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RESEARCH ARTICLE

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Ringing data reveal a significant decline in first-year willow warblers *Phylloscopus trochilus* at Gotland, Sweden—an effect of climate change?

Ringmärkningsdata visar att årsungar av lövsångare *Phylloscopus trochilus* minskar betydligt på Gotland – en effekt av klimatförändringen?

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One of the most widespread passerines breeding in Europe, the willow warbler *Phylloscopus trochilus*, has declined considerably. Here, we analyse the production of offspring in the southern subspecies of willow warbler at Gotland, Sweden, by utilizing data on post-juvenile moult of first-year birds from standardized ringing during 1990–2024, and comparing our findings with meteorological data. The number of first-year birds ringed in post-juvenile moult stage 0–4, which means that they are hatched in the vicinity, varied greatly, with an annual average of 317 (range 50–591) individuals and a significant negative trend over time. During 1990–2006, the number was relatively stable at 431 ± 85 (SD), followed by decreasing numbers and higher variation 2007–2024. Compared to 1990–2006, the number of ringed first-year willow warblers in moult stage 0–4 decreased by 74 % (112 ± 44) from 2016 onwards, and was negatively related to temperature during the incubation and the nestling period, but not

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during the fledgling period. There was no significant relationship between precipitation and the number of birds ringed. We discuss the results with respect to increased temperature during breeding, following climate change, involving negative effects on offspring productivity.

Keywords: population trend, offspring production, breeding success, increasing temperature

Recent climate change, coupled with other human-induced factors such as land use, influence global biodiversity, including birds, negatively (Sala et al. 2000, Davison et al. 2024). The milder climate has notably influenced phenology—the timing of seasonal events in animals and plants (c.f. Phillimore et al. 2016, Hällfors et al. 2020, Lomas Vega et al. 2021, Hanmer et al. 2022). Numerous studies indicate that long-distance migratory birds in recent decades are arriving earlier in spring and depart earlier after breeding in autumn (cf. Cotton 2003, Hellström et al. 2023). Additionally, there is evidence of declining populations in a number of passerine species in recent years and it has been shown in North America that changes in phenology have impacts on demography (Youngflesh et al. 2023). In Europe, a species that has experienced a considerable decline in numbers, by 40 % since 1980, is the willow warbler *Phylloscopus trochilus*, which is one of the continent's most common breeding birds (PECBMS 2025). In Britain, studies from the early 2000s revealed a decline in willow warbler populations in the south, while an increase was noted at the same time in the north, which was primarily caused by differences in chick survival rates (Morrison et al. 2016).

The willow warbler is a widespread species with a breeding range that spans much of the northern and central Palearctic, from Ireland in the west to the Bering Strait in the east (BirdLife International 2024). In Sweden it breeds in most of the country, with an estimated population of about 13 million pairs (Ottosson et al. 2012). Two subspecies are recognized in Europe: the southern subspecies, *P. t. trochilus*, and the northern subspecies, *P. t. acredula*. Additionally, there is a third subspecies, *P. t. yakutensis*, in the eastern part of the breeding range. The willow warbler winters in tropical Africa, with the southern subspecies migrating to West Africa, while the northern subspecies winters in eastern and southern Africa (Hedenström and Pettersson 1987, Fransson and Hall-Karlsson 2008). Willow warblers breed in various open woodlands and build the nest in close contact with the ground (Bellamy et al. 2009).

The number of willow warblers ringed in Sweden has declined in recent years, both nationally (Fransson et al. 2024) and at various bird observatories (cf. Hellström et al. 2024), as well as in the Swedish Bird Survey's regular inventory of singing birds (Green et al. 2024). In Sweden, the southern subspecies occupies the southern and central parts, while the northern subspecies inhabits the northern part. This study utilizes 35 years of standardized ringing data from the southernmost part of Gotland in the Baltic Sea, where the Sundre Bird Observatory conducts ringing activity. To explore the productivity and population trends of the regional willow warbler population over time, we utilized data on post-juvenile moult. This approach allows us to gather information from first-year birds that are definitively born in the vicinity, belonging to the southern subspecies. We then compared the annual numbers of first-year willow warblers with local temperature and precipitation data.

Material and methods

THE STUDY AREA AND RINGING ACTIVITIES

The Sundre Bird Observatory (SBO) carries out ringing of birds at Hoburgen, Sweden (56°55'N, 18°08'E), located on the southwestern tip of the island Gotland in the Baltic Sea (Figure 1). Standardized trapping using mist nets has been performed annually since 1990 from 25 July to 15 September. Trapping starts 1h before sunrise and continues at least until 10:00. The number of mist nets used is 18 and nets are checked every 30 minutes. Data collection include determination of age, wing length, body mass, amount of fat (ordinal scale 0–6; Pettersson and Hasselquist 1985), and post-juvenile moult stage of first-year birds (ordinal scale 0–6; see

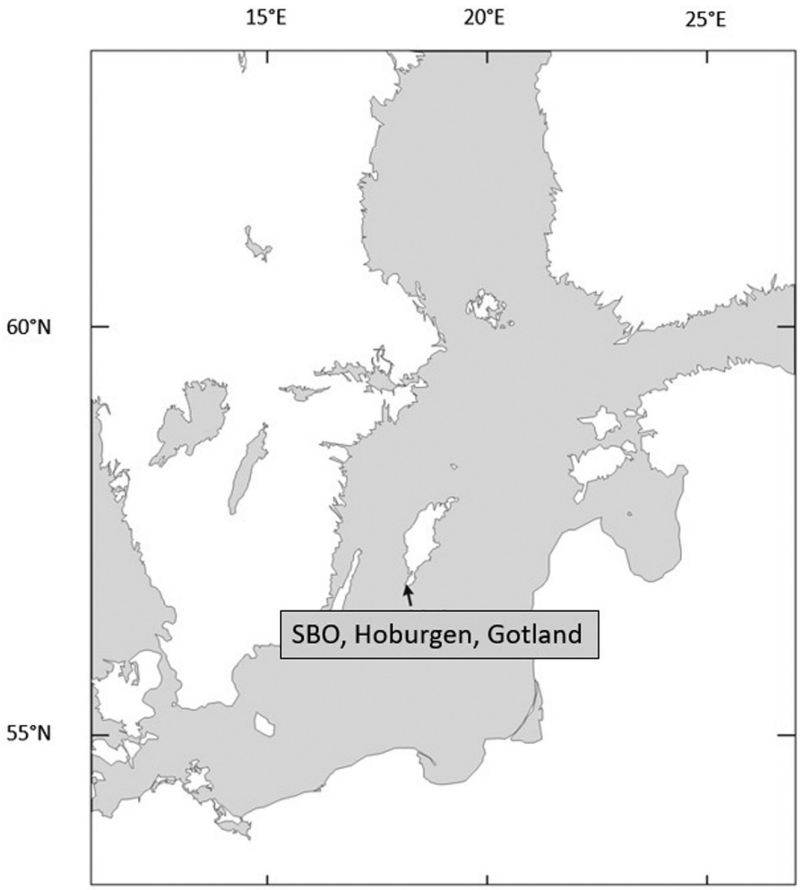

FIGURE 1. Location of the Sundre Bird Observatory (SBO) at Hoburgen, Gotland, Sweden, (56°55′N, 18°08′E) in the Baltic Sea.
– Karta som visar Sundre fågelstation vid Hoburgen, Gotland (56°55′N, 18°08′Ö).

Bensch and Lindström 1992, with addition of stage 0, referring to moult not initiated).

The total number of willow warblers ringed in the period 1990–2024 was 27,637, with an annual average of 790, range 272–1462. The vast majority (96.2 %) of birds with information on age were first-year, on average 757 ± 253 (SD) ringed per year, while adult birds were less common with an average of 30 ± 19 ringed per year. A few birds (0.4 %) were not determined to age.

