesser Black-backed Gulls in the data, separated by age.

	Sexed with dissection	Sexed with unknown methods	Not sexed
Adults	8	48	15
Juveniles	2	14	6
Total	10	62	21

I performed the sexing for the LBBGs based on sexing method from morphometrics described by Hallgrimsson and others (2016). I used different models for adults and juveniles in order to determine their sex with strong reliability. For adults LBBGs the model used in this study for sexing was:

$$\text{SEX.adult} = 0.265 * \text{Head length} + 0.606 * \text{Bill depth} + 0.140 * \text{Tarsus length} - 50.375$$

According to Hallgrimsson and others (2016) the values for 95% sexing probability for females and males were below -1.13 and above 0.23, respectively. For the juvenile LBBGs the sexing model used in this study was:

$$\text{SEX.juvenile} = 0.099 * \text{Head length} + 0.327 * \text{Tarsus length} - 31.381$$

According to Hallgrimsson and others (2016) the values for 80% sexing probability for females and males were below -0.336 and above 0.930, respectively.

I performed the sexing for all 95 LBBG individuals on this study. I also included those ten individuals, whose sex had been confirmed by dissection, into the sexing, as I wanted to test the reliability of the Hallgrimsson's method (hereafter HM) for them. After I had performed the sexing, I compared the sexing result from HM to the pre-determined sex of the museum specimen. If the two suggested different sex, I chose the result that I had determined myself with the HM except for those individuals with confirmed sex.

2.5. Morphological measurements

I measured the wing, head and bill length in addition to bill depth and tarsus length from all 95 LBBG individuals. I measured the wing length using a 600 mm steel ruler and the other

measurements using 150 mm digital caliper. I measured the wing length using so-called maximum method, in which the wing was pressed against the ruler and the primaries straightened (Hario 1986). I took the wing measurement always from the individual's left wing and measured it to the nearest 1 mm. I measured the head length with caliper from the posterior ridge to the tip of the bill to the nearest 0.1 mm. Bill length was taken with caliper from the tip of the upper bill to the beginning of the chin and measured to the nearest 0.1 mm (Figure 3). Bill depth was taken from the specific part of the bill showed in the Figure 3. In order to take the bill depth measurement properly I had to press the upper and lower parts of the bill together. Tarsus length was taken from the front of the tarsometatarsal bone at the toe joint to the end of the bone below the ankle joint and measured with the digital caliper to the nearest 0.1 mm (Figure 4).

I took every measure twice and compared the results in order to assure the repeatability. Finally, for each metric I took the mean of the original and repeated measurements and used that mean as the final measurement in all comparisons.

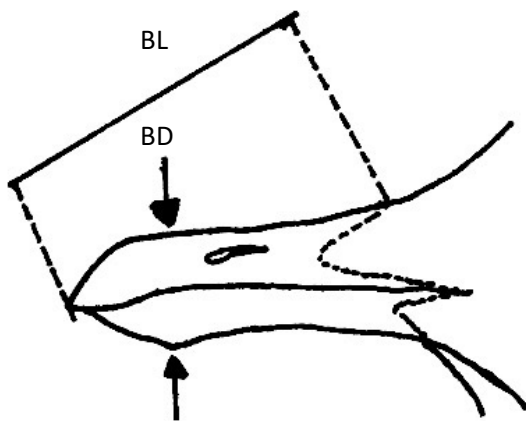


Figure 3. Measurement of bill length (BL) and bill depth (BD). Both measures were taken with a digital caliper to the nearest 0.1 mm.

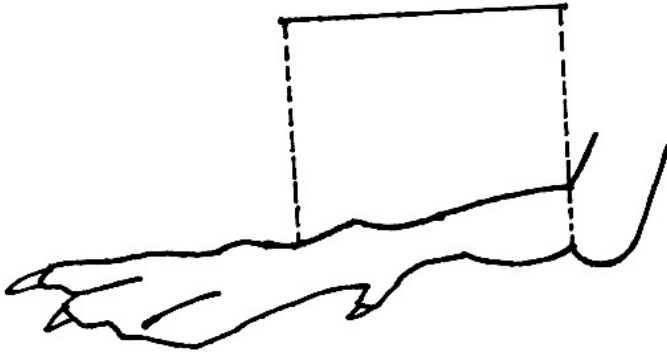


Figure 4. Measurement of tarsus length. The measure was taken with a digital caliper to the nearest 0.1 mm.

2.6. Feathers

I also studied the feathers of the adult LBBGs and performed wing-tip measurements based on the instructions by Gull Research Organisation (hereafter GRO) available on their official website (GRO 2018). The wing feathers of gull species are moulted and grown annually (Grant 1982) and according to studies these feathers may show signs of asymmetry if an individual is experiencing high level of environmental stress (Bustnes et al. 2002, 2007). As urban animals are suggested to be under greater environmental stress than their rural counterparts, I wanted to include the plumage asymmetry into the study as well.

On this study I focused on the primary feathers of adult LBBGs. Similarly to the other members of family Laridae, the LBBG has 11 primaries, of which the outermost is vestigial. The primaries are numbered outwards from the outermost large primaries to the innermost, and hence the largest primary is referred to as P10 and the smallest P1 (Figure 5).

