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RESEARCH PAPER

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Territory occupation sequence and population change 2005–2019 in a satellite versus core area for Grasshopper Warblers *Locustella naevia*

Revirbesättningens ordning och populationsförändringar hos gräshoppsångare Locustella naevia *i ett satellitområde jämfört med ett kärnområde 2005–2019*

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BECAUSE OF habitat preferences and variation at a landscape level, a species' distribution tends to show a level of aggregation. In the Grasshopper Warbler *Locustella naevia*, the distribution is linked to suitable breeding habitats of open grassy and herbaceous grounds, often adjacent to water. Consequently, the presence of the Grasshopper Warbler at landscape level will consist of core and satellite areas. In theory, birds can sense habitat quality and should occupy territories within those areas based on territory quality. It might also result in different population trends between different areas in the landscape. I tested these assumptions through a 15-year study in a satellite area, comparing the results to a nearby core area. In both areas, the males occupy a territory based on the perceived attractiveness, and general patterns of the territory utilization were similar between areas. Territory density was lower and the males arrived later in the satellite area, thereby confirming the satellite/core area relationship between the study areas. In the core area, no significant change in population size was noted, while in the satellite area, the population decreased significantly.

Keywords: breeding ecology | habitat quality | territory selection | population decline | long-term survey | Passeriformes

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Introduction

The Swedish population of Grasshopper Warbler *Locustella naevia* had a peak in around 1990, after which the population suffered a decline of roughly sixty percent (SLU Artfakta 2019, Green *et al.* 2022). The species was included in the national Red List in 2005, as a Near Threatened (NT) species (Gärdenfors 2005). It was still considered as NT in the 2010 national Red List (Gärdenfors 2010) although the decline had ceased at about the turn of the century. In the red lists of 2015 and 2020 the Grashopper Warbler was placed in the category of Least Concern (LC) (SLU 2020). Hence, during my study period 2005–2019, the national population fluctuated about a steady level (Green *et al.* 2022).

Due to habitat preferences, the mobility of the species, habitat variation and fragmentation (patch size and isolation) at a landscape level, a species' distribution tends to show different levels of aggregation and population sizes (Andrén 1994). The Grasshopper Warbler requires for breeding specific types of grass/herb-rich open or semi-open areas, often in connection to water (Gilbert 2012). Some such habitats are large, some small. For many populations, a large fraction of the individuals may regularly occur in so called "sink" habitats where populations may persist by being locally maintained by continuous immigration from more-productive "source" habitats nearby (Pulliam 1988). Consequently, Grasshopper Warbler occurrence at the landscape level will consist of core areas with many territories and satellite areas with fewer territories.

In theory, birds can sense habitat quality and should occupy areas and territories within these areas accord ing to territory quality. This has been shown to be the case in other bird species (see for example Lanyon & Thompson 1986, Bensch & Hasselquist 1991). Hence, Grasshopper Warbler males could be expected to distribute themselves among different territories according to habitat quality, in sequence from the best to the worst. Thus arrival dates between different territories could be used as a measure of territory quality (Sergio & Newton 2003, a full review of the strengths and weaknesses of this assumption is found in Johnsson 2007). Therefore, I hypothesized that a negative population trend in the Grasshopper Warbler would be easier to detect in a satellite area compared to a core area, and that within each area the territories that were most attractive should be colonised first.

In this study I aim to test these predictions by comparing the records of a 15 year-long study in a potential satellite ("sink") area with those from a core ("source") area, separated by only two kilometres distance. The satellite area resides along Kumlaån (Kumla River) and the core area in Björka lertag, a nature reserve and Natura 2000 site, which are both located in Kumla, southern Sweden. In the latter the Grasshopper Warbler population have been monitored extensively since 1983 and in the 10 years that preceded this study, up to 12 singing males (mean of 6.6, median of 6.5) were noted at Björka lertag. Population densities of Grasshopper Warbler have been observed to be variable; in Finland populations typically includes 3–8 pairs/km^2, but densities of up to 20–50 pairs/km^2 have locally been observed in optimum habitat (Hagemeijer & Blair 1997, del Hoyo *et al.* 2006). The observed population densities in Björka lertag (prior to this study) translates to up to 36 singing males/km^2 (mean/median value of approximately 20 singing males/km^2). Hence, in this study this site is classified as a high quality site and is referred to as the core area in this study.