COMPILATION OF RINGING DATA

Ringed willow warblers were divided according to age (cf. Svensson 2023) into first-year and adult birds (second calendar year or older). First-year birds where then divided by moult stage with 0–4 representing locally hatched birds performing dispersal movements prior to migration, and 5–6 birds in migration mode (Lawn 1984, Hedenström and Pettersson 1987, Lindström et al. 1996). Locally hatched willow warblers in stage 0–4 belong to the subspecies *P. t. trochilus*, whereas birds in stage 5–6 form a mix of *P. t. trochilus*, ready to migrate, and passing *P.t. acredula* from the north. Hence, we used the number of first-year birds in moult stage 0–4 per year in assessing the population development of *P. t. trochilus* at Gotland, Sweden. We applied a Spearman rank correlation test to identify if there is a trend between year and the number of first-year birds in moult stage 0–4 and 5–6, respectively, with number of birds on the y-axis and year on the x-axis.

On days with high numbers of trapped birds, e.g. in connection with extensive local movements of moult stage 0–4 birds early in the period or high numbers of migrating birds on stopover later in the season, moult stage and fat score may not have been recorded due to time restrictions; in total 14 % of first-year birds in 1990–2024. During data compilation first-year birds that were not classified to moult stage, were assigned either stage 0–4 or stage 5–6 based on the average proportion in each moult stage for a certain date, based on all first-year birds with a determined stage during the period 25 July–15 September 1990–2023 (Appendix 1).

The ringing period (25 July–15 September) does not fully cover the period of birds in moult stage 0–4 (Figure 2). To evaluate whether the timing of breeding has changed (e.g. started earlier) during the period 1990–2024, and thereby possibly affected the number of trapped local first-year birds (stage 0–4), we analyzed median dates for first-year birds in moult stage 3 and 4 using a Spearman rank correlation test (median date on the y-axis and year on the x-axis).

To investigate potential changes in the condition of local first-year birds during the period 1990–2024 we compared the body mass of first-year birds in moult stage 4 over time, for males (with wing lengths 67 and 68 mm) and for females (wing lengths 63 and 64 mm), respectively, according to Svensson (2023).

In an attempt to predict the development of the breeding population in the area we used the number of first-year birds ringed and estimates of the annual survival of first-year and adult birds, respectively across cohorts; e.g. the number of 0–4 birds in year 1 (N1) × first year survival = N2, and N3 = N2 × adult survival+the number of 0–4 birds in year 2 × first year survival, and so on up to the fifth calendar year. The annual survival of first-year birds was set to 25 % and the annual survival for adult birds to 50 % (Pratt et al. 1991, Fransson and Hall-Karlsson 2008). The number of survivors per year was then summed for the respective year 1994–2025, and the relative number per year calculated with the population level set to one for 1994.

ENVIRONMENTAL DATA

In order to evaluate the relationship between the production of first-year birds and the prevailing climate change, we compiled data of local temperature and precipitation for the period 1990–2024 for Hoburgen, Gotland (Swedish Meteorological and Hydrological Institute (SMHI) 2024). We divided the breeding season into three phases, incubation (27 May–10 June), nestling period (11 June–25 June) and fledgling period

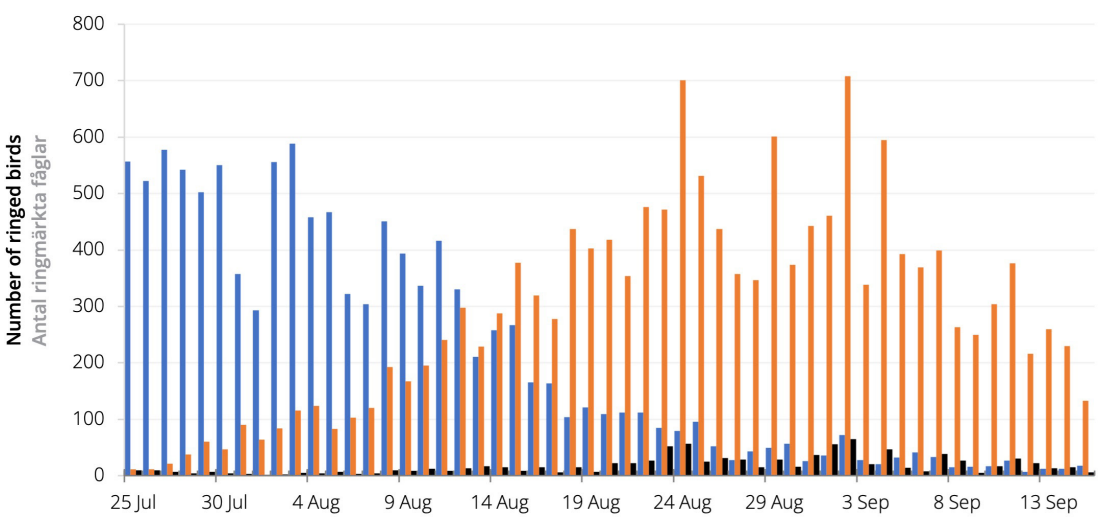

FIGURE 2. The number of ringed willow warblers *Phylloscopus trochilus* per day; first-year birds in juvenile moult stage 0–4 (in blue) and in stage 5–6 (in orange) respectively, and adult (in black) birds, during the period 25 July–15 September at Hoburgen, Gotland, Sweden, 1990–2024.
– Antalet ringmärkta lövsångare *Phylloscopus trochilus* per dag under perioden 25 juli–15 september vid Hoburgen, Gotland, 1990–2024; årsungar i ruggningsstadium 0–4 (blått) respektive 5–6 (orange), och vuxna (svart).

(1 July–25 July; start of ringing) based on female arrival to the area in spring (Hedlund et al. 2015) and time for nest building, egg-laying, incubation and nestling period, according to Arvidson and Nilsson (1983). Note that the time periods chosen are approximate, as detailed data of the reproduction biology for willow warbler from the area is lacking. We analysed potential trends in climate data using linear regression (temperature and precipitation, respectively, on the y-axis and year on the x-axis). Further, we plotted the number of ringed stage 0–4 birds per year against temperature and precipitation data of the respective period, and identified potential trends using a Spearman rank correlation test (number of birds on the y-axis and temperature or precipitation, respectively on the x-axis). This resulted in a significant negative correlation between temperature during the breeding season and the number of ringed first year birds in moult stage 0–4 at both the incubation and nestling periods (below) suggesting a negative effect of increased temperature on offspring production. Successively fewer first-year birds ringed may be due to a decreasing breeding population as confirmed by the results from the Swedish Bird Survey in the area (Swedish Bird Survey data from fixed routes; Martin Green, Lund University, pers. comm.). To compensate for the effect of the decreasing breeding population, i.e. to reveal the potential effect of temperature on the number of local first-year birds, we detrended data on the number of birds ringed in moult stage 0–4 during the period (below), by using the residuals of the trend (linear regression; $y = -11.108 + 22{,}610$). Accordingly, negative residuals show a lower number of first-year birds ringed than expected from the decreasing trend.

Results

TIMING OF MOULT AND MIGRATION

The number of moulting first-year birds (moult stage 0–4), i.e. considered being from the local breeding population, decreases during the season, forming the vast majority of individuals early in the season (July) but very few in September (Figure 2). Consequently, the number of first-year birds in migration phase (moult stage 5–6) increases during the period, from almost none at the start of the ringing period in July, to forming the vast majority from late August onwards. The ringing period covers the period of migration well, whereas the period of first-year birds in post-juvenile moult, performing local movements, is not fully covered. Adult birds

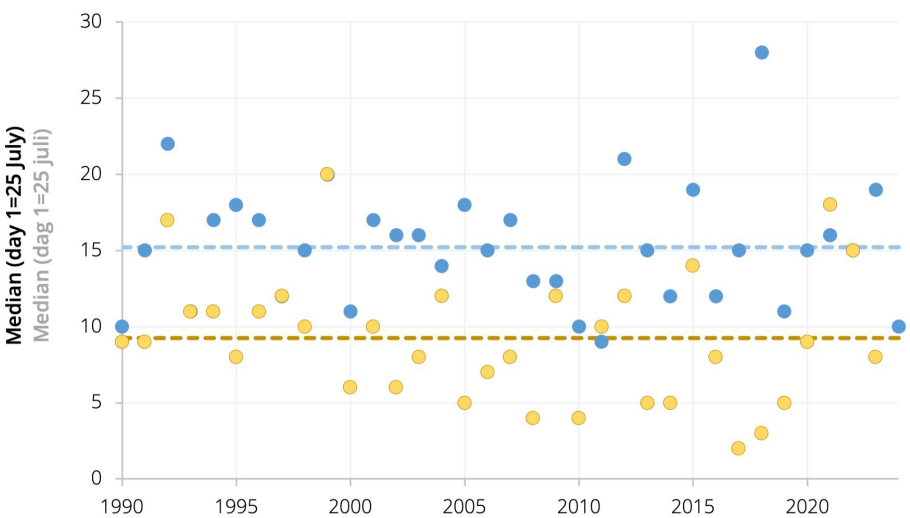

FIGURE 3. Median date of ringed first-year willow warblers *Phylloscopus trochilus* in juvenile moult stage 3 (yellow) and 4 (blue) during the period 1990–2024 at Hoburgen, Gotland, Sweden. The Y-axis shows day number from start of ringing; 1=25 July. Dashed lines show the overall averages.

