

Breeding biology of the Lapland Bunting *Calcarius lapponicus* in Lapland, Sweden

PETER GIEROW & MARTIN GIEROW

Abstract

We have studied a population of individually colour ringed Lapland Buntings at Ammamäs, Swedish Lapland in 1984–1989. Pairs arrived together at the study site at the time of snow melting (late May to early June). Territorial behaviour (i.e. singing by the males) usually lasted about 10 days. In 1986 and 1987 males sang throughout the incubation period (20–25 days); in the latter year this may have been caused by extensive nest predation. Females were most often seen feeding close to their nests, while males were less confined to their territories. Some observations of territorial birds feeding together in flocks were made during the breeding season. The territory density at the study site was 29/km² which is a slight increase compared to figures from before 1984. Egg-laying was highly synchronized and more than 75 % of the females initiated their clutch within 6 days after the first egg in the first clutch was laid. The average clutch size decreased with progress of the breeding season (–0.057 eggs/day). Clutch size decreased with calendar day in a bi-phasic pattern, decreasing slowly between 28 May and 13 June (–0.02 eggs/day) and more rapidly between 14–20 June (–0.09 eggs/day). The average clutch sizes for these two periods differed significantly (5.59 vs. 5.02). The lower clutch size late in the season may at least

partly be caused by younger females breeding later and having smaller clutches. Females that were known to be old (3K+) had significantly larger clutches than young (2K) and unringed (3K+) females (5.74 and 5.31, respectively). The former group (3K+) on average laid their first eggs on 11 June compared to 14 June for the latter (2K and 3K+). 53 % of the females started to incubate before the clutch was complete, resulting in a 1–2 days hatching asynchrony. Nestlings remained in the nest until they were 10–11 days old. 92 % of the unpredated eggs hatched and only 6 % of the nestlings died during the nest period. During five of the study years, 14 % of the nests were predated. In the sixth year (1987), as much as 88 % of the nests were lost by predation. Thus, predation seemed to have a rather low impact on the population during normal years. However, in the year after the large nest predation (1988) the density of breeding birds reached its minimum suggesting that at least short term effects can occur.

Peter Gierow, 739 Amigos Way, Apt 1B, Newport Beach, CA 92660, USA

Martin Gierow, Getingevägen 58, S-222 41 Lund, Sweden

Introduction

The distribution of the Lapland Bunting encompasses the arctic and subarctic zones of both the Palearctic and Nearctic. Of the four races described, three have rather limited distributions (Williamson 1968). *C.l. coloratus* is found only on the Kamchatka Peninsula, *C.l. subcoloratus* in eastern Greenland, and *C.l. alascensis* in Alaska. The nominate race *C.l. lapponicus*, on the other hand, is almost circumpolar and can be found in arctic to subarctic North America (except Alaska), on western Greenland, in the Scandinavian alpine mountain range, and along the Soviet coast of the Arctic Ocean all the way to Bering Strait.

C.l. alascensis has been studied for a number of years and is relatively well described (Custer & Pitelka 1977, Tryon & MacLean 1980). For the nominate race there exists a thorough report describing a coastal population in northern Canada (Hussell 1972) and a study from two separate years on western Greenland (Madsen 1982, Fox et al. 1987). No systematic studies have been performed on the Scandinavian population, despite that the Lapland Bunting is among the more numerous species on the alpine heath of the Scandinavian mountains (Svensson et al. 1984) and the easy accessibility of these mountains.

By comparing earlier studies of the breeding biology, it is evident that several differences occur between different populations. In an effort to shed more light upon this, a Scandinavian population has been studied for six consecutive seasons, since 1984, at Ammamäs in Swedish Lapland (56°50' N, 16° 20' E). The area studied, a 1 km square, has been described in detail by Svensson et al. (1984), and is since 1964 part of a long term standardized bird census program.

Methods

The work in the field was, during all years, performed from early June to the beginning of July. The breeding conditions, however, differed considerably between the seasons. In 1984 spring was very early, resulting in a ground virtually free of snow already on 1 June. Spring also came early in 1986, a year otherwise characterized by the occurrence of Geometrid moth caterpillars *Epirrita autumnata* also on the alpine heath. In all other years spring was late to very late. It should also be noted that there was a high predation of eggs and chicks in 1987.

The number of breeding birds was estimated by mapping territories of singing males. The visits, usually 8, were performed as early as possible in each season and evaluated according to the standards used in the Swedish breeding bird census (Anon. 1970).

