

Local variation in sex ratios in three species of wintering ducks: the need for large-scale sampling

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This study investigates the hypothesis that site characteristics and flock size influence the sex ratios of wintering ducks by examining three species: the Mallard (*Anas platyrhynchos*), the Goldeneye (*Bucephala clangula*), and the Long-tailed Duck (*Clangula hyemalis*) in the Gulf of Gdańsk, southern Baltic. Birds were counted in mid-January along approximately 160 km of shoreline in the western part of the Gulf of Gdańsk and the estuarine sections of the Vistula River on the southern Baltic coast. Only flocks in which the sex of all individuals was identified were included in the analysis. The sex ratios of the three study species varied across the five habitat types within the study area but did not vary with species-specific flock size. In Mallards the lowest proportion of males was recorded along the open seacoast and municipal beach, suggesting that these areas are primarily occupied by paired birds. The higher proportion of males at other sites is likely due to the shift of unpaired individuals to these locations, where the overall number of this species is the highest. In the Goldeneye the highest percentage of females was observed in the most sheltered areas, while the lowest percentage, alongside low individual numbers, occurred along the open seacoast. These patterns suggest that Goldeneye density and sex ratio are influenced by female tolerance to adverse weather conditions, as this species shows the greatest size difference between males and females among the species studied. Long-tailed Ducks exhibited a more uniform sex ratio across the study area, likely due to their frequent movements to access areas with abundant food resources. This study highlights spatial variations in duck sex ratios within a single water body and underscores the need for large scale sampling to obtain representative sex ratio estimates.

1. Introduction

The sex ratio often varies temporally and spatially in bird populations (e.g. Nichols & Haramis 1980, Meissner & Krupa 2017, Brides *et al.* 2017, Fox *et al.* 2018) and is a crucial

component of population structure, as they are closely related to demography, behaviour, and population dynamics (Donald 2007, Lee *et al.* 2011, Székely *et al.* 2014, Larsson 2022). Hence, adult sex ratios can provide useful information on population structure and potential differences in

survival rates of males and females (Donald 2007). For many bird populations, sex ratios differ from equilibrium and are mostly biased towards males (e.g. Even *et al.* 2001, Kosztolányi *et al.* 2011, Brides *et al.* 2017, Serrano-Davies *et al.* 2022, but see: Jaatinen *et al.* 2010, Grieves *et al.* 2024). Skewed sex ratios in a species may arise from various factors, including unequal sex ratios at fertilization or differences in sex-specific mortality rates among juveniles and adults. However, sex-specific adult mortality is the most significant predictor of the adult sex ratio (Székely *et al.* 2014).

The duck species studied in this context exhibit balanced sex ratios both as embryos and at the hatching stage (Blums & Mednis 1996). However, the sex ratio among adult ducks in the temperate zone is biased towards males in all the studied species (e.g. Campbell 1977, Nichols & Haramis 1980, Larsson 2022, Wood *et al.* 2021, Meissner & Witkowska 2023). Sex difference in post-fledging survival rates is the main factor responsible for skewed adult sex ratio, because in ducks only females participate in incubation and chick-rearing and are therefore more vulnerable to predator pressure during breeding (Bellebaum & Mädlow 2015, Lehtikoinen *et al.* 2018, Wood *et al.* 2021).

An unbalanced sex ratio may have consequences on pairing behaviour. A low number of females forces very early pairing. By early pairing females gain increased foraging efficiency and survival due to male defence and vigilance, while males benefit from increased mate acquisition and improved female condition (Rodway 2007). That is why, in Northern Hemisphere ducks, a pair bond is established in autumn or early winter, and the male must remain close to his partner and actively defend her from other males until insemination occurs and the female begins incubation (Cramp & Simmons 1977). Remaining, unpaired, males cause the male-biased sex ratio, which in winter period may vary between habitats and sites on a local (Pounder 1976, Campbell 1977, Meissner & Witkowska 2023), regional (Nilsson 1976, Rodway *et al.* 2015, Larsson 2022) and continental scale (Carbone & Owen 1995, Brides *et al.* 2017). In local breeding populations, male-skewed sex ratios are likely to affect critical

demographic rates such as breeding success, particularly in species experiencing a long-term decline in the proportion of females (Pöysä *et al.* 2019, Homolková *et al.* 2024). Moreover, trends in sex ratios at individual sites may not reflect patterns observed at larger spatial scales, as demonstrated in the Common Pochard (*Aythya ferina*) (Brides *et al.* 2017, Frew *et al.* 2018). Therefore, extensive monitoring is necessary to record the proportion of males and females for an accurate assessment of the population's structure.

