Sex, age, and site fidelity as determining factors of productivity in a confined community of Common Whitethroat

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(*Med et dansk resumé: Køn, alder og stedtrohed som bestemmende faktorer for produktivitet i en afgrænset population af Tornsangere*)

Abstract Fecundity and mortality among both young inexperienced and older experienced individuals are crucial for the population development of birds. To evaluate population dynamics, we examined productivity of eggs and fledglings, as well as site fidelity of males and females, in a Common Whitethroat *Curruca communis* population of 72 breeding pairs on the island of Hjelm, Denmark, during the breeding seasons of 1975 and 1976. Site fidelity was prominent with 85% of breeding males and 44% of females originally being hatched on the island or breeding at least one year earlier. Native breeding males returned to their former territory and nest site (90% within 100 m), while native females were more dispersed. Birds of unknown origin and age (2cy+) constituted 35% of the community but supplied more than three times the number of females (44) compared with males (13). Young native males (2cy) arrived later than older native males (3cy+) and required markedly more time to have the first egg in the nest. About 42% of all breeding pairs produced two clutches. Young native females (2cy) delivered remarkably fewer second clutches (15%) compared to older native (3cy+, 68%) and non-Hjelm-native females of unknown age (2cy+, 36%). The experienced older birds produced more eggs over the season (7.49/7.95 eggs per male/female) than the first-time breeders (5.20/5.31 eggs per male/female). Despite high breeding density (2.9 nests per ha), food availability was apparently plentiful, and since no ground-living predators and only few predatory birds were present, most eggs (90%) subsequently led to fledglings. I propose that advanced spring arrival of Common Whitethroat during the last 50 years in the warmer climate, and the linked capacity to produce two clutches leading to substantially more fledglings, are keys to the recovery of the NW European population, which was declared threatened in 1969.

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Introduction

Quantification of fecundity and mortality is essential in the study of population dynamics of birds (Greenwood & Harvey 1982). Experience and site fidelity are important elements for the ability of individuals to optimise the balance between fecundity and mortality and produce high numbers of offspring, thereby enabling the population to prosper (Greenwood 1980). Young first-time breeders commonly produce less offspring than experienced older breeders (Verhulst & Nilsson 2008). Site fidelity, which means the tendency of birds to return to the same area or even to the specific site where they were hatched, or to occupy the same suitable nesting site as the year before, is another determinant of breeding success in many bird species (Payevsky 2016).

To evaluate these phenomena requires precise knowledge and identification of individual birds and quantification of their production of eggs and fledglings. This requirement can be met by ringing of all breeding birds and fledglings and daily identification of all observed individuals over the breeding season. This pronounced logistic challenge is possible to overcome in a relatively closed bird population of suitable size in a habitat that prevents random emigration and immigration during the breeding season and, at the same time, includes a manageable size of the breeding population but with enough numbers to permit solid statistical analysis. This challenge has traditionally been solved by studies of birds in nest boxes that can be followed closely (Haartman 1951, Berndt & Sternberg 1971), while species nesting in the vegetation require extra attention and a considerable fieldwork to catch the individuals, ring them, identify, and observe them and find their nests for the breeding season's one hundred days.

The Common Whitethroat *Curruca communis* (hereafter only Whitethroat) is the most widespread passerine bird species in Denmark today (Vikstrøm & Moshøj 2020). This remarkable status has developed since 1969, when the species was declared threatened in NW Europe (Berthold 1973) in 1974, and with Winstanley *et al.* (1974) postulating that "alarming is the bird's failure to make any sort of recovery. Having investigated the possible causes of the decline, the authors are convinced that the Whitethroat is the victim of a recent climatic deterioration in its winter quarters, the drought-stricken Sahel Zone of West Africa." In contrast, the recent recovery of the Whitethroat populations in a warmer climate could be the result of a prolonged breeding season due to earlier arrivals and higher total numbers of fledglings from two rather than one clutch per season. This theory is supported here by our detailed population dynamic study.

The study was first and foremost inspired by the high density and relatively confined population of Whitethroats on the island of Hjelm. Secondly, the declaration in 1969 of the species being threatened in NW Europe by recurrent draughts in the Sahel region called for an in-depth study of the species' population dynamics. The objective of this study was to quantify the population dynamics of individually identified Whitethroats on the island during the breeding season of 1976; in 1975 and the year before many birds had been ringed and observed to identify their territory, age, and origin. I was optimistic that our population study could contribute to the understanding of the status and the critical bottlenecks in the future development of the species. Our specific hypotheses were that: 1) Site fidelity would be strong, particularly for males, 2) Individuals' production of eggs and fledglings would benefit from early spring arrival through higher probability of producing more eggs including a second clutch, 3) Sex and age and natal dispersal would play important roles as drivers of the dynamics of the population.

Study site

Situated in Kattegat 6 km off the mainland of Jutland (Fig. 1) Hjelm (56°8'0"N 10°48'10"E) is a close to perfect location for population dynamic studies of breeding passerines like Whitethroat. The breeding habitat was the 25-ha large, and 45 m high morainic hill surrounded by the 37-ha large and otherwise flat island with dry open grasslands and beaches. The hilly plateau was a very suitable breeding ground for Whitethroat, while the flat lowlands were unsuitable as nesting habitat.

Hjelm offered several advantages for population studies. The isolation of the island prevented random intrusions of breeding birds from neighbouring areas, while the study area of 25 ha supported a sufficiently large population (72 breeding pairs) to offer data for convincing analyses with statistical significance. At the same time, the study area was not too large to be carefully examined every day to make sure that all breeding pairs and their nests were under permanent monitoring.

The island no longer had any human inhabitants, so there would be no disturbing or destructive activities taking place. After 125 years with agricultural use, the plough was parked in 1965, and the farmer went ashore. Since then, a wild flora and fauna had spread across the 15 ha of former fields. In 1975-1976, when the present study took place, regrowth was still in an early phase generating perfect conditions for a very large population of Whitethroats. Since then, regrowth continued

