

A 30-year (1988–2017) study of Mute Swans *Cygnus olor* in Riga, Latvia

RUSLANS MATROZIS

Latvian Ornithological Society, Skolas iela 3, Rīga, LV-1010, Latvia.

E-mail: matruslv@inbox.lv

Abstract

Ringling of Mute Swans *Cygnus olor* in Riga and its surrounding area (*c.* 500 km²) has been undertaken since January 1988. Numbers breeding in this area currently amount to *c.* 40 pairs, with *c.* 150–200 swans wintering in the region. A total of 2,446 individuals were ringed over a 30-year period (1988–2017), and 42,968 sightings or recoveries of these birds were recorded, with an average of 16 sightings per swan (up to 544 sightings for one individual). During the study, 295 (12.1%) individuals were seen abroad, with the longest migration distances being to the Netherlands (1,267 km) and the Ukraine (1,238 km) in severe winters. Sightings of 144 swans ringed in other countries were also recorded in Riga, mostly (54.2%) from Lithuania. The mean date on which migrating swans were first identified in Riga each spring was 11 March (range: 26 February–4 April during 2004–2017). Two spring migration waves were detected: the first was a continuous period of 3–4 weeks from the initial arrival day, while the second, at the end of May and beginning of June, was of non-breeding swans migrating to their moulting sites. First successful breeding was observed during the 3rd and 4th calendar years of life, but most swans (68%) started breeding between the ages of 4–6 years. Longest runs of successive successful breeding seasons (*i.e.* without skipping a year) were 10 years (male) and 11 years (female). Oldest successful breeders were 15+ years (for a male first ringed as an adult) and 16+ years (female), whilst the maximum number of cygnets produced during the life-time of one swan was 46 (for a male) and 59 (for a female). Hatching locations were known for 197 swans and five subsequently found breeding were all < 10 km from their natal territory, indicating that natal dispersal typically occurred over short distances. Of the 2,446 ringed swans, 620 were found dead or re-sighted in at least two winter periods, of which most (87%) were sighted in at least 5 winters, up to a maximum of 16 winter seasons. Only 4.5% were sighted or recovered > 10 years after ringling; the maximum age recorded was 17 years (male) and 18+ years (female). Polish morph Mute Swans were rarely observed in Riga; only 14 such individuals were ringed in total (0–3 per year between 2004 and 2017), representing 0.57% of all swans ringed during the study.

Key words: breeding phenology, individual life-histories, Latvia, migration, Mute Swan, Polish morph, ring re-sightings.

The first breeding of Mute Swans *Cygnus olor* within the borders of modern-day Latvia has been described in historical publications, with colonial breeding and also hunting of swans on the shallow coastal waters of Lake Papes (west Latvia) reported from *c.* 1777 up to 1844 (Bernoulli 1779; Beseke 1792; Andre 1845). During the mid-19th century, breeding was only reported for captive swans on the artificial ponds and lakes of large properties, but from 1882 onwards single swans also occurred in some public places. In 1935 a pair of wild Mute Swans was first observed breeding on the coastal Lake Engures in western Latvia (Transehe 1939) and 1–3 pairs occasionally bred at the same lake thereafter, although in some years they were shot by local hunters because the species was not protected by law during the breeding season. It was not until 1957 that the Mute Swan was included in the list of protected birds for Latvia, which made it illegal to hunt the species at any time of year. In the same year, parts of Lake Engures and some other shallow coastal lakes in western Latvia were protected for waterbirds occurring at these sites, and the protection measures had a positive effect on the number of Mute Swans breeding in the area, which started to increase.

The first national count of Mute Swans breeding in Latvia was undertaken in 1964, when the population was estimated at *c.* 40–60 breeding pairs (Vīksne 1968). In 1972, 80–100 pairs were recorded at 31 sites (Lipsbergs 1979), but the suitability of waterbodies for nesting swans was considered more carefully during the first census of Mute Swans breeding across the Soviet Union in 1974, resulting in more

accurate estimates for Latvia of at least 220 pairs on 37 waterbodies (Jogi *et al.* 1976). By the time of the second swan census across the Soviet Union, in 1978, the breeding population in Latvia had increased to at least 350 pairs on 77 waterbodies (Lipsbergs 1983), and the third census in 1987 found at least 350 pairs on 116 waterbodies (Lipsbergs 1990a). From the 1980s onwards, breeding Mute Swans started to occupy waterbodies in central and eastern parts of Latvia, and in 1981 they reached the border of Riga city. At least 500 pairs were counted on 198 waterbodies in 1992 (Lipsbergs 1995), and in 1997 about 600 pairs were reported (Kalniņš 1998).

During the 21st century, the number of Mute Swans breeding in Latvia is considered to be stable and is estimated at about 500–600 pairs (BirdLife International 2015). A geographical assessment of Mute Swan populations in western and central Europe established that swans from Latvia belong to the Scandinavian-Baltic group (Wieloch 1991), which is mostly sedentary in the western part (in Denmark, Sweden and north Germany) and more migratory in the eastern part of its range (Poland, Finland, western Russia and the Baltic States).