Among other factors, a significant difference in body mass between male and female ducks may influence the sex ratio observed in wintering populations at a given site. Birds maintain some of the highest body temperatures among animals, relying on internal metabolic heat production to offset heat loss in cold environments (Ruben 1996). Moreover, mass-specific energy expenditure is significantly and negatively associated with body mass (Furness & Speakman 2008). Consequently, energy requirements for basic maintenance increase as body size decreases (Kendeigh 1970). Therefore, females, which are smaller than males, have a lower physiological tolerance to low temperatures and are especially susceptible to periods of harsh weather and food shortage (Nichols & Haramis 1980, Jorde *et al.* 1984, Meissner & Markowska, 2009). Therefore, female ducks tend to prefer moderate winter climates in temperate zones, as they require relatively more energy for daily survival (Sayler & Afton 1981). As a result, higher proportion of females was observed in places well protected against wind and with lower susceptibility to waves (Nilsson 1970a, Nichols & Haramis 1980, Woolington 1993). These size differences between males and females also have an impact on differential migration of sexes, where females winter further south in milder climate condition than males (Carbone & Owen 1995, Evans & Day 2001). Moreover, males prefer to winter near the breeding grounds, but their larger size and social dominance over females force the latter to winter further south (Nichols & Haramis 1980, Hepp & Hair 1984, Carbone & Owen 1995). There is also a hypothesis that, in some duck species, the sexes have different flocking tendencies, with males or females being more common in larger flocks or in

areas with higher conspecific abundance (Nilsson 1970a, Owen & Dix 1986, Kestenholtz 1990). However, it was not fully confirmed in other studies (Woolington 1993, Söderholm 2003, Rodway 2006, Meissner & Witkowska 2023).

This study aimed to test the hypothesis that the sex ratio in wintering ducks is influenced by site characteristics and flock size. We examined three species differing in size and habitat requirements. The Mallard (*Anas platyrhynchos*) is an omnivorous dabbling duck adapted to an extremely wide range of habitats. In winter, it forages mostly on various plants and, to a lesser extent, aquatic invertebrates (Delnicki & Reinecke 1986, Combs & Fredrickson 1990, Dabbert & Martin 2000). It is the largest species among those compared in this study and winters in large numbers across Europe, including in urbanized areas (Cramp & Simmons 1977, Figley & VanDruff 1982, Meissner *et al.* 2015, Wetlands International 2025). The mean body mass of male Mallards is about 1150 g, while that of females is approximately 1000 g (Cramp & Simmons 1977). Thus, males are about 14% heavier than females. The Goldeneye (*Bucephala clangula*) is smaller than the Mallard, with male body mass around 1050 g and female body mass about 730 g (Cramp & Simmons 1977). This represents the largest sex-based difference in body mass among the species studied, with males being approximately 42% heavier than females. The Goldeneye belongs to the diving ducks, obtaining food from the bottom of waterbodies. Its main prey in winter includes molluscs, crustaceans, and polychaetes in various proportions (Cramp & Simmons 1977, Custer & Custer 1996, Bourget *et al.* 2007). The Goldeneye winters in large numbers in Europe, primarily in freshwater or brackish habitats, but also in coastal areas (Cramp & Simmons 1977, Wetlands International 2025). The Long-tailed Duck (*Clangula hyemalis*), another diving duck, is smaller than the Goldeneye, with male body mass around 780 g and female body mass about 700 g (Cramp & Simmons 1977). Thus, males are approximately 12% heavier than females, a difference similar to that observed in the Mallard. It spends winter mainly in offshore marine habitats, feeding mainly on bivalves as well as crustaceans, fish, and fish eggs (Skov & Kube

1996, Jamieson *et al.* 2001, Forni *et al.* 2022). The Baltic Sea is its main wintering site in Europe (Skov *et al.* 2011, Wetlands International 2025).

2. Materials and methods

2.1. Bird counts

The study was conducted in mid-January from 1988 to 1995 in the western part of the Gulf of Gdańsk and the estuarine sections of the Vistula River (southern Baltic coast) (Fig. 1). Birds were counted in January during the weekend closest to the middle of the month, along approximately 160 km of shoreline, with each individual or group of birds recorded separately. Only flocks in which the sex of all birds was identified were

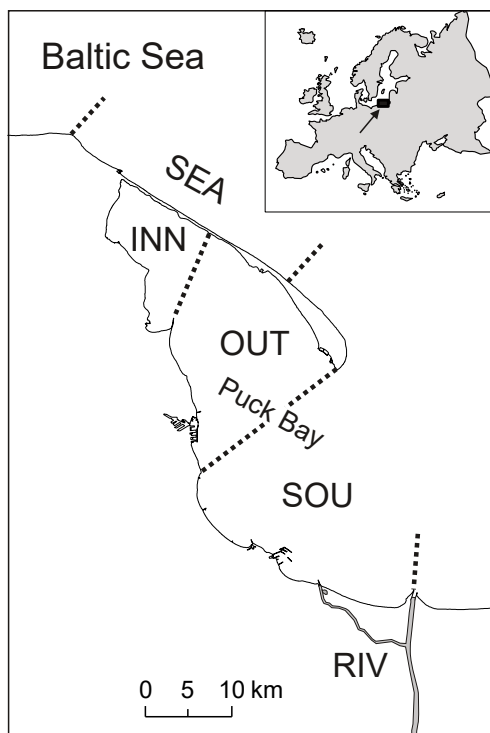


Fig. 1. Study area. The boundaries between the distinguished parts of the study area (see Table 1) are shown with dotted lines.