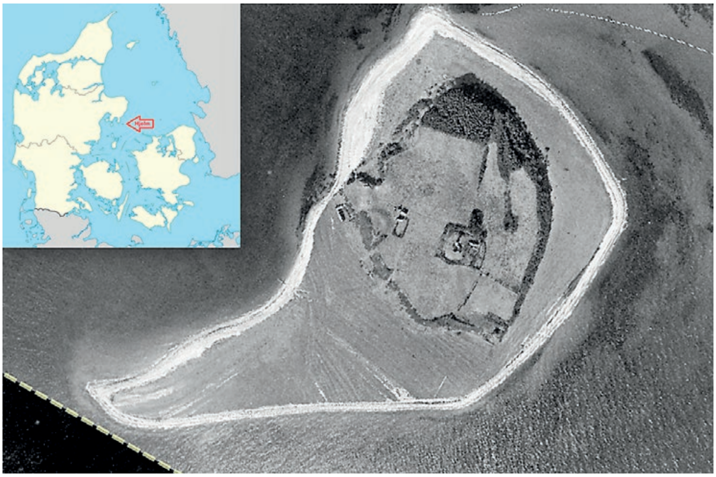

Fig. 1. The island of Hjelm is located in Kattegat 6 km off the mainland coast of Jutland. The central hilly plateau with the former fields together with bushy slopes to the lowlands constituted the breeding area for Whitethroat. In the center stands the lighthouse at 45 m above sea level, and to the west lies the abandoned farm buildings. Aerial photo from 1974. Source: Kort- og Matrikelstyrelsen/Danish Cadastra Office.
Øen Hjelm ligger i Kattegat 6 km ud for den jyske fastlandskyst. Det centrale bakkede plateau med de tidligere marker udgjorde sammen med busk- og træbevoksede skråninger mod lavlandet yngleområdet for Tornsanger. I midten på øen står fyret i 45 m over havet, og mod vest ligger de forladte landbrugsbygninger. Luftfoto fra 1974. Kilde: Kort- og Matrikelstyrelsen.

and the hilly plateau became covered by dense forest, which to-day is unacceptable as a breeding habitat for Whitethroat (details in Hansen 2021).

No ground-living predators (i.e. viper *Vipera berus*, cat *Felix catus*, red fox *Vulpes vulpes*, mice *Myomorpha*, brown rats *Rattus norvegicus* or weasels *Mustelidae* live on Hjelm. Apart from occasional visits of migrating predatory birds like Sparrow Hawk *Accipiter nisus*, Eurasian Hobby *Falco subbuteo*, and Red-backed Shrike *Lanius collurio*, the island housed only two predators in 1976: Hooded Crow *Corvus cornix* (6 pairs) and Eurasian Magpie *Pica pica* (2 pairs). Furthermore, the abundance of food in the large colonies of gulls undoubtedly reduced the need of these two predators to prey on the nests of smaller passerine birds.

The lack of predators meant that the breeding population of Whitethroat on Hjelm during 1975-1976 was characterised by stability, fidelity and firm relationships between male and female in solid breeding pairs, in stark contrast to other descriptions of Whitethroat communities (Siefke 1962, Diesselhorst 1968, Emmrich 1972, Payevsky 1999). During the 1976-season only two individuals were lost to predators. In late May, a Red-backed Shrike killed a 2cy breeding male. Later the same day a likely breeding 2cy+ female also was lost. Both kills took place in mist nets. Moreover, a second clutch nest with pulli was plundered by some predator in July. Those very few and documented cases of predation on Hjelm stand in sharp contrast to predation as the main cause behind 51.8% failed breeding attempts in British Whitethroats in a study based on 3176 mapped nests (Mason 1976).

Finally, it is worth considering that Hjelm, when surrounded by rather shallow 'warm' seas, has a stable and dry summer climate like other localities in southern Kattegat including Røsnæs and Sjællands Odde (Sand-Jensen & Vestergaard 2017). However, it is beyond the scope of this article to explore this climatic premise.

Methods

The present study is based on two main methods of data collection that were practiced throughout the breeding season 24 April - 17 September 1976: 1. daily systematic capture of passerines for ringing and collecting metric data, 2. daily identification rounds and active search for nests of Whitethroat in the field.

The most important prerequisites for a successful in-depth field study of the population dynamics were created since 1970, where the standardised ringing of migratory birds, especially in the spring months, was established. The effort was consistent and systematic with 10 hours of daily catching by 2-3 experienced bird ringers using 30-35 stationary mist nets, evenly distributed over the 25-ha moraine hill that includes both the former fields (15 ha) and the overgrown slopes (10 ha). Only inclement weather was allowed to disrupt this routine.

Hjelm supported an extraordinarily large breeding population of Whitethroat. Already in August 1970, we caught and ringed 137 individuals, primarily 1cy birds. In the following years, we ringed (number of nestlings in brackets) 1971: 150; 1972: 206; 1973: 106 (5); 1974: 204 (60); 1975: 497 (314) and culminating in the year of this study 1976 with 671 (415). Thus, over the years 1970-1975, we ringed 1300 individual Whitethroat including 379 nestlings.

Fig. 2. Every Whitethroat caught during the years 1973-1976 was tagged with a unique color code and an aluminum ring, which allowed identification of every specimen observed or caught in the field. Photo: KH.
Alle Tornsangere fanget i årene 1973-76 blev mærket med en unik farvekode og en aluminiumsring, som tillod identifikation af hvert enkelt individ observeret eller fanget i net på øen.

From 1973 onwards, all adults were marked with two coloured plastic rings plus the traditional aluminium ring forming a unique code for every individual (Fig. 2). The 314 nestlings in 1975 and 415 nestlings in 1976 all received a single plastic ring of the same colour for siblings in the same clutch as well as an individually coded aluminium ring.

During the breeding season of 1976, we identified 109 specimens (two died) of Whitethroat, which had been ringed on Hjelm in previous years as pulli, juveniles or adults. The 109 individuals comprised 47 individuals ringed as pulli in 1975 and 62 older birds ringed as adults in 1975 or earlier. The oldest bird was ringed in 1971. In 1976, we also caught and ringed 58 additional individuals of unknown age and origin as part of the total breeding population of 167 individuals. Because of the two lost individuals, 165 tagged individuals form the basis of the analysis.

We have applied the same age code as used by the Zoological Museum in Copenhagen since 1996. 2cy+ means a full-grown bird from an earlier year (i.e. in its 2nd calendar year or more; Euring code 4), 2cy means born the year before (Euring code 5), and 3cy+ means a bird in its 3rd calendar year or older (Euring code 6). Please note that these Scandinavian transcriptions of the Euring codes are not the same as those used by BTO in UK.

Fig. 3. The original field map from 1976 illustrates the density of breeding pairs that had to be checked to ensure accurate data. The map is dotted with the individual color codes used (males above, females under), which were recorded with the corresponding ring number for each breeding bird.
Dette originale kort fra 1976 illustrerer tætheden af ynglepar, der skulle kontrolleres for at sikre nøjagtige data. Cirklerne på kortet viser de individuelt anvendte farvekoder (hanner over, hunner under), som er angivet med det tilsvarende ringnummer for hver ynglefugl.