To answer my question on if the two areas had a similar population development I first investigated if there really was a satellite area/core area relationship between my study sites. I did this by looking at the population density and territory occupancy in the (presumed) satellite and core area. In addition, I investigated if males arrived at a similar time to the satellite area compared to the core area of Björka lertag and if I could find evidence for an active territory choice within each area.

Method

STUDY AREAS

The core area Björka lertag is a nature reserve, formed in 1997 and expanded in 2012, of approximately 33 ha. The area is characterized by a mosaic of open water surfaces, reedbeds, bushes and deciduous forest. In 1969 a brick manufacturer begun excavating clay and farmland was turned into a clay-pit. Some parts were subsequently used as a landfill, while other parts were left to develop freely. Over time a rich birdlife developed and Grasshopper Warblers began to breed in the area in the mid-1980s (see for example Engzell 1996, Teljå 1996,

for more information about the area). Grasshopper Warblers (and successively other species) have been monitored there since 1983.

The satellite area is approximately 47 ha and includes about 500 m of the stream Kumlaån, downstream from Nykvarn, at ~59.1049, 15.4328 (GCS WGS 1984). In the studied stretch of Kumlaån the water retains its natural winding path (Figure 1). The nature of the stream varies; the western part can perhaps best be described as a reen ("very slowly-flowing stream <5 yards wide; of the order of 1 foot/minute"), whereas the eastern part it better described as a river, according to Yapp's classification of habitats (Yapp 1955). Approximately 25–30 m (15–80 m) on each side of the stream was not cultivated, constituting the main habitat for Grasshopper Warblers. The vegetation on the banks and the uncultivated land surrounding the stream is mostly made up of tall grasses, including Common Reed *Phragmites australis*, and tall herbaceous vegetation, for example the Common Nettle *Urtica dioca*. European

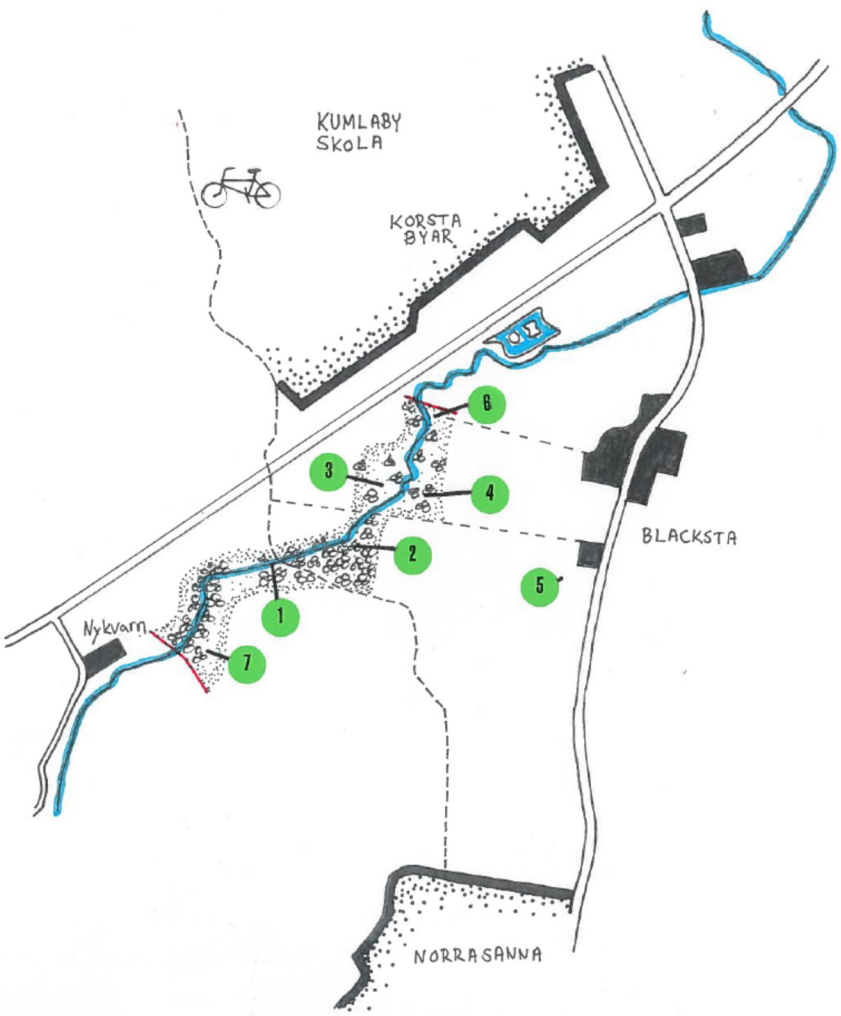

FIGURE 1. Simplified map over the Grasshopper Warbler *Locustella naevia* study area. Blue colour represents water. The red lines delimit the monitored stretch of Kumlaån. Green circles with numbers and arrows mark territories.
— *Förenklad karta över studieområdet* för gräshoppsångare Locustella naevia. *Blå färg representerar vatten. Röda linjer avgränsar den inventerade sträckan av Kumlaån. Gröna cirklar med nummer och pilar markerar territorier.*