included in the study, representing about 50% of all flocks recorded. Each person counting birds was assigned a coastal section of 10 to 16 kilometres to walk. The boundaries between sections were placed at natural divisions along the coastline, and it was assumed that the likelihood of counting the same bird flocks twice was low and did not significantly affect the quality of the data collected. Single birds were omitted from the analyses. There were 520 singleton Mallards (males exclusively), 160 Goldeneyes (98 males and 62 females), and 1110 Long-tailed Ducks (893 males and 217 females). These accounted for 2.1%, 0.8%, and 1.3% of all birds of these species, respectively. The total number of flocks included in analyses was 894 in Mallard, 1766 in Goldeneye and 1322 in Long-tailed Duck.

Not all first winter Goldeneye males obtain adult plumage in January and some of them may be still indistinguishable from females, especially when observing in large flocks from a large distance. In Long-tailed Duck first-year males in January resemble adults, while in Mallards the difference in plumages between first-year and adult males are very subtle and in these two species young males are easy distinguishable from females (Cramp & Simmons 1977).

2.2. Study area

The western part of the Gulf of Gdańsk is a water body with diverse environmental conditions. It includes the open sea, exposed to winds, and Puck Bay, which is shallower and sheltered from winds, particularly those blowing from the westerly sector, which account for 40–50% of all winds in the region, and even more during the winter (Majewski 1990, Cieślíkiewicz & Cupiał 2024). The wind waves are much higher in the areas exposed to the wind, *i.e.* on the coast of the open sea and along the southern coast of the Puck Bay. Whereas, in the inner and outer parts of the Bay of Puck, the size of the waves is much smaller (Cieślíkiewicz *et al.* 2017). The inner part of the Puck Bay is the shallowest part of the study area and freezes over most quickly and to the greatest extent, while the outer part is only partially covered by ice during harsh winters

(Korzeniewski 1993). In the seasons under study, winter weather in January was mild and only in 1993 partial icing occurred on the inner and, to a lesser extent, outer parts of the Bay of Puck and parts of the estuarine section of the Vistula. In January 1993 waterbirds stayed numerously in all parts of the study area, hence it is assumed that differences in ice cover had no influence on sex ratio in bird flocks.

Five parts of the study area were identified based on wind cover, susceptibility to icing, depth, slope steepness, bottom characteristics, and phyto- and zoobenthos abundance (Herra & Wiktor 1985, Korzeniewski 1993, Kruk-Dowgiałło 1998, Gic-Grusza *et al.* 2009, Dyrz 2017, Badur & Cieślíkiewicz 2018, Janas *et al.* 2019, Sokołowski *et al.* 2021, Miernik *et al.* 2023) (Table 1, Fig. 1). This division corresponds to the ecosystem units of the Gulf of Gdańsk based on the morphology and dynamics of water masses that determine the living conditions of bottom vegetation and fauna as well as the environmental quality of coastal water masses (Andrzejewicz *et al.* 2004, Błęńska & Osowiecki 2015). The boundary between inner and outer part of the Puck Bay is widely used in other studies, while its southern part is characterised by greater depths, the absence of reed beds and the presence of urban beaches where people feed the birds intensively (Korzeniewski 1993, Meissner & Ciopcińska 2007). Due to the low number of Long-tailed Ducks in the inner part of the Puck Bay, the inner and outer parts were combined in the analyses for this species.

2.3. Data analysis

The mean bird number per 1 km of coastline was used to determine the part of the study area of greatest importance for each of the three species. It was assumed that gregarious behaviour of ducks (Owen & Black 1990) combined with a heterogeneous availability of resources leads to a concentration of individuals on sites with the best quality (Loring *et al.* 2013, Pap *et al.* 2013, Cervencel *et al.* 2015). To compare densities of studied species between parts of the study area, the Kruskal-Wallis test was used with post-hoc Dunn test (Zar 2010). Using a Generalized Linear

Table 1. Characteristics of the study area parts distinguished in this study.

