Age of first breeding in the Common Eider
Somateria m. mollissima population in the northern Baltic Sea

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The Baltic/Wadden Sea Common Eider (*Somateria m. mollissima*) population may have declined by one-third between 1991 and 2000, based on counts carried out on the species wintering grounds, Denmark in particular. However, less drastic reductions have been reported from the breeding grounds, mainly in Finland and Estonia. It has been hypothesized that this discrepancy might arise from an earlier debut breeding attempt of subadult individuals. An increase in adult mortality may allow a larger proportion of subadult individuals to start breeding and arrive to the breeding grounds at a younger age than before. Consequently, their numbers might mask the decline of the adult population. Accordingly, the decline of the entire population would then be discernable only on the joint wintering grounds in the south, where all age classes occur together. Yet this study found no tendency towards earlier debut breeding in a declining Eider population in the Gulf of Finland. On the contrary, debut breeding was delayed as the population declined and the adult mortality increased. Later debut breeding and diminished population size were both related to poor fledging success three years earlier (i.e., the mean maturation age), which in turn was an outcome of mass mortality among ducklings. Debutants originating from small year classes (resulting from heavy duckling losses) took more time to become mature and made a smaller contribution to the population growth rate than recruits of large year classes. Environmental conditions (e.g., food, pathogens) might affect the development of an individual, with late debutants having lower fitness than early debutants. The discrepancy between the size of the wintering stock and that of the breeding stock of Baltic/Wadden Sea Eiders might result from a decreasing fledging rate in the north and, to a lesser extent, from increased adult mortality.

1. Introduction

In long-living bird species, responses to decreasing population densities include enhancement of fecundity or survival, changes in the immigration : emigration ratio, and decreasing age of debut breeding, i.e., the first entry into the breeding population (e.g., Newton 1998). Decreasing age of debut breeding has been demonstrated in studies in which adult survival has been intentionally reduced (e.g., by culling; Coulson et al. 1982), or where the reduction of adults has otherwise been

extensive (as in bycatch mortality of albatrosses in long-line fisheries; Croxall et al. 1990). In these situations, an increasing proportion of non-breeders would then become reproductive and recruit into the breeding population.

The proximate factor is believed to be the relaxation of competition for resources (e.g., mating partners, food resources and nesting territories), which existed prior to the adult reduction (e.g., Coulson et al. 1982). The resulting increase in recruits would then become a compensating factor, acting in a density-dependent manner. In most waterfowl, however, the cue of lowered adult survival must be received on the wintering grounds, as pairing occurs on the wintering grounds and the male follows the homing female to her breeding grounds (e.g., Rohwer & Andersson 1998).

Northern Baltic Common Eiders *Somateria m. mollissima* are strictly migratory, breeding on the coasts of Finland, Sweden and Estonia and wintering mainly in Denmark (Noer 1991). Only adults occupy the breeding territories in the spring (Hario et al. 2002), as non-breeding subadult individuals tend to stay in the south. On the wintering grounds, a decrease of 36% in the total population took place between 1991 and 2000 (Pihl et al. 2001, Desholm et al. 2002). Despite this trend, no equally consistent reduction has been reported from the breeding grounds of the same population (Desholm et al. 2002). To explain this discrepancy, Desholm et al. (2002) offered several hypotheses, two of which they considered likely. The first proposes that population declines remain undetected in some breeding areas (notably in Sweden), and the other proposes that the phenomenon is due to a decrease in the age of debut breeding. The present study explores the latter hypothesis.

The earlier-debut-breeding hypothesis predicts that as breeding numbers drop, an increasing proportion of non-breeders would become reproductive and recruited into the breeding population by simply decreasing the age of debut breeding. This surplus would sustain stable numbers on the breeding grounds despite the overall population decrease found on the wintering grounds at least in the short term. It thus creates a 'buffering' effect against the population low (sensu Desholm et al. 2002). This scenario assumes that it is mainly the adult stock that has declined.

In the present study, evidence of this effect was sought in a fluctuating Common Eider population on Finnish breeding grounds. The hypothesis predicts an earlier debut-breeding age if the population declines, and a corresponding delay if the population increases. The analysis here is based on data collected on marked Eider females whose age was known at the time of debut breeding and which spans over both population phases (increase, decrease/levelling off).