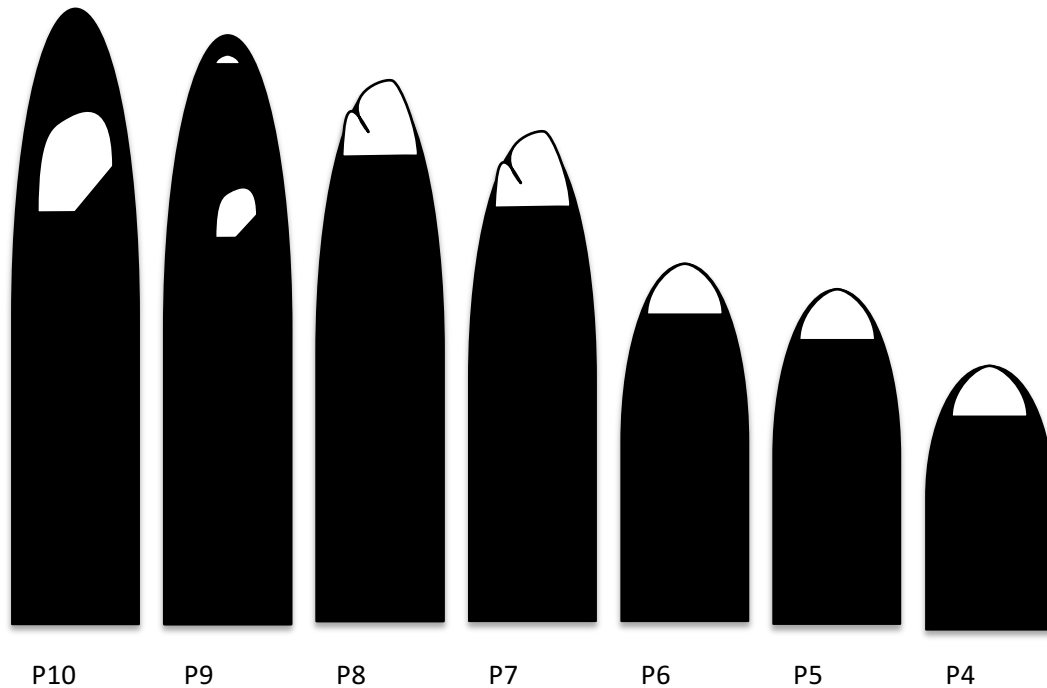


Figure 5. Illustration of black-tipped primaries of an adult nominate Lesser Black-backed Gull. The primaries are numbered outwards from the outermost large primaries to the innermost. The vestigial 11th outermost primary is ignored here as well as the innermost primaries from 3rd to 1st. In the LBBG the primaries from P8 to P4 are typically white-tipped, P9 often as well and P10 occasionally. P10 usually has the white mirror that differs in size between individuals. Sometimes the mirror is also visible in P9.

I studied the primaries of every adult LBBG and documented the following information: number of black-tipped primaries (NB), pattern of black on the innermost primary with black (TI), pattern of the tip on P10 (T10), the color of the tongue on the inner web of P10 (TN), the length of the white mirror in P10 (W10), the number of white mirrors in primaries in both wings (NW) and the number of primaries with white tips (WHT). These wing tip measurements were based on the instructions by GRO (2018) and documented according to a protocol (Appendix 1). I calculated the number of black-primaries (NB), as I wanted to see if the GEN 8–10 individuals would have less black in their feathers compared to the GEN 1–7 individuals. I assumed that the lack of black feathers would indicate a lack of melanin pigment.

The small white mirrors on the largest primaries are distinctive characteristics of the adult LBBGs (Figure 5). They usually appear only on P10, occasionally also on P9. I calculated the number of white mirrors on primaries on both wings. I compared the number of white mirrors on each wing, as I wanted to see if the mirrors on both wings were symmetrical or asymmetrical in relation to one and other (Figure 6). I also measured the length of the white

mirror on P10 to nearest 0.1 mm using a 150 mm digital caliper. The measurements were taken along the feather's shaft (GRO 2018).

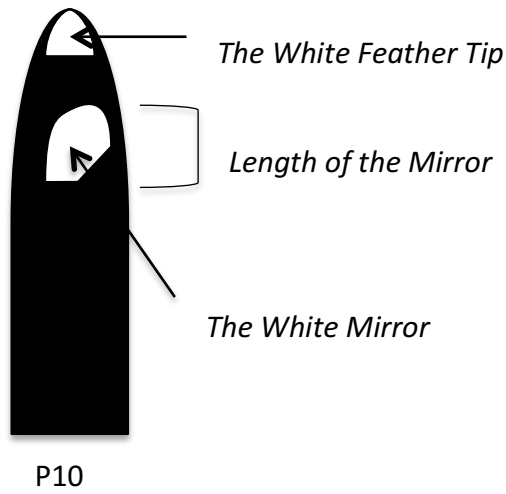


Figure 5. An illustration of the longest primary feather (P10) of an adult nominate Lesser Black-backed Gull.