Name and abbreviation	Midpoint coordinates	Total length of the coast	Characteristics
Open sea (SEA)	54.760 N 18.522 E	31.6 km	Fully exposed to winds. Highest water waves in windy conditions. Sandy bottom. Lack of coastal plants and reedbeds. About 11 km with rows of piles overgrown with periphyton. Depth increasing rapidly with distance from shore. Benthic fauna (molluscs, crustaceans and polychaetes) in moderate densities. Very low number macrophytes.
Inner part of the Puck Bay (INN)	54.723 N 18.488 E	34.3 km	The shallowest part of the study area. Good wind protection. Waving very low. Usually at least partially iced over in moderate winter. Sandy bottom. Very high densities of zoo- and phytobentos. Coast overgrown by plants and often by reedbeds.
Outer part of the Puck Bay (OUT)	54.627 N 18.646 E	28.0 km	Moderately protected from western and northern winds. Waving in winter usually low. Moderate waving only for eastern wind. Bottom mainly sandy with some areas of mud and coarse sediment. High spatial variability of zoo- and phytobenthos densities. Sandy coasts with low number of reedbeds.
Southern part of the Puck Bay (SOU)	54.420 N 18.717 E	36.1 km	Fully exposed only to north-eastern and eastern winds. Sandy bottom. Lack of coastal plants and reedbeds. Depth increasing slowly with distance from shore. About 15 km of municipal beaches, where people regularly feed birds. High densities of benthic fauna. Low and moderate densities of macrophytes.
Riverine habitats (RIV)	54.310 N 18.932 E	27.0 km	Shallow (mainly 3-4 m deep) estuarine sections of the Vistula River and a small coastal lake. Banks are vegetated and partially with reedbeds. Muddy and sandy bottom. Good wind protection. Waving very low. No recent data on zoo- and phytobentos. Very high number of wintering bentophages suggests a high density of zoobenthos.

Model (GLM) (McCullagh & Nelder 1989), the proportion of males (response variable) was modelled as a function of part of the study area (categorical explanatory variable) and flock size (continuous variable) in each of the three species separately. Preliminary analyses with the use of ‘performance’ R package (Lüdecke *et al.* 2021) revealed a significant deviation from normality of residuals in all three models. As proportion of males shows only positive values and their distribution was right-skewed, we employed a GLM with a gamma error distribution and a logarithmic link function (Dunn & Smyth 2018), which brought the distribution of the residuals close to a normal distribution. Performance of obtained models were assessed using the ‘performance’ R package (Lüdecke *et al.* 2021). In the models concerning Goldeneye and Long-tailed Duck, the variance inflation factor (VIF)

was below 2.0, indicating low multicollinearity. In contrast, for the Mallard, the VIF exceeded 100, revealing extremely high collinearity, with variance over 100 times greater than in the case of orthogonal predictors (Hair *et al.* 1995). After excluding the smallest flocks of two and three birds, the VIF value dropped to 7, which is considered acceptable, as values below 10 are generally not regarded as problematic for multicollinearity (Dormann *et al.* 2012). As a result of this exclusion, the number of Mallard flocks included in the analysis decreased to 630. In all models there were no influential observations and no deviations from linearity. Only in the case of the Goldeneye and Long-tailed Duck was slight heterogeneity of variances observed, which is typically not problematic for GLMs, especially when sample sizes are sufficient (Hair *et al.* 1995). Therefore, it was

assumed that there are no major deviations from the assumptions of the linear model that could affect obtained results.

The open sea coastal area is fully exposed to winds from the prevailing directions in winter and characterized by the highest waves (Table 1) In some duck species the proportion of males wintering in such conditions is expected to be high (Nilsson 1970a, 1976, Campbell 1977). Hence, when determining the effect of part of the study area on proportion of males, the open sea was set as the baseline for comparisons. We performed post-hoc comparisons using linear contrasts with the package ‘emmeans’ (Length 2021). The statistical significance of observed differences was evaluated considering $P < 0.05$. All analyses were performed in R 4.4.2. Differences in body mass between males and females were calculated using a weighted

average of the data provided by Cramp and Simmons (1977), taking into account differences in bird numbers between different samples.

3. Results

The highest number of Mallards was recorded in outer and inner parts of the Puck Bay and in the riverine habitats. Their densities in southern part of the Puck Bay and in the seacoast were significantly lower (Fig. 2). The Goldeneye also revealed lower densities in these two parts of the study area, but the highest number in the inner part of the Puck Bay and in riverine habitats (Fig. 2). In contrast to these two species, Long-tailed Duck densities were highest along the open seacoast and in the riverine habitats with significantly lower numbers in Puck Bay (Fig. 2).