The overall aim of this study was to use the insights of a long-term ringing programme to improve our understanding of the movements and demography of Mute Swans in Riga. In particular, it sought to understand the magnitude and frequency of swan movements, both within Latvia and exchanges with other countries. The timings of seasonal movements related to events in the annual cycle, such as breeding, moulting and wintering, were also quantified.

Finally, such long-term data on individual swans allowed assessments of important demographic information such as lifespan and breeding performance, including the age of first successful breeding and life-time reproductive success.

Methods

Study area

The study was undertaken in Riga (the capital city of Latvia; 307 km²; 56.57°N, 24.07°E) and the surrounding area, extending to a total study area of *c.* 500 km². First breeding by Mute Swans in the city of Riga was observed on the shallow Lake Mašēnu, very close to the city boundaries, in 1981. Over the next four decades, swans occupied 50 of the waterbodies most suitable as breeding territories, and in good breeding years numbers reached 40 pairs. In the early years, the first breeding pairs notably avoided contact with the public and tried to use waterbodies with abundant aquatic vegetation. Growth of the local population was slow initially and over the first decade it reached only 10–15 breeding pairs. In the warm winter of 1987/88, however, many swans stayed to overwinter in Riga and its surroundings, and at the end of this season many changed their behaviour and started to accept additional food (mostly white bread) offered by the public, in some cases taking it from the hand. This provided local bird ringers an opportunity to catch some of the swans for ringing, and swans ringed in other countries were also observed during this winter. Up to 2002, Mute Swans were ringed and subsequently either re-sighted alive or recovered dead in Riga, usually in winter,

because from early spring to late autumn most avoided direct contact with humans. A further change in swan behaviour occurred in spring 2002, when the birds started to approach the public for food, a practice which continued into summer and autumn.

Mute Swans started wintering in the Riga district during the early 1980s, when they were first seen on the coast of the Gulf of Riga near the city of Jūrmala, and at some inland waterbodies which had not frozen. Numbers increased from some tens of swans in the mid-1980s up to 300 in winter 1992/93 (Stīpniece & Matrozis 2001), but later stabilised at *c.* 150–200 swans in winter each year. Riga city has many feeding and resting places used by the swans, mostly on the Daugava River, which is also an important migration route for the birds as they move to breed on waterbodies in inland parts of Latvia, Lithuania and Belarus, and particularly during their moult migrations to the large coastal lakes of western Latvia, the shores of the Riga Gulf, and also to the Pärnu Bay coastline in Estonia. All of the most important wintering sites for Mute Swans in Riga are situated on, or close to, the Daugava River.

Mute Swans observed in Latvia belong to the “Scandinavian-Baltic group” (Wieloch 1991) and most migrate over distances in excess of 600–1,000 km per year. The following types of migration are recognised: 1) return migration between the wintering and breeding grounds (undertaken by breeders and non-breeders, involving a 250–800 km movement in each season); 2) a moult migration (undertaken by non-breeders, of 30–150 km) mostly to the shallow coastal lakes of Latvia (to the west

and northwest of Riga) and to the coast of Pärnu Bay in Estonia; 3) migration of breeders and young swans to wintering grounds (up to 250–800 km); and 4) migration of non-breeders from moulting locations to other stopover sites or directly to wintering sites (up to 250–800 km).

Ringings and re-sightings

Ringings of Mute Swans wintering in Riga and its surroundings commenced in January 1988 (Fig. 1). From 1988 to 1999, custom-made thin aluminium swan rings with a black or red coloured number were used, while from 2000 thicker aluminium rings with black alphanumeric codes manufactured

by “Aranea” (Poland) were fitted to the swans. The thicker aluminium rings were more durable, were more difficult for the swans to remove or lose, and could easily be read through binoculars over the entire lifetime of a swan (up to 20 years, based on this study). In addition, the black colour text on these rings was durable and readable over many years (some swans have rings that still show partial colouration after 15–17 years). Some swans were regularly seen using their bill to open the ring’s lock, so to reduce ring loss many were reclosed, in some cases several times. In addition to the metal rings, small number of plastic leg-rings (Ogilvie 1972) and neck-collars were also used:

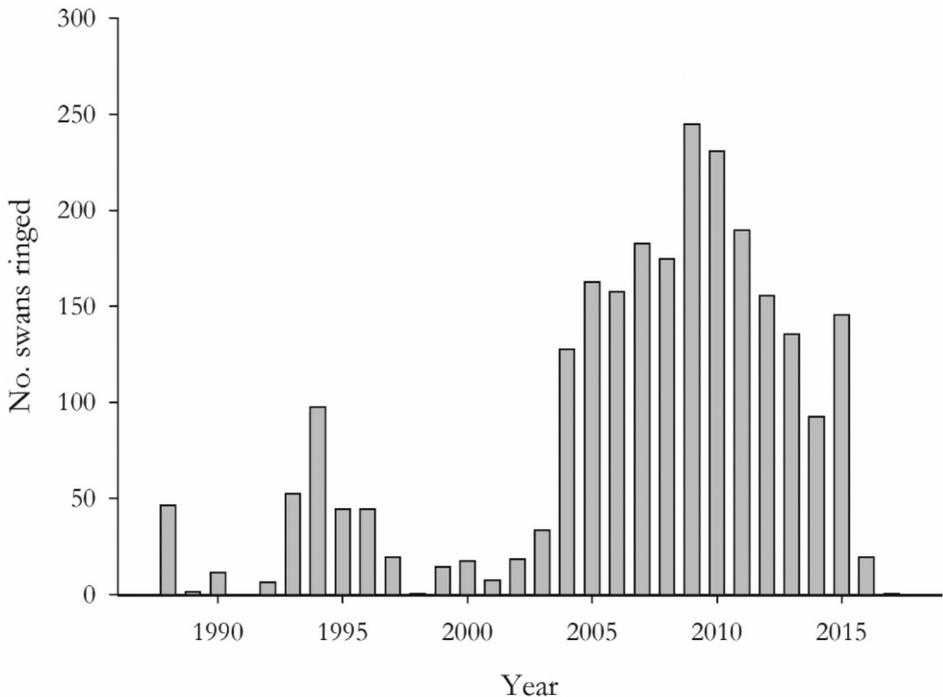


Figure 1. Total number of Mute Swans ringed for the first time in Riga ($n = 2,446$ for years 1988–2017 inclusive).

98 neck-collars (blue with white codes CT00–99, in 2004–2009) and 18 leg-rings (in 2011–2012). All plastic rings and collars were provided by Pelle Andersen-Harild (Denmark).

The swans were caught by using white bread to attract individuals to the shore, whereupon they were caught by hand. Between 1988–2003 Mute Swan ringing was possible mostly in winter months, but from 2004 it was possible to catch and ring swans throughout the year. The sex of each individual was determined by cloacal examination. Precise age could be determined for 53% of caught swans based on their plumage characteristics, whilst for the remaining 47% (*i.e.* individuals caught as adults of unknown age) only a minimum age could be estimated; ages for the latter are therefore given with the suffix +, whereby 15+ refers to an individual with a minimum age of 15. It was also noted whether each captured swan was a “Polish morph” individual, based on plumage and skin characteristics (Bacon 1980). Ringing activity was discontinued in spring 2016, in part because it was judged that sufficient data had been obtained to answer the questions set out in this paper, and in part because of difficulties in finding replacement volunteers to co-ordinate a long-term ringing study of a common, abundant species such as the Mute Swan.

All ringed Mute Swans re-sighted or recovered were identified by reading the ring code, usually using binoculars but in some cases by eye without any optics or by using a telescope, on identifying live birds in the field. Up to the 2000s all information collected (ringing, re-sighting and recovery data) was stored in hand-written journals,

but later data were transferred to a Microsoft “Access” database. Nowadays this database contains not only all information about any ringed Mute Swan seen in Riga but all re-sightings and recoveries of swans ringed in Riga reported elsewhere in Latvia and abroad, with one re-sighting or recovery referring to one observation of a ringed swan in one location during one calendar day.

Additional information about Mute Swan numbers has also been collected, including the number of adult (white plumage) and young (brown plumage) swans at the most important feeding sites for the species in Riga, as well as at their breeding sites, which are monitored from April to late autumn. Information about the use of moult sites by Mute Swans, including numbers and phenology of moulting swans, was obtained through repeated surveys to check for ringed birds at the main moulting location in Riga, the Daugava River, every 3–5 days during late June and July during the study. Additional information about moulting places of swans outside of Riga was obtained from the locations of swans re-sighted or recovered during the moult period. Such information allowed the numbers of swans, as well as the timing and duration of their moult period, to be determined.

Results

During the thirty years of the study (1988–2017), a total of 2,446 Mute Swans were ringed in Riga and its environs (Fig. 1). Overall, 42,968 records of 2,235 ringed swans were collected, of which 96% (41,536) were from Riga and the surrounding area (Fig. 2). Most were seen alive; only 164 swans were

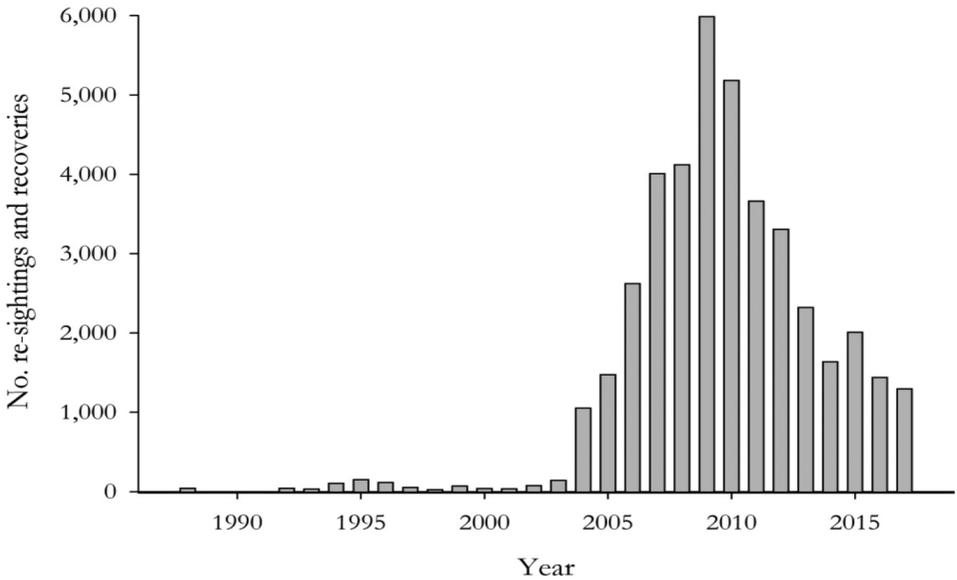


Figure 2. Timing of 41,479 re-sightings and 57 recoveries of ringed Mute Swans in Riga ($n = 41,536$ records, for years 1988–2017 inclusive).