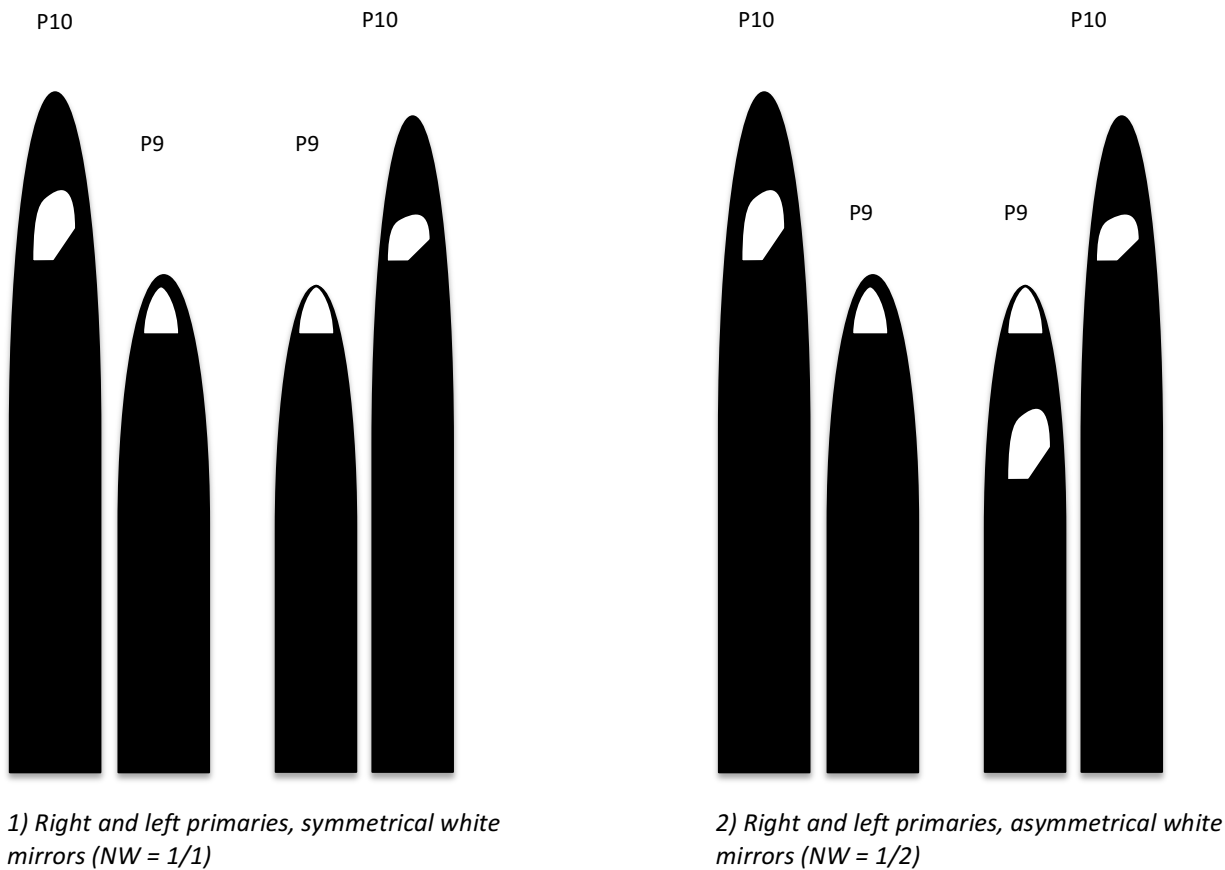


Figure 6. Example of symmetry and asymmetry in number of white mirrors in the primaries of the nominate Lesser Black-backed Gulls. NW is referring to the number of white mirrors in the primaries (white tips not counted)

2.7. Statistical analysis

All statistical analyses were performed using SPSS software, version 25.0 for Windows (SPSS2017). I used the 95% confidence limit in all analyses. Differences at the level of $P \leq 0.05$ were reported as significant. I plotted the means with their standard errors by using R 3.5.3.

3. Results

3.1. Sexing adults and juveniles

Adults

The sexing results by HM for adult LBBGs were 54 females and 23 males. I sexed all individuals with HM values above 0.23 as males and those with HM values below -1.13 as females. Individuals with HM values between -1.13 and 0.23 were sexed as males if they had a head length larger than 117.0 mm.

Altogether sexing results showed 72% consistency with the sexes that had been determined beforehand. For females the HM results were 96.7% in line with the sexes that had been determined for the individuals previously. In other words, of those individuals that had been determined as females in the collection, 29 out of 30 were identified as females as well by the model. For males the HM results were 57.7% in line with the sexes that had been determined beforehand for the individuals. Of those individuals that had been identified as males in the LBBG collection, 15 out of 26 were identified as males by the model.

Of the eight adults that had been sexed reliably by dissection, four were females and four males. The model sexed all females correctly as females (100% consistency) but only one of the four confirmed males was sexed as male (25% consistency). The HM values for these incorrectly sexed males were -3.80, -2.01 and -1.90, which means that according to the HM they should have been females with probability of over 95%. All incorrectly sexed adult males were urban individuals and had been encountered between 2000 and 2004 from Helsinki and its neighboring areas.

The final results for sexing of adults, when both the HM result and the confirmed sexes were taken into the account, were 47 females and 26 males. The number of sexes is presented in the Table 3, separated by urban and rural individuals.

I performed the non-parametric Kruskal-Wallis-Test in order to see if there was a significant difference between the values from sexing results between adult urban and rural males and females (Figure 7). There was no difference between the sexing results of rural and urban females ($p = 1.00$). However, the difference between rural and urban males was slightly more significant ($p = 0.3$). The test showed a significant difference between the sexing results of rural females and rural males ($p < 0.001$) as well as between urban females and rural males ($p < 0.001$). The difference between rural females and urban males was significant ($p = 0.04$), although not to the same extent as in the previous cases. There was no significant difference between urban females and urban males ($p = 0.43$).

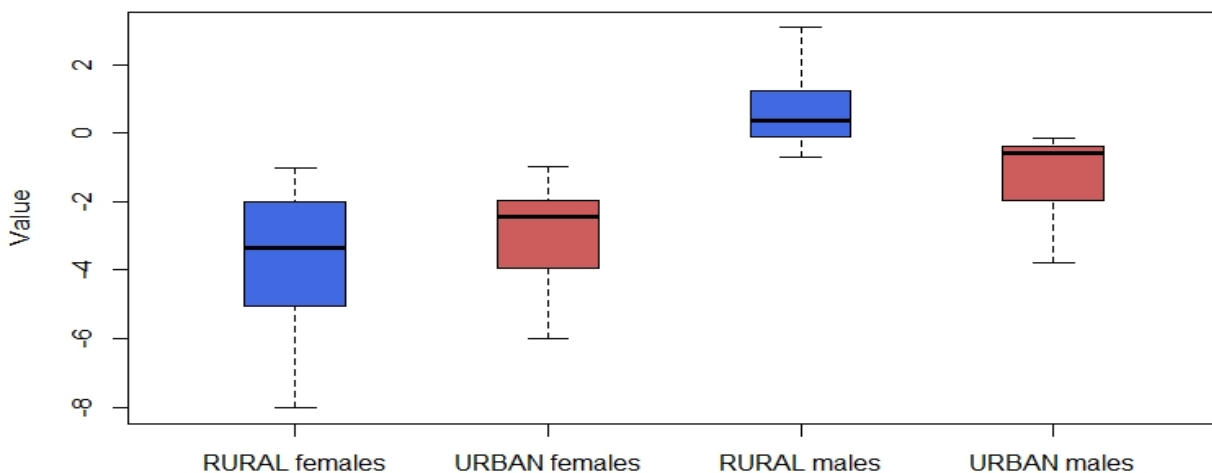


Figure 7. The sexing results for rural and urban nominate Lesser Black-backed Gulls from the morphometrics plotted by the sexing values. The mean values for rural females, urban females, rural males and urban males were -3.63, -2.92, 0.65 and -1.13, respectively.

Juveniles

The sexing results by HM for juvenile LBGs were 14 females and 10 males. I sexed all individuals with HM value above 0.930 as males and all individuals with HM value below -0.336 as females. If an individual had a HM value between -0.336 and 0.930, I identified the sex based on the head length.