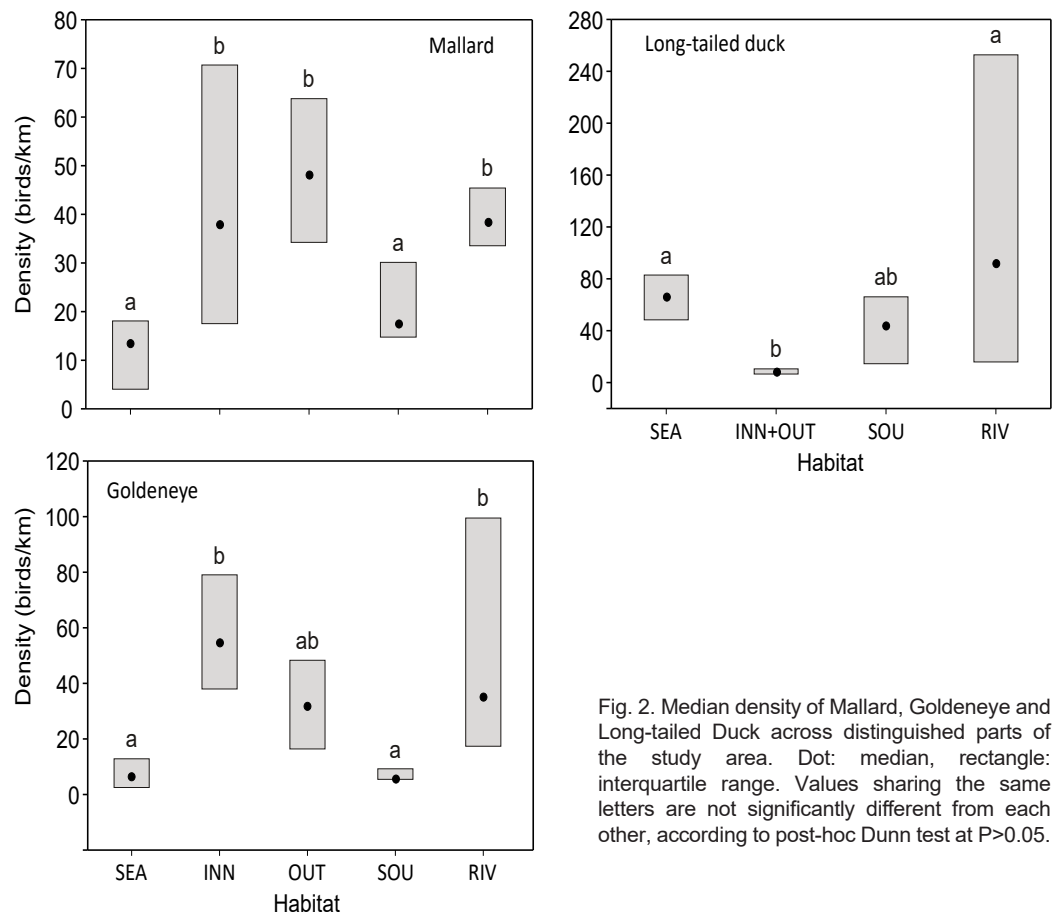


Fig. 2. Median density of Mallard, Goldeneye and Long-tailed Duck across distinguished parts of the study area. Dot: median, rectangle: interquartile range. Values sharing the same letters are not significantly different from each other, according to post-hoc Dunn test at $P > 0.05$.