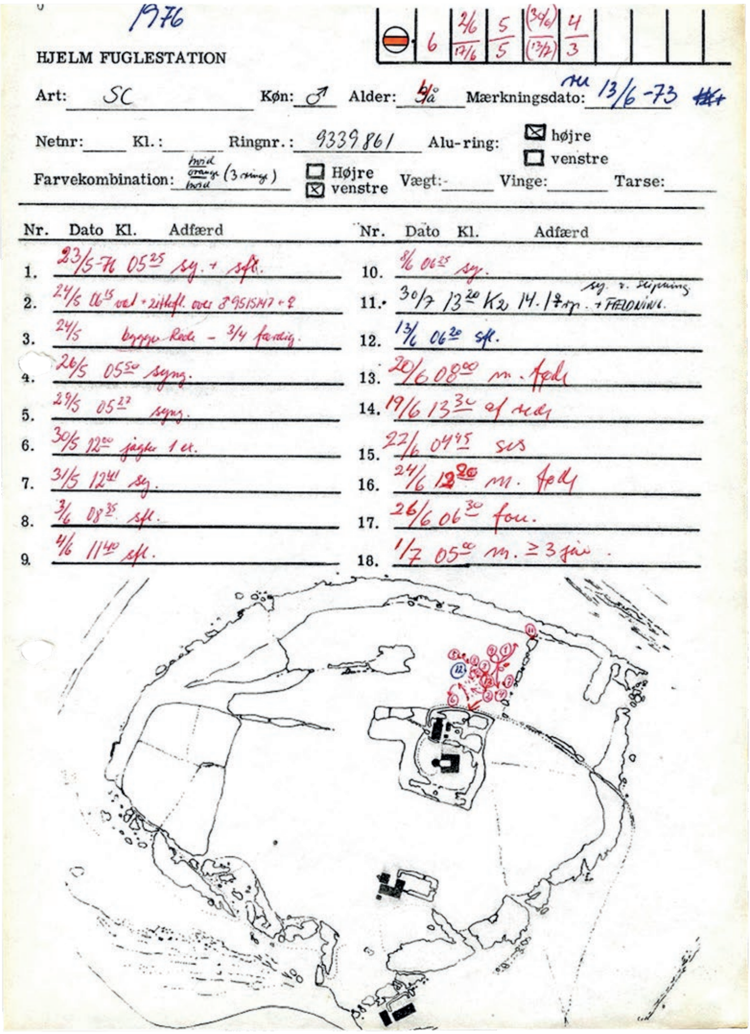

Fig. 4. The first page of the original field map from 1976 illustrating the location of a breeding individual (male) and his movements during the breeding season, which is defining the territory. Red letters: sightings in the field. Black letters: caught and controlled in a mist net.
Første side af et originalt feltkort fra 1976 der rummer data om et ynglende individ (han) og dets bevægelser i ynglesæsonen, som derved definerer territoriet. Røde bogstaver: observationer i marken. Sort tekst: fanget og kontrolleret i net.

For every individually tagged bird, we produced an individual sheet in a logbook with a map of the island, where all registrations of that particular individual were written and jotted down, e.g., caught in mist net, date and time, metric values, weight and control of incubation patch (Figs 3 & 4). Likewise, all observations of the colour-tagged individuals in the field, including nests, were mapped with time and location. Later, special maps were used to record dimension and height above the ground of all nests and metric data for pulli when they were ringed. Finally, we noted the development of individual clutches, including number of eggs and pulli.

Results

The breeding population and its productivity

The breeding population in 1976 included 72 pairs, all producing a first clutch, with 28 males and 30 females of these also producing a second clutch (Tab. 1). When the productivity is presented in a traditional manner as total egg production relative to number of pairs, the mean value will be 6.43 eggs per pair. Median date for the first laid egg was 10 June. In total, the 463 eggs gave rise to 415 fledglings, i.e. a high success rate of 90% relative to egg numbers.

Analysed in finer detail, age, sex, and site fidelity were important for the quite varying numbers of produced

Tab 1. Breeding population and egg productivity of males and females and non-breeding males according to traditional reporting with no separation of data into age and origin of birds.
Ynglebestand og ægproduktivitet for hanner og hunner og ikke-ynglende hanner i henhold til traditionel rapportering uden adskillelse af data for fuglenes alder og oprindelse.

All population	N	Nonbreeder	1 clutch	2 clutches	Productivity[4]	First egg median
Male	87	15[1] (+1 not sexed)	72	28	6.43 eggs	10 June
Female	78	6[2]	72[3]	30	6.43 eggs	10 June

[1] 15 males and [2] six females are included in the total population, but not in further calculations as they did not breed (details in Tab. 2-4). [3] Differences in numbers of one or two clutches between males and females are due to the fact that two males each had two females (bigamy) and two females received a new male partner each. [4] Only breeding birds included.

Tab. 2. Breeding of second calendar-year birds (2cy) hatched and ringed on Hjelm the year before and breeding in 1976 for the first time.
Yngleaktivitet for et år gamle (2k) individer, der er klækket og ringmærket på Hjelm året før, og som ynglede i 1976 for første gang.

2cy	N	Nonbreeder	1 clutch	2 clutches	Productivity[2]	First egg median
Male	33	8[1]	25	3	5.20 eggs	16 June
Female	13	0	13	2	5.31 eggs	8 June

[1] Of these eight males five left the island shortly after, and the remaining three never found a partner. These individuals are included in the total numbers, but not in the sex-related evaluation. Moreover one male with a nest was killed by a small raptor but is not included. [2] Only breeding birds included. Furthermore, a ringed individual of unknown sex was noted 25 May, but not observed later. This individual is included in total numbers, but not in sex-related data.

Tab. 3. Breeding birds older than two years (3cy+) ringed on Hjelm as adults in 1975, or in earlier years.
Ynglefugle der er to år eller ældre (3k+) og ringmærket på Hjelm som voksne i 1975 eller tidligere år.

3cy+	N	Nonbreeder	1 clutch	2 clutches	Productivity[3]	First egg median
Male	41	6[1]	35	22	7.49 eggs	3 June
Female	20	1[2]	19	13	7.95 eggs	4 June

[1] Two males were injured in mist nets, two males disappeared after two days on the island, and two males remained unpaired. [2] One female was observed once 11 June, but never seen later. [3] Only breeding birds included.

Tab. 4. Breeding birds of unknown age (2cy+) and origin.
Ynglefugle af ukendt alder og oprindelse.

Age unknown	N	Nonbreeder	1 clutch	2 clutches	Productivity[1]	First egg median
Male	13	1	12	3	5.42 egg	17 June
Female	44	5[2]	39	14	6.13 egg	14 June

[1] Only breeding birds. [2] Two females remained unpaired, one female was killed, one died in a mist net, one nest was never found and the female not identified, but no fledglings were produced; the nest was probably lost to predation or bad weather.

eggs and fledglings by the different groups (Tab. 2-4).