Both sexes considered the sexing was 70.1% consistent with the sex that was originally stated in the museum specimens. For females the HM results were 85.7% in line with the sexes that had been determined for the individuals beforehand. Of those individuals that had been identified as females in the collection, six out of seven were identified as females as well by the model. For males the HM results were 55.6% in line with the sexes that had been determined for the individuals beforehand. Of those individual that had been identified as males in the collection, five out of nine were identified as males by the model.

The two individuals that had been sexed reliably by dissection were both females and classified as urban individuals. One of them was correctly sexed as females by the model, while another was incorrectly sexed as male with HM value of 1.05. Thus, the consistency between the HM values and the confirmed sexes was 50.0 %.

The final results from sexing of juveniles, when both the HM result and the confirmed sexes were taken into the account, were 14 females and eight males. The number of sexes is presented in the Table 3, separated by urban and rural individuals.

Table 3. The sexing results for urban and rural nominate Lesser Black-backed Gulls.

	Males	Females	Total
ADULTS			
URBAN	8	12	20
RURAL	18	35	53
Total	26	47	73
JUVENILES			
URBAN	2	5	7
RURAL	6	9	14
Total	8	14	22
TOTAL	34	61	95

Finally, I performed the non-parametric Kruskal-Wallis Test in order to see if there was a significant difference between the values from sexing results between juvenile urban and rural males and females. There was no difference between the rural females and urban males ($p = 1.00$) or between the rural males and urban males ($p=1.00$). The difference between rural females and rural males was significant ($p = 0.02$). The difference between the urban females and rural males was significant as well ($p = 0.02$) but the difference between rural females and urban males was non-significant ($p = 0.70$). The difference between urban females and urban males was also non-significant ($p = 0.59$).

3.2. Morphological measurements

The mean lengths and standard deviations for each metrics for adults are presented in the Tables 2 and 3. Both adult and juveniles were separated as females and males and both sexes as urban and rural individuals. I also analyzed the repeatability of the measures I had taken. The repeatability of each of the five metrics exceeded 99.9 percent. I calculated the correlation between the original and repeated measurements for each metric. The correlation between the original and repeated measurement was high (WING $r = 0.999$, HEAD $r = 0.998$, BILL $r = 0.999$, BILL DEPH $r = 0.996$, TARSUS $r = 0.998$). The p value was less than 0.0001 in all cases, which indicates strong correlation between the original measurements and the repeated ones.

I compared the means of each metric between adult rural and urban females and rural and urban males with Equal Variance *t-test* of independent samples. Since the sample size was less than 30 in all groups except the adult rural females, I first tested if the means of each metrics were normally distributed among the groups. I tested the normal distribution with two tests, Kolmogorov-Smirnov and Shapiro-Wilk test. If the two tests indicated the normal distribution ($p > 0.05$), I continued using the *t-test*. However, if either one of the tests indicated that the sample was not normally distributed, I used the non-parametric Mann-Whitney U-test instead.

According to the Kolmogorov-Smirnov test and the Shapiro-Wilk test of normality, the wing and bill length, bill depth and tarsus length were all normally distributed. Thus, I compared those metrics of urban and rural females with the independent *t-test*. The head length, on the other hand, was not normally distributed according to the test, and thus I used the Mann-Whitney U-test for the comparisons of head length of rural and urban sexes. I tested the

variances of the wing length, bill length, bill depth and tarsus length with Levene’s test for equality of the variances. According to the Levene’s test, all metrics of the data sets had equal variance and thus the Equal Variance *t*-test was used.

The results from the Equal Variance *t*-test and Mann-Whitney U-test for the adult urban and rural sexes are presented in the Tables 4 and 5. There was no difference in wing lengths between rural and urban males or between rural and urban females (Tables 4 and 5). Similarly the tarsus lengths between rural and urban males and females did not show notable differences (Figure 8). However, while in males the bill lengths did not differ between rural and urban individuals, in females the urban individuals had slightly longer bills than the rural individuals (Table 4 and 5, Figure 10).

Table 4. Comparison of the wing length, head length, bill length, bill depth and tarsus length of adult rural and urban nominate Lesser Black-backed Gull males. *P* value and *t* are from an independent samples *t*-test for wing, bill length, bill depth and tarsus and from Mann-Whitney U-test for head.

	RURAL males (n = 18)			URBAN males (n = 8)			<i>t</i>	<i>P</i> value (** U-test)
	Mean	SD	Range	Mean	SD	Range		
Wing length (mm)	434.9	11.4	419.0–459.0	430.4	9.2	424.0–441.5	0.979	0.34
Head length (mm)	119.6	2.6	116.5–127.0	114.2	4.9	104.5–119.9	–	0.002* *
Bill length (mm)	51.8	2.2	46.1–55.4	51.6	3.3	46.4–56.8	0.195	0.847
Bill depth (mm)	16.8	0.9	14.8–18.6	16.4	0.6	15.4–17.1	1.105	0.280
Tarsus length (mm)	65.5	2.9	60.5–72.3	64.0	3.0	59.6–68.8	1.166	0.255

In addition to the bill length, also the bill depth was slightly larger in urban females compared to rural females. However, the difference in bill length was only slightly significant ($p = 0.04$), while the difference in bill depth was not statistically significant ($p = 0.08$). The bill depth between rural and urban males did not differ much. The mean head length between the rural and urban females was also more or less the same between the groups (Table 5).

The most significant difference in the morphological traits between rural and urban individuals was in head length between rural and urban males. The comparison of means

suggested that the urban males had notably smaller heads than rural males (Figure 11). According to the Mann-Whitney U-test, the difference between mean head lengths was statistically significant ($p = 0.002$). The head length was the only metric in adult males that showed clear difference between the two groups. All in all, the urban males seemed to be slightly smaller in size than their rural counterparts, while the females seemed to be quite similar in size to one and other (Tables 4 and 5).

Table 5. Comparison of the wing length, head length, bill length, bill depth and tarsus length of adult rural and urban nominate Lesser Black-backed Gull females. *P value* and *t* are from an independent samples *t*-test for wing, bill length, bill depth and tarsus, and from Mann-Whitney U-test for head.