reported as dead (7.3% of the ringed swans). The number of re-sightings of ringed swans during the study ranged from 1–544, with an average of 16 re-sightings per bird. Over the first 16 years (1988–2003), 1,129 re-sightings and recoveries were collected in total, of which 88% were collected during the winter periods; in contrast, between 2004–2017 40,397 re-sightings and recoveries were collected (Fig. 2), of which 35% were from the winter seasons. In total, 295 individuals (12.1%) were re-sighted in 13 countries outside Latvia (Fig. 3; Fig. 4). Moreover, 144 Mute Swans ringed elsewhere, from nine different, countries were observed within Riga (Fig. 3).

Choice of wintering area

A total of 620 ringed swans (a subset of the total sample size of 2,446) were reported

across all wintering sites in at least two seasons, of which 87% were reported in at least 5 winter seasons, 13% were recorded in at least 6 winter seasons, and for some individuals the wintering sites in up to 13–16 seasons were known. Approximately two-thirds of these 620 swans wintered in one location, for an average of 5–6 seasons, but others changed wintering areas for many possible reasons, such as breeding phenology, safe and comfortable wintering, and accessibility of food in previous seasons. Winter site fidelity also likely depended on wintering conditions, as many swans try to stay at, or close to, one wintering site during the whole wintering season, but *c.* 20% of them move south and southwest to spend the remaining part of winter in a warmer climate. Most records of ringed swans observed in different locations during a

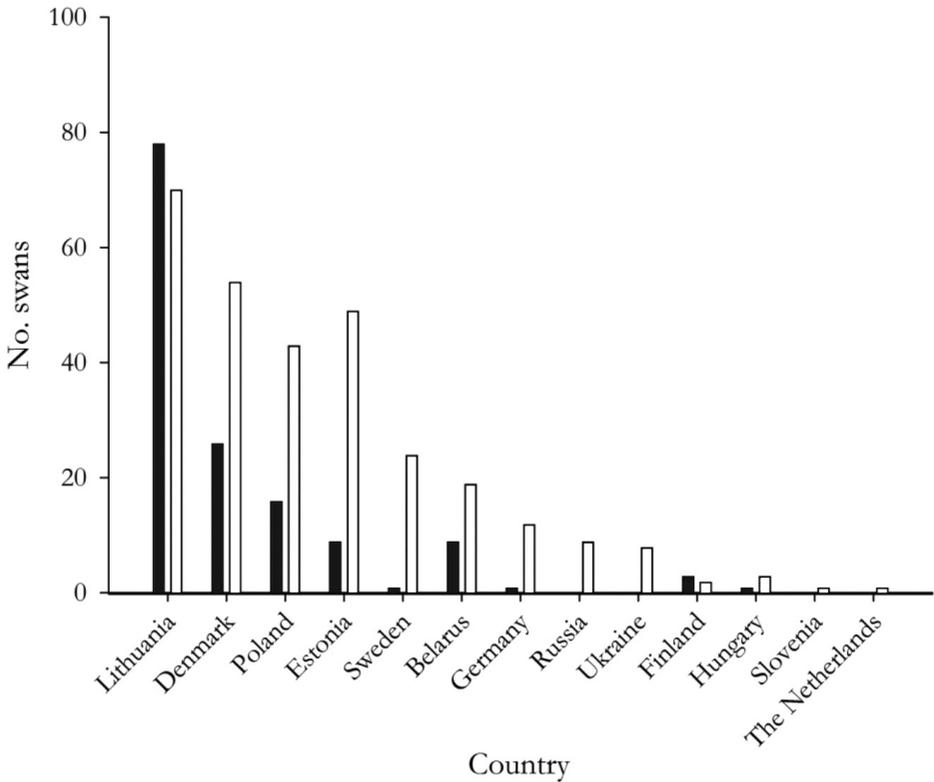


Figure 3. From 2,446 ringed swans in Riga, 295 individuals (12.1%) were re-sighted or recovered abroad in one of 13 countries (white bars), while a total of 144 swans ringed in one of nine other countries were observed in Riga (black bars).

single winter season were typically observed in early winter (up to the middle of January, after which ice cover in Riga forces many swans to move to the ice-free Baltic Sea coast); later in the winter, only occasionally did single swans move to other sites.

The longest distance moved by a swan between two wintering locations in different seasons was 1,108 km (Fig. 4). This female, hatched in 2001 (ring Latvia Riga EE022) spent the first winter (2001/02) in Riga, the next winter (2002/03) it was re-sighted in Hungary, on the 3rd and 5th winter there

was no information about wintering places (not in Riga), but in the 4th and from 6th–16th winters this swan was seen again in Riga.