– Mediandatum för ringmärkta årsungar av lövsångare *Phylloscopus trochilus* i ruggningsstadie 3 (gult) och 4 (blått) under perioden 1990–2024 vid Hoburgen, Gotland. Y-axeln visar dagnummer från start av ringmärkningen; 1=25 juli. De streckade linjerna visar respektive medelvärde under perioden.

occur in low numbers during the entire period, but are more frequent in the second half of the period.

The annual median date of first-year birds in moult stage 3 and 4 during the period 1990–2024 revealed no trend ($r_s = -0.23$, $p = 0.19$ and $r_s = 0.06$, $p = 0.72$ respectively; Figure 3) suggesting that the time of hatching and subsequent post-juvenile moult of first-year birds is unchanged during the period. Hence, the number of first-year birds in moult stage 0–4 ringed during 1990–2024 does not seem to have been affected by a phenological change in moult period and can thereby be considered as an unbiased estimate of the annual number of local first-year birds.

TRENDS IN THE NUMBER OF RINGED FIRST-YEAR BIRDS

The number of ringed first-year birds in moult stage 0–4 varied greatly during the period 1990–2024, with an annual average of 317 (range 50–591) ringed birds and with a significant negative decrease over time (Spearman rank correlation; $r_s = -0.69$, $p<0.001$; Figure 4). During the period 1990–2006, the number of stage 0–4 birds was relatively stable with an average of 431 ± 85 (SD) birds, followed by decreasing numbers and larger variation between 2007–2024. Compared to 1990–2006, the period 2007–2024 showed a decrease of 51.5 % (209 ± 134), and 74.0 % (112 ± 44) from 2016 onwards. Thus, the number of local first-year birds (*P. t. trochilus*) decreased considerably during the period, in particular since 2016.

In addition, the annual number of ringed first-year birds in moult stage 5–6 (average: 441 ± 142; range 204–826) also decreased during the period ($r_s = -0.53$, $p = 0.0010$). The reduction is not as strong as for birds in moult stage 0–4, particularly there is no dramatic decline in 2016–2024 (Figure 5). Moult stage 5–6 first-year birds are a mixture of local willow warblers (*P. t. trochilus*) and passing willow warblers from the north (*P. t. acredula*).

The body mass of first-year birds in moult stage 4 did not change over time (Figure 6). This applies to both males (linear regression with body mass on the y-axis and year on the x-axis; $t = -0.34$, $p = 0.69$) and females ($t = 0.44$, $p = 0.66$) and gives no indication that the condition of ringed local first-year birds has changed over the period 1990–2024.

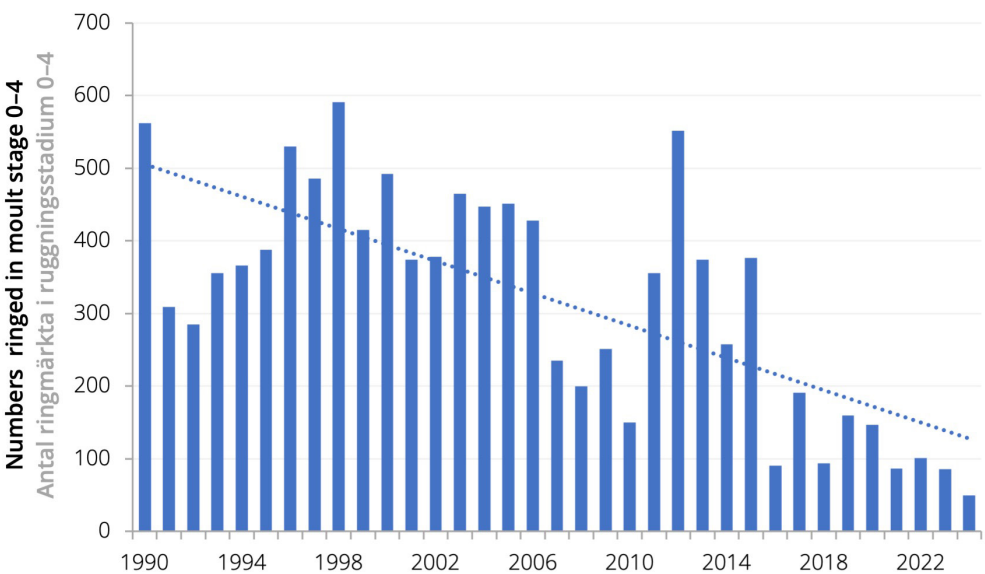

FIGURE 4. The number of ringed first-year willow warblers *Phylloscopus trochilus* in post-juvenile moult stage 0–4 in 1990–2024 at Hoburgen, Gotland, Sweden.
– Antalet ringmärkta årsungar av lövsångare *Phylloscopus trochilus* i ruggningsstadium 0–4 under perioden 1990–2024 vid Hoburgen, Gotland.

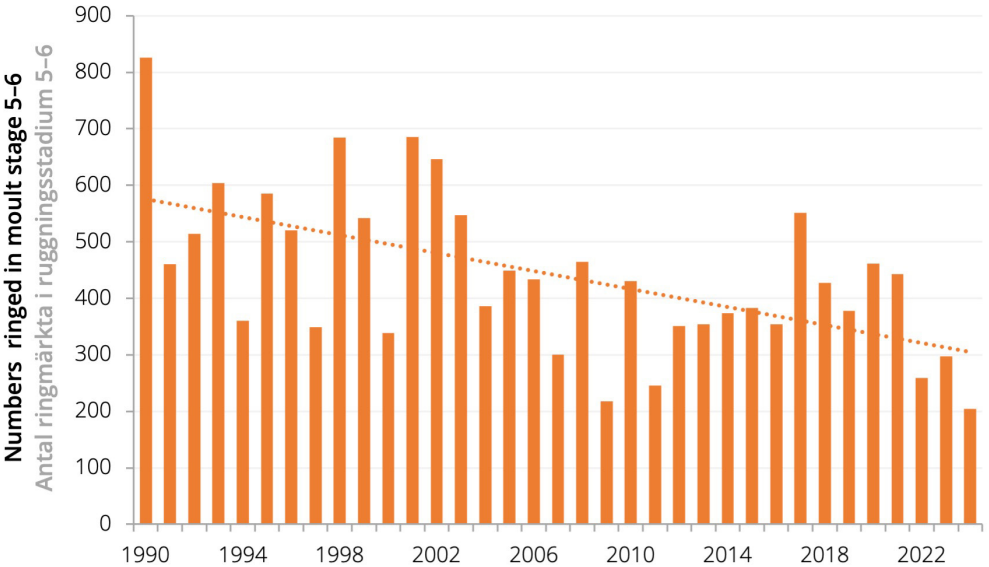

FIGURE 5. The number of ringed first-year willow warblers *Phylloscopus trochilus* in post-juvenile moult stage 5–6 in 1990–2024 at Hoburgen, Gotland, Sweden.
– Antalet ringmärkta årsungar av lövsångare *Phylloscopus trochilus* i ruggningsstadium 5–6 under perioden 1990–2024 vid Hoburgen, Gotland.