Ringed birds involved predominantly three methods: (a) mist nets, in suspected territories, combined with recorded song and a plastic decoy painted to resemble a male, (b) mist nets alone, but placed close to localized nest, and (c) cages, with an approximate height of 40 cm and a diameter of ≤ 1 m, baited with seeds and placed on appropriate rocks. Captured adult birds were banded with a standard metal ring and an individual combination of three coloured plastic bands. Nestlings were banded with a metal ring and one plastic band, a different colour for each year.

The search for nests was facilitated by following females whenever they were spotted and by closely monitoring their movements. Other parts of the study area were actively checked according to their suitability as nesting habitat. In addition, nightly expeditions were undertaken during the incubation period, during which the area was systematically searched by 3–4 persons, walking 10–20 m apart, in order to flush females off their nests.

The nests were visited once or twice a day during egg-laying, start of incubation, and hatching to get these events properly timed. Otherwise nests were only checked every third or fourth day. The incubation starts was determined by examining the eggs of a clutch in a dark tube, transilluminated by a flashlight (Enemar & Arheimer 1980). The eggs were numbered according to laying sequence, whenever possible.

In addition to data collected by ourselves, information from 1964 to 1983 was obtained from a nest card file of the study area. The date of the first egg laid in a clutch has been calculated using an incubation period of 12 days (own estimate, see below). Data on clutch sizes have only been included if they have been confirmed by repeated visits or by transillumination of the eggs, or when collected from nests in the early phase of hatching (number of hatchlings \leq number of eggs).

Results and discussion

Arrival

The arrival of Lapland Buntings to their breeding grounds usually coincides with the melting of the snow, i.e. in Ammamäs at the end of May to early June. We have been able to follow the start of the breeding season during some of the years with a late spring. These years, the males and the females appeared to arrive simultaneously to the study area, and were often seen moving around, pairwise, looking for food at the edge of the melting snowfields. During late springs Lapland Buntings have been observed in the middle of May at lower elevations, below the tree limit, awaiting the snow melt. Regarding the North American populations it has been reported that the males usually arrives 2–3 days before the females (Hussel 1973), whereas on Greenland differences between the sexes ranging from a few days to two weeks have been observed (Madsen 1982, Fox et al. 1987). Two weeks or more have also been noted for the Alaskan race (Williamson & Eminson 1971, Tryon & MacLean 1980). Both the nominate race in North America (Drury 1961, Hussel 1972) and the Alaskan race (Tryon & MacLean 1980) have been reported to form pairs only when having arrived to the breeding grounds. Mikheev (1939) studied the nominate race on the Russian tundra during one breeding season, and observed the arrival of large flocks of males to a river delta at the onset of snow melt. The females arrived on average nine days later, were more dispersed but stayed well separated from the males. As the spring advanced, the birds broke up pairwise and spread over the tundra. Whether our and Mikheev's observation is a feature characteristic for the European populations or a response to late springs remains to be examined, however.

Formation of territories

The territorial behaviour has varied between the years. During 1984, 1985 and 1988 the males stopped singing at the time of the start of incubation, resulting in a song period not longer than 10 days. In fact, almost no observations of males were made until the feeding of nestlings began. During 1986, however, the males continued to sing throughout the entire incubation

Table 1. Number of territories and nests located within the 1×1 km study area. *Antal revir och bon som lokaliseras inom studieområdet (1×1 km).*

	1984	1985	1986	1987	1988	1989	Mean Medel	1963–83 ¹
Territories <i>Revir</i>	29	32	31	31	25	27	29.2	23.4
Nests <i>Bon</i>	9	20	27	25	16	19	–	–

¹ from Svensson et al. 1984.

period, and in some cases, until a few days after the appearance of the first hatchlings, i. e. altogether 20–25 days. A similar pattern was observed 1987, but the long song period might have been caused by extensive predation upon the nests that year. Direct confrontations between males have been observed a few times, but only at the beginning of the breeding season. This was also the period when the plastic decoy and the taped song were most successful. However, direct attacks against the decoy have only been noted three times. The number of territories has been relatively constant throughout our investigation (see Table 1), which implies that population density alone does not account for the differences in behaviour between the years. Other factors, such as availability of food and females might be involved. Mikheev (1939) reports about intensive territorial fighting among the males, and singing throughout the entire breeding cycle. A similar behaviour was noted in the Alaskan race (Seastedt & MacLean 1979, Tryon & MacLean 1980), but conflicting observations have been made (Rowell 1957, Drury 1961, Hussell 1972).