As the overall recruitment rate and adult mortality in the studied Common Eider population was known, the interaction between the debut breeding age and the variations in recruitment rate and adult mortality, respectively, were also studied. The relationship was expected to be negative (i.e., younger debut age coinciding with elevated adult mortality and recruitment) for regulation to occur (negative density-dependence; e.g., Turchin 1999). Assuming this expectation of negative density-dependent regulation was correct, yearlings would be able to adjust their physiological maturation according to the cues of adult mortality already received on the wintering grounds. However, if no density-dependent relationship exists, then all birds might be physiologically mature at the same age, perhaps entering the population randomly.

2. Material and methods

The study was conducted at the Söderskär Game Research Station, central Gulf of Finland (60°07'N, 25°25'E; see Hario & Selin 1988). The Common Eider population there has been monitored with nest counts since 1948. The Eider produces only one clutch in a given year. Thus, the number of active nests appears a reliable estimate of the population size for a given year.

2.1. Recruitment rate and fledging rate

During nest counts at Söderskär, female Eiders were captured, ringed, or recaptured on their nests, using a long-handled dip-net. Each year, females were caught no earlier than day 20 of population incubation (median date) to avoid nest desertion (*sensu* Laurila & Hario 1988). Females captured for the first time (unringed) were scored as "re-

cruits", and their share of the total catch was used to indicate the overall recruitment rate (% catchable portion of the population). The remaining ringed females represented "old breeders". Once recruited, the females appear to faithfully return to the same breeding islet for years (only 3 out of 255 females controlled at nests in adjacent archipelagos within 10–20 km had previously nested at Söderskär, M. Hario & K. Selin, unpublished data). Annually, an average of 53.7% of incubating females were captured (median 53.9%), with the range of annual variation being comparatively small (SE = 1.9; 95% of capture proportions within 49.8–57.6%).

The effect of recruitment rate on population size is strong (Hario & Selin 1988). Here, the relationship between the annual debut breeding age and the recruitment rate is explored. As close agreement exists between the recruitment rate and the fledging rate, or fledglings/nest from 3 years before (mean maturation age; Hario & Rintala 2006), the response of the debut breeding age to the fledging rate is also explored. The figures for the annual fledging rate and recruitment rate (years 1967–2004) are from Hario & Rintala (2006).

2.2. Data on debut age

The true age of most females captured for the first time was often not known, but since 1982 many have been ringed as day-old nestlings; hence their age at debut breeding is known (for ringing waterfowl nestlings using plasticine-filled rings, see Blums et al. 1994, 1999). The grand total of female nestlings ringed at Söderskär during 1977–2001 was 6,576. By 2004, 236 (3.6%) of these had been recorded breeding at Söderskär (and only 1 outside Söderskär; M. Hario & K. Selin, unpubl.). The low recovery rate is due to heavy duckling mortality, a common feature in all Common Eider studies (Hario & Rintala 2006).

The present study only uses data on first entries in which the recorded age of first breeding was no more than 5 years. Older first-time encounters are assumed to result from escaped previous capture. This selection is reasonable because the focus is based on an assumption of earlier debut breeding, not overall debut breeding. The sample for analysis included 170 debut-breeding cases from 1982–

2004 (as the nestling-ringing project started in 1977, the first potential 5-year-old individuals entered the population in 1982), with a rate ranging between 2 and 24 and averaging 8.5 (± 5.4 SD) recruits per year. However, in 1998–99 no nestling-ringed females entered the population and the recruitment rate was exceptionally low (see later), and in 1987 only one such female was recorded, so these years were excluded, leading to a data set for 22 years. The distribution of the debut breeding age is compared among three population phases: population increase (by 10% annually in 1975–85), population decrease (by 7% annually in 1986–99) and the current levelling-off or recovery (by 5% in 2000–04).

2.3. Adjusting mortality rates

Mortality rates were converted from survival rates determined from capture-recapture data (Hario et al. 2009). The data consist of capture histories of 6,393 breeding females at Söderskär in 1960–2007, with a probability estimate of an individual's chance of survival from a given year to the next. Time-dependent female survival is estimated following standard procedures applied to ringed individuals. The annual apparent survival of female Eiders averaged 0.882 (± 0.864…0.899 95%CI). Here, only data from 1967–2004 were inclusively used to allow a comparison with reproduction and recruitment data. As only breeding females (i.e., those found at a nest) were sampled, no younger cohorts are included in the analysis and, consequently, no age-dependent survival was included in the time-dependent model, which was selected using Akaike's Information Criterion (AIC; see Hario et al. 2009).