The 46 2cy birds comprised 28% of the 167 individuals in the breeding population (Tab. 2). The figures show a significant difference in site fidelity between 2cy males and 2cy females (Chi-square test, Yates' correction, $P < 0.05$) in that more than twice the number of 2cy males (33) compared to 2cy females (13) were birds originally hatched on the island. However, 2cy females were faster than 2cy males to get breeding going, so that 2cy females had the first egg in the nest nine days earlier than pairs with 2cy males. Furthermore, 2cy females were significantly more inclined to produce two clutches compared to the 2cy males (Chi-square test, Yates' correction, $P < 0.05$; Tab. 2). Thereby, 2cy females were slightly more productive (5.31 eggs per female) than 2cy males (5.20 eggs per male).

Also, among older native birds (3 cy+), the sex ratio was remarkably skewed with twice as many native males compared to native females in the pairs (Chi-square test, Yates' correction, $P < 0.05$; Tab. 3). Among older birds, significantly higher proportions produced two clutches compared to younger birds (2cy birds; Chi-square test, Yates' correction, P < 0.01; Tab. 2 and 3). Thus, older birds producing more clutches and laid more eggs than younger birds for both sexes. Older males and older females produced eggs at an earlier date than 2cy birds. Older males were, on average, 13 days in advance with the first laid egg compared with young males in the pairs, while old females were three days ahead. See statistics in Fig. 5 C.

Among the 57 Whitethroats of unknown age and origin (2cy+), the ratio between males and females was quite the opposite compared to that of birds hatched on Hjelm (Tab. 4). Among these birds, females were three times more abundant than males. It is remarkable that 13 foreign males (some 19% of all breeding males) only produced one clutch in their pairs and had a modest production (5.42 eggs), while female foreigners produced more eggs (6.13 eggs). The production of the foreign 2cy+ males was close to that of 2cy males, indicating that a large proportion of young inexperienced males must be among the foreigners. In contrast, 14 of the 25 foreign females delivered a healthy production of two clutches. The productivity of these foreign females (6.13 eggs per individual) was halfway between the productivity of young native (5.64 eggs per individual) and older native females (7.95 eggs per individual). Males and females of unknown age and origin were late starters of breeding. The median date for the first laid egg was between 14 and 17 June.

Timetable and productivity compared with site fidelity

The breeding population consisted primarily of native birds that had been hatched on Hjelm in earlier years or had lived there earlier, probably also breeding. This was the status of about 85% males and 44% females, all in all adding up to 65% of the whole community. These native individuals arrived earlier to the island than the foreign individuals (Fig. 5A).

The dates of arrival and the first laid egg are essential

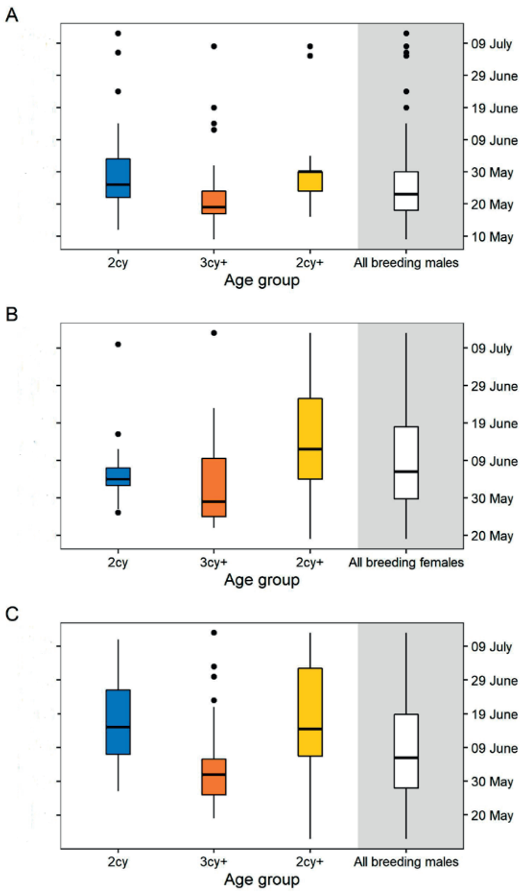

Fig. 5A. Date of arrival on the island of 87 males that took part in the breeding season in 1976. They consisted of 38% native 2cy birds (blue, N = 33), 47% native 3cy+ birds (orange, N = 41), and 16% 3cy+ birds of unknown age and origin (yellow, N = 13). Older males (3cy+) arrived significantly earlier than both 2cy birds (P = 0.02) and 3cy+ birds (P = 0.05; One-way Anova, Tukey post-hoc test).

A. Ankomstdato til øen for de 87 hanner, der deltog i ynglesæsonen i 1976. De bestod af 38 % hjemmehørende 2k-fugle (1 år gamle, dvs. i deres 2. kalenderår/cy; blå, N = 33), 47 % hjemmehørende 3k+-fugle (orange, N = 41), og 16 % 2k+ fugle af ukendt alder og oprindelse (gul, N =13). Ældre hanner (3k+) ankom signifikant tidligere end både 2k fugle (P = 0,02) og 2k+ fugle).

B. Date of the first egg in three age groups of females. Second calendar year females (2cy) only include 13 individuals and older females (3cy+) 20 individuals, which are too few for reliable statistical analysis, though the difference between medians is marked. Egg laying of older females (3cy+) happened significantly earlier compared with 44 females of unknown age (2cy+, P = 0.026; One-way Anova, Tukey post-hoc test).

B. Dato for det første æg i tre aldersgrupper af hunner. Et år gamle hunner (2k) omfatter kun 13 individer og ældre hunner (3k+) 20 individer, hvilket er for få til pålidelig statistisk analyse, selvom forskellen mellem medianerne er markant. Æglægning hos ældre hunner (3k+) sker signifikant tidligere sammenlignet med 44 hunner af ukendt alder (2k+).

C. Older males of native origin (3cy+, N = 35) produce the earliest egg in the nest, significantly earlier than both second calendar year males (2cy, P = 0.002, N = 25) and males of unknown age (2cy+, P = 0.008, N = 12); One-way Anova, Tukey post-hoc test). 22 of 35 older males produced a second clutch (Tab. 3).

C. Ældre hanner af hjemmehørende oprindelse (3k+, N = 35) producerer det tidligste æg i reden, betydeligt tidligere end både 1 år gamle hanner (2k, P = 0,002, N = 25) og hanner af ukendt alder (2k+, P = 0,008, N = 12). 22 af 35 ældre hanner producerede to kuld (Tab. 3).

for the ability to produce two clutches and more fledglings. A clutch with five eggs requires parental care for 31 days (5 days for laying eggs, 11 days for hatching, 15 days for feeding the nestlings and later juveniles (Siefke 1962; own observations). This time requirement brings a late second clutch in conflict with the start of the moulting cycle, which started on Hjelm about 15 July (unpubl. data). In general, our data showed that the first egg in the first clutch must be laid no later than 8 June, if a second clutch is to be finished before the moulting period begins. Almost none of our 72 breeding pairs produced a second clutch after this date.