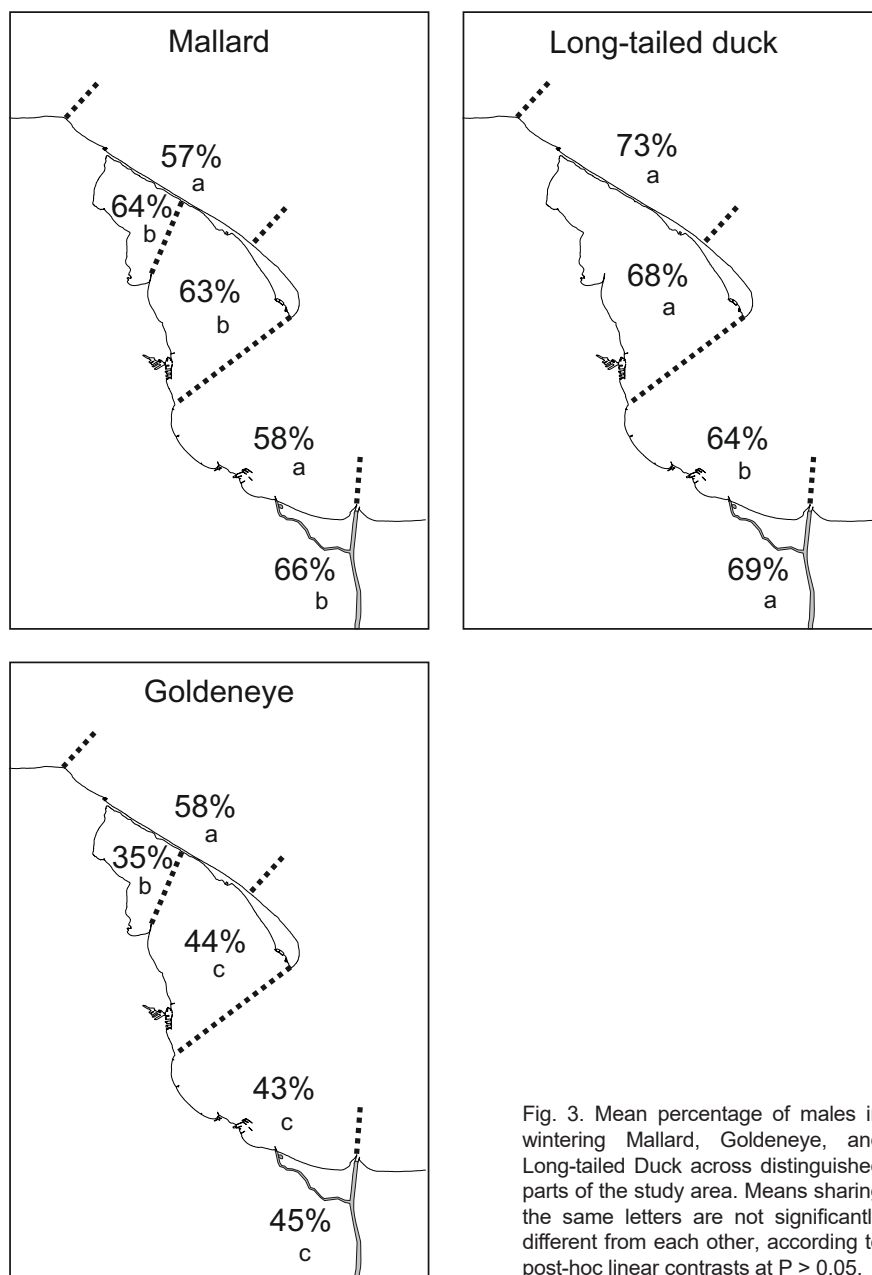


Fig. 3. Mean percentage of males in wintering Mallard, Goldeneye, and Long-tailed Duck across distinguished parts of the study area. Means sharing the same letters are not significantly different from each other, according to post-hoc linear contrasts at $P > 0.05$.

Conspicuous variability of mean densities of Goldeneye and Long-tailed Duck in riverine habitats is due to the appearance of very high numbers of these species only in the last four years of the survey.

The proportion of males in all three species differed significantly between distinguished parts

of the study area (Tables S1, S2, S3). In Mallards, the percentage of males was highest in the estuarine section of the Vistula River and in the inner and outer parts of the Puck Bay. In the open seacoast and the southern part of Puck Bay, the percentage was significantly lower (Fig. 3). Contrary to the Mallard, the proportion of males

in Goldeneyes reached its maximum in the open sea coastal section fully exposed to winds, while it was lowest in the inner part of Puck Bay. In other parts, the proportion of males in this species had intermediate values (Fig. 3). In Long-tailed Ducks, the proportion of males in flocks was more evenly distributed across the study area, with a significantly lower value only in the southern part of Puck Bay (Fig. 3). For all three species, there was no significant relationship between the proportion of males in a flock and flock size (Tables S1, S2, S3).

4. Discussion

The most of ducks from temperate zone show seasonal monogamy and male-biased sex ratio (Nilsson 1970a, Rohwer & Anderson 1988). Thus, a large number of males have little opportunity for reproduction. The pairing process occurs very early and in Mallard almost all females are paired in January (Johnson & Rohwer 1998, Jonsson & Gardarsson 2001). Once a pair bond is established, paired males remain close to their mates, engaging in mate guarding (Goodburn 1984, Meissner & Markowska 2009). Male attendance offers paired females benefits of increased social status, better access to food and less harassment from conspecifics, whereas males' benefit is mate acquisition (Ashcroft 1976, Hepp & Hair 1984, Rohwer & Anderson 1988). The lowest proportion of male Mallards along the section of the open seacoast and the southern part of Puck Bay suggests that this area is mainly occupied by paired birds. Paired males achieve a higher hierarchical position in the flock than unpaired ones (Bossemma & Roemers 1985) and show a tendency to remain at the wintering site during deteriorating weather conditions, while unpaired males left these sites, resulting in a less skewed sex ratio (Meissner & Witkowska 2023). Strong aggression by paired males towards unpaired ones (Hepp and Hair 1984, Johnson & Rohwer, 1998, Schummer *et al.* 2020) results in the latter being forced out of areas where females with their mates are present (Meissner & Witkowska 2023). Hence, a shift in the occurrence of unpaired males toward sites offering better

overwintering conditions seems a likely explanation for their higher proportion among Mallards observed in the inner and outer Puck Bay and the estuarine section of the Vistula River, where the number of wintering birds of this species was significantly higher than in two other areas. Females remaining with their partners in open sea suboptimal habitat experience less pressure from conspecifics in accessing food in the form of periphyton overgrowing rows of wooden piles (Table 1). In the southern part of the Puck Bay the proportion of males was also low, as it was in open sea coast. Mallards concentrated here mainly along municipal beach, where 89% of all birds of this species observed in this part of the study area were noted. Along the municipal beach, people intensively feed waterbirds in winter and Mallard shows strong tendency to stay in large number in such places due to additional food resources available (Avilova & Eremkin 2001, Meissner *et al.* 2015, Witkowska *et al.* 2024). Exploiting abundant anthropogenic food resources may be profitable especially for females, which are smaller than males by about 14% of their body mass and thus are more sensitive to low temperatures in winter (Pattenden & Boag 1989, Jónsson 2010). Therefore, females remained here together with males they paired with, resulting in a lower proportion of males at such sites. This is in line with the study conducted in an urbanized area documenting the sex-dependent response of Mallards to temperature changes during the winter period. In severe weather conditions, females remained with their paired mates, whereas unpaired males possibly left the town (Meissner & Witkowska 2023).