The role of the male territory as feeding area was studied in three pairs during one season, 1984. The female was very seldom seen outside the male territory; mostly she was seen searching for food in the proximity of the nest. The males, on the other hand, were not at all confined to the area they claimed by singing. One of the males was frequently seen leaving his own territory, passing through most of his neighbour's territories to a section where he was searching for food, often accompanied by a male from a third territory. Observations from other years confirm this behaviour. At one point in the nestling period as many as seven males and two females were observed searching for food in an area of 20×20 m. During the same two hour period one additional male and four females were seen within 100 m of this area. Since several of the birds were banded it was possible to identify them as birds with nests within a 250 m radius from the feeding area. It is likely that they were exploiting an unusual concentration of caterpillars. In Alaska, the males have been reported to utilize the defended area to a considerably higher degree (Tryon & MacLean 1980). They stayed within their territories in 65 % of the cases whereas the beha-

viour of the females was more in accordance with our observations as they remained within the territory 83 % of the time.

Breeding density

The number of territories in our study area was on average $29/\text{km}^2$ (Table 1), which was considerably higher than the result from the standardized mapping 1964–83 in the same area (Svensson et al. 1984). However, the discrepancy in the number of territories between the two counts during the span of our study was very low, ± 1 –2 pairs (Svensson, pers. comm.). A slow increase of the numbers from the first years can be seen in the standardized census, but whether this represents a true tendency or not remains to be seen. Interestingly, the Lapland Bunting has been reported to be expanding on the Kola peninsula recently (Mikhailov & Filchagov 1984). Population densities show a great deal of variation, from 17–50 pairs/ km^2 (Wynne-Edwards 1952) to more than 200 (Rowell 1957, Custer & Pitelka 1977). The higher figure often represents rather small, optimal areas. In addition, very large variations have been reported within a population between different years (Lien et al. 1974, Custer & Pitelka 1977). Fluctuations of this magnitude have not been observed in our population (Svensson et al. 1984), but tendencies to form higher densities in a small section of the study area have been observed in certain years.

Nesting data

The nest is built by the female alone. The male can be seen with nesting material, but this is only part of his courtship ritual (see also Drury 1961). The nest is usually localized to the side of a small protrusion of the ground, next to a willow or birch sprig. Areas with tufts of grass and fairly scarce vegetation were often preferred, whereas dense growths of willows and flats of pure bog were usually avoided. Birds that could be followed for several years did usually not move more than 100–150 m from one year to another (Gierow & Gierow unpubl.)

One nest, out of 104 examined by us, was lined with grass alone. The material most frequently used was

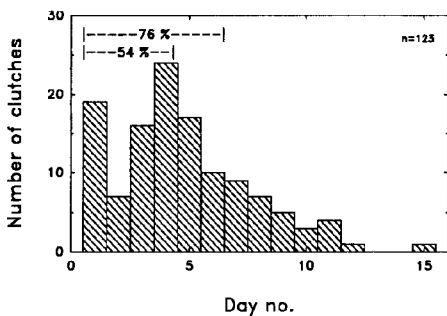


Fig. 1. Onset of egg laying in relation to the first egg of the season. All clutches of a season have been ordered in relation to the day (day no. 1) of the first egg in the earliest nest in that season. Only years with $n \geq 5$ have been included.

Ägglägningsstart för alla kullar ordnade i relation till den dag då första ägget lades i den tidigaste kullen (day no. 1) under respektive säsong. Enbart år med fem eller fler registrerade kullar har använts vid analysen.

white Ptarmigan feathers, from just a few up to a dozen or more. They were occasionally replaced by or supplemented with dark wader feathers. In addition, hairs from reindeer were often included in the lining of the nest. An extremely well insulated nest contained 10 Ptarmigan feathers, an abundance of hair and a few tufts of fur from a vole.

When the lining was almost complete, the female laid one egg a day until the clutch was full, and only on rare occasions did a break in the laying occur. The egg laying was well synchronized within the population (Fig. 1). More than 50 % of the females had started their clutch four days after the arrival of the first egg in the

earliest nest, and more than 75 % after the sixth day. Thereby, the onset of the breeding season became slightly more synchronized than in the Alaskan race (Custer & Pitelka 1977), and considerably more synchronized than in a population on Greenland (Madsen 1982). It has been suggested that northern populations, due to the late spring and thus a shorter breeding season, would be more synchronized by necessity (Madsen 1982). This might have been further accentuated in our study area since it was situated on a northern slope. A study by Williamson & Eminson (1971), in which a southern population of Lapland Buntings were substantially less synchronized than a northern population, further supports this theory.