	RURAL females (n=35)			URBAN females (n=12, *n=11)			<i>t</i>	<i>P value</i> (**U-test)
	Mean	SD	Range	Mean	SD	Range		
Wing length (mm)*	415.1	14.7	378.0–446.5	420.2	14.1	396.5–439.5	-1.061	0.29
Head length (mm)	109.0	5.0	98.4–117.3	110.1	3.6	100.5–114.7	–	0.47**
Bill length (mm)	48.0	2.6	42.2–53.5	49.7	2.4	44.9–55.3	-2.087	0.04
Bill depth (mm)	15.3	0.8	13.9–17.2	15.8	0.9	14.6–17.2	-1.801	0.08
Tarsus length (mm)	61.5	3.2	54.1–68.7	62.1	3.4	54.8–66.6	-0.647	0.52

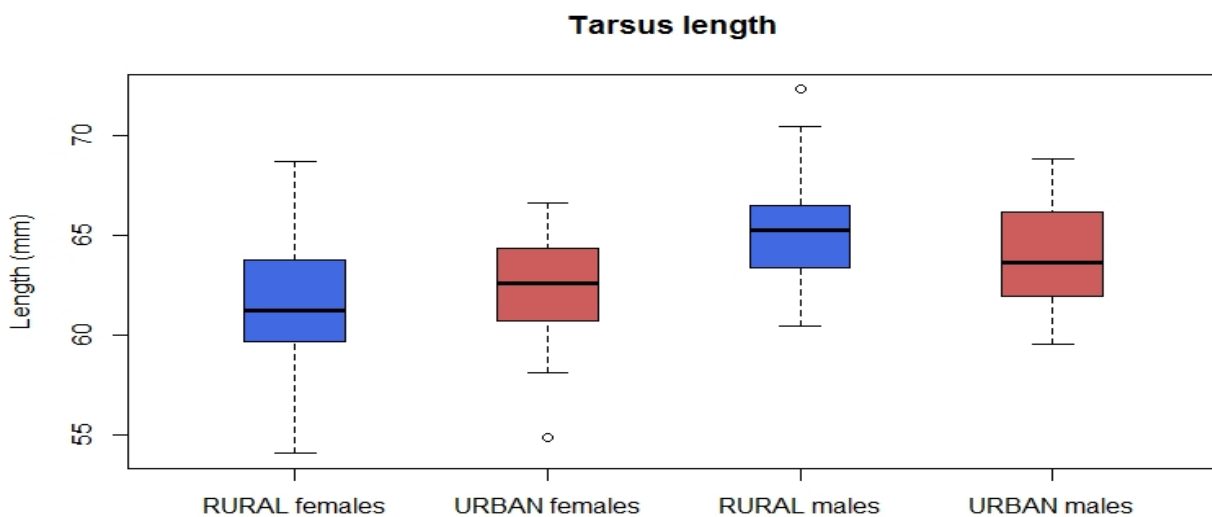


Figure 8. The mean differences of tarsus length between adult urban and rural Lesser Black-backed Gulls. The standard errors are indicated.

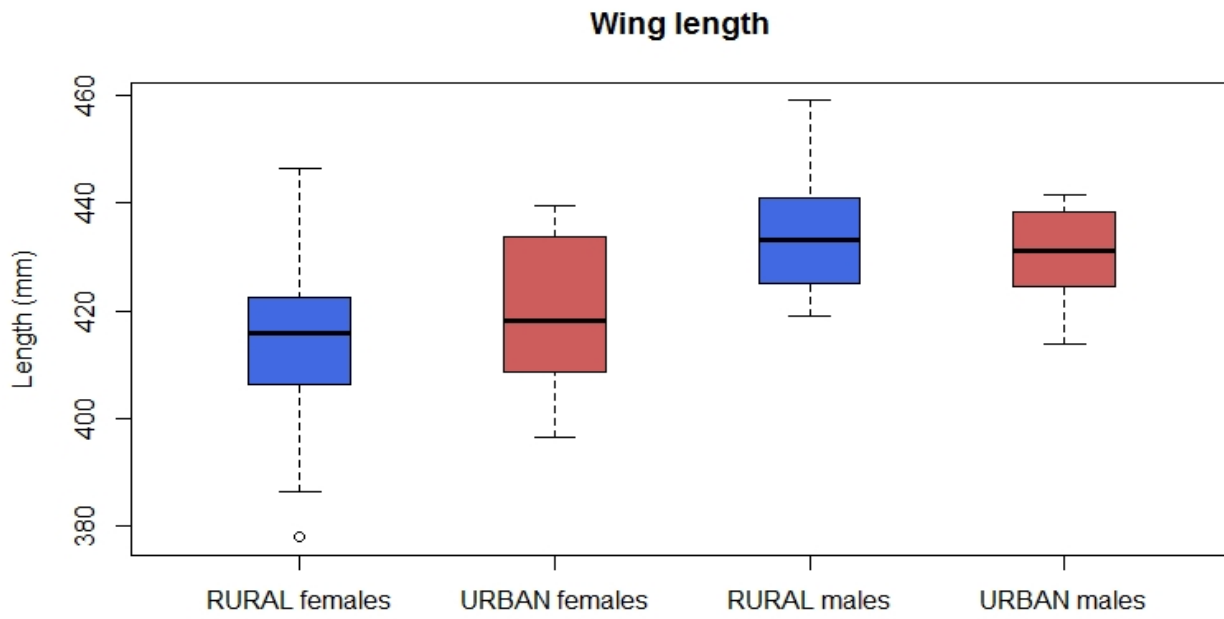


Figure 9. The mean differences of wing length between adult urban and rural Lesser Black-backed Gulls. The standard errors are indicated.