2.4. Statistical methods

The data on debut breeding and dependent variables (recruitment age, fledging rate and mortality parameters) were described and analysed using standard statistical methods with two-tailed hypotheses (Zar 1999). A critical $\alpha \leq 0.05$ was applied to reject a null-hypothesis (H_0). To minimize variables' deviation from the assumed normal distribution (R for Pearson correlations), arcsine
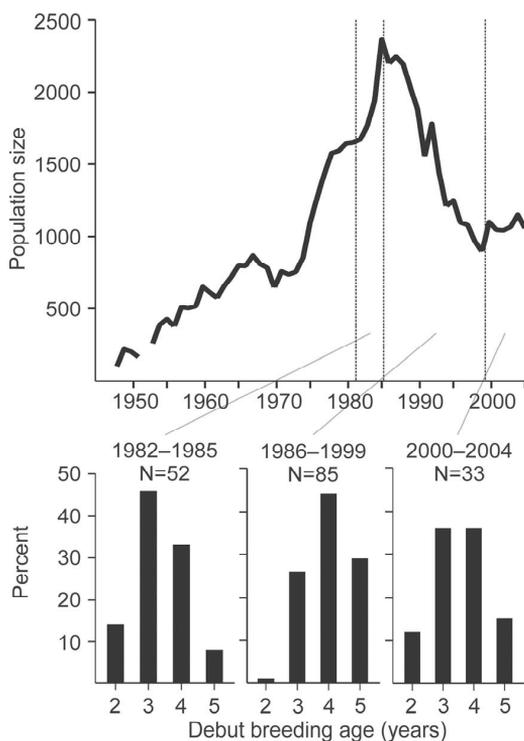
Fig. 1. The population trend of Söderskär Common Eiders in 1948–2005 (pairs, upper graph, no count data in 1952), and the proportional distribution of different debut breeding ages during three different population phases at Söderskär (the phases indicated by vertical lines).

square-root transformation was used to the % data (recruitment rate and mortality) and square-root transformation to the fledging-rate data. For data on the debut breeding age, the original values were used, because transformations did not improve the normality of distributions.

3. Results

Based on nest counts, a pronounced peak in the trajectory of the Söderskär Common Eider population density was detected, realised as a 10% annual increase in 1975–85 and 7% annual decrease in 1986–99 (Fig. 1). After this, a slight recovery prevailed.

During the peak, there was no association between a specific recruitment age (2, 3, 4, or 5 years; no yearlings were found breeding) and a particular phase of the population trajectory (the increasing

phase 1982–85 vs. the decreasing phase 1986–99; $\chi^2_3 = 12.88$, P > 0.1; Fig. 1), suggesting no response by the debut breeding age to the reduced nesting density. The debut breeding did not occur at an earlier age during the population decline in 1986–99. As a matter of fact, it was delayed by one year (median 4 [n = 85] against 3 [n = 52]; Mann-Whitney U = 3133.0, P < 0.001). After the decline had ceased, i.e., in 2000–04, the breeding age decreased again (median 3.5 [n = 33] against 4 [n = 85]; U = 1798.5, P = 0.024).

The annual mean age of debut breeding tended to become earlier with an increasing recruitment rate, although the relationship was not statistically significant (R = –0.30, t = –1.42, df = 20, P = 0.170). As the recruitment rate is highly dependent on the fledging rate three years before (Hario & Rintala 2006), there was a significant negative relationship between debut breeding age and fledging rate three years before (R = –0.71, t = –4.18, df = 17, P = 0.0006; Fig. 2). The age of debut breeding significantly increased with the increase in the mortality of adult females (R = 0.59, t = 3.23, df = 20, P = 0.004; Fig. 3).