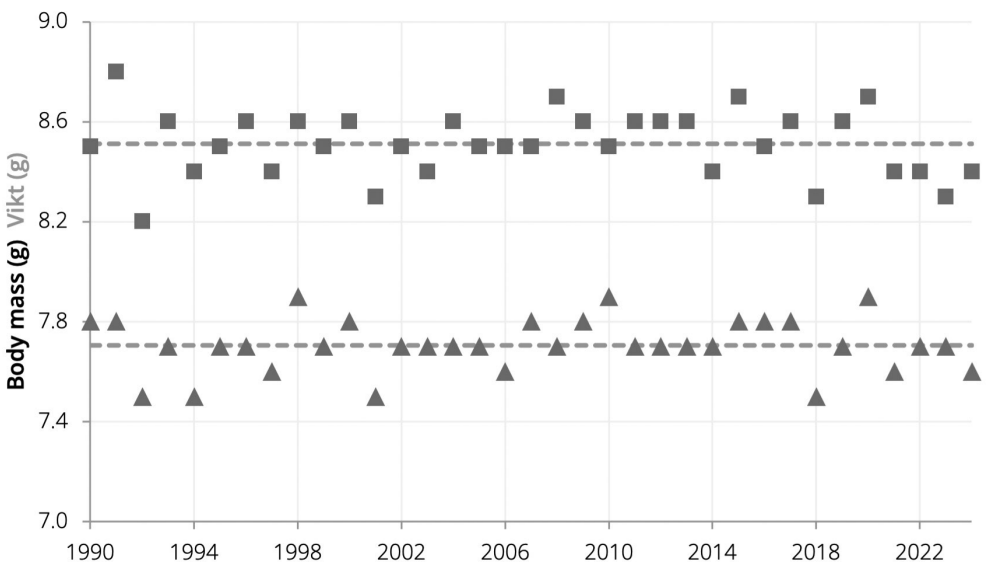

FIGURE 6. Average body mass (g) of ringed first-year willow warblers *Phylloscopus trochilus* in moult stage 4 in 1990–2024 at Hoburgen, Gotland, Sweden. Females (triangles); males (squares). Dashed lines show the overall averages.
– Medelvikt (g) för ringmärkta årsungar av lövsångare *Phylloscopus trochilus* i ruggningsstadium 4 under perioden 1990–2024 vid Hoburgen, Gotland. Honor (trianglar); hanar (fyrkanter). Streckade linjer visar medelvärde.

RELATIONSHIP WITH ENVIRONMENTAL DATA

Variation in temperature during the respective phases; incubation, nestling and fledgling periods, at Hoburgen, Sweden during 1990–2024 is shown in Figure 7, and for precipitation as supplementary data in Appendix 2. Although there is a tendency of increased temperature and less precipitation during 1990–2024, there is a clear trend only in temperature during the nestling period (Table 1), with temperatures above average, 16.3 ± 1.3°C, from 2016 onwards (except for in 2024), compared to 14.0 ± 1.4°C during 1990–2015. The amount of precipitation varies greatly between years, on average 78 ± 34 mm (sum of the respective period), but does not show a clear trend (Table 1).

Plotting of the number of ringed first year birds in moult stage 0–4 against temperature data during the breeding season revealed a significant negative correlation during both incubation and the nestling period, but a non-significant relationship during the fledgling period (Table 2). No significant correlation occurred between precipitation and the number of ringed first-year birds in moult stage 0–4 (Table 2).

Detrended data (residuals) of the number of ringed birds in moult stage 0–4 against temperature (Figure 8), revealed predominantly negative residuals, i.e. a lower number of ringed birds than expected, in years with high temperatures. Of the eight warmest years, seven and eight showed negative residuals at the incubation period (Figure 8a) and at the nestling period (Figure 8b), respectively. Moreover, also years with low temperature showed negative residuals, as in 1991 and 1994 (Figure 8a). The low number of ringed birds in 1991–1992 (Figure 4) occurred during the coldest year followed by a year with high temperature. The low number of ringed birds in 2007–2008 corresponds to years with high temperatures, in which is also the case in 2016, 2018 and 2021. Further, the high numbers of ringed birds in 1996–1998 and 2011–2012 (Figure 4) occurred at average temperatures (Figure 8). Thus, temperature conditions during the incubation and nestling

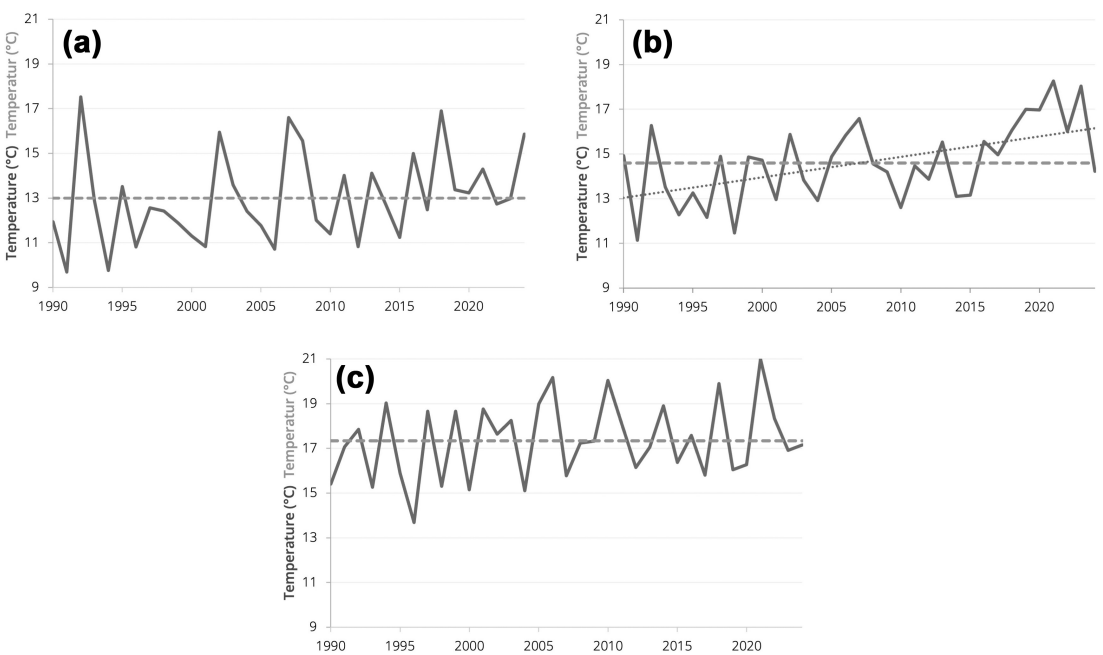

FIGURE 7. Average temperature (°C) during (**a**) the incubation period (27 May–10 June), (**b**) the nestling period (11–25 June), and (**c**) the fledgling period (1–25 July), in willow warblers *Phylloscopus trochilus* at southern Gotland, Sweden in 1990–2024. Data for Hoburgen, Gotland, Sweden, from the SMHI. Dotted line shows significant trend (see Table 1) as linear regression and hatched lines the overall averages.
– Medeltemperatur (°C) under (**a**) ruvning (27 maj–10 juni), (**b**) boungefas (11–25 juni), och (**c**) som flygga (1–25 juli), för lövsångare *Phylloscopus trochilus* på södra Gotland 1990–2024. Data från SMHI för Hoburgen, Gotland. Streckade linjer visar medelvärde och punktlinje visar trend som linjär regression.

TABLE 1. Trends (linear regression statistics) in temperature and precipitation at Hoburgen, Gotland, Sweden, during 1990–2024 during the respective period of willow warbler *Phylloscopus trochilus* incubation, nestling and fledgling.
– Trender (linjär regression) för temperatur och nederbörd vid Hoburgen, Gotland, 1990–2024 under lövsångarens *Phylloscopus trochilus* faser för ruvning, boungar respektive flygga ungfåglar.

