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ORIGINAL ARTICLE

Neckband loss and its effect on apparent survival estimates in Greylag Geese (*Anser anser*): variation with season, sex and age

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Abstract

Mark-recapture studies enable us to estimate population parameters such as survival, if marks do not impact survival and if marks are not lost. Mark loss can result from external wear and damage, but also behavioural factors may be important and could explain differences between seasons or sexes. We studied Greylag Geese (*Anser anser*) in eastern Netherlands, ringed with neckbands, leg bands and metal rings (912 geese), observed weekly during 1997–2019 (131,625 observations). Given the double marking and high annual resighting probabilities (neckbands: 0.974, leg rings: 0.639), we quantified neckband loss and the effect of neckbands on apparent survival, using multistate mark-recapture models. Annual neckband loss was 0.038, was higher in males (0.056) than females (0.021) and increased with years since marking, up to 0.098 for males more than 8 years after marking. Neckband loss tended to be higher during December–May than June–November, with most losses occurring in March–April. Both the higher loss in males and the peak in spring in both sexes could result from intraspecific fighting (pulling each other's neck and neckband). Survival was underestimated in Cormack-Jolly-Seber models that did not account for neckband loss, by up to 0.096 for adult males 6–7 years after marking. Thus, ignoring neckband loss may give erroneous survival differences between sexes and seasons, and overestimate the effect of ageing on survival (i.e. senescence). We did not detect an effect of neckbands on mortality, but statistical power for this test was limited. Neckband loss, although lower nowadays than in studies of decades ago, still impacts survival estimates and should be considered in mark-recapture studies.

Keywords Ageing · Multistate models · Neck collar · Retention · Ring loss · Senescence

Zusammenfassung

Der Verlust des Halsbandes und die Auswirkung auf die Überlebensrate bei Graugänsen (*Anser anser*): Unterschiede je nach Jahreszeit, Geschlecht und Alter

Markierungs- und Wiederfangstudien helfen uns bei der Einschätzung von Populations-Parametern wie z.B. der Überlebensrate, wenn die Markierungen selbst keinen Einfluss auf die Überlebensrate haben und nicht verlorengehen. Das Verlieren von Markierungen kann an äußerer Abnutzung und Beschädigung liegen sein, aber auch verhaltensbedingte Faktoren können eine Rolle spielen und gefundene Unterschiede zwischen Jahreszeiten oder Geschlechtern erklären. Im Osten der Niederlande untersuchten wir Graugänse (*Anser anser*), die mit Hals- und Fußbändern sowie Metallringen markiert waren (912 Gänse), und beobachteten sie wöchentlich im Zeitraum von 1997-2019 (131.625 Beobachtungen). Angesichts der doppelten Markierung und der hohen jährlichen Wiederbeobachtungs-Wahrscheinlichkeit (Halsbänder: 0,974, Beinringe: 0,639) haben wir mit Hilfe von mehrstufigen Markierungs- und Wiederfangmodellen den Verlust von

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Halsbändern und die Auswirkung von Halsbändern auf das Überleben quantifiziert. Der jährliche Halsbandverlust betrug 0,038, war bei Männchen höher (0,056) als bei Weibchen (0,021) und nahm mit den Jahren seit Markierung zu, auf bis zu 0,098 bei Männchen mehr als 8 Jahre nach ihrer Markierung. Das Verlieren von Halsbändern war im Zeitraum Dezember-Mai tendenziell höher als im Zeitraum Juni-November, wobei die meisten Verluste im März-April auftraten. Sowohl der höhere Verlust bei den Männchen als auch die Spitze im Frühjahr bei beiden Geschlechtern könnten auf innerartliche Kämpfe (gegenseitiges Ziehen am Hals und am Halsband) zurückzuführen sein. In Cormack-Jolly-Seber-Modellen, die den Verlust des Halsbandes nicht berücksichtigten, wurde die Überlebnsrate bis zu 0,096 für erwachsene Männchen 6–7 Jahre nach der Markierung unterschätzt. Daher kann die Nichtberücksichtigung des Halsbandverlustes zu verfälschten Unterschieden in der Überlebensrate zwischen den Geschlechtern und den Jahreszeiten führen und die Auswirkungen der Alterung auf die Überlebensrate (d. h. die Seneszenz) überbewerten. Wir konnten keine Auswirkung der Halsbänder selbst auf die Sterblichkeit feststellen, wobei die statistische Aussagekraft dieses Tests allerdings begrenzt war. Der Verlust von Halsbändern ist heute zwar geringer als in Studien vor Jahrzehnten, wirkt sich aber immer noch auf die Überlebensschätzungen aus und sollte bei Wiederfangstudien berücksichtigt werden.

Introduction

Following individual animals with unique marks enables us to estimate population parameters such as survival and dispersal (White and Burnham 1999). To obtain accurate estimates, two issues of marks need to be addressed: (1) the direct effect on the parameter of interest, which should be minimal, and (2) the retention over the period of interest, which should be maximal. Especially for the first issue, it is important to quantify the second issue simultaneously, because e.g. a low estimate of apparent survival may in fact originate from mark loss (cf. Nelson et al. 1980; Alisauskas and Lindberg 2002). The direct effect of marks can differ between population parameters, as marks may decrease survival but not dispersal (Alisauskas et al 2012).