The average date for the first egg was 11 June, as shown in Table 2. The average date for individual years has been plotted against the average clutch size in Fig. 2, and shows a decrease in clutch size the later the spring was (-0.057 eggs/day, $r = -0.57$, $p < 0.05$). This result is well in accordance with reports from other bird species in the Ammamäs area (Arheimer 1982, 1987, Svensson 1986, 1987). Depicting clutch size as a function of calendar day results in a bi-phasic pattern (Fig. 3). The number of eggs in a clutch decreased slowly between 28 May and 13 June (0.02 eggs/day, $r = -0.113$, $n = 78$), and was followed by a more rapid decline between 14 and 20 June (0.09 eggs/day, $r = -0.215$, $n = 50$). The average clutch size during these two periods, 5.59 ± 0.69 and 5.02 ± 0.98 , respectively, were significantly different from each other (t-test, $p < 0.001$). Hussell (1972) reports about a decrease in clutch size of approx. 0.12 eggs/day (Fig. 6, p.331), but in a more linear fashion throughout the breeding season. A pattern similar to ours has been noted in a study of the Reed Bunting *Emberiza schoeniclus* in northern Finland (Haukioja 1970).

Table 2. Clutch size and date of laying of the first egg during the study years in comparison with data in the nest card file from 1964–1983. Values are expressed as mean \pm standard deviation.

Kullstorlek och datum för första ägg respektive år i jämförelse med uppgifter från bokortarkivet för åren 1964–1983. Värdena är givna som medelvärde \pm standardavvikelse.

	Clutch size Kullstorlek						Mean Medel	S.D.	N	1 st egg I:a ägg	N
	3	4	5	6	7	8					
1964–1983	3	7	29	32	3	1	5.37	0.91	(75)	11/6	(53)
1984	–	–	1	4	–	–	5.8	0.8	(5)	30/5	(3)
1985	1	1	7	12	3	–	5.63	0.92	(24)	15/6	(13)
1986	–	1	8	16	1	–	5.65	0.63	(26)	5/6	(21)
1987	–	2	13	7	2	–	5.38	0.77	(24)	15/6	(10)
1988	1	4	4	6	–	–	5.00	1.00	(15)	14/6	(14)
1989	1	1	12	2	–	–	4.94	0.68	(16)	14/6	(14)
Total	6	16	74	79	9	1	5.39	0.86	(185)	11/6	(128)

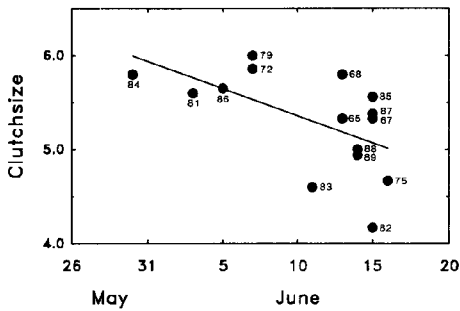


Fig 2. Average clutch size in relation to average calendar date for the first egg of all clutches in different years. The number of clutches used for calculation of clutch sizes was 5–9 prior to 1985 and 15–26 from 1985 and thereafter.

Medelkullstorlek i förhållande till medeldatum för äggläggningsstart respektive år. Antal kullar varierar mellan 5–9 för åren fram till 1985 och mellan 15–26 kullar från och med 1985.

To a certain extent the decline in clutch size could be explained by early nest predation, resulting in production of smaller replacement clutches. However, we were not able to find any such clutches even during years with very high nest predation. The only indication towards this was a male who was seen copulating with a female a few days after that "his" nest had been lost. It has been suggested that the decrease could be a result of young females laying smaller clutches later in the season (Arheimer 1982). Since several of the banded females returned the following season, it was possible to divide our material into two groups, one including only 3K+ females and one all the others, i. e. young females (2K) and unbanded 3K+ females. The resulting average clutch size for the two groups was 5.74 ± 0.73 ($n=14$) and 5.31 ± 0.86 ($n=86$), respectively, which is statistically different from each other ($p < 0.05$). Further analysis of these two groups, utilizing data from nests where the date of the first egg could be accurately determined and omitting the first years when only a few nests of previously banded females could be localized, reveals that they also differ regarding to their onset of egg laying. Thus, the average date for 3K+ females was $11 \text{ June} \pm 2$ ($n=11$) and for the second group $14 \text{ June} \pm 3$ ($n=23$) (U-test, $d=2.34$, $p < 0.05$).