Raspberry *Rubus idaeus* is also common on the banks. In addition, there is also a high proportion of tree and bush vegetation, dominated by Common Alder *Alnus glutinosa*. The Grasshopper Warbler has been noted in the area as a regular singing, and probably breeding, species since at least the mid-1980s (Engzell unpubl.). The area was surveyed during 2005–2019.

MONITORING

Core area in Björka lertag

The methodology used to monitor Björka lertag aims to map individual territories of all species in the area and is described in detail in BIN (Statens naturvårdsverk 1978), updated version by Naturvårdsverket (2012) and in Engzell & Waern (2005). The methodology for territory mapping includes 8–10 or 12 visits, but could be increased to cover monitoring of night-active species. During 2005–2019, monitoring has been carried out by me and Hans Waern, with around 8–12 visits targeting night active birds (like Grasshopper Warblers). This in addition to the day/morning visits (during which Grasshopper Warblers are also regularly noted). From 2008 the visits targeting night active species were made in the same three distinct time periods as in the satellite area. From each visit, the position of the sightings of grasshopper warblers (mostly singing males, but also other nesting behaviours/found nests are included) were marked on a map. After all visits were executed, swarms of sightings on the map were evaluated to identify territories. To identify as a territory there had to be sightings from several visits to each territory, and simultaneous registrations between neighbouring territories were taken into account to determine whether it is one, two or more territories. The number of sightings needed to classify as a territory depended on the number of valid monitoring visits (visits made when grasshopper warblers were present and possible to locate). If the number of valid visits were 8–10, three sightings from valid visits were required to identify a territory. However, if the number of valid visits were lower than 8–10, two sightings from valid visits were required.

Satellite area along Kumlaån

To compare the populations of grasshopper warblers in the two areas, a less time consuming monitoring method was used in the satellite area along Kumlaån. This method was based on a method used by Kvismare Bird Observatory in 1976–1978 for monitoring Grasshopper Warblers (Pettersson & Sondell 1979). This method is in turn based on a method used to monitor night singing birds on the Island of Öland (Rodebrant 1973, 1976). Each year I made three visits in May and June to cover the main period of singing males. From 2008 the visits were done in 3 distinct periods. The first visit was carried out in the beginning of May (approximately week 18–19), the second in mid-to late May (approximately week 20–21) and the third in the beginning of June (approximately week 22–24). This methodology was used in order to both monitor the number of singing males, and to approximate when the birds arrived to the area and specific territories.

At each visit I walked at a normal walking pace along a predetermined route with short five-minute stops that allowed access to the whole area. I noted all singing Grasshopper Warbler males on a chart. The singing positions of the males were used to determine the central part of the territories, but no attempt was made to determine territory boundaries or breeding success. In order to qualify as a territory, a singing male should have been noted during at least two out of the three visits. In years with late arriving birds, I made a fourth visit, to confirm whether new birds, recorded on the third visit, established territories (the original method, as used in Kvismaren, was two visits with a third visit to males only heard once). I tried to avoid bad weather such as rain and hard winds, but six visits were (by necessity) made in slightly rainy weather and three were made in slightly windy weather. Visits were made either late in the evenings or in the early morning hours to coincide with song activity (median start time: 23:00 (n=24) or 04:30 (n=14)).

Data treatment and statistics

In this study, areas that qualified as occupied according to the methods described above, in at least one of the study years, is referred to as a territory. This area can be occupied or unoccupied in different years. Occupancy is a measurement of how many of the study years a territory was occupied. In this study, territories occupied in at least six out of 15 years is categorized as "high occupancy", and the territories occupied two to three out of 15 years is categorized as "low occupancy".

Single year occupancy indicates that the territory was occupied in one of 15 study years.

Statistical analysis has been performed with Spearman Rank correlations and χ^2 statistics, calculated using free online calculators found on Social Science Statistics (https://www.socscistatistics.com/) and/or Office for Research Development and Education website (Wessa 2017). I assumed, unless disclosed by the presentation of the results, all tests to be two-tailed.