At the main wintering site on the Dārziņu Old River (near the Riga city boundary), the proportion of young swans (*i.e.* individuals within their first year of life) in January was on average 23% (range: 11–38%, 2002–2017). The age structure of Mute Swans wintering at the site in 2015/16, based on data recorded for 140 ringed birds of known age identified, was as follows: 1st year of life



Figure 4. The locations of re-sighted and recovered swans that were ringed in Riga, or ringed elsewhere and subsequently re-sighted or recovered in Riga, during the present study.

= 21% ($n = 29$), 2nd year of life = 6% ($n = 9$), from 3rd to 9th year of life = 58% ($n = 81$), and 10th–17th year of life = 15% ($n = 21$).

River Daugava as an important Mute Swan migration route

A total of 1,368 Mute Swan counts were made on the River Daugava, in the Ķengarags district of Riga, during 2002–2017 inclusive; the number of counts per year ranged between 10–156, with a mean \pm s.d number of 86 ± 44 counts carried out per year. This is the most important site for feeding swans by members of the public throughout the year; monthly peak counts recorded a mean of 32 ± 21 Mute Swans over the study

period (Fig. 5). The regular re-sightings of ringed swans have illustrated the migration phenology for individuals which spend the winter outside of Riga. The mean date on which the first migrating swans were seen in Riga each spring, based on the arrival of non-resident ringed swans, was 11 March (range: 26 February to 4 April during 2004–2017), with the timing apparently dependent on weather conditions in late winter. Re-sightings of ringed swans, together with the count data (Fig. 5), showed increasing numbers of migrating swans in two spring periods. The first was during the 3–4 weeks following the initial arrival date, when mass migration of breeders and non-breeders

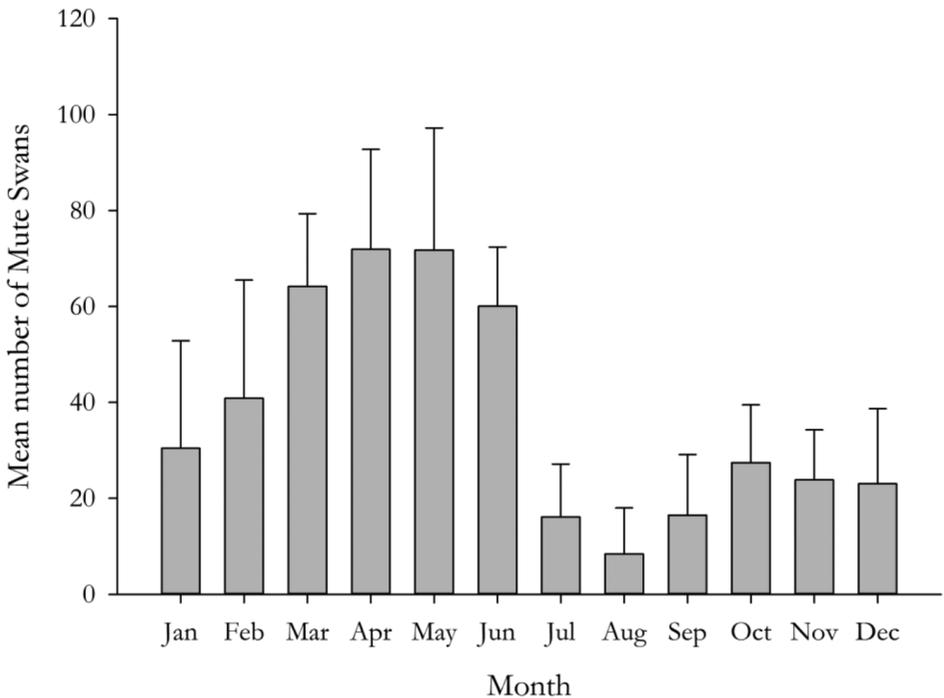


Figure 5. The mean (\pm s.d.) number of Mute Swans counted during surveys in each month on the River Daugava, in the Kēngarags district of Riga, between 2002 and 2017.

(mostly local swans) was observed. The second occurred at the end of May and beginning of June, when non-breeders (birds of local, Lithuanian and Belarusian origin) migrated through Riga to their moulting sites.

Breeding age and phenology

Over the period 2004–2017, 555 cases of breeding by ringed swans were recorded. For 22 males and 38 females of known age (ringed as cygnets or during their 2nd year of life, when was possible to determine their age) known to have bred, first successful breeding occurred in the 3rd year (1 male and 1 female) and 4th year of life

(3 females). Of the breeding swans of known age, most (68%) of these individuals, 16 males and 25 females, started to breed when aged 4–6 years old. Each year, on average 41% of ringed Mute Swans (range: 15–68% during 2004–2017), including individuals of known and unknown age, started breeding for the first time. The longest runs of successive successful breeding (*i.e.* without skipping a breeding season) observed among all 555 ringed birds observed breeding was 10 years (male) and 11 years (female). The oldest successful breeders were 15+ years old (male) and 16+ years old (female). The maximum number of cygnets produced during the life-time of one individual swan

was 46 (male) and 59 (female). Of the 197 swans with known hatching locations, five (3 females and 2 males) found breeding subsequently were all within 10 km of their natal territory, indicating that natal dispersal occurred typically over short distances. Breeding in Riga started in April, with the first eggs laid mostly during the second part of this month, and the first cygnets observed from the end of May (from 24th) to the first days of June. The first flying young swans were observed from the 21st September to the middle of October.