A significant negative relationship between annual fledging rate (no time lag) and adult female mortality was found ($r_s = –0.560$, n = 33, P < 0.01). At Söderskär, low fledging rate (number of fledglings/nest) is an outcome of high duckling mortal-
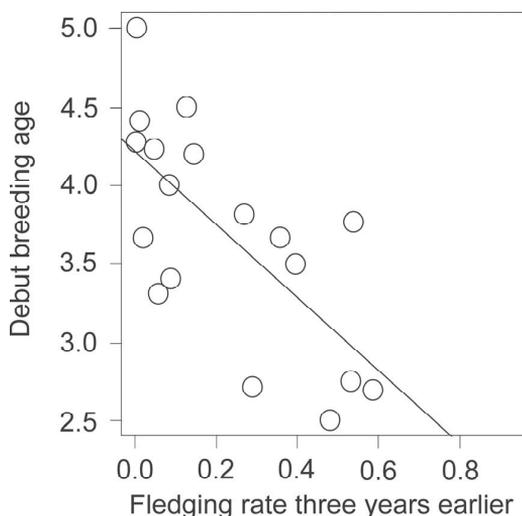

Fig. 2. Relationship between mean debut breeding age and the fledging rate of the study population three years earlier.
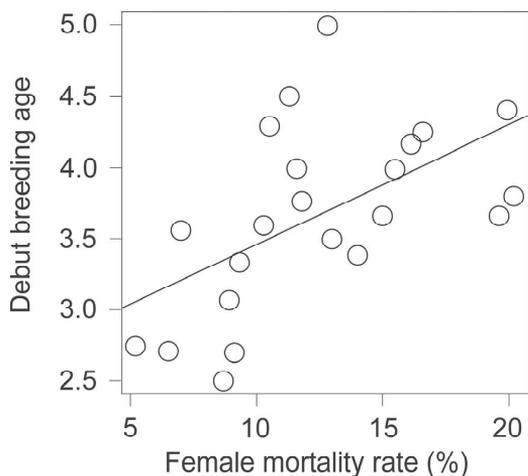
Fig. 3. Relationship between the adult female mortality and the mean age of first breeding at Söderskär in 1982–2004 (no data in 1987 and 1998–99).

ity, not of small initial output (clutch size) or poor hatching result (Hario & Rintala 2006). Thus, the higher the duckling mortality during the chick-rearing period, the higher the adult mortality of the same year.

4. Discussion

This study reported no evidence of an earlier debut breeding age with a decreasing population density of the Common Eider at Söderskär. This finding questions the hypothesis that a low Common Eider population would result in a higher recruitment rate of subadult birds. However, it does not question the hypothesis of the 'buffering' effect *per se*. Indeed, the studied population did decline partly because there was no 'buffering' effect.

The phenomenon of a decrease in debut breeding age is known from previous culling and removal studies, as well as from reports on various environmental hazards, in which the breeding densities of bird populations drop far below the normal year-to-year fluctuation (e.g., Newton 1998, Gaston 2004). Circumstantial evidence for this response in eiders has been reported from Denmark in connection with two Avian Cholera incidents, when 80–90% mortality in breeding females was subsequently compensated for by recruitment rates exceeding the normal range (although the age of newcomers was not reported; Desholm et al. 2002). This finding has been taken as evidence of a pool of non-breeders waiting for an opportunity to nest, which further implies the existence of resource competition within a population (e.g., for nesting habitat). No such effect was found at Söderskär, where fewer adults coincided with later debut breeding, and where nesting habitat is a constant supply. Also, there are no mammalian or avian predators at Söderskär that would curtail access to good breeding habitat (cf. Kilpi & Öst 2002).

The increasingly strong male-biased sex ratio in the Baltic Sea (Lehikoinen et al. 2008) indicates there may be increasing demand for females. As males presently outnumber females during the spring migration into the Gulf of Finland as well (Kilpi et al. 2003), an increasing proportion of males may not have found a mate on the wintering grounds, for genuinely-paired males would not be travelling alone but would be mate-guarding (Hario et al. 2002, Hario & Hollmén 2004). One could anticipate that this sex bias *per se* forms a strong visible cue for prospective young females on the wintering grounds. However, as they do not seem to give the appropriate response by pairing earlier, competition for resources may not be the driving force behind the variation of debut breeding age in our Eider population.

A highly significant negative relationship was found between mean debut breeding age and the fledging rate of the population three years before, implying that year classes that suffered high mortality during their growth period (as ducklings) needed more time to become mature. The resulting recruiting stock was consequently smaller, but its relation to debut breeding age was suggestive at best. This finding is important, however, considering the discordant sample sizes: the debut age was based on an annual mean of only 8.5 individuals, whereas the numbers of recruits averaged 134 individuals for the same years.