The date of arrival could be determined with high accuracy for every male. The males started singing immediately upon arrival and were registered at once during the daily observations. The males were also restless and often caught in the mist nets. A similarly accurate determination of the date of arrival was not possible for the females, which show a less visible behaviour. In many cases, the females were not observed until they started feeding the nestlings. On the island of Christansø northeast of Bornholm in the Baltic Sea, the females arrive 7.5 days later than the males, as an average (Lausten & Lyngs 2004). The same delay may exist on Hjelm.

On Hjelm, the first native 3cy+ male arrived on 8 May, and 25 and 50% of the 3cy+ males population arrived on 16 May and 24 May, respectively. Young native 2cy males arrived later; the first individual on 12 May and the 25% and 50% of the population had not arrived until 22 May and 4 June, respectively. Thus, the first 50% of the old males arrived 11 days earlier and over a shorter period than young males. The last 15% of the population, the foreign males (2cy+) arrived later than both groups of native birds; 25 % arrived before May 30 and 50% before 4 June (Fig. 5A).

In all three groups, a few males arrived markedly later than the most individuals. Among seven males that fell outside the main group of individuals (Fig. 5A and 5C), only one male produced offspring. The remaining six did not form pairs and left the island after a short visit of one or a few days.

As stated above, the arrival of the females could not be accurately determined due to their skulking behaviour. However, it was possible to determine when they laid the first egg by observing the nests. This event can be used to estimate the day of arrival by applying the same time frame as for males for establishing of pairs and the delay for delivering the first egg. It was assumed that the females spent 5-10 days after arrival before the first egg was laid. The data showed that older females laid their first egg appreciable earlier than 2cy females and females of unknown age and origin (Fig. 5B). Using the estimated delay between arrival and egg production, the older native females can be assumed to arrive on May 29 on average, 2cy natives on June 4, and foreign females on June 12. According to the observation of the first egg, there is no doubt that the older native females have more time for breeding than the two other groups.

Ultimate site fidelity

Site fidelity, or philopatry, is a common phenomenon among birds and mammals (Greenwood 1980). It is defined as an organism's tendency to stay in or habitually return to a particular area. Natal site fidelity, where animals return to their birthplace to breed, is also very common. It is well known since half a century ago that female birds are much less inclined to show site fidelity than males (Howard 1960).

The breeding birds on Hjelm showed high site fidelity, particularly among the males (Tab. 5). In 1976, 35 males and 20 females bred in the age category 3cy+, who were all tagged on Hjelm during the breeding season in a previous year. Of these, 30 males and 16 females had a well-documented breeding course in both 1975

Tab. 5. Comparison between the same individual territories in 1975 and 1976. 3cy+ males predominantly returned to the exact same territory as they occupied the year before, or close by. This was not the case for females, who were more dispersed. See also Fig. 6.
Sammenligning mellem samme individers territorier i 1975 og '76. 3k+ hanner vendte helt overvejende tilbage til nøjagtig samme territorium, som de besatte året før, eller tæt på. Dette var ikke tilfældet for hunnerne, som fordelte sig mere tilfældigt på øen. Se også Fig. 6.

Sex	***	**	*	0	Sum
Males	13	5	9	3	30[1]
Females	0	3	3	10	16[2]

*** represents the same territory, ** within max 50 m from the territory occupied the year before, * within 50-100 m from the territory occupied the year before, 0 more than 100 m from the territory of the year before. [1] Five males and [2] three females were not observed breeding the year before; therefore, these reduced numbers compared to figures in Tab. 3. In the statistical analysis, numbers in ** and * were combined to increase numbers in the cells.

and 1976. This enabled a comparison between the two breeding seasons, as all observations and catches of the colour-tagged birds had been recorded on individual species maps in both 1975 and 1976.

The males returned with high preference to the same territory and breeding site as the year before, or very close to it. A typical breeding territory occupies a circle with a radius of about 25 m and an area of 2000 m². 13 males occupied the same territory as the year before, while five and nine males, respectively, occupied territories placed up to 50 and 100 m away from the former territory. Only three males occupied territories more than 100 m away and with no observable connection to the former territory. Thus, 27 males (90%) exhibited high site fidelity with respect to territory (Fig. 6).

In contrast, only six of 16 females (38%) had breeding sites within 100 m of their last-year breeding spot, and most females were widely dispersed on the island, in agreement with the much higher natal dispersal of females compared with males. Thus, males of Whitethroat show extreme site fidelity also at the micro-level of a few square meters, while females behave quite indifferently.

A Chi-square contingency table (Fowler *et al.* 1998) showed a significant difference in the distribution of males and females ($P < 0.01$, three columns and two rows; Tab. 5).

Discussion

This study documents the importance of sex, age, and site fidelity for the productivity of eggs and fledglings in a confined community of Whitethroats. I discuss, firstly, a method to estimate the total age distribution in the closed community based on the productivity in two groups with known age. Secondly, I discuss the profound differences in productivity between age groups and between males and females. Thirdly, I discuss the possible underlying reasons for the recent increase in the national population of the species by evaluating the importance of having a higher proportion of breeding pairs with two rather than one clutch annually in the light of the last 50 years of global warming.

Site fidelity and sex ratios for native and foreign birds

The unknown age distribution for the large group (57 individuals; 34% of the breeding population; Tab. 4) of 2cy+ breeding birds is a challenge for evaluation of the entire community. The group of foreign birds consisted of 13 males and 44 females forming a sex ratio opposite to that of birds originating with certainty from Hjelm, with many more males (85%) than females (44%). This reversed sex ratio among foreigners makes sense, because it requires a substantially higher arrival of foreign females than males if all available males from Hjelm are to receive a partner, and thereby contribute to the breeding success of the community.

The sex and the breeding success are known for all 57 individuals of unknown age and origin, and this enables me to estimate their likely age distribution by using the well-known breeding success of the remaining population of known age. I assume that none, or very few, of the 57 individuals derived from the island. Since 1970, 1300 individuals of Whitethroat have been ringed on Hjelm (374 were hatched on the island), so the existence of birds hatched on Hjelm among the birds of unknown origin must be close to zero.