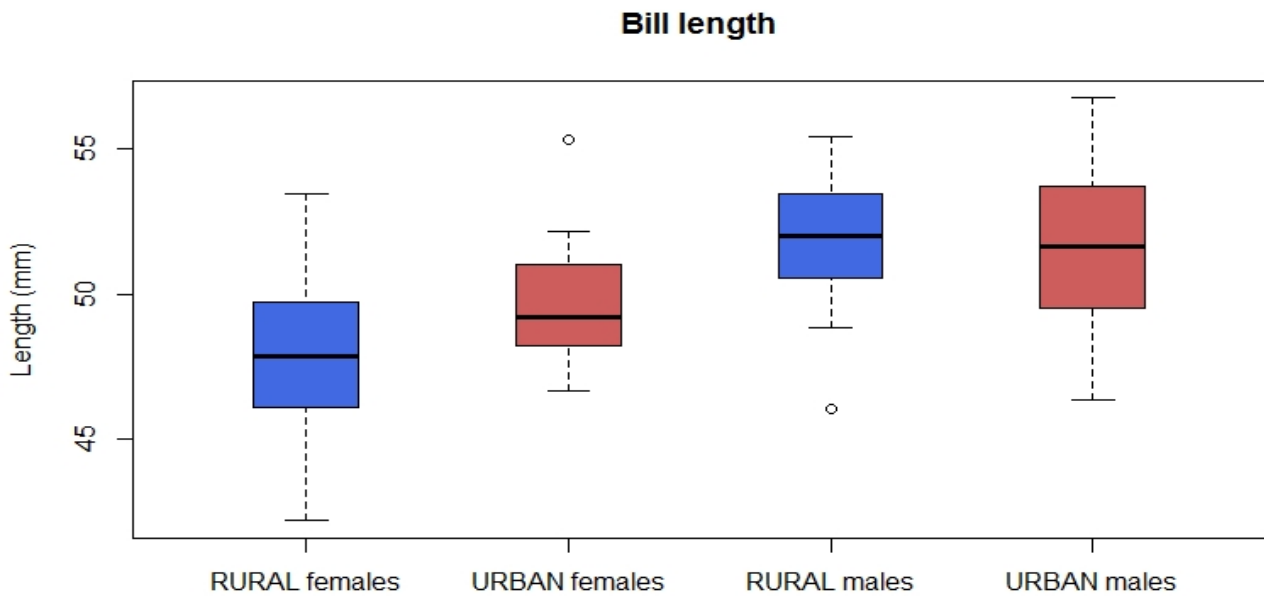


Figure 10. The mean differences of bill length between adult urban and rural Lesser Black-backed Gulls. The standard errors are indicated.

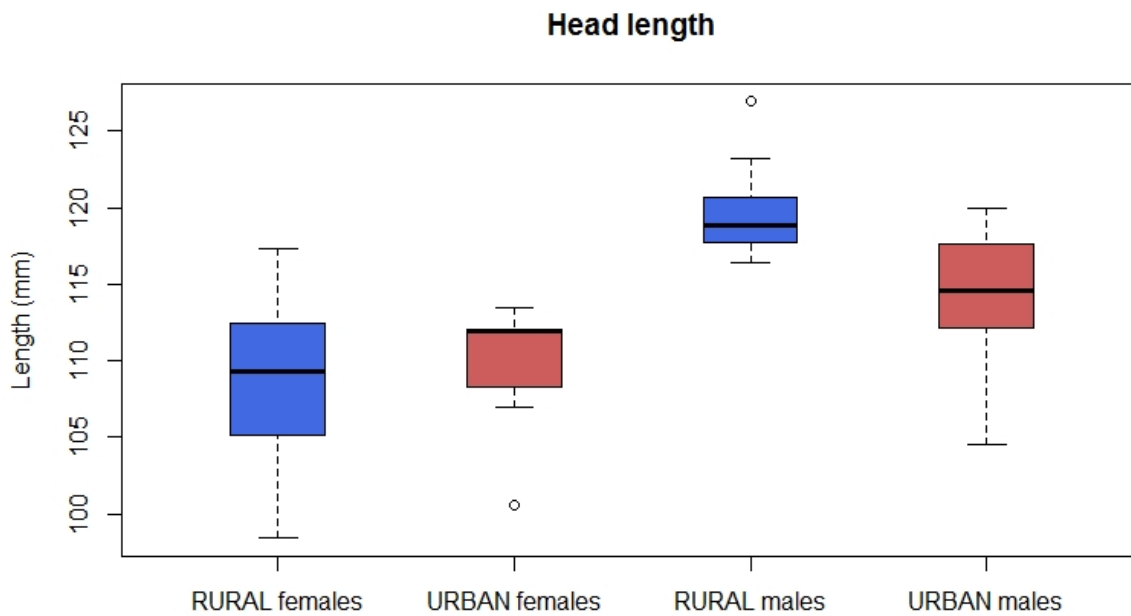


Figure 11. The mean differences of head length between adult urban and rural individuals. The standard errors are indicated.

3.3. Comparisons between urban and rural individuals

Adults

For pairwise comparisons between the adult urban and rural males and females I conducted one-way analysis of variance (ANOVA) for the wing length, bill length, bill depth and tarsus length. As stated earlier, all these variables were normally distributed and had equal variances, and thus ANOVA could be applied. As the head length was not normally distributed, I used non-parametric Kruskal-Wallis Test for pairwise comparisons of head length instead of one-way ANOVA. I also applied Bonferroni correction for all pairwise comparisons.

The results from the two analyses for adults are presented in the Table 6. The rural females and rural males differed significantly from one and other in all variables measured (Table 6). The differences in measured variables were also significant between rural females and urban males, although the head and tarsus length did not show notable difference between the sexes. Urban females differed from rural males in wing, head and tarsus lengths as well as in bill depth, but the difference in bill lengths between the two was not significant (Table 6). The urban females and urban males did not differ from each other in any of the variables.

According to the ANOVA, there was no difference between the mean tarsus length of urban males and urban females.

Table 6. The pairwise comparisons between the rural and urban females and males. The P values are from one-way ANOVA or *from Kruskal-Wallis Test. W= wing length, HE = head length B = bill length, BD = bill depth and T = tarsus length. P values of < 0.05 are in bold.