The inclusion of groups of two and three birds in the GLM analysis resulted in very high collinearity in the model. Groups of two Mallards consisted of 87% paired birds, with the remaining 13% being two males. In groups of three individuals, the majority (81%) comprised two males and one female, while all other cases consisted of three males. This is due to the typical pairing behaviour of this species (Cramp & Simmons 1977). The GLM analysis, including groups of two and three birds and accounting for high collinearity, produced the same results, with the same significant differences between

designated parts of the study area in the post-hoc test.

Among the three species studied, the difference in body mass between males and females was largest in the Goldeneye. Similar to another study on the sex ratio of this species (Campbell 1977), the lowest percentage of Goldeneye males was found in the inner Puck Bay, the area most sheltered from the predominant western and north-western winds. Wind speed is important in increasing physiological cold stress (Krishnan *et al.* 2023), so topographical features of the area surrounding a water body and prevailing wind patterns may contribute to differences in sex ratios at a site (Bennett & Bolen 1978, Krishnan *et al.* 2023). The proportion of males was intermediate in the rest of the Puck Bay and the estuary of the Vistula River, which are somewhat less sheltered from the winds. Along the open seacoast the percent of males was the highest together with low number of birds stayed there. Hence, the density and the sex ratio of Goldeneye reflect differences in tolerance towards adverse weather conditions of females. Especially since, in this species males are larger than females by 42% by body mass (Cramp & Simmons 1977). Therefore, the smaller and lighter Goldeneye females are predicted to select habitats with more moderate winter weather conditions (Campbell 1977, Sayler & Afton 1981), as they require relatively greater amounts of energy for existence and have lower resistance to food shortages during periods of low temperatures and long winter nights. However, in the Goldeneye, some first-year males may still be difficult to distinguish from females in January (Cramp & Simmons 1977). These young males, with no clearly visible signs of breeding plumage, remain unpaired, but their presence lowers the proportion of males in flocks. Nevertheless, the number of juvenile males wintering in northern latitudes seems to be rather low (Nilsson 1970a, Sayler & Afton 1981). Therefore, their presence may have only a minor influence on the obtained results.

In non-breeding period the Long-tailed Duck reveals strong preference to open seas habitats (Cramp & Simmons 1977). Therefore, its number was the lowest in inner and outer parts of the Puck Bay and the highest along the open seas

coast, as the open sea areas gather the vast majority of wintering Long-tailed Ducks in the Baltic (Skov *et al.* 2011). The high numbers of birds of this species in the Vistula estuary is due to large flocks entering this part of the river at dawn and remaining there until dusk (authors' unpublished data). This behaviour of Long-tailed Ducks was observed only in last four years of the study and its cause is unknown, but these birds were observed diving frequently there, which suggests foraging. The sex ratio in the Long-tailed Duck is the most balanced among the species studied. Only in the Long-tailed Duck the percent share of males in the inner and outer parts of the Puck Bay was similar to open seacoast. Movements of Long-tailed Ducks over Hel Peninsula, between these parts of the study area, are observed quite frequently (authors' unpublished data). Whereas, in Vistula estuary Long-tailed Ducks stay only during daytime with large number of birds arriving in the morning and departing before night. It is likely that the small concentrations of this species outside the open sea are short-lived and involve males and females in similar proportions that are present in the open sea resulting in not significant differences in male proportions between these areas. Only along southern coast of the Puck Bay the proportion of males was significantly lower. The sexually-selected behaviour and the formation of large groupings in areas of abundant food may explain the differences in winter distribution of both sexes in wintering sea ducks, which was found in Harlequin Duck (*Histrionicus histrionicus*), a sea duck similar in size to Long-tailed Duck. In this species, unpaired birds were more likely to move to exploit sites with abundant food resources, where they obtained nutritional benefits and facilitated courtship and mate sampling (Rodway 2006). If such behaviour also applies to the Long-tailed Duck, it may explain the observed movements of birds between regions of the study area and only slight differences in the proportion of males in this species.