It is assumed that the birds of unknown age and origin are a mixture of young (2cy) and older birds (3cy+). If this was not the case, the egg productivity would most likely be the same as one of the two groups of birds of known age, and this was not the case (Tab. 6). The question then was what mixture of young and older birds gives the best correspondence with the observed productivity of the foreign birds. The best fitting estimate of age distribution among the 57 foreign birds was, for males, 11 young (2cy) and one older (3cy+) and, for females, 30 young and 15 older individuals (Box 1).

The results are supported by the marked differ-

Tab. 6. Breeding population and productivity in 1976 of birds of known age (2cy and 3cy+) and birds of unknown age (2cy+) and origin.
Ynglebestand og produktivitet i 1976 for individer af kendt alder (2k og 3k+) og individer af ukendt alder (2k+) og oprindelse.

Age	Males	Females	Total breeding population[1]	Number of eggs (male/female)[2]
2cy	34	13	47	5.20-5.31
3cy+	41	20	61	7.49-7.95
2cy+	13	44	57	5.42-6.13
Sum	88	77	165	6.43

[1] Territorial, but unpaired individuals are included in the total breeding population. [2] Breeding birds only are included in the calculations of productivity of the total population.

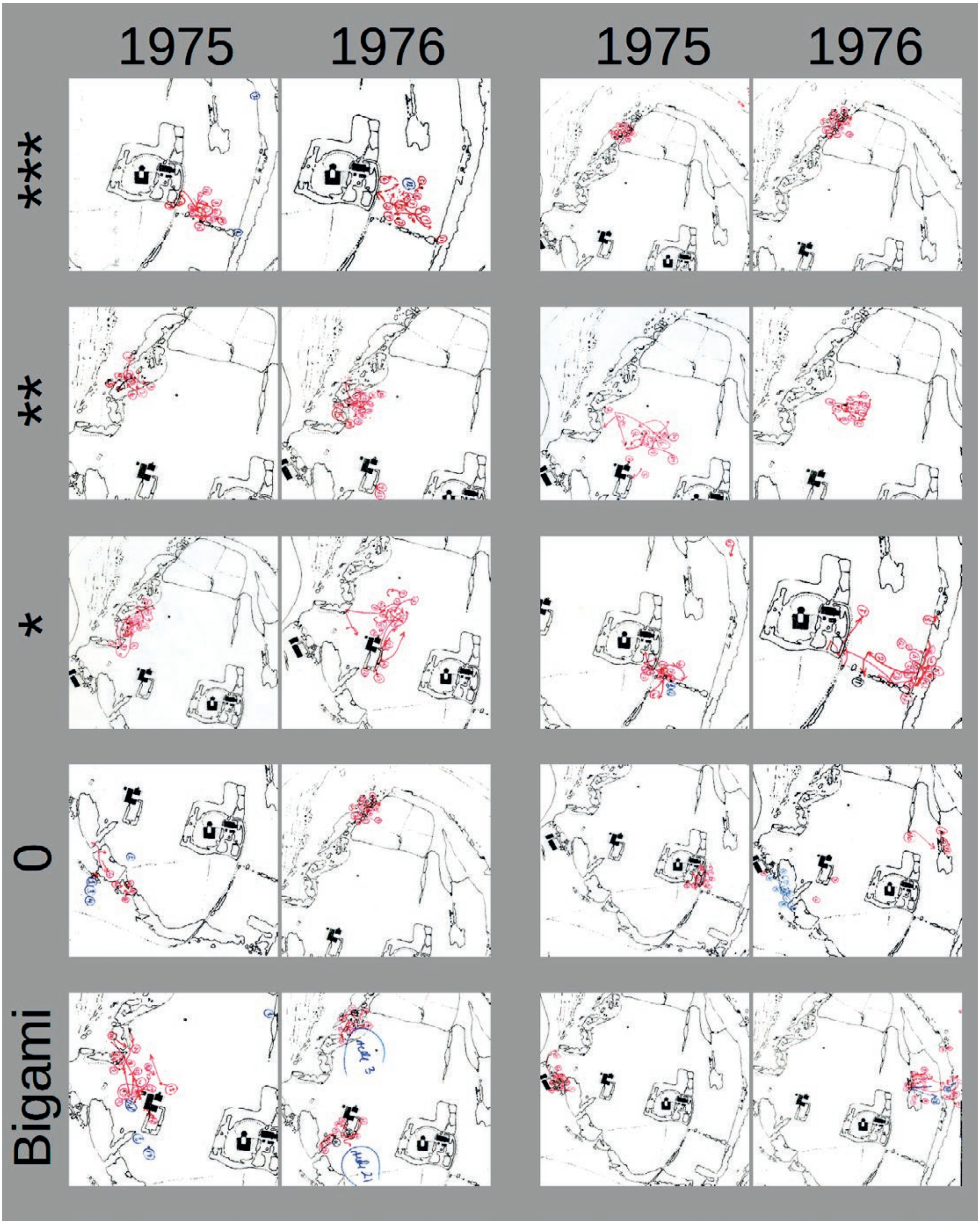

Fig. 6. Examples of territories of older 3cy+ males from 1975 and 1976 distributed on the four categories used in Tab. 5 (two examples for each category). Also, two cases of bigamy are shown, where site fidelity seems to play a role. The same data as in Tab. 5. Maps are scanned from the original field logs. The colors of the pencil (red and blue) are irrelevant.
Eksempler på territorier for nogle få af de ældre (3k+) hanner fra 1975 og '76 fordelt på de fire kategorier anvendt i Tab. 5 (to eksempler for hver kategori). To tilfælde af bigami er også vist, hvor stedtrohed også synes at spille en rolle. Samme data som i Tab. 5. Kortene er scannet fra de originale feltkort. Farverne på skriften (rød og blå) er irrelevante.

Box 1. Estimated age distribution among foreign birds

We know the productivity of the three groups of birds (Tab. 2-4). Thus, we can estimate the likely mix of young and old birds until we hit the age distribution of foreign birds that corresponds to the observed productivity (assuming that productivity of young and older foreign birds is comparable to that of native Hjelm birds).
If x1 was the proportion of 2cy males, 1-x1 would be the proportion of older males (3cy+). The same argument would apply for females.
For males: 5.20 x1 + 7.49 * (1-x1) = 5.42; x1 = 0.904, and in the numbers of young foreign males: x1*13 = 11.75 ~12.
For females: 5.31 x2 + 7.95 * (1-x2) = 6.13; x2 = 0.689, and in the numbers of young foreign females: x2* 44 = 30,3 ~30.

ence in site fidelity between males and females among birds hatched on Hjelm versus foreign birds. While the male:female ratio among native 2cy birds was 33:12, the estimated ratio for foreign 2cy birds was almost exactly the reverse: 12:30.