Moulting sites and phenology of non-breeding Mute Swans

The most important moulting sites for non-breeding Mute Swans that migrated (*e.g.* identified by ring code in spring) through Riga were the coastal lakes in western Latvia (Babītes, Kanieris, Engures) and the Pärnu Bay coast in Estonia (south of Pärnu city), which are 30–150 km from Riga. Up to 4,000 individuals gather to moult on these waterbodies (R. Matrozis, pers. obs.). In some years single swans or small groups (up to 13) remained in Riga to moult, mostly on the Daugava River near Ķengarags and on Lake Juglas.

Observations made of 36 ringed swans (21 males, 12 females and 3 of unknown sex) moulting at Daugava River near Ķengarags were as follows: the first moulting birds (which had lost their flight feathers and were unable to fly) were recorded in mid-June (from 18 June) to early July, and all of them ($n = 7$) were 2nd calendar year swans. Adult swans (*i.e.* aged in their 3rd calendar year or more) began to moult later, mostly in mid-July, but some still had old primary feathers

up to the first days of August. Most swans moulted their flight feathers from mid-July to the end of August. The flightless period took at least 38 days, but the swans arrived at their moulting sites approximately 1–2 weeks before they lost their flight feathers and remained for another *c.* 1–2 weeks after they regained their flight ability. The shortest periods between two sightings in Riga, before and after moult, of ringed swans which moulted outside of Riga were 67 and 76 days. Most swans arrived at the moulting sites at the beginning of June and the first swans completed their moult and returned to Riga from mid-August onward, although most remained away until October.

Longevity and mortality

According to the ringing and re-sightings data, the life-time longevity for *c.* 90% of Mute Swans ringed in Riga was about 8 years. The remaining 10% of ringed swans survived beyond this, with the current maximum age for Mute Swans ringed in Riga of 17 years old for males and 18+ years old for females, which will undoubtedly increase as these individuals remained alive at the time of reporting. Only 4.5% of birds were observed alive 10 or more years after ringing. The highest mortality rate was recorded in the first four years of life, as 78% of swans of known age did not live beyond the age of four and hence only 22% of swans survived to reach the typical age of first breeding (4–6 years old). Higher mortality was noted in the first five months of the year (January to May), accounting for 71% of annual mortality, highlighting the importance of the winter period for regulating of the population. The database contained information about

164 ringed swans, which were reported dead, but for only 14 individuals (8.5%) was the most likely cause of death known, which was collision with electrical or railway wires. Other causes of mortality were unknown, due to the lack of *post-mortem* investigations on dead swans.

Observations of Polish morph

First observed in 2003, only 14 Polish morph individuals were ringed during the study, accounting for 0.57% of the 2,446 Mute Swans ringed in Riga. Of these, eight were female, three were male and for the remaining three birds the sex was unknown. The largest numbers of ringed Polish morph swans observed were seen in April and May, when birds from neighbouring countries (believed to be of Belarus and Lithuanian origin) migrated through Riga to their moulting places. Some ringed Polish morph swans were identified in up to four spring seasons. Only single families with Polish morph cygnets were observed in Riga, and in general the origin of such swans observed during the spring migration was not known.

Discussion

The long-term study of ringed Mute Swans provides valuable information about migration routes, distances, phenology and other aspects of Mute Swan population in the eastern part of the species' home range. It was possible to collect records of ringed swans in Riga throughout the whole year, because swans were regularly attracted by additional food, mostly white bread, which was provided by the public. Based on the field observations of the volunteer swan counters in the study

area between 2004–2017, at least 90% of swans approached members of the public who showed a desire to feed them. It seems that such behaviour of Mute Swans in Riga city is not typical for other regions of Eastern Europe and so represents a good opportunity to study this species. The average number of re-sightings for an individual ringed swan in Riga was 16, which is quite high in comparison with 2.3 records per ringed individuals in Eastern Germany (Heinicke 2007), and 5.9 and 0.7 for colour-ringed and metal-ringed individuals, respectively, in Hungary (Kovács *et al.* 2018).

The flight feather moulting phenology for the majority of non-breeding Mute Swans in Riga was similar to the phenology reported for the west part of Swedish seacoast (Mathiasson 1973). Natal dispersion of Mute Swans originating from Riga was up to 10 km from the hatching site, but only five such records were collected, which is not enough to make any robust conclusions. For example, average natal dispersal distances in Germany, where swans are mostly sedentary, were 59 km (Heinicke 2007), and 37.9 km in Hungary (range: 0–165 km) (Kovács *et al.* 2018).

The longest recorded migratory distances for Mute Swans ringed in Riga were typically observed during the coldest winters: 1,238 km to Ukraine in January 2010 and 1,267 km to the Netherlands in December 2010. Studies of Mute Swans ringed in the Baltic States similarly found that the individuals may make long distance migrations, with one bird travelling 1,716 km from Lithuania to the United Kingdom (Švažas *et al.* 2001), and a Mute Swan ringed in the Russian arctic was subsequently sighted wintering *c.* 3,000

km to the southwest in Budapest, Hungary (Rees *et al.* 2019).