	RURAL females	URBAN females	RURAL males	URBAN males
RURAL females		W: 1.00 HE: 1.00* B: 0.25 BD: 0.43 T: 1.00	W: < 0.001 HE: < 0.001* B: < 0.001 BD: < 0.001 T: < 0.001	W: 0.03 HE: 0.14* B: 0.003 BD: 0.005 T: 0.27
URBAN females	W: 1.00 HE: 1.00* B: 0.25 BD: 0.43 T: 1.00		W: 0.03 HE: < 0.001* B: 0.14 BD: 0.006 T: 0.03	W: 0.60 HE: 0.47* B: 0.56 BD: 0.51 T: 1.00
RURAL males	W: < 0.001 HE: < 0.001* B: < 0.001 BD: < 0.001 T: < 0.001	W: 0.03 HE: < 0.001* B: 0.14 BD: 0.006 T: 0.03		W: 1.00 HE: 0.21* B: 1.00 BD: 1.00 T: 1.00
URBAN males	W: 0.03 HE: 0.14* B: 0.003 BD: 0.005 T: 0.27	W: 0.60 HE: 0.47* B: 0.56 BD: 0.51 T: 1.00	W: 1.00 HE: 0.21* B: 1.00 BD: 1.00 T: 1.00	

Juveniles

I also performed pairwise comparisons for juvenile rural and urban females and males. As the sample size of juveniles was overall smaller than that of adults, and as only the bill length and bill depth were normally distributed, I used the non-parametric Kruskal-Wallis-Test. I performed the pairwise comparisons only when the difference between the groups was notably significant ($p < 0.01$). According to this test there was no significant difference in wing

lengths between the four groups ($p = 0.27$). In addition, no differences were noted in bill depths and tarsus lengths between the groups. There was a small significant difference in bill lengths between rural and urban females and males ($p = 0.02$). The head length showed by far the most notable difference between the four groups ($p = 0.002$). The results from the pairwise comparison for the head length are presented in the Table 7.

Table 7. The pairwise comparisons of head length of juveniles. The four groups compared pairwise are urban and rural females and males. The P values of <0.05 are in bold.

	RURAL females	URBAN females	RURAL males	URBAN males
RURAL females		1.00	0.01	0.76
URBAN females	1.00		0.005	0.43
RURAL males	0.01	0.005		1.00
URBAN males	0.76	0.43	1.00	

3.4. Feathers

The wing tip measurements showed notable constancy between both urban and rural individuals and between the sexes. Neither the pattern of the black in the innermost primary with black (TI), nor the color of the tongue in P10 (TN) varied much between the urban and rural individuals or the sexes. Also the mean number of white mirrors in primaries was similar between the groups (Table 8). I used Kruskal-Wallis one-way analysis of variance for the wing tip measurements, as the measurements were not normally distributed. There was only little difference between the number of black primaries (NB) between urban and rural individuals and between the sexes ($p = 0.08$). The length of the white mirror in P10 showed almost no difference between the groups. Also the mean number of white tip feathers was similar between the urban and rural males and females (Table 8). The symmetry in white

mirrors showed slight difference between the groups, although not statistically significant ($p = 0.06$).

Table 8. The mean values from the wing tip measurements of the rural and urban individuals.

	RURAL males and females (n=53)			URBAN males and females (n=21)		
	Mean	SD	Range	Mean	SD	Range
Number of black primaries (NB)	7.15	0.50	6–9	7.52	0.81	6–9
Number of white tipped primaries (WhT)	6.00	0.96	5–9	5.81	1.03	4–8
The length of the white mirror in P10 (W10)	28.92	8.87	0.00–41.58	26.72	12.99	0.00–45.80
Number of white mirrors (NW)	1.03	0.27	0–2	1.00	0.55	0–2

4. Discussion

Contrary to the first hypothesis of this study, urban LBBG males seem to be similar or slightly smaller in size compared to rural LBBG males. The wing and bill length as well as the bill depth show almost no difference between urban and rural LBBG males. However, based on the results urban LBBGs have notably smaller heads than their rural counterparts. As the other anatomical structures between the two groups were more or less similar in size, the results give an impression that the smaller heads of the urban LBBGs are not in relation to the rest of the measures. However, as the significance of this difference varies depending on the statistical analyses used, larger sample size of urban LBBG males would be needed in order to emphasize this difference more. All in all, the differences between the urban and rural LBBG males are unexpected in the light of previous studies on morphological changes in urban birds (Auman et al. 2008; Evans et al. 2009). These results do not show consistency with the previous study on urban Silver Gulls that suggested that urban male gulls would be larger in size and in overall greater body condition than their rural counterparts (Auman et al. 2008). As I could not measure the mass of the birds, the possible differences in body condition between urban and rural LBBGs are unknown.

There seem to be no difference in the length of tarsus between the urban and rural LBBGs, in contrast to my second hypothesis. In fact, of all morphological measures the tarsi show the

least differences between the groups. The length of tarsi does not vary between urban and rural juveniles either. This seems to indicate that there is no difference between the offspring quality of urban and rural LBBGs. In many other studies, the tarsus lengths in particular have showed notable difference between urban and rural bird populations, and thus the findings from this study are surprising and interesting (Richner 1989; Liker et al. 2008; Partecke 2014).

In contrast to my third and last hypothesis, there seem to be no difference in plumage patterns between urban and rural LBBGs. Indeed, the wing tip measurements from my study show notable consistency between the two groups. To my knowledge, there are only a few studies previously on the plumage patterns of nominate LBBG. Furthermore, there seem to be no previous studies that would compare the wing tip measurements of different groups. The wing-tip measurements showed almost no difference between the urban and rural individuals. Surprisingly, even the lengths of the white mirrors in the primary feathers showed high constancy among both sexes and habitats. There was slightly more mirror asymmetry in urban LBBGs compared to rural LBBGs. However, the overall number of asymmetries in this trait was notably small. The wing tip measurements from this study supported strongly the previous observations by Hario (1986). Interestingly, the function and importance of the white mirrors and other white patterns in the primaries of LBBG are still largely unknown. According to my study, it seems that there is only a little variation in these patterns between different individuals. I did not observe any sex-specific differences in the plumage characteristics either.

The sexual size dimorphism in nominate LBBGs was apparent in this study. The rural males and females differed from each others in every measure taken in the study. The rural males were significantly larger than rural females and they had longer wings, heads, bills and tarsi. Rural males had also larger bill depths than the females. The size dimorphism among the juveniles was not as clear, which may indicate that the size of the juveniles is more dependent on the specific age of the individual than of the sex. On the other hand, in Hallgrímsson's and others study (2016) on the LBBG, also the juveniles showed significant sexual dimorphism. The differing results between that study and the study of mine may be due to the relatively small sample size of juveniles in my study. The head length, however, seemed to show clear

sexual size dimorphism already in juveniles and the rural males had notably larger heads than the rural females.