In each of the three species studied, flock size had no effect on the observed sex ratio. However, the flock sizes used in the analyses exceeded 100 birds in only 8.5%, 3.5% and 2.3% of the Mallard, Goldeneye and Long-tailed Duck respectively, and the number of flocks above 300

individuals ranged in these species from three to seven. There is only one publication that demonstrated such a trend and included flocks of more than 1,000 individuals (Owen & Dix 1986), whereas another study, which also analysed flocks of this size, found no such relationship (Evans *et al.* 2001). Moreover, the sex ratio of ducks in large flocks is very difficult to determine, and the error in estimating the number of birds in flocks of approximately 1,000 individuals can be as high as 10% (Nilsson 1970a). Therefore, in our study, we avoided determining sex ratios in such large flocks. Thus, on the one hand, the variability in flock size in our study may not be sufficient to demonstrate a possible effect of flock size on sex ratio. On the other hand, however, sex ratios in duck flocks may be strongly influenced by the habitat conditions in which the birds stay than by flock size. In general, more smaller duck females than males has been observed in shallower and more calm water bodies (Nilsson 1970a, Campbell 1977, Saylor & Afton 1981, this study), which was related to larger food requirements of the females making it necessary for them to feed longer or more frequently than the males (Nilsson 1970b, Kaminski & Prince 1981, Munday & Rose 2022). Therefore, the marked differences in sex ratios between different parts of the study area may also reflect local differences in food resources.

Intersexual competition for food has been identified as an important factor influencing sex ratios in duck groupings during winter (*e.g.* Hepp & Hair 1984, Alexander 1987, Choudhury & Black 1991). However, by January, all Mallard females and the majority of female Goldeneyes and Long-tailed Ducks are paired and protected by their mates from aggression by other individuals (*op. cit.*). Therefore, the sex ratio of ducks at a given site seems to be a result of the interaction of various ecological and behavioural traits that compromise against different selection pressures, such as sexual segregation within habitats and intersexual competition for food (Nilsson 1970a, Campbell 1977, Saylor & Afton 1981, Duncan & Marquiss 1993).

The sex ratio at breeding and wintering sites is a fundamental demographic parameter that provides valuable information on the differential

survival rates of the sexes. This offers important insights into population dynamics and can indicate demographic factors contributing to population decline (Donald 2007, Brides *et al.* 2017). However, differences in sex ratios between closely located areas of the study site also have implications for planning further research on the sex structure of wintering ducks and highlight the need for large-scale sampling to obtain representative estimates of the sex ratio for a given species as it was shown for Common Pochard (Brides *et al.* 2017, Frew *et al.* 2018). Furthermore, in such surveys, bird counts should be conducted across a variety of habitats, including areas sheltered from the wind as well as those exposed to stronger wave action, since this factor appears to significantly influence local differences in sex ratio. In species such as the Mallard, which often rely on food provided by humans, the sex ratio may differ between sites where birds are fed and sites where they are not. This factor should therefore also be taken into account.

Paikallinen vaihtelu talvehtivien sorsalintujen sukupuolijakaumassa kolmella lajilla: Laajamittaisen havainnoinnin tarve

Tässä tutkimuksessa tarkastellaan hypoteesia, jonka mukaan alueen ominaisuudet ja parven koko vaikuttavat talvehtivien sorsalintujen sukupuolijakaumaan. Tutkittavana oli kolme lajia: sinisorsa (*Anas platyrhynchos*), telkkä (*Bucephala clangula*) ja alli (*Clangula hyemalis*) Gdańskinlahdella, eteläisellä Itämerellä. Linnut laskettiin tammikuun puolivälissä noin 160 km:n pituisella rantaviivalla Gdańskinlahden länsiosassa ja Veikseljoen suistoalueilla eteläisellä Itämeren rannikolla. Analyysiin sisällytettiin vain ne parvet, joissa kaikkien yksilöiden sukupuoli voitiin määrittää. Kolmen tutkitun lajin sukupuolijakaumat vaihtelivat tutkimusalueen viiden eri elinympäristötyypin välillä, mutta eivät lajikohtaisen parven koon mukaan. Sinisorsalla pienin koiraiden osuus havaittiin avoimella merenrannalla ja kaupunkirannalla, mikä viittaa siihen, että nämä ovat pääasiassa pariutuneiden lintujen alueita. Muiden alueiden suurempi koiraiden osuus

johtuu todennäköisesti pariutumattomien yksilöiden siirtymisestä näille alueille, joissa lajin kokonaismäärä on suurin. Telkällä suurin naaraiden osuus havaittiin suojaisimmilla alueilla, kun taas pienin osuus, yhdessä yksilömäärän kanssa, esiintyi avoimella merenrannalla. Nämä mallit viittaavat siihen, että telkän tiheys ja sukupuolijakauma liittyvät naaraiden sietokykyyn epäsuotuisia sääolosuhteita kohtaan, sillä tutkituista lajeista telkällä on suurin kokoero koiraiden ja naaraiden välillä. Allilla sukupuolijakauma oli tasaisempi koko tutkimusalueella, mikä johtuu todennäköisesti lajin aktiivisesta liikkumisesta alueille, joilla oli runsaasti ravintoa. Tutkimus korostaa sorsalintujen sukupuolijakauman alueellista vaihtelua yhden vesialueen sisällä ja osoittaa, että edustavien sukupuolijakauma-arvioiden saamiseksi tarvitaan laajamittaista havainnointia.

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Online supplementary material

Supplementary material available in the online version of the article includes Tables S1-S3.