Assuming that 3K+ females would choose older, more experienced males as partners, one would expect a similar difference by dividing the males into two groups. However, this was not the case. Males that were known to be 3K+ had an average clutch size of 5.33 ± 0.84 ($n=18$), which did not differ from the group of unbanded males (5.40 ± 0.81 , $n=82$).

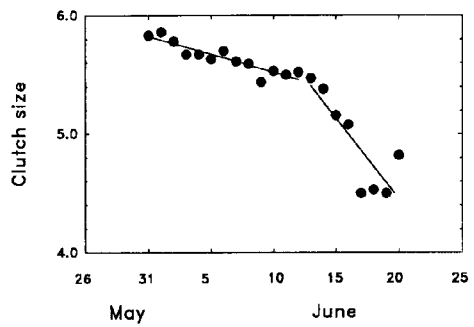


Fig. 3. Clutch size in relation to calendar date. The average clutch size for different calendar dates has been depicted as running means of three days.

Kullstorlek i förhållande till kalenderdatum. Medelkullstorlek för olika datum avsett som rullande tredagars medelvärden.

The relationship between clutch size and the day of the first egg of the season is shown in Fig. 4, resulting in a decrease of 0.11 eggs/day ($r = -0.35$, $n = 123$, $p < 0.001$). A decline of 0.07 eggs/day has been reported for the Alaskan race (Custer & Pitelka 1977). This pattern has been described for a number of species producing a single brood every year (see Hussel 1972).

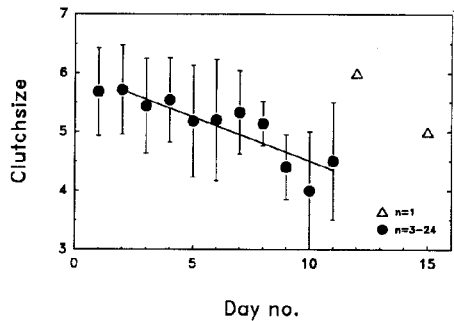


Fig. 4. The average clutch size as a function of day of laying relative to the first egg of the season. Each clutch has been grouped daywise in relation to the day (day no. 1) of the first egg of the earliest nest of that season. n refers to the number of clutches in a daygroup.

Medelkullstorlek som funktion av äggläggning i förhållande till första ägget i tidigaste kullen för säsongen. n = antal kullar.

We have also been able to follow the clutch sizes of 14 females for two years or more. Eight of them did not change at all, whereas three increased by 1, 1, and 2 eggs, respectively, and one decreased by one egg. The remaining two females varied their clutch size up and down by one during the three and four years, respectively, they could be followed. No relationship in the fluctuations of the clutch sizes and of the average date of the first egg could be detected, despite the fact that the latter could change 10 days from one year to another. Custer & Pitelka (1977) followed eight females in Alaska, and only one of them changed its clutch size.

Incubation, hatching and nestling period

By transillumination of the eggs it became evident that the Lapland Bunting often began incubating before the completion of the clutch. 53 % of the females started incubating while one egg or more were still missing ($n = 43$). No obvious pattern could be discerned but, normally, at least 3–4 eggs appeared to be required before the female started incubating. Hussell (1972) suggested that a clutch of five eggs was usually incubated steadily 2 days before completion, and a clutch of six eggs 2.5 days in advance. The incubation, which was performed by the female alone, lasted for 12.4 ± 0.7 days ($n = 24$), when calculated from laying to hatching of the last egg in the clutch. Similar results have been reported by others (Williamson 1968, Hussell 1972, Madsen 1982).

When incubation started before the clutch was complete the hatching period became extended, usually by 1–2 days. The nestlings remained in the nest until they were 10–11 days old, even though they were fully capable to leave the nest, when disturbed, at the age of 8 days. Very short nestling periods have been reported by several investigators, e. g. 7.4 days by Maher (1964) and 6–11 days by Williamson & Eminson (1971), but it is possible that this is a result of too much activity around the nest. Other factors, such as latitude, i. e. day length (Karplus 1952), and pressure from predators (Williamson & Eminson 1971) have also been reported to affect the duration of the nestling period.

Production and predation

After omitting nests that had been subject to predation, 97 nests remained to be used for examination of hatching success. 535 out of 583 eggs hatched, i. e. 92 %. No differences were observed between different clutch sizes. Both Hussell (1972) and Madsen (1982) report a hatching-frequency of 90 %. The survival of the hatchlings could be followed among 325 of them until they were 6–8 days or older. Only 19, i. e. 6 %, died during this period. In other words, 87 % of the eggs resulted in

a nestling that reached the age when it could be banded. Combining these numbers with the average clutch size, 5.39 eggs, and an adult survival of 46.5 % from one season to the next (Gierow & Gierow, unpublished), 23 % of the young must survive from when they were banded to the following season in order to maintain a steady population.