The results of long-term monitoring of ringed swans provide information about their productivity over the swans' entire lifespans. For breeding swans in Riga the maximum numbers of cygnets produced during the life-time of one swan was 46 (male) and 59 (female), which is higher than the 41 and 50 reported from a similar long-term study in the United Kingdom (Coleman *et al.* 2001). Otherwise, the maximum successful breeding age was quite similar, with 15+ years for males and 16+ for females in Riga, and 18 years old for both sexes in the United Kingdom (Coleman *et al.* 2001).

The longevity data from the Riga study showed that the oldest birds reached more than 18 years. In quite rare cases Mute Swans can reach more than 20 years old, for example, the oldest ringed swan from Sweden reached 24 years 11 months (Fransson & Pettersson 2001). In December 2008 the oldest swan in Denmark was found dead, at an age of least 40 years old (Anonymous 2009); however, the oldest Mute Swan with a Danish ring, which was at least 42 years and 9 months old, was found dead on the Baltic seacoast of Latvia in spring 2010 (Matrozis 2010). To get such information on ringed birds in the future, researchers should either use strong metal rings or else they must replace old rings that show damages or metal fatigue with new rings. Among the individuals that were recovered dead, the exact causes of death were difficult to determine without the help of a veterinarian to conduct *post-mortem* analyses. However, collisions were the main

identified cause of death, as swans are known to have poor manoeuvrability when in flight and can strike both natural (*e.g.* trees) and man-made (*e.g.* wind turbines and power lines) objects (Rees 2012). The results from Latvia therefore agree with numerous previous studies of Mute Swans from across their range that flying collisions and other traumatic accidents are a major source of mortality (*e.g.* Esselink & Beekman 1991; Perrins & Sears 1991; Mathiasson 1993; Pennycott 1999; Wood *et al.* 2019).

The ringing programme in Riga highlighted a low level (0.57%) of occurrence of Polish morph individuals, whereas in some parts of eastern Europe Polish morph individuals account for up to 20% of the total number of Mute Swans (Bacon 1980). In the Baltic States such Mute Swans were first observed in Lithuania in 1987 (Wieloch & Czapulak, 1991), in Latvia in 1988 (Lipsbergs 1990b), and were considered to be quite rare in the subsequent ten years (Kalniņš 1997). Most observations of the *immutabilis* form in Riga were reported during the spring migration from mid-April to the end of May. Such birds may have been of Lithuanian origin, which is bordered with Poland, which in turn has one of the largest percentages of this morph in Europe (Wieloch & Czapulak 1991).

Acknowledgements

This study of Mute Swans in Riga, made over thirty years, was undertaken on a voluntary basis and was only possible thanks to more than 300 observers who reported their records of ringed swans. I am immensely grateful to several active participants, who over many years spent their time and budgets visiting the main sites for ringing,

reading rings and counting swans: Dmitry Boiko, Jānis Dreimanis, Silvija Priedniece, Oļegs Mizīņenko, Mārtiņš Kalniņš, Arnis Arnicāns and Juris Vīgulis. I also thank Pelle Harild-Andersen (Denmark) for providing the neck-collars and leg-rings used in this study. Special thanks go to Ričardas Patapavičius (Head of the Lithuanian Bird Ringing Centre) for cooperative information exchange on the re-sightings and recoveries of Mute Swans in the region. The author is grateful to Eileen Rees and Kevin Wood for the substantial assistance during the preparation of this article.