	Temperature Temperatur				Precipitation Nederbörd			
Period Fas	coefficient koefficient	SE standarfel	t	p	coefficient koefficient	SE standarfel	t	p
Incubation Ruvning	0.057	0.033	1.74	0.09	–0.28	0.15	–1.81	0.08
Nestling Boungar	0.091	0.025	3.64	<0.001	–0.23	0.31	–0.75	0.46
Fledgling Flygga	0.039	0.028	1.38	0.18	–0.22	0.46	–0.48	0.64

periods appears to have a significant impact on the offspring production in the area. In particular years with high temperatures, but also years colder than normal, result in fewer birds ringed, while average temperatures may result in higher numbers of ringed birds.

Based on the assumption of an annual mortality of 0.75 for first-year birds and 0.5 for adult birds, the estimated development of the breeding population is strongly affected by the number of stage 0–4 birds (Figure 9). The population showed recovery after the first period of higher temperatures (2007–2008) and reduced number of moult stage 0–4 birds, but remains at a low level following 2016, with temperatures above average and low reproduction.

TABLE 2. Correlation (Spearman rank correlation statistics) between the number of ringed first-year willow warblers *Phylloscopus trochilus* in moult stage 0–4 and the average temperature and sum of precipitation, respectively, during the periods for incubation, nestling and fledgling, at Hoburgen, Gotland, Sweden, during 1990–2024.
– Korrelation (Spearman rank-korrelation) mellan antalet ringmärka årsungar av lövsångarens *Phylloscopus trochilus* i ruggningsstadium 0–4 och medeltemperatur respektive total nederbörd vid Hoburgen, Gotland, 1990–2024 under faserna för ruvning, boungar respektive flygga ungfåglar.

	Temperature Temperatur		Precipitation Nederbörd	
Period Fas	r_s	p	r_s	p
Incubation Ruvning	–0.50	0.002	0.31	0.071
Nestling Boungar	–0.45	0.006	0.26	0.14
Fledgling Flygga	–0.29	0.091	0.27	0.12

Discussion

The willow warbler has experienced a dramatic decline in the breeding population across Europe since the early 1980s (PECBMS 2025). This is evident also at the island Gotland, Sweden, where the breeding population of *P. t. trochilus* has decreased by 34 % during 1998–2022 (data from the Fixed routes of the Swedish Bird Survey; Martin Green, Lund University, pers. comm.). In the present study, we show that the production of offspring, assessed as the number of ringed first-year birds in moult stage 0–4, has decreased by 74 % from the average during 1990–2006 to the average during 2016–2024. Comparison with environmental data in the area revealed that this decline is related to increased temperature conditions during the incubation and nestling periods. The relationship between the number of first-year birds in moult stage 0–4, and temperature revealed an effect of temperature on offspring production; a decrease in numbers of ringed birds was associated with higher temperatures, whereas an increase in numbers occurred at average temperatures. In particular, temperatures above average during the nestling period seem to have contributed to the decrease in offsprings (birds in moult stage 0–4) from 2016 onwards. In contrast, we found no effect of temperature during the fledgling period on the number of ringed first-year birds. Moreover, body mass of birds in moult stage 4 has remained unchanged over the years, suggesting that the condition of surviving fledglings has not been affected over time. Hence, the bottleneck appears to occur during the incubation and nestling periods.

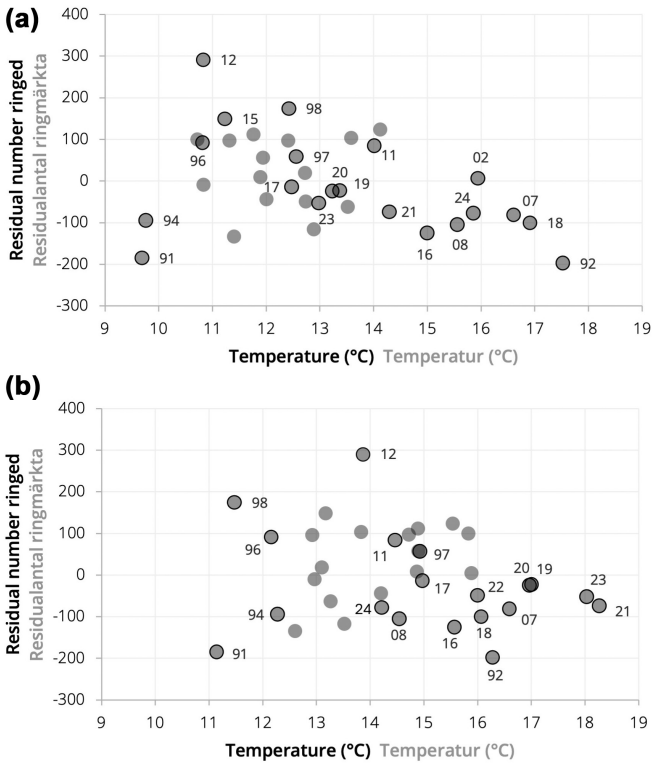

FIGURE 8. The relationship between the average temperature during (**a**) incubation (27 May–10 June), (**b**) the nestling period (11–25 June), and detrended data of the number of ringed first-year willow warblers *Phylloscopus trochilus* in moult stage 0–4 at Hoburgen, Gotland, Sweden, during 1990–2024 (residuals from Figure 4). Numbers indicate years (19NN/20NN) discussed in the text; circles highlighted with black outline.
– Förhållandet mellan medeltemperatur under (**a**) ruvning (27 maj–10 juni), (**b**) boungefasen (11 juni–25 juni), och avvikelser (residualer) från trend i figur 4 för antalet ringmärkta lövsångare *Phylloscopus trochilus* i ruggningsstadium 0–4 vid Hoburgen, Gotland, 1990–2024. Siffrorna visar år (19NN/20NN) vilka diskuteras i texten; cirklar markerade med svart kant.

First-year birds in moult stage 5–6, being a mixture of local willow warblers, *P. t. trochilus*, and passing willow warblers, *P. t. acredula*, from the north, show a less dramatic decrease in number of ringed birds. This might indicate that the population of passing *P. t. acredula* has not decreased in the same magnitude as the local *P. t. trochilus* population in Gotland.

Based on the number of ringed local first-year birds Figure 9 illustrates the estimated development of the local breeding population, being stable up to 2007, thereafter being more variable, and from 2019 substantially reduced. Evidently, the current population has a considerably lower capacity to produce offspring, irrespective of local temperature conditions. The development may be reversed only if the productivity increases (cf. Morrison et al. 2016), or if first-year and adult survival improves over time (e.g. in wintering areas), counterbalancing the low productivity. If nothing changes, we can foresee a continued decrease in numbers of first-year birds in moult stage 0–4 from 2025 onwards.

Several long-distance migrating Afro-Palearctic passerines, and in particular species that winter in the tropic sub-Saharan zone, display substantial population declines as opposed to short-distance (within-Europe/North Africa) migrants which are generally less affected (Sanderson et al. 2006, Ockendon et al. 2012). This has led to the conclusion that survival during migration and in particular in wintering areas may be of significance,