The effect of predation has not been included in the figures above. On average, 14 % of the nests were lost to predators during five of the years. In the sixth year, however, as much as 23 out of 26 located nests were subject to predation, i. e. 88 %. Since the nestlings in the remaining three nests were all recently hatched when our field season ended it is doubtful if any offspring was produced that year. 25 % of the nests were lost during the period prior to hatching, and 8 % of the remaining nests thereafter. Madsen (1982) reported a predation frequency of 7.5 %, with all losses restricted to when there were eggs in the nests. Hussell & Holroyd (1974), on the other hand, recorded an average of 77 %, and similar numbers have been found in populations in Alaska (Custer & Pitelka 1977), evenly distributed throughout the breeding season.

Our results indicate that predation, in the area studied, has a rather limited impact on the population in normal years. However, since the density of breeding birds (see Table 1) reached its lowest point in 1988, the year after a year with extensive predation, it is possible that at least short term effects can occur. Another interesting observation is that the clutch size also reached a low value in 1988 (see Table 2), perhaps indicating an influx of young females to replace older females lost to predators in the previous year. But further studies are required to verify this.

Potential predators in our study area were Ravens, Red Foxes, Longtailed Skuas, Mew Gulls and ermines, with the two first mentioned being most likely candidates as judged from observations around the nests. Ravens and Arctic Foxes were regarded as responsible for the nest predation on Greenland (Madsen 1982). The skua was ruled out by Hussell & Holroyd (1974), since examination of disgorged pellets revealed mostly bones from already fledged birds, and they instead suggest the Arctic Fox as being the most important nest predator.

In summary, our results show that the Lapland Bunting is well adapted to its environment. The breeding season is highly synchronized, making it possible for the majority of the population to produce fledglings within 4–5 weeks of the onset of snow melt. In addition, the decline in clutch size that occurs as the season proceeds, seems at least in part to be due to young females breeding later than adults and producing smaller clutches. However, it still remains to be shown whether this is due to that they are young or that they breed later in the season.

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Sammanfattning

Lappsparvens *Calcarius lapponicus* häckningsbiologi i Lappland

Lappsparvens utbredning inbegriper de arktiska och subarktiska delarna av både Palearktis och Nearktis. Fyra raser finns beskrivna varav en, nominatrasen *C. l. lapponicus*, har en cirkumpolär utbredning. Flera studier av lappsparvens häckningsbiologi har gjorts (Alaska, norra Kanada, västra Grönland) men ännu så länge inga på den skandinaviska populationen. Det har visat sig vara stora skillnader i häckningsbiologi mellan olika lappsparvpopulationer och därför har vi sedan 1984 studerat lappsparv vid Ammarnäs i södra Lappland. Studieområdet (1 km²) har beskrivits i detalj av Svensson m fl (1984).

Metoder

Fälтарbetet har varje år pågått från början av juni till början av juli. Häckningsförutsättningarna har varierat betydligt mellan åren. 1984 kom våren tidigt och det var i princip snöfritt den 1 juni. Ett annat tidigt år var 1986 som också bjöd på riklig

tillgång på fjällbjörkmätarlarver *Epirrita autumnata*. De övriga våramna har varit sena till mycket sena. 1987 var det hög predation på både ägg och ungar.

Antalet häckande par bestämdes genom att revirkartera de sjungande hanarna. Vanligtvis gjordes åtta inventeringar så tidigt som möjligt på säsongen. De utvärderades sedan enligt Svensk häckfågeltaxeringsstandard. Fågeln fängades med hjälp av nät, bandspelarsång och en målad lockfågel av frigit eller i mjärdar med frön som lockbete. De adulta fåglarna märktes med aluminiumring och tre färgringar. Boungar ringmärktes med aluminiumring och en färgring, en unik färg för varje år.

Bon letades upp genom att honor följdes och lämpliga områden söktes igenom. Undersökningsområdet gick även igenom systematiskt nattetid av 3–4 personer för att försöka skrämna honorna från deras bon. Bon besöktes 1–2 gånger per dag i samband med äggläggning, ruvningsstart och kläckning, annars var 3–4 dag. Äggen genomlystes med en transilluminator för att bestämma ruvningsstart. Uppgifter om lappsparrvens häckningsbiologi 1964–1983 har vi hämtat från LUVREs bokortsregister. En ruvningsdag på 12 dagar (egna uppgifter) har använts för att beräkna dagen för första ägget i kullen.