Unexpectedly, the sexual size dimorphism was significantly less apparent in the urban LBBGs. Urban males were slightly smaller in all morphological traits than their rural counterparts, while the urban females were slightly larger in size compared to rural females. Although only a few morphological measures, the head length in males and the bill length in females, showed clear differences between the urban and rural individuals, the results indicate that the sexes in urban areas are more similar to each other in size. Thus, it seems that the sexual dimorphism in LBBGs have become notably reduced in urban areas compared to rural areas.

The more similar size of urban and male LBBGs can make it difficult to distinguish the sexes from each other by only morphological measures. This seems to be the case also in my study, as the Hallgrimsson's and others (2016) sexing method sexed most of the urban male gulls incorrectly. As the method clearly sexed most of the urban males as females, it seems that the reliability of Hallgrimsson's and others method should be re-evaluated when the data consists of urban gull individuals. However, more studies of this matter are needed, as the sample size of urban gulls was relatively small in my study.

To my knowledge, there are no previous studies that would have indicated that urbanization could reduce the sexual dimorphism in any bird species. In that sense, the findings from this study are surprising and extremely interesting. It is difficult to speculate what could be the underlining reasons for the reduced sexual dimorphism. According to previous studies, there is no difference in feeding behavior between male and female LBBGs (Götmark 1984; Coulson & Coulson 2010; Juvaste et al. 2017), which could offer an explanations why males have slightly reduced in size in urban areas while females have slightly increased in size. Furthermore, it is unknown if this change in sexual dimorphism is an adaptive response to changed environment and new selection pressures or if it is a result from increased chemical contaminants or malnutrition. All in all, larger sample size would be needed in order to investigate this phenomenon more.

Apart from the relative small sample size, there are a couple of critical points that are important to acknowledge in this study. First, it can be argued to what extent the gulls found

from urban areas actually fed in urban sites during their lifetime. One of the main assumptions of this study was that part of the morphological differences would result from the different diet of the urban LBBGs. According to previous studies utilizing satellite tracking, different individuals of LBBG are highly specialised in their foraging (Juvaste et al. 2017). Gulls seem to base their choice of foraging area on the different trade-offs of distinct food sources. The most important trade-offs are related to how much time can be invested on flying to the foraging area and searching for food versus the time that is safe to be away from the breeding site without leaving nestlings vulnerable to predation (Juvaste et al. 2017). Thus, especially during the breeding season, it is crucial for gulls to balance between these two and try to optimise their allocation of time (Juvaste et al. 2017). Based on this, one can assume that the LBBGs living in the urban environment would most likely also feed there, as by doing that they could save the valuable time especially during the breeding season. If the breeding parents forage mostly in urban areas, they would also feed their chicks with the anthropogenic food, which would in turn effect on the development of the fledglings.

Second, as my data consisted of both gulls collected directly from urban areas and those collected within ± 50 km range from urban areas, it could be questioned how realistic it is to assume that the gulls outside urban areas may rely on the urban resources. However, the pivotal study by Juvaste and others (2017) supports the hypothesis that also LBBGs near urban areas would feed in build-up habitat. Based on this study, even during the breeding period gulls may forage in areas as far as 50 km away from their nests, if these areas guarantee high resource abundance and easily accessible food (Juvaste et al. 2017). Thus, the longest feeding trips by the LBBGs were performed to waste dumps and fur farms, which represent "fast food hot spots" for gulls in terms of resource abundance and access (Juvaste et al. 2017). My data included a couple of individuals collected directly from waste dumps, which may also indicate that these kinds of food sources are important for LBBGs.

Another critical point for this study that can be raised is related to the migration behaviour of the LBBG. LBBGs spend the better part of their life outside Finland in their wintering areas in East Africa. In addition to the six to eight months of each year individuals spend in these areas, the LBBGs also spend the first two or three years of their lives exclusively in Africa (Moreau 1972; Hario 2013; Valkama & Piha 2013). Thus, one could argue to what extent the urban or rural conditions and food sources in Finland are responsible for the changes in

morphological traits between the groups and which effects could be traced back to the wintering areas instead. On the other hand, researchers still know little about the behaviour and foraging methods of LBBG in Africa. It is not known, for instance, if LBBGs are looking for areas resembling their breeding sites or if they continue foraging for food in the same way they do in Finland. If urban LBBGs utilize more or less similar urban areas in their wintering grounds in Africa as well, they might be subjects to similar environmental factors as in their urban breeding grounds in Finland.

As stated previously, the successful urbanization has been one of the key factors contributing to the global increase of many gull species (Cramp 1971; Jonsson 1998; Burger & Gochfeld 1996). As the endangered nominate LBBG has started to nest and feed more and more in urban areas, it would be interesting to study if the urbanization of this species had an effect on the ongoing decline of LBBG. Indeed, it seems that LBBG is doing even better in some urban areas than its competitor Herring Gull (Rapp 2018). However, more studies on the overall urbanization process of LBBG are obviously needed. My study is one the first of its kind to demonstrate that there are morphological differences between the rural and urban LBBGs. As the results from this study were mostly unexpected and differed from the results of previous studies, it is important to replicate this study with a larger sample size in the future. Furthermore, it is important to study other urban gull species as well in order to see if the reduced sexual dimorphism is a more common phenomenon among urban gulls.

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8. Appendix

Appendix 1. The protocol for morphological measurements used on this study.

INFORMATION ON THE SPECIMEN		NUMBER OF THE SPECIMEN	
Location (from the label):		Date:	
Year (from the label):		Collection:	
Ring number:			
Ringing place:			
TYPE:		URBAN / RURAL	
Label information:			
MEASUREMENTS			
WING LENGTH (mm):		1.	2.
HEAD LENGTH (mm):		1.	2.
BILL LENGTH (mm):		1.	2.
BILL DEPTH (mm):		1.	2.
TARSUS LENGTH (mm):		1.	2.
AGE:			
Calendar Year:			
WING TIP MEASUREMENTS			
NB:	TI:	TN:	W10 (mm):
NW:	WHT:		
SEXING			
Morphometry		Anatomical (sexed by dissection)	
LEGEND:			
NB = number of black tipped primaries		TI = pattern of black on innermost primary with black (1-3)	TN = color of the tongue in P10 (1-3)
T10 = pattern of the tip on P10 (1-5)		W10 (mm) = length of the mirror on P10 (measured along the feather's shaft)	NW = number of white mirrors in both wings
WHT = number of primaries with white tips			