Smaller year classes are possibly of poorer quality, with individuals remaining 'runts' for their entire lives. No ultimate explanation for the possible quality difference among year classes can be offered, but various pathogens (viruses, parasites) may play an important role here, along with the deteriorating nutritional conditions during the ducklings' growth period. These represent factors pos-

sibly shaping the overall quality of year classes (but see Christensen 1999; for a review of pathogens, see Friend et al. 2001).

We found a coincidence of increased adult mortality in years of increased duckling mortality. This could indicate that there are deteriorating environmental conditions or occurrences of highly virulent pathogens acting on both age classes simultaneously. However, adult mortality only explains 2% of the annual variation in population size, whereas the corresponding figure is 61% for the reproductive rate (fledglings/female) at Söderskär (Hario et al. 2009).

The present study does not question the hypothesis of the 'buffering' effect by the debut breeding age *per se*, but a further hypothesis is put forward to explain the discrepancy in population trends between the wintering grounds (consistent decline) and the breeding grounds (not equally consistent decline) from the early 1990s until 2000. This is set by the low recruitment rate of the late 1990s, which applied to larger areas than just Söderskär or the Gulf of Finland. Anecdotal evidence points to a universally poor fledging result not only in the Gulf of Finland but over the entire south-western Archipelago (henceforth SW Archipelago), the core area of the northern breeding grounds of Common Eiders. This area hosts 150,000 pairs of Eiders and therefore has a much more profound effect on the countrywide population trajectory than that of the Gulf of Finland with only 20,000 pairs (Desholm et al. 2002).

Hario & Rintala (2006) showed that the Eider population of the SW Archipelago was in a growth phase in 1991, while at that time the population in the Gulf of Finland was already decreasing (Fig. 4). The SW Archipelago population peaked in 1997, after which it abruptly turned to the present decline. Yet in 1999, preceding the 1999–2000 winter count in Denmark, it was still at roughly the same level as it had been in 1991 (at the time of the previous winter count in Denmark), but was already suffering from similar reproductive failures and duckling mortalities as the population of Gulf of Finland did (Hario & Rintala 2006). As immature (non-breeding) cohorts can constitute a substantial part of an Eider population (20–30%; Almqvist et al. 1975, Coulson 1984), the overall poor fledgling production during the late 1990s in the northern Baltic Sea can very well explain the
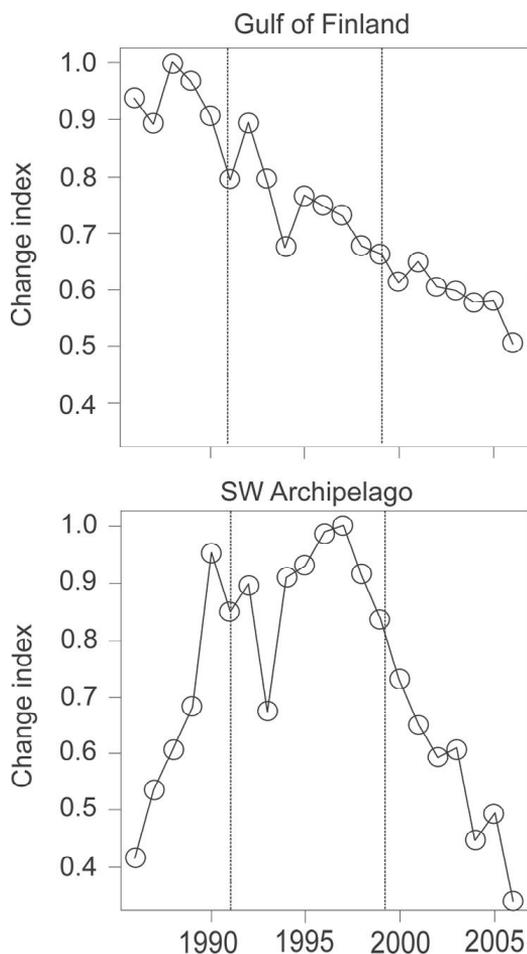

Fig. 4. Population trajectories of Common Eiders in the Gulf of Finland and in the south-western Archipelago during 1986–2006 according to the national Archipelago Bird Census scheme (redrawn from Hario & Rintala 2007). The maximum index of both series is set at 1.0. The vertical dashed lines denote the state of the population at the time of the mid-winter counts in Denmark (in 1991 and 1999).