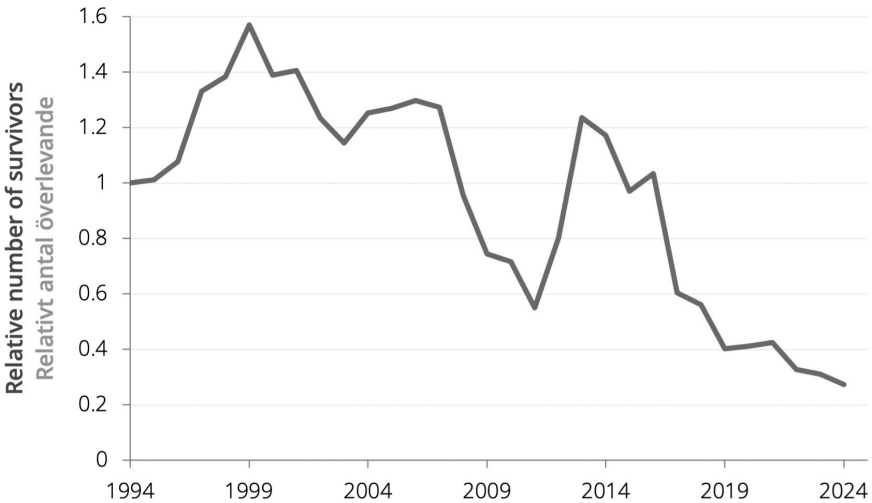

FIGURE 9. An estimate of the local breeding population of willow warbler *Phylloscopus trochilus* at Gotland, Sweden based on the assumption of annual mortality of 0.75 and 0.5 for first-year and 2cy–5cy birds respectively, and calculated from the number of ringed first-year birds in moult stage 0–4 in 1990–2024 at Hoburgen, Gotland, Sweden. Note that the estimate only represents a proxy for the number of breeding birds and population level was set to one for 1994.
– Skattad häckningspopulation för lövsångare *Phylloscopus trochilus* på södra Gotland, baserat på antagande om 75 % dödlighet för årsungar (1k–2k) och 50 % dödlighet för vuxna fåglar (2k–5k), beräknat utifrån antalet ringmärkta årsungar i ruggningsstadium 0–4 vid Hoburgen, Gotland, under 1990–2024. Observera att beräkningen endast utgör en teoretisk skattning av häckningsbeståndet där startåret 1994 har fått värdet 1.

especially since adult survival may vary greatly between years (Morrison et al. 2016). The subspecies *P. t. trochilus* winters in forests and wooded savannah habitats in the sub-Saharan zone of western Africa (Salewski et al. 2002, Heldbjerg and Fox 2008). Here, the willow warbler exhibits itinerancy over a large area in relation to greenness in vegetation, from arrival in October-November until northward migration in April (Salewski et al. 2002, Lerche-Jørgensen et al. 2017). The habitat in the region is deteriorating, due to both human related habitat change (Vickery et al. 2014), and climate change involving increased warming and increasingly variable precipitation, including periods of draught (Niang et al. 2014, Janes et al. 2015). These changing circumstances may influence survival and thus population development (Vickery et al. 2014, Telensky et al. 2020).

However, the importance of survival during non-breeding season for population abundance has been questioned due to within-species variation in population trends, as for willow warbler *P. t. trochilus* in Britain (Morrison et al. 2016). Morrison et al. (2016) demonstrated that the decline in willow warbler population in southern Britain is driven primarily by decreased productivity; the number of fledglings produced per nesting attempt, which according to Hanmer et al. (2022) is coupled to phenological shifts due to increased temperature. The mechanism behind this is unknown. As climate change progresses, migratory passerines not only arrive earlier in spring but start the autumn migration earlier (cf. Cotton 2003). The initiation of spring-migration is driven by increasing winter temperatures in sub-Saharan Africa, and the timing of autumn departure has advanced after increased summer temperatures at breeding sites (Cotton 2003). Decreased productivity may be due to insufficient food resources following climate change, either as decreased food abundance or a mismatch between the requirements for chicks and insect availability (Both et al. 2006, Møller et al. 2008, Martey et al. 2017). Further, Hanmer et al. (2022) discusses potential temperature-related mechanisms causing the decrease in offspring productivity in willow warblers, and found an association between earlier primary moult and brood patch re-feathering in adults and negative population trends, indicating poor breeding success with increased warming. Apart from earlier breeding, advances in initiation of moult may be due either to a higher proportion of nest failures in warm years,

or alternatively, to advanced gonad regression triggered by increased temperature, and hence earlier cessation of breeding as demonstrated experimentally in common starling *Sturnus vulgaris* (Dawson 2005). This may result in a reduced possibility of replacement broods and diminished extent of fledgling care (Hanmer et al. 2022). Moult-breeding overlap has been shown to affect parental care and subsequent survival/fitness of offspring in both European pied flycatcher *Ficedula hypoleuca* and Eurasian blue tit *Cyanistes caeruleus* (Hemborg and Lundberg 1998, Svensson and Nilsson 1997).

Consistent with our results, Telensky et al. (2020), studying migratory species that winter in sub-Saharan Africa, including *P. t. trochilus*, concluded that poorer breeding productivity was associated with warmer springs at breeding sites. In addition, they found higher adult survival to be related to water availability in sub-Saharan wintering areas. Further, reduced breeding success in years with higher pre-hatching temperatures has also been shown in the pied flycatcher (Lomas Vega et al. 2021). Moreover, Martey et al. (2017) modelled population trends of willow warbler in Britain, and found an optimum breeding season temperature in population growth and abundance at 11°C (assessed as temperature during the entire breeding season from April to July). This is consistent with our findings; lower offspring production at high temperatures, and higher numbers of first-year birds at average temperatures. It is also interesting to see that years with low temperatures (1991 and 1994) resulted in lower offspring production. Given the above, the potential for adaptation to the global warming in terms of arrival to breeding sites and initiation of breeding, is a key question. The willow warbler shows a large degree of protandry, where males arrive in advance of females to breeding sites (cf. Hedlund et al. 2015). In a study of a breeding population of willow warbler in central Sweden covering 38 years, it was shown that the degree of protandry increased over time since males have advanced their arrival time at the breeding site much more than females (Hedlund et al. 2022). This was evident both at a population level and within breeding pairs. This indicates, in agreement with our findings concerning median date for birds in moult stage 3 and 4 over time, that breeding of willow warbler in the area has not advanced significantly over the period. Moreover, ringing-data from SBO at Hoburgen during spring migration (a mix of local and passing willow warblers) reveal significantly earlier arrival for males since 1999 onwards, but no change in median date for females (SBO, pers. comm.).

Obviously, more studies are required to pinpoint the underlying mechanisms causing population declines in long-distance sub-Saharan migrating passerines. The picture is complex, i.e. future research needs to address conditions in wintering areas, at breeding sites and along migration routes. With regard to our findings, we encourage detailed studies of breeding biology, including the potential effect of moult breeding overlap, and how variability in temperature might affect offspring production. Here the pan-European ringing-initiative 'Constant Effort Sites' with standardized trapping at specific sites during spring-summer (Peach et al. 1996) may provide an important source of information to reveal both temporal trends and regional discrepancies.

Up to now, Europe, including Scandinavia, has been subject to an increase in temperature above the global average and further projections from climate modelling suggest that temperatures across European land areas will continue to increase throughout this century (IPCC 2021). Thus, with continued increases in temperature, the future of the southern subspecies of willow warbler *P. t. trochilus* population in Europe is at risk.

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Svensk sammanfattning

Lövsångaren *Phylloscopus trochilus* är en av Europas vanligaste fågelarter med en utbredning som sträcker sig över stora delar av norra och centrala Palearktis (PECBMS 2025, BirdLife International 2024). I Europa förekommer två underarter; den sydliga *P. t. trochilus* och den nordliga *P. t. acredula*. Lövsångaren häckar i olika typer av skogs- och buskmarksmiljöer och bygger boet på marken (se Bellamy m. fl. 2009). Övervintring sker i tropiska Afrika söder om Sahara; den sydliga i västra Afrika och den nordliga underarten i östra och södra Afrika (Hedenström och Pettersson 1987, Fransson och Hall-Karlsson 2008). I likhet med flertalet andra långdistansflyttare (Sanderson m. fl. 2006, Ockendon m. fl. 2012) har lövsångaren minskat, med 40 % sedan 1980, i Europa som helhet (PECBMS 2025). I Sverige, där den sydliga underarten förekommer i de södra och centrala delarna, och den nordliga i den norra, har minskningen konstaterats både i svensk ringmärkning och genom Svensk häckfågeltaxering (Fransson m. fl. 2024, Green m. fl. 2024). Undersökningar i Storbritannien har visat att lövsångaren minskade i söder samtidigt som den ökade något i norr, framför allt på grund av skillnader i häckningsframgång/produktivitet (antal flygga ungar per häckning; Morrison m. fl. 2016). Fortsatta studier i Storbritannien har visat på förskjutningar i olika livscykel-händelser som häckning och ruggning, kopplat till temperaturförhållanden under häckning, vilket påverkat populationsutvecklingen negativt (Hanmer m. fl. 2022).