Ankomst

Lappsparrvens ankomst till häckningsplatserna vid Ammarnäs brukar sammanfalla med snösmältningen, d v s slutet av maj till början av juni. Under några sena vårar har vi lyckats följa början av häckningen. Hanen och honan verkade anlända samtidigt till studieområdet och sågs ofta söka föda och röra sig tillsammans. Hos andra lappsparrsvraser har man funnit att honan anländer efter hanen och att parbildningen sker på häckningsplatsen. En häckningsstudie av nominatrasen från den ryska tundran visade dock att lappsparrarna höll ihop i flockar. Dessa lämnade de sedan parvis för att uppsöka sin häckningsplats.

Reviretablering

Hanarnas revirbeteende varierade mellan åren. 1984, 1985 och 1988 slutade hanarna sjunga i samband med att honorna började ruva vilket resulterade i en sängperiod på knappt 10 dagar. 1986 däremot fortsatte hanarna att sjunga under hela ruvningsperioden, i vissa fall även några dagar efter att de första ungarna kläckts (totalt 20–25 dagar). Hanarna sjöng under en lika lång period även 1987, men detta kan ha berott på att den höga bopredationen detta år. Antalet revir i studieområdet har varit ganska konstant under alla år och kan därför inte i sig själv förklara skillnaden i beteende mellan åren.

Under 1984 studerade vi revirutnyttjandet hos tre par. Honorna var mycket sällan utanför hanens sängrevir och sökte mest föda i närheten av boet. Hanarna höll sig däremot inte alls inom sina sängrevir. Till exempel passerade en hane ofta genom sin grannes revir för att nå en plats där han sökte föda. På denna plats var han ofta tillsammans med en tredje hane. Även andra år har liknande observationer gjorts. Vid ett tillfälle under häckningssäsongen sågs sju hanar och två honor söka föda tillsammans på en yta av 20 × 20 m.

Ytterligare en hane och fyra honor sågs inom 100 m från denna plats. Alla dessa fåglar häckade inom en radie av 250 m från födosöksplatsen. Troligen var det en osedvanligt riklig förekomst av fjällbjörkmätarlarver som lockat dem samman.

I en studie av lappsparrv från Alaska visade sig hanarna stanna betydligt mer inom sina revir (65 % av tiden inom reviret).

Revirtäthet

Antalet revir inom studieområdet var i medeltal 29/km² (Tabell 1), vilket är en ökning jämfört med siffror från före 1984. Lappsparrven har även rapporterats öka på Kola-halvön under senare tid. Populationstätheter i andra delar av artens utbredningsområde visar på stora variationer, från 17–50 par/km² upp till 200 par/km². Man har även funnit stora variationer i populationstäthet inom samma population mellan olika år. Ammarnäs-populationen har ej visat stora svängningar mellan år, men tendenser till höga tätheter inom vissa begränsade delar av studieområdet har noterats.

Häckningsuppgifter

Boet, som honan bygger själv, placeras oftast vid sidan av en tuva nära en vide- eller björkkvist. Öppna områden och tuvmarker föredrogs vid bobygget, medan täta vidensnår och rena myrar undveks. Honor som återvände för att häcka för andra året placerade oftast sitt bo mindre än 100–150 m från fjölårets boplats. Bona fodrades oftast med några få till ett dussin vita rippfjädrar samt renhår. Ett extremt välisolerat bo innehöll 10 rippfjädrar, mycket renhår och några tussar sorkpås. Endast ett bo av 104 undersökta var fodrat med enbart gräs.

Populationen uppvisade en mycket väl synkroniserad äggläggning. Mer än hälften av honorna påbörjade sin kull inom fyra dagar och över 75 % inom sex dagar efter det att första ägget lagts i det tidigaste boet för säsongen. Därmed är äggläggningen i denna lappsparrvpopulation mer synkroniserad än i andra populationer. Första ägget lades i medeltal 11 juni (Tabell 2). I Figur 2 har medeldatum för första ägg avsatts mot medelkullstorleken för respektive år. Figuren visar att kullstorleken minskar ju senare våren är (−0.057 ägg/dag, $r = 0.57$, $p < 0.05$). Då kullstorleken avsätts mot kalenderdag erhålls en bimodal fördelning (Figur 3). Kullstorleken minskade långsamt mellan 28 maj och 13 juni (0.02 ägg/dag), medan den minskade snabbare mellan 14 och 20 juni (0.09 ägg/dag). Medelkullstorlekarna för dessa två perioder skiljde sig signifikant åt (5.59 respektive 5.02 ägg, t -test $p < 0.001$).