Results

In total, the number of singing males varied between zero and four in the satellite study area (mean 1.9 +/− 0.5, median two; Table 1), distributed between seven different territories during 2005–2019 (Figure 1). Of these territories, the occupancy varied from high in Territory 3 (occupied in 10 out of 15 years) and Territory 1 (six out of 15 years), to low (two to three out of 15 years) or single year occupancy in the other territories (Table 1).

Corresponding numbers of territory occupancy in the core area was 12 territories with high occupancy (occupied in 6–15 years), 20 territories had a low occupancy (two to three years) and single year occupancy occurred in 11 territories. One territory was occupied in 15 out of 15 years and five others were occupied in 10 years or more. There was no statistically significant difference in the general occupancy pattern between the satellite and core area (χ^2 (n=50)=0.4627; p>0.05).

Territory quality, measured as number of years of occupancy in the time period 2008–2019, correlated with the number of times the territory was the first one to be occupied in the satellite area (r_s=0.808, p<0.05; Figure 2). These two parameters were also found to correlate in the core area in 2005–2019 (r_s=0.532, p<0.05).

The population density, using the uncultivated area surrounding the river as a boundary, varied between 0 and 0.09 singing males/ha, with a mean and median of 0.04 singing males/ha in the satellite area (0–9 males/km^2, with a mean/median of four). Those figures falls in the lower range of Grasshopper Warbler density, as given by Hagemeijer & Blair (1997). The density at Björka lertag during the same period was

TABLE 1. Occupation of different territories (T) by singing males of Grasshopper Warblers *Locustella naevia* in a study area by Kumlaån, during the years of 2005–2019, and the total number of singing males in each year. * marks the first occupied territory in 2008–2019.
— Revirbesättning av sjungande hanar av gräshoppsångare Locustella naevia *i studieområdet vid Kumlaån under åren 2005–2019, samt det totala antalet hanar varje år. * markerar det först besatta reviret under åren 2008–2019.*

Year *År*	T 1	T 2	T 3	T 4	T 5	T 6	T 7	Sum singing males *Summa sjungande hanar*
2005	X	X	X	X				4
2006			X	X				2
2007	X		X					2
2008	X	X*	X					3
2009	X*		X*	X				3
2010	X*				X			2
2011						X*		1
2012		X*					X	2
2013								0
2014			X*					1
2015						X*		1
2016	X*		X				X	3
2017			X			X*		2
2018			X*					1
2019			X*					1
Sum *Summa*	6	3	10	3	1	3	2	

0.18 to 0.52 singing males/ha, with a mean of 0.35 and a median value of 0.36 (18–52 males/km^2, with a mean/median value of 35–36). That is well within (or some years even a bit higher) the figures given for densities from optimum habitat (Hagemeijer & Blair 1997, del Hoyo *et al.* 2006).

The difference between the two study sites extends also to time of arrival. Only in one of 12 years (2008–2019) did I note singing males in the beginning of May (before 11 May) in the satellite area, as compared to nine times in the same 12 years at Björka lertag (χ^2 with Yates correction: χ^2 (n=24)=8.4; p<0.01). Most males arrived to the satellite study site in mid to late May, but nearly as many arrived in late May or in the beginning of June (Table 2). For reference, the arrivals to the core study site had a different pattern during these same years (Appendix 1). There the number of early arrivals (late April to early May) were only slightly lower than in mid to late May and only a few males arrived late (early June). This difference between the two sites is statistically significant (χ^2 (n=163)=14.495; p<0.05).

During the period from 2005 to 2019, this small satellite population had a negative population trend (Spearman Rank Correlation, r_s=−0.599; p<0.05: Figure 3). In contrast, there was no statistically significant trend in the core population of Björka lertag (r_s=−0.192, p=0.49). The population in the core area remained stable at 6–17 singing males over the period 2005–2019, with a mean of 11.7 and a median of 12 males (see Appendix 1).

Discussion

In the beginning of this study I predicted that the (then presumed) satellite area along Kumlaån was less attractive to Grasshopper Warblers than the study area at Björka lertag, because males seemed to arrive there later. This prediction seems to have been verified in this study by a lower population density and differences in the time of arrival to the areas, both underlining a satellite/core area relationship between the two areas (discussed in more detail below). It was further strengthened in 2021, when I got results indicating that

FIGURE 2. Relationship between the number of years each Grasshopper Warbler *Locustella naevia* territory by Kumlaån were occupied in 2008–2019 and the number of times each territory was the first to be occupied in the same years. Territories 1 and 3 were noted on the same date in 2009 and were given the values 2.5 and 3.5, respectively. Two territories were occupied in only one year and never the first one to be occupied (territories 4 and 5). Statistically significant trend line is shown.