Mark loss can only be studied when individuals have been equipped with multiple marks, as done in birds (e.g. Clausen et al. 2015), reptiles (e.g. Rivalan et al. 2005) and mammals (e.g. Bradshaw et al. 2000), or when specific individuals can still be identified with the remaining marks in combination with special body features or high site fidelity (e.g. Allen et al. 2019). In birds, unique marks have been e.g. metal leg rings, larger coded or coloured leg rings, and in species with long necks such as geese and swans also neckbands (Helm 1955; Craighead & Stockstad 1956; Ballou & Martin 1964). Neckbands are well visible from a distance and thus yield higher resighting probabilities (e.g. Juillet et al. 2010; and own data). This results in a higher power to detect differences in e.g. survival between different sexes or ages, but also in a higher risk of obtaining misleading results if these differences in fact concern differences in mark loss.

Mark loss is especially relevant when studying long-lived species. Mark loss has been studied mostly in middle and large-bodied birds and was found to be on average around 0.025 annually for leg rings on waders, gulls and geese (Thomas 1979; Spendelow et al. 1994; Persson 2000; Thorup 2000; Ward 2000; Burns et al. 2010; Allen et al. 2019) and on average around 0.11 for neckbands on geese (Ballou and Martin, 1964; Fjetland 1973; Craven 1979; Zicus and Pace 1986; Hestbeck and Malecki 1989; Johnson and Sibly 1989; Samuel et al. 1990, 2001; Campbell and Becker 1991; Johnson et al. 1995; Schmutz and Ely 1999; Menu et al. 2000; Persson 2000; Wiebe et al. 2000; Alisauskas and Lindberg 2002; Coluccy et al. 2002; Conn et al. 2004; Reed et al. 2005; Juillet et al. 2010; Clausen et al. 2015) and around 0.30 for swans (Nichols et al. 1992). The causes of mark loss are assumed to be wear, accumulating over time, by natural causes such as scratching against rocks and mussel beds (Allen et al. 2019), temperature fluctuations, solar UV irradiation, and possibly salty water (but see Ludwig 1967; Gaston et al. 2013), and damage by non-lethal lead shot from hunting (Persson 2000; Alisauskas and Lindberg 2002; own observations). In line with this accumulating wear, mark loss probabilities have been reported to increase with the age of the ring (Zicus and Pace 1986; Samuel et al. 1990; Campbell and Becker 1991; Johnson et al. 1995; Samuel et al. 2001; Coluccy et al. 2002; Allen et al. 2019).

Apart from these wear effects, other, behavioural causes may contribute to ring loss. We hypothesize that ring loss is highest in the season with the highest amount of preening behaviour, as during preening birds may also pull the marks (e.g. Clausen et al. 2020) or in the season with the most intraspecific fighting, which can also result in pulling and removing neckbands of conspecifics (Campbell and Becker 1991; Johnson et al. 1995). These possible seasonal effects may bias seasonal survival estimates. Furthermore, these seasonal behavioural effects on ring loss may differ between sexes. In many goose species, neckband loss was found to be higher for males than females (Fjetland 1973; Johnson et al. 1989; Samuel et al. 1990; Campbell and Becker 1991; Johnson et al. 1995; Persson 2000; Wiebe et al. 2000; Samuel et al. 2001; Alisauskas and Lindberg 2002; Coluccy et al. 2002; Conn et al., 2004). Thus, it is important to understand a potential behavioural component of ring loss, especially when within-year survival probabilities are considered but also to understand why sexual variation in ring loss may exist. Furthermore, a behavioural cause of ring loss might distort studies of apparent survival in relation to e.g. age, or personality (cf. Kralj-Fišer et al. 2010).

We quantify seasonal and sexual variation in neckband loss in a population of Greylag Geese (*Anser anser*) in the southwestern part of the Gelderse Poort, the Netherlands. We also quantify the direct effect of neckband presence on apparent survival (hereafter referred to as 'survival'). Here, 1087 individuals were marked, and followed by weekly visits and additional sightings of citizen scientists during 1997–2019. The high resighting probability and the use of multiple marks per individual (neckband, metal ring, coded plastic leg ring) allow us to estimate neckband loss probabilities for both sexes over years and seasons with multistate mark-recapture models. We further compare these models that account for neckband loss with models that do not, to quantify the importance of including neckband loss for accurately estimating survival while simultaneously assessing the direct effect of neckband presence on survival.