36% gap in the flyway winter-count data in Denmark between 1991 and 2000.

Finding evidence for this idea would require age- and cohort-specific survival estimates for each year. Such data are not available for Baltic Eiders. However, the cohorts that were born at Söderskär in 1994–96 were exceedingly small due to large-scale nesting failures (duckling mortalities) at that time. The fledging rates for those years were only 0.08, 0.057 and 0.009 (Hario & Rintala 2006), leading to low recruitment rates three years

later in 1997–99, with only 7.9%, 5.9% and 7.4% of breeding females scored as "recruits". These figures are the lowest in the entire 1967–2004 data set collected at Söderskär (Hario & Rintala 2006).

It is worth noting that these duckling die-offs did not affect the numbers of ringed nestlings, because the mortality only started after the young entered the water. The present material is unique in that it covers the entire pre-fledging period of ducklings, not just the 2–3 weeks prior to fledging as usually in waterfowl studies. There were no significant changes in the ringing effort, i.e., the percentage of ringed nestlings from the total stock of Söderskär nestlings, during those critical three years of 1994–96 (a mean of 7.9% against a mean of 7.5% for all years). However, no nestling-ringed females were recruited in 1998–99. A similarly low fledging success applied to most of the monitoring areas around the Finnish coasts for the same years (Hario & Rintala 2002).

To sum up, neither of the hypotheses put forward in Introduction were confirmed. There was no tendency of subadult Eiders to become physiologically mature at the same age, and they did not enter the breeding population randomly. Instead, they entered the population according to the fledging result of their year class, with small year classes entering at a later age than large ones. Contrary to the debut-breeding-age hypothesis, the debut breeding age was delayed when the population declined and adult mortality increased. Apparently the decreasing population size in 1991–2000 in Denmark was not due to increasing adult mortality, but to a decreasing fledging rate in the north.

Haahkan sukukypsyysikä ei aikaistunut kannan laskiessa Suomenlahdella 1990-luvun lopulla

Itämeren haahkakannat ovat olleet tuntuvassa laskussa 1990-luvulta lähtien. Talvehtimisalueilla kannat laskivat 36 % vuosina 1991–2000, mutta pesimäalueiden tiedot ovat hajanaisemmat ja osittain ristiriidassa tämän kanssa. Useimmilla alueilla lasku on ollut lievempää tai laskua ei ole havaittu lainkaan, tai sitten se on ajoittunut toisin kuin talvilaskentojen tuloksissa. Tätä ristiriitaa on selitetty hypoteesilla, jonka mukaan kannan laskiessa esiaikuiset ikäluokat olisivat tulleet sukukypsiksi aikaisemmin kuin ennen ja siirtyneet pesimäalueille, joilla ne kompensoisivat pienentynyttä aikuiskantaa. Tämän "puskuriefektin" vaikutuksesta kokonaiskannan pudotus ei näkyisi pesimäalueilla vaan pelkästään talvialueilla (joilla siis koko kanta on kerralla paikalla).

Söderskärin riistantutkimusasemalla keskisellä Suomenlahdella sukukypsyysiän mahdollinen muutos oli testattavissa pesäpoikasina rengastettujen haahkojen kontrolliaineistosta. Kannanlaskun vuosina 1986–99 rekrytoitumisen otaksuttua aikaistumista ei kuitenkaan tapahtunut, vaan mediaani sukukypsyysikä oli itse asiassa yhden vuoden korkeampi (neljä vuotta) kuin kannannousun vuosina 1982–85.

Sukukypsyysiän ja rekryytin koon välillä havaittiin negatiivinen riippuvuus (korkea sukukypsyysikä – vähän rekryyttejä). Pienten vuosiluokkien debytantit tulivat myöhään sukukypsiksi, eikä niiden harvalukuinen joukko korvannut aikuiskuolevuutta, ja kanta laski. Pienet vuosiluokat olivat voimakkaan pienpoikaskuolevuuden seurausta. Talvialueilla havaittu kannanlasku saattaa olla paremminkin seurausta esiaikuisten ikäluokkien pienenemisestä huonon poikastuoton seurauksena pohjoisilla tuotantoalueilla kuin kohonneesta aikuiskuolevuudesta.

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