— Sambandet mellan antalet år gräshoppsångarreviren Locustella naevia *längs Kumlaån var besatta åren 2008–2019 och antalet gånger reviren blev det första upptagna reviret under samma år. Revir 1 och 3 noterades på samma datum 2009 och fick värdet 2,5 respektive 3,5. Både revir 4 och 5 var endast besatta ett år och var aldrig de första reviren att besättas. Statistiskt signifikant trendlinje visas.*

TABLE 2. The time of arrival of Grasshopper Warbler *Locustella naevia* males to the study area by Kumlaån in the years 2008–2019.
— Gräshoppsångarhanarnas Locustella naevia *ankomst till studieområdet vid Kumlaån under åren 2008–2019.*

Year *År*	Late april- beginning of May Slutet av april till *början av maj*	Mid to late May *Mitten till slutet av maj*	Late May to early June *Slutet av maj till början av juni*
2008	0	1	2
2009	0	3	0
2010	0	0	2
2011	0	0	1
2012	0	1	1
2013	0	0	0
2014	0	1	0
2015	0	0	1
2016	2	1	0
2017	0	1	1
2018	0	1	0
2019	0	1	0
Sum *Summa*	2	10	8

there are significantly less arthropods (potential prey) in the satellite area as compared to the core area Björka lertag (Engzell unpubl.).

The reasons for the observed difference in population trend between the areas could be several. It is noteworthy, however, that no significant differences in the general occupancy pattern was detected between the satellite and core area. Interestingly, within both study areas some territories were more frequently occupied than others. In addition, the territories that were more frequently occupied correlated with another measure of habitat quality, as they were more often the territory that was occupied first, in the respective area. The observed pattern that the territories that are more often occupied between years also most often were occupied first within a year indicates that Grasshopper Warbler males do try to settle in territories according to territory quality/attractiveness, similar to what have been observed in other species (Lanyon & Thompson 1986, Bensch & Hasselquist 1991). That Grasshopper Warblers in the studied areas share this ability is important, especially when applying different

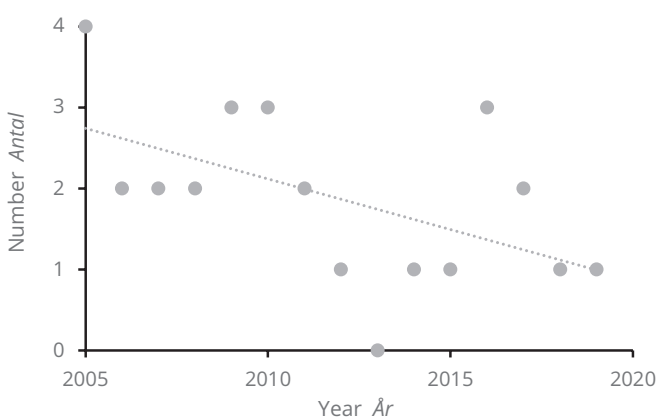

FIGURE 3. Number of singing Grasshopper Warbler *Locustella naevia* males during 2005–2019 in the study area by Kumlaån. Statistically significant trend line is shown.
— Antalet sjungande hanar gräshoppsångare Locustella naevia *2005–2019 i studieområdet vid Kumlaån. Statistiskt signifikant trendlinje visas.*

ecological theories (like source–sink dynamics) both in this and in future studies.

The statistical difference in the time of early arrival in the two areas, with less birds arriving early in the satellite area, could be because the males actually arrive later to the (assumed) suboptimal habitat. But it could also be a side effect of the differences in the population size between the two study sites, since it is expected to detect more extreme arrival dates in larger populations due to more tries (i.e. more birds). Thirdly it could be a result of differences in monitoring activity between the two sites (also due to more tries). On the other hand the difference in the arrival pattern was not only detected in the early arriving males, more birds also arrived late in the satellite area compared to the core area in Björka lertag. Hence, the differences seen in early arrivals are probably not due to the difference in population size (as a large population is also expected to generate more extremely late arrivals, not just early arrivals). However, as fewer visits and less observation time was spent in the satellite area compared to the core area, it is possible that this difference is due to, or enhanced by, the differences in monitoring effort between the two sites.