Denna studie omfattar resultat från 35 år med standardiserad ringmärkning vid Sundre fågelstation, Hoburgen, Gotland (56°55'N, 18°08'E). Ringmärkning har skett under perioden 25 juli–15 september 1990–2024, med 18 slöjnät, från en timme innan soluppgång till minst 10:00. Datainsamling omfattar ålder, vinglängd, vikt, fettstatus (skala 0–6) och pullruggning (skala 0–6). Årsungar blir flyttningsbenägna först när ungfågelruggningen nått ruggningsstadium

5–6 (Lawn 1984, Hedenström och Pettersson 1987, Lindström m.fl. 1996), dvs årsungar i pullruggningsstadium 0–4 har lokalt ursprung. För att skatta populationsutvecklingen för lövsångaren på södra Gotland, följdes den årliga ungfågelproduktionen i form av antalet ringmärkta årsungar i pullruggningsstadium 0–4. Sambandet mellan antalet ringmärkta årsungar i pull 0–4 per år och temperatur respektive nederbörd under häckningsperioden analyserades med data från SMHI, Sveriges meteorologiska och hydrologiska institut, för Hoburgen, Gotland, där häckningen delades upp i tre faser, ruvning (27 maj–10 juni), boungar (11–30 juni) och flygga ungfåglar (1–25 juli); se figur 7 respektive appendix 2. Totalt ringmärktes under perioden 27 637 lövsångare, i genomsnitt 790 (272–1462) per år, varav 96,2 % utgjordes av årsungar. 14 % av de ringmärkta årsungarna saknade klassning av pullruggningsstadium. Dessa gavs antingen pullruggningsstadium 0–4 eller 5–6 baserat på fördelningen av de som bedömts vid det datum de fångats (se appendix 1).

Ringmärkningsperioden 25 juli–15 september täcker flyttningsperioden för lövsångare vid Hoburgen, Gotland väl (årsungar i pullruggningsstadium 5–6), medan perioden då de lokala årsungarna genomför så kallade ungfågelrörelser (stadium 0–4) bara delvis täcks (figur 2). I och med den pågående klimatförändringen anländer flyttfåglar allt tidigare till häckningsområdena (Cotton 2003, Hellström m.fl. 2023). Tidigareläggning av häckningen skulle kunna innebära att även perioden för pullruggning förskjuts, dvs påverka fångsten av årsungar i pullruggningsstadium 0–4 över tid. Analys av mediandatum för ungfåglar i stadium 3 och 4 under 1990–2024 visade dock ingen trend (figur 3), dvs antalet årsungar i pullruggningsstadium 0–4 kan antas utgöra ett tillförlitligt mått på ungfågelproduktionen under perioden.

Antalet ringmärkta årsungar i pullruggningsstadium 0–4, dvs lokala ungfåglar av *P. t. throchilus*, varierade avsevärt under perioden, 50–591 (i genomsnitt 317) per år, med en signifikant negativ trend över tid (Spearman rank-korrelation; $r_s = -0{,}69$, $p < 0{,}001$; figur 4). Antalet var relativt stabilt, 431 ± 85 (standardavvikelse) per år under 1990–2006, följt av minskande antal och högre variation under 2007–2024; från 2016 och framåt noteras en minskning med 74,0 % (112 ± 44). Vikten för årsungar i ruggningsstadium 4 var konstant under perioden för såväl hanar (linjär regression; $t = -0{,}34$, $p = 0{,}69$) som honor ($t = 0{,}44$, $p = 0{,}66$) (figur 6) vilket indikerar att tillgången på föda för överlevande flygga ungfåglar varit oförändrad. Analys av sambandet mellan antalet ringmärkta årsungar i pullruggningsstadium 0–4 och temperaturförhållanden under häckningsperioden visade på en signifikant negativ korrelation under både ruvnings- (Spearman rank-korrelation; $r_s = -0{,}50$; $p = 0{,}002$) och boungefasen ($r_s = -0{,}45$; $p = 0{,}006$), men inte under perioden som flygga ungfåglar ($r_s = -0{,}29$; $p = 0{,}091$), dvs förhöjd temperatur under tiden i bo resulterade i färre ringmärkta årsungar. En fördjupad utvärdering av förhållandet mellan temperatur och antalet ringmärkta årsungar i pullstadie 0–4 visade på temperaturens betydelse på ungproduktionen i området (figur 8). Högre temperaturer, som t. ex. 2007–2008 samt under 2016, 2018 och 2021, resulterade i färre ringmärkta årsungar, medan genomsnittliga temperaturer innebar fler årsungar; t. ex. under 1996–1998, och 2011–2012. Kompenserat för att häckningspopulationen i området minskat (se figur 9) ringmärktes under perioden 2016–2024 färre årsungar än förväntat i samband med höga temperaturer under framför allt boungefasen (figur 8).

Orsaken till lövsångarens tillbakagång är oklar, och sannolikt komplex, då förhållandena under såväl häckning, övervintring som utmed flyttvägar, t. ex. passagen över Sahara, kan påverka överlevnaden och därmed populationsutvecklingen. Dessutom kan utvecklingen för den nordliga och sydliga underarten se olika ut i och med att de har olika häcknings- och övervintringsområden. Mot bakgrund av att flertalet långdistansflyttare som övervintrar i tropiska Afrika uppvisar minskande populationer har det antagits att förhållandena i övervintringsområdet och/eller under flyttningen har stor betydelse för populationsutvecklingen (Sanderson m.fl. 2006, Ockendon m.fl. 2012), speciellt som överlevnaden kan variera betydligt mellan år (Morrison m.fl. 2016), t. ex. beroende på varierande temperatur och nederbörd i övervintringsområdet i västra Afrika (Vickery m.fl. 2014, Telensky m.fl. 2020). Detta har ifrågasatts i och med skillnader i populationsutveckling inom arter, t. ex. lövsångare, med samma övervintringsområde. Snarare kan förhållanden under häckningssäsongen spela roll för utvecklingen, där produktiviteten, dvs antal flygga ungar per häckningsförsök, avgör om populationen ökar eller minskar (Morrison m.fl. 2016). Vad som påverkar produktiviteten är inte

klarlagt. Minskad överlevnad kan bero på otillräckliga födoresurser till följd av klimatförändringen, antingen som minskad tillgång på insekter i sig, eller en obalans i tid mellan ungarnas behov och förekomsten av insekter (Both m. fl. 2006; Møller m. fl. 2008; Martey m. fl. 2017 och referenser däri). Vidare kan enligt Hanmer m. fl. (2022), minskad produktivitet hos lövsångare kopplas till temperaturförhållanden genom påverkan på förhållandet mellan häckning och den adulta ruggningen. En tidigareläggning av ruggningsfasen pga. ökad temperatur (se Dawson 2005) kan inverka negativt på t. ex. ungomvårdnad, med minskad överlevnad som resultat (Hanmer m. fl. 2022). Martey m. fl. (2017) modellerade populationstrenden för lövsångare i Storbritannien och fann ett optimum för populationstillväxt vid 11°C (räknat på hela häckningssäsongen från april till juli). Detta överensstämmer med våra resultat; lägre ungfågelproduktion vid speciellt höga temperaturer, och högre antal årsungar vid mer genomsnittliga temperaturer (figur 8).

Skattad utveckling av häckningspopulationen av lövsångare på södra Gotland utifrån antalet ringmärkta ungfåglar per år (figur 9) visar på kraftigt minskad häckfågelpopulation i och med den minskade ungfågelproduktionen fr o m 2016. För att vända utvecklingen krävs antingen högre överlevnad av adulta fåglar och/eller ökad ungfågelproduktion. Både överlevnaden under övervintring och flyttning (Vickery m. fl. 2014) och produktiviteten (Hanmer m. fl. 2022, Telensky m. fl. 2020) tycks påverkas negativt av ökande temperatur som en följd av den pågående klimatförändringen. Prognoserna för framtiden är att temperaturen kommer att fortsätta att öka (IPCC 2021) varför populationsutvecklingen, åtminstone för den sydliga rasen av lövsångare (*P. t. trochilus*), i Europa är oroande.