For older birds (3cy+) the tendency was the same, but the results were less distinct, probably due to smaller numbers. While the male:female ratio was 41:20 for native birds, it was 1:9 for foreign birds. Again, a reversed ratio for native versus foreign birds, but the estimate is based on very small numbers.

These theoretical calculations are meaningful. Female Whitethroats on Hjelm, young as well as older individuals, exhibited only half the site fidelity of the males. It follows, that double the number of foreign females than males must enter the breeding population on Hjelm, if an equal match between males and females is to be maintained in the breeding population. Accepting these calculations, the community of Whitethroat on Hjelm in 1976 consisted of 79 2cy birds and 77 3cy+ birds, a percentage distribution close to fifty-fifty.

Diving further into the age question, we found 45 2cy-males and 43 2cy-females. However, nine 2cy males did not breed successfully, so the breeding population consisted of 36 2cy males (35 natives) and 43 2cy females (13 natives). Among older birds (3cy+), 42 were males and only 35 were females.

Site fidelity is prevalent

The marked differences in site fidelity between males and females observed on Hjelm agree with common principles among birds (Greenwood 1980, Payevsky 2016), but is described here in detail for a confined population for the first time for Whitethroat. Admittedly Balsby & Hansen (2010) reported the phenomenon for males of Whitethroat but based on very few data. Nine 2cy males were captured and colour-tagged in hedge rows between agricultural fields on the south side of Fussing Lake, Denmark (56°28'N, 9°54'E) in May and June 1995, 1996, and 1997. Of a total of these nine males, five were recovered one year later at the same locations.

Site fidelity can be described as the extent of dispersal from the birth site to the breeding site. The most widely used definition of such dispersal is that by Howard (1960): "Dispersal of an individual vertebrate is the movement the animal makes from its point of origin to the place where it reproduces or would have reproduced if it had survived and found a mate." This definition refers only to juveniles undergoing a permanent movement from birth site to first breeding or potential breeding site and can perhaps more correctly be termed natal dispersal. It is different from breeding dispersal, which is the movement of individuals between successive breeding sites.

Sex differences in natal dispersal has previously been described for passerines, e.g., Pied Flycatcher *Ficedula hypoleuca* (Haartman 1951, Berndt & Sternberg 1971), where males to a greater extent than females return to the earlier breeding habitat, like the Whitethroats on Hjelm. Payevsky (2016) mentions 18 non-passerines and 24 passerines with a sex-related bias of dispersal and mortality, confirming the principle of much greater female natal dispersal. Whitethroat is not among the studied species, but the closely related Lesser Whitethroat *Curruca curruca* and Barred Warbler *Curruca nisoria* are included and show the same pattern. Concerning sex-related natal dispersal, the case is clear-cut on Hjelm with only 44% of all females being of native origin compared with 85% of all males. For the whole community, 65% of all breeding birds were of native descent.

Age-related differences in egg productivity were profound. Older experienced native birds (3cy+) were markedly more productive than both younger native birds (2cy) breeding for the first time and birds of unknown age and origin (2cy+). Older birds produced 7.49 and 7.95 eggs in males and females, respectively, compared to 5.20 and 5.31 eggs for young male and female first-time breeders, respectively. I found that an earlier

The breeding Common Whitethroats on Hjelm showed great year to year site fidelity with especially many males settling in the same territory several years in a row. Photo: Leif Bolding.
De ynglende Tornsangere på Hjelm viste stor stedtrohed fra år til år med især mange hanner, der slog sig ned i det samme territorium flere år i træk.

(age-related) arrival date to Hjelm was closely positively related to the date of the first egg and the ability to produce and raise two clutches rather than only one clutch during the summer.

These data document the frequent occurrence of delivering two clutches in the Hjelm community. This stands in stark contrast with the older literature (Glutz von Blotzheim 1991), which generally doubts the existence of two clutches for Whitethroat, although breeding localities mentioned were located further to the south in Germany than Hjelm (Siefke 1962 in Mecklenburg, Emmerich 1971 on Rügen, and Diesselhorst 1968 in South Bavaria) or at the same geographical latitude as Hjelm in South Sweden (Persson 1971, Enemar 2001). The validity of these evaluations may be doubtful, however, considering that the researchers had not colour-tagged their birds and therefore lacked the ability to monitor each individual closely every day as we did.

Mason (1976) evaluated 3176 nest record cards of Whitethroats from the British Isles and wrote ”second broods, but only a small proportion, were recorded for …” but without offering the exact numbers. Finally, Sell & Nielsen (1986) examined (as part of their master's thesis) a breeding population of 37 pairs of Whitethroat in hedges surrounding conventional agricultural fields in East Jutland. According to their paper each breeding pair was visited every second day. Despite the apparently careful fieldwork, they reported only one second clutch, which is markedly different from our findings on Hjelm.

Jensen (2002) reported similar results to our findings. He writes: ”I have studied the Whitethroat in detail during many years using ringed birds. I have found that this species often produces two broods but has a complicated mating system with frequent changes of mates or shifts of territory between the broods”. In 1970 and 1971 he found that eight males (47.1%), with certainty based on examination of nests, delivered two clutches (Jensen 1971). Jensen worked in the locality Kagsmosen near Copenhagen.

From several observations in Sweden, Enemar (2001) proposed “that some Whitethroats might be double-brooded in the coastal areas of south-western Sweden, probably only in seasons when conditions happen to be optimal”. Further Enemar speculates “that if the Swedish Whitethroats are at all capable (programmed) to raise two clutches in a suite, then perhaps the conditions required for a second breeding attempt to be triggered after a successful first clutch are very rare."

Our careful identification and daily observation of all individuals and all nests clearly showed that 42% of the breeding pairs on Hjelm produced two clutches in 1976, and at least 27% produced two clutches in 1975. Thus, the main strategy of Whitethroat must be, whenever possible, to produce two clutches. It appears illogical that the species in SW Sweden and further to the south in Germany should have a less efficient breeding strategy. However, it is evident that the optimal research conditions on Hjelm have made observations and firm conclusions easier. Moreover, breeding conditions were also optimal as the island was virtually free of predators, which meant the pairs lost no eggs and no pair bonds were split. Thus, the community on Hjelm could show the true breeding potential of the species, when it is not experiencing loss rates of 30-50% or more of all breeding attempts, as in other studies (Siefke 1962, Diesselhorst 1968, Mason 1976). I also believe that field work without close control of the identity of individual birds and all nests are problematic and might lead to doubtful conclusions.

I conclude that the Whitethroat is programmed to deliver two clutches both in Central Europe, S Sweden and in Denmark. However, the timetable of the individual bird in spring determines whether the birds succeed in producing two clutches. The birds need to arrive in due time to go through two cycles of raising young, when each cycle requires at least 31 days. If the two-clutch-strategy is to be successful, according to our Hjelm-data the first egg in first clutch must be laid no later than 8 June.