Liknande mönster har rapporterats för många arter som endast föder upp en kull per år. Till en del skulle detta kunna förklaras av tidig bopredation med omläggningar och därmed lägre kullstorlek som följd. Vi har dock inte hittat en enda omläggning i vårt studieområde trots att vi haft år med hög bopredation. Det har föreslagits att mönstret kan förklaras av att unga honor lägger små kullar och bildar par senare på säsongen. Vi har kunnat testa detta eftersom många ringmärkta honor återvänt till vårt studieområde mellan åren. Vårt material har delats i två grupper, en bestående av enbart kända gamla honor (3K+) och den andra bestående av unga (2K) och ej ringmärkta (3k+) honor. Gruppen innehållande kända gamla honor hade signifikant större medelkullstorlek än den andra gruppen (5.74, $n = 14$ mot 5.31, $n = 86$). De två grupperna skiljde sig också signifikant åt vad gäller medeldatum för första ägget, 11 juni för de gamla honorna och 14 juni för de andra gruppen. En likadan uppdelning av materialet för hanarna visade att det inte fanns några skillnader i kullstorlek (gamla hanar 5.33 ägg, unga och omärkta hanar 5.40 ägg). För 14 honor har vi häckningsuppgifter från två år eller mer. Åtta

honor hade oförändrad kullstorlek medan tre ökande kullen med 1, 1, och 2 ägg, och en minskade med 1 ägg. Två honor hade kullstorlekar som ändrades upp eller ned med 1 ägg under de tre respektive fyra år som de kunde följas. Vi fann inget samband mellan ändringar i kullstorlek och medeldatum för första ägg, trots att det senare kunde variera upp till 10 dagar mellan olika år.

I Figur 4 analyseras sambandet mellan kullstorlek och datum då säsongens första ägg lades. Figuren visar att kullstorleken minskade med 0.11 ägg/dag.

Ruvning, kläckning och matning

Genomlysning av äggen visade att 53 % av lappsparrhonorna började ruva innan kullen var fullagd, vilket medförde att kläckningen blev utdragen över 1–2 dagar. Ruvningen sköttes av honan ensam och varade i medeltal 12.4 dagar räknat från läggning till kläckning av det sista ägget. Ungarna stannade oftast i boet tills de var 10–11 dagar, trots att de vid störning kunde lämna boet då de var 8 dagar gamla.

Häckningsframgång och predation

Kläckningsframgången kunde fastställas i 97 bon som ej utsatts för predation. 535 av 583 ägg, d v s 92 % av äggen, kläcktes. Endast 6 % av ungarna dog innan de uppnått en ålder

på 6–8 dagar, d v s den ålder då de kunde ringmärkas. Genom att kombinera denna dödlighetsfrekvens för boungar med en medelkullstorlek på 5.39 ägg och en adult överlevnad mellan år på 46.5 %, innebär detta att 23 % av de ringmärkta ungarna måste överleva till nästa häckningssäsong för att populationsstorleken skall vara stabil.

Under fem av de sex studieåren blev i medeltal 14 % av bona rövade. Det sjätte året (1987) däremot blev 23 av 26 bon (88 %) rövade. Eftersom ungarna i de tre återstående bona alla var nykläckta då vi avslutade fältarbetet är det tveksamt om någon enda unge i vårt studieområde överlevde detta år. Dessa uppgifter antyder att bopredationen under normala år har en begränsad påverkan på häckningsframgången. Eftersom tätheten av häckande lappsparrar i studieområdet var som lägst 1988, d v s året efter den höga bopredationen, verkar bopredationen åtminstone kunna ha korttidseffekter på populationsstorleken. Vidare var kullstorleken som lägst 1988, vilket kan antyda att många unga honor detta år ersatte ett större bortfall av gamla honor året innan.

Sammanfattningsvis visar våra studier att lappsparrar är väl anpassad till sin häckningsmiljö. De har en mycket synkroniserad häckningssäsong där majoriteten av populationen får ut sina ungar 4–5 veckor efter snösmältningen. Vidare verkar det som den med häckningssäsongen minskande kullstorleken delvis kan förklaras av att de sent häckande honorna är unga och lägger små kullar.