References

- Andre, C. 1845. *Oekonomische Neuigkeiten und Verhandlungen Zeitschrift 1844*. Erster Band. Verlag der J.G. Calve'schen Buchhandlung, Prague, Czech Republic.
- Anonymous. 2009. World's oldest swan found dead in Denmark. *Science Daily*, 14 February 2009.
- Bacon, P.J. 1980. A possible advantage for the 'Polish' morph of the Mute Swan. *Wildfowl* 31: 51–52.
- Bernoulli, J. 1779. *Reisen durch Brandenburg, Pommern, Preussen, Curland, Russland und Polen in der Jahren 1777 und 1778*. Fritsch, Leipzig, Germany.
- Beseke, J.M.G. 1792. *Beitrag zur Naturgeschichte der Vogel Kurlands*. Mitau und Leipzig, Russia and Germany.
- BirdLife International. 2015. *European Red List of Birds. Cygnus olor* (Mute Swan). Office for Official Publications of the European Communities, Luxembourg.
- Coleman, A.E., Coleman, J.T., Coleman, P.A. & Minton, C.D.T. 2001. A 39 year study of a Mute Swan *Cygnus olor* population in the English Midlands. *Ardea* 89 (Special Issue No. 1): 123–133.
- Esselink, H., & Beekman, J.H. 1991. Between year variation and causes of mortality in the non-breeding population of the Mute Swan *Cygnus olor* in the Netherlands, with special reference to hunting. *Wildfowl* (Special Supplement No. 1): 110–119.
- Fransson T. & Pettersson J. 2001. Svensk ringmärkningsatlas. Vol. 1. Stockholm.
- Heinicke, T. 2007. Höckerschwan. In T. Heinicke & U. Köppen (eds.), *Vogelzug in Ostdeutschland I – Wasservogel Teil 1*, pp. 29–43. Ber. Vogelwarte Hiddensee Publication No. 18. Vogelwarte Hiddensee, Schleswig-Holstein, Germany. [In German.]
- Jogi, A., Lipsberg, Y. & Nedzinskas, V. 1976. The number and seasonal distribution of the Eastern Baltic population of the Mute Swan. Bird migration. Tallin, Valgus: 175–184. [In Russian.]
- Kalnins, M. 1997. Reports of the “Polish” morph of the Mute Swan *Cygnus olor immutabilis* Yarrell in Latvia. *Swan Specialist Group Newsletter* 6: 26–27.
- Kalniņš, M. 1998. Swan' 97. *MMD: Med bas, Makšķerēšana, Daba* 1: 26–27. [In Latvian.]
- Kovács, G., Szinai, P., Karcza, Z. & Winkler, D. 2018. Movements of Mute Swan *Cygnus olor* (Gmelin, 1789) (Anseriformes) based on Hungarian ringing data. *Acta Zoologica Bulgarica* 70: 75–81.
- Lipsberg, Y. 1979. Numbers and distribution of Mute Swan in Latvia. *Ornitologija* 14: 126–132. [In Russian.]
- Lipsberg, Y. 1983. Mute Swan. Birds of Latvia. Territorial distribution and number. Riga, Zinātne: 33–34. [In Russian.]
- Lipsbergs, J. 1990a. Results of swan census in Latvia in 1987. *Putni dabā* 3: 19–26. [In Latvian with English summary.]
- Lipsbergs, J. 1990b. The first recoveries of the “Polish” morph of the Mute Swan *Cygnus olor immutabilis* Yarr. In Latvia. *Putni dabā* 3: 142–144. [In Latvian with English summary.]

- Lipsbergs, J. 1995. The results of swan census in Latvia in 1992. *Putni dabā* 5.2: 95–97. [In Latvian with English summary.]
- Mathiasson, S. 1973. A moulting population of non-breeding Mute Swans with special reference to flight-feather moult, feeding ecology and habitat selection. *Wildfowl* 24: 43–53.
- Mathiasson, S. 1993. Mute Swans, *Cygnus olor*, killed from collision with electrical wires, a study of two situations in Sweden. *Environmental Pollution* 80: 239–246.
- Matrozis, R. 2010. The oldest European Mute Swan found on seacoast near Akmenrags. *Putni dabā* 2010/1–2: 64. [In Latvian.]
- Ogilvie, M.A. 1972. Large numbered leg bands for individual identification of swans. *Journal of Wildlife Management* 36: 1261–1265.
- Pennycott, T.W. 1999. Causes of mortality in Mute Swans *Cygnus olor* in Scotland 1995–1996. *Wildfowl* 50: 11–20.
- Perrins, C.M. & Sears, J. 1991. Collisions with overhead wires as a cause of mortality in Mute Swans *Cygnus olor*. *Wildfowl* 42: 5–11.
- Rees, E.C. 2012. Impacts of wind farms on swans and geese: a review. *Wildfowl* 62: 37–72.
- Rees, E.C., Cao, L., Clausen, P., Coleman, J., Cornely, J., Einarsson, O., Ely, C., Kingsford, R., Ma, M., Mitchell, C.D., Nagy, S., Shimada, T., Snyder, J., Solovyeva, D., Tijssen, W., Vilina, Y., Włodarczyk, R. & Brides, K. 2019. Conservation status of the world's swan populations, *Cygnus* sp. and *Coscoroba* sp.: a review of current trends and gaps in knowledge. *Wildfowl* (Special Issue No. 5): 35–72.
- Stipniece, A. & Matrozis, R. 2001. The Mute swan (*Cygnus olor*) wintering in Latvia (1984–2001). *Acta Biologica Universitatis Daugavpiliensis* 1: 45–50.
- Švažas, S., Patapavičius, R. & Dagys, M. 2001. Recent changes in distribution of wintering populations of waterfowl established on the basis of Lithuanian ringing recoveries. *Acta Zoologica Lituanica* 11: 235–242.
- Transehe, N.v. 1939. Hockerschwane (*Cygnus olor*) als Brutvogel des Engures-Sees. *Korrespondenzblatt des Naturforschender Vereins zu Riga* 63: 39–41.
- Vīksne, J. 1968. Results of Mute Swan and White-tailed Eagles counts in Latvia in 1964. *Communications of the Baltic Commission for the study of bird migration* 5: 76–80. [In Russian.]
- Wieloch, M. 1991. Population trends of the Mute Swan *Cygnus olor* in the Palearctic. *Wildfowl* (Supplement No. 1): 22–32.
- Wieloch, M. & Czapulak, A. 1991. *Cygnus olor immutabilis* in Poland. *Wildfowl* (Supplement No. 1): 304–309.
- Wood, K.A., Brown, M.J., Cromie, R.L., MacKenzie, C., Newth, J.L., Pain, D.J., Perrins, C.M. & Rees, E.C. 2019. Regulation of lead fishing weights results in mute swan population recovery. *Biological Conservation* 230: 67–74.