Possibly, males that settled in the satellite area arrived in the general (larger) area and had to move around a bit in the landscape in order to find the best free territory. Yet, other factors, such as age or other state dependent factors, could also play a role. For example, site fidelity (not investigated in this study) could also be an important underlying factor. It could, for example, be that the degree of site fidelity is different (for several reasons) in a core area or in a satellite area. Results from bird ringing in the core area in Björka lertag implies a rather high site fidelity in male Grasshopper Warblers there, as several have been retrapped in the area in successive years (see for example Engzell 2017b). A high site fidelity could make early arrivals more advantageous (in the local competition for the best territories). However, it could also make late arriving males more prone to stay in suboptimal territories, than to search for better quality territories in satellite areas (at least far from the core area).

Not adopting the same monitoring effort in the satellite area as in the core area potentially makes the figures on population density difficult to compare. The simplified monitoring method with only three visits used in the satellite area, is better suited to monitor population change over time than to give accurate numbers on the "true" number of singing males each year compared to the more extensive method used in the core area. But even taking that into account, the difference in population density is so large that it would take twice (eight individuals) the maximum number of males noted (four individuals) to reach the lowest figure for the population density in Björka lertag. Therefore, the indicated difference is probably real, despite the differences in monitoring methods. Yet, the numbers on population density observed from the satellite area could be slightly underestimated if some males have gone undetected.

The differences in population development between a core and a satellite population (some caution is of course warranted, given the small sample size and differences in monitoring methods) underline the importance of monitoring the Grasshopper Warbler on a broad, national level. Early warning of decline would be possible to obtain if separate trends were calculated for sites of different habitat quality: core sites with records in many years versus sites with records in few years. Although the national decline did not continue during my study period, my study may still throw some light on the cause of the previous decline. It may, at least in part, have been a result of habitat quality change.

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Svensk sammanfattning

På grund av habitatpreferenser och variation på en landskapsnivå tenderar en arts utbredning att visa en nivå av aggregering. Hos gräshoppsångaren *Locustella naevia* är fördelningen kopplad till lämpliga häckningsmiljöer av specifika öppna gräs- och örtrika marker, ofta i anslutning till vatten. Följaktligen kommer gräshoppsångarens förekomst på landskapsnivå att bestå av kärnområden och satellitområden med färre revir. I teorin kan fåglar känna av livsmiljökvalitet och bör besätta områden och revir inom dessa områden utifrån revirkvalitet. Detta kan resultera i skillnader i populationstrender mellan olika delområden i landskapet. Här testade jag dessa antaganden genom att utföra en 15 år lång studie i ett satellitområde och jämföra resultaten med ett kärnområde i samma region. Resultatet visade att hanarna, i både satellitområdet och kärnområdet, besätter reviren utifrån deras attraktivitet. Det generella mönstret för revirens utnyttjande var liknande i bägge områden. Revirtätheten var lägre och hanarna anlände senare till satellitområdet. Därigenom bekräftade studien att det rådde ett satellit-/kärnområdesförhållande mellan de bägge studieområdena. I kärnområdet noterades ingen signifikant förändring av populationsstorleken under studietiden, medan populationen i satellitområdet minskade signifikant. Implikationen av resultaten från inventeringar av gräshoppsångare diskuteras kort, liksom den möjliga orsaken till tidigare populationsminskning.

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Appendix 1

The time of arrival of Grasshopper Warbler *Locustella naevia* males in the study area Björka lertag in the years 2008–2019 and the total number of territories holding males.
— Gräshoppsångarhanarnas Locustella naevia *ankomst till studieområdet i Björka lertag under åren 2008–2019 samt det totala antalet revirhållande hanar.*

Year *År*	Late April–early May *Slutet av april–början av maj*	Mid–late May *Mitten–slutet av maj*	Late May–early June *Slutet av maj–början av juni*	Number of territory holding males *Antalet revirhållande hanar*
2005	–	–	–	9
2006	–	–	–	9
2007	–	–	–	14
2008	9	5	0	14
2009	6	10	1	17
2010	6	5	2	13
2011	6	7	1	14
2012	9	2	1	12
2013	2	7	1	10
2014	0	6	3	9
2015	5	5	2	12
2016	4	2	0	6
2017	6	2	4	12
2018	5	6	1	12
2019	1	11	0	12
Sum *Summa*	59	68	16	