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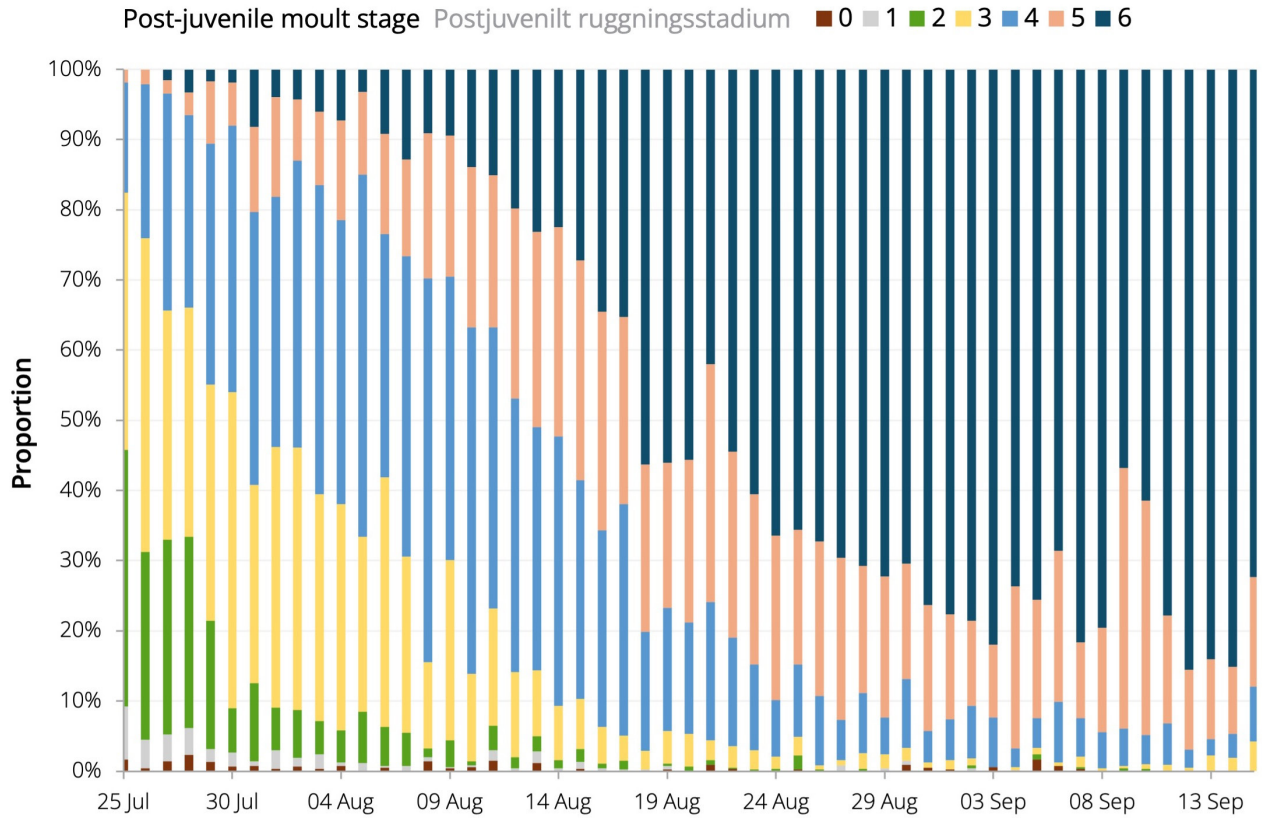
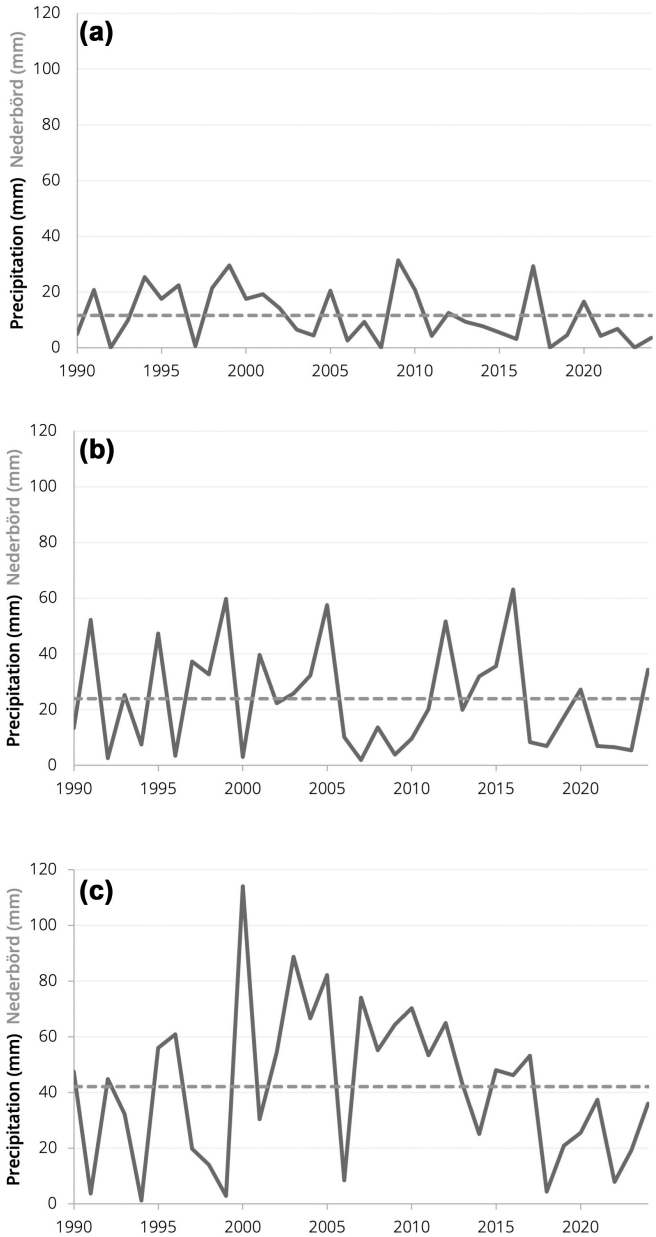
Appendices



APPENDIX 1. The average proportion (%) of first-year willow warblers in different stages of post-juvenile moult (0–6) per day during the ringing period 25 July–15 September at Hoburgen, Gotland, Sweden, 1990–2023. Stage 0 means that post-juvenile moult has not started and stage 6 that moult is completed. The proportion of the respective moult stage per day was used to assess the stage of undetermined first-year birds.

– Andelen (%) årsungar i olika pullruggningsstadier (0–6) per dag under ringmärkningsperioden 25 juli–15 september vid Hoburgen, Gotland. Stadium 0 innebär att pullruggningen (den postjuvenila ruggningen) ej är påbörjad och stadium 6 att ruggningen är fullt genomförd. Andelen för respektive pullruggningsstadium per dag användes för att skatta stadium för ungfåglar för vilka stadium inte bestämts.



APPENDIX 2. The amount of precipitation (mm), and linear regression-statistics, during (**a**) the incubation period (27 May–10 June; t = –1.81, p = 0.080), (**b**) the nestling period (11–25 June; t = –0.75, p = 0.46), and (**c**) as fledglings (1–25 July; t = –0.48, p = 0.64), in willow warblers at southern Gotland, Sweden in 1990–2024. Data for Hoburgen, Gotland, Sweden, from the SMHI. Hatched lines show the overall averages

– Mängd nederbörd (mm) under (a) ruvning (27 maj–10 juni; t = –1,81, p = 0,080), (b) boungefas (11–25 juni; t = –0,75, p = 0,46), och (c) som flygga (1–25 juli; t = –0,48, p = 0,64), för lövsångare på södra Gotland 1990–2024. Data från SMHI för Hoburgen, Gotland. Streckade linjer visar medelvärde.