Population plasticity and global warming

The Whitethroat population has experienced a remarkable recovery since the gloomy scenario of decline in 1969-1970 (Winstanley *et al.* 1974). As of today, it is the most widespread passerine in Denmark (Vikstrøm & Moshøj 2020), and the population has grown from an estimated magnitude of some 358 000 breeding pairs in 1993-1996 to 393 000 pairs in 2014-2017 (Meltofte *et al.* 2021). This recovery calls for an explanation.

The high productivity of the Whitethroat community on Hjelm with a two-clutch-strategy offers a likely explanation for the actual comeback as a result of global warming, promoting an earlier arrival in spring and therefore increased opportunities for an extended breeding season (see further below).

At least two advantages are the results of an earlier arrival. The first is the enhanced competition for prime territories, which clearly are occupied according to arriving first on the site. The second is the improved ability to produce two clutches, when the tight timetable is somewhat extended.

At the end of the breeding period, pairs going for two clutches must meet another time threshold, the onset of moulting (Pimm 1973). This threshold may be regarded as a hormonally determined, firmly set threshold. However, our observations of moulting in the 1976-population revealed that initiation was spread over an extended period of some 19 days (15 July to 4 August) and with 11 August as the latest date for a not yet moulting bird. This considerable time frame leaves enough room for phenotypical plasticity to work on the stop block and move it further into late summer opening a window for a second clutch.

Tøttrup *et al.* (2006) have shown with data from Christiansø east of Bornholm in the Baltic Sea that passerine species wintering in Africa arrived successively much earlier in spring during the period 1976-1997. Karlsson & Ehnbom (2021) showed the same development for southern Sweden. Earlier spring arrivals could likely be important for the probability of Whitethroat to produce two clutches. On Christiansø, spring arrival of Whitethroat was advanced by a healthy 10 days for the first individual and 3-4 days for the median passage of the population. This development has probably been ongoing until the present time with now an estimated seven days' earlier arrival for the population as such. Unfortunately, no reliable breeding data exist for determining whether the Whitethroat is exploiting this possibility for earlier breeding.

However, we can refer to an excellent study of Eurasian Reed Warbler *Acrocephalus scirpaceus* in a 3-ha large fishpond in SW Poland over two periods 1980-1983 and 2005-2012 (Halupka *et al.* 2021). The Reed Warbler is a long-distance migrant wintering in sub-Saharan Africa, like Whitethroat. Average temperature on the breeding site rose 1.5 °C between the two periods, and consequently the breeding season of individual females (from building of the first nest till the end of caring for the last fledglings/last nest failure) was extended with two weeks compared to the 1980s. In the 2000s, females produced 75% more fledglings annually than females in the 1980s (2.8 vs. 1.6 per clutch). The proportion of females raising a second clutch increased from 2.7% to 23.6% between the first and the second study period, while the share of females that did not produce any young annually decreased from 48.1% to 15.5%. The higher offspring production in recent years was related to more successfully fledged clutches and an earlier start of breeding, which secured more time to re-nest in case of failures.

Halupka *et al.* (2021) concluded that prolonged reproductive seasons might be beneficial for some species. Identifying causes and consequences of changes in the duration of breeding seasons may be essential to predict demography of populations under changing climatic conditions. The same conclusion applies to Whitethroat, I suppose.

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Resumé

Køn, alder og stedtrohed som bestemmende faktorer for produktivitet i en afgrænset population af Tornsangere

Vi undersøgte produktiviteten af æg og unger, samt stedtrohed hos hanner og hunner i en Tornsanger-population på øen Hjelm (Fig. 1) i Danmark i ynglesæsonerne 1975 og '76. Formålet var at beskrive populationsdynamikken (Tab. 1).

Stedtrohed var fremherskende med 85 % af de ynglende hanner og 44 % af hunnerne oprindeligt udklækket på øen eller konstateret ynglende på øen mindst et år tidligere. Indfødte ynglende hanner vendte også i meget høj grad tilbage til deres tidligere yngleterritorium (90 % inden for 100 m), mens indfødte hunner fordelte sig mere spredt på øen (Fig. 6). Fugle

About 42% of all breeding pairs produced two clutches, with experienced native females (3cy+) producing most (68%). Photo: Flemming Bomholdt.
Omkring 42 % af alle ynglepar producerede to kuld med erfarne indfødte hunner (3k+) producerende flest (68 %).

af ukendt oprindelse og alder (2k+; dvs. i andet kalenderår eller ældre) udgjorde 35 % af bestanden, men inkluderede mere end tre gange så mange hunner (44) som hanner (13) (Tab. 4).

Unge indfødte hanner (2k) ankom senere end ældre indfødte hanner (3k+) og behøvede markant længere tid for at få det første æg i reden (Fig. 5A-C).

Omkring 42 % af alle ynglepar producerede to kuld. Unge indfødte hunner (2k) leverede bemærkelsesværdigt færre 2.-kuld (21 %) sammenlignet med ældre indfødte (3k+; 68 %) og fremmede hunner af ukendt alder (2k+; 36 %) (Tab. 2, 3, 4).

De erfarne ældre fugle producerede væsentligt flere æg i løbet af sæsonen (7,49/7,95 æg pr. han/hun) (Tab. 3) end de førstegangsynglende (5,20/5,31 æg pr. han/hun) (Tab. 2). På trods af høj yngletæthed (72 reder på 25 ha) var der tilsyneladende rigelig føde tilgængelig, og da ingen jordlevende rovdyr og kun få rovfugle var til stede, førte de fleste æg (90 %) efterfølgende til udfløjne unger.

Ynglefuglene på Hjelm viste høj stedtrohed, især blandt hannerne (Tab. 5). Stedtrohed, eller philopatry, er et almindeligt fænomen blandt fugle og pattedyr (Greenwood 1980), men det er velkendt, at hunner er meget mindre tilbøjelige til at udvise stedtrohed end hanner. Hunner på Hjelm, unge såvel som ældre individer, udviste kun halvt så meget stedtrohed som hannerne.

Mine beregninger (Box 1) viser, at Tornsanger-samfundet på Hjelm i 1976 bestod af 79 2k-fugle og 77 3k+-fugle, en procentvis fordeling tæt på 50/50.

Jeg foreslår, at den fremrykkede forårsankomst af Tornsanger i det varmere klima i løbet af de sidste 50 år og den dermed forbundne kapacitetsforøgelse til at producere to kuld, så der produceres væsentligt flere udfløjne unger, er en nøgle til at forstå den succesfulde genopretning af den nordvesteuropæiske bestand af Tornsanger, som ellers var blevet erklæret udryddelsestruet i 1969.

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