Methods

Study area

We studied a Greylag Goose population in the southwestern part of the Gelderse Poort, the Netherlands, situated between the cities of Nijmegen and Arnhem and the German border (51°51′N, 05°55′E). The Gelderse Poort consists of floodplains along the river Waal, dykes, waterbodies, swamps, reedbeds, unmanaged grassland, agricultural fields (dairy farms with crop production), forest patches and urban areas. The study area consisted of parcels of agricultural and natural land use. Greylag geese have been present here since 1977 (Brouwer et al. 1985), during the study period with around 1750 pairs (Majoor and Van Diermen 2013) and are almost exclusively residential (Voslamber et al. 2010).

Capture and marking

Between 1997 and 2015, 1087 Greylag Geese have been individually marked with metal rings, coloured plastic leg rings and/or neckbands. Greylag Geese were caught during their moulting period which, in the Netherlands, is mainly in June (end of May–half July). Most geese (93.5%, 1016 of 1087) were ringed during June, the rest mainly in July ($n = 69$) and only two birds in August. The catches were concentrated on families (i.e. adults with goslings). A group of around five to ten people were driving the birds, causing the geese to walk or swim in the direction of a funnel-shaped net ending in a corral (e.g. Persson 1994; Kampp and Preuss 2005). Geese were sexed by cloacal examination. All birds received a metal ring from the Dutch Centre for Avian Migration and Demography on one of their tarsi (aluminium, but steel in the last years). From 1999 onwards, almost all birds (except for too small goslings) also received on the other tarsus a coded plastic leg ring with the same code and colour as the neckband, and of the same material (see below). Neckbands were used on all adults, and young that were large enough, and were dark green with white unique inscriptions. This resulted in 53 geese being ringed with metal only (mainly small goslings), 112 geese ringed with metal + plastic leg ring (small goslings, 1998–2015), 151 geese with metal + neckband (mainly 1997–1998) and 771 geese ringed with metal + plastic leg ring + neckband (from 1998 to 2015). Because all neckbanded birds always received one or two other ring types, we were able to evaluate neckband loss.

We used three types of neckbands (all with inner diameter 48 mm, 1.5 mm thick, overlap glued with Bison Hard PVC-glue) that differed slightly: (A) 1997–2012: laminated PVC, manufactured by WSV Kunststoffen B.V., Utrecht, the Netherlands, height 45 mm, weight 11 g, overlap 20 mm, engraved to depth 0.2–0.3 mm by University of Groningen, the Netherlands ($n = 840$); (B) 2010–2011: laminated PVC, manufactured by M.Z. di Zanini Ivan & C. S., Milan, Italy, weight 13 g, but otherwise the same as type A ($n = 90$); (C) 2012–2015: modified acrylic (Gravoglas 2-plex), manufactured and engraved by Pro-Touch Engraving Ltd., Saskatoon, Canada, height 55 mm, weight 15 g, overlap 25 mm, engraving depth 0.3 mm ($n = 157$). Types A and B were delivered as sheet and were rounded manually with pliers in hot water. Type C was already perfectly rounded when delivered. Because of this, type C was glued more tightly than types A and B, and water and dirt could enter voids between overlapping parts in types A and B more easily.

Observations

Weekly observations of the geese were generally conducted by a single observer (BV) from 1997 to 2016 when site-specific resightings were recorded via a 7 × binocular or 20–60 × telescope using a car as shelter ($n = 93{,}833$ sightings). BV also noted whether a marked goose still had all its marks. Additionally, observations were reported by volunteer observers throughout 1997–2019 ($n = 45{,}795$ sightings). All sightings were entered in the citizen science platform of www.geese.org (Ebbinge et al. 2020), from which an export was made up to and including December 2019, in early January 2020. Wrong ring reports were identified by BV (e.g. unused codes, codes reported before ringing or after death, or neckband readings more than a year after the previous observation) and if possible corrected or else excluded. Under good light conditions, neckbands can be read from a distance of up to 500–600 m. Because of the many roads in the area, good coverage was achieved. There was no difference in readability of the neckbands between habitats. However, metal and plastic leg rings could mainly be read under special conditions and was more time-consuming (at closer ranges, mainly on sandbanks along the river and in short vegetation). In total, neckbands were reported 136,246 times (936 geese), coded plastic leg rings 3942 times (212 geese) and metal rings 527 times (69 geese).

Data selection

Of in total 139,628 ring reports, we excluded 139 dead recoveries and 5 recoveries of rings without a bird, resulting in a dataset of live resightings only. We excluded 164 birds that never received a neckband, because these were young juveniles, still too small for a neckband, and therefore likely had a different survival which introduces confounding variation in survival between neckbanded and leg-ringed birds. However, when a bird received a neckband during a recapture, it was included from that point onwards ($n=3$). Furthermore, we excluded birds that received a new neckband during a recapture as replacement of the worn old one ($n=7$) or because the old one had been lost ($n=4$), since survival and neckband retention cannot be decoupled here. Thus, in total, 131,625 resightings were included, of 912 individuals (442 females, 470 males). At ringing, 233 females were juvenile and 209 were adult, while of males 245 were juvenile and 225 adult. These neckbands comprised type A (332 females, 335 males), type B (44 females, 46 males) and type C (66 females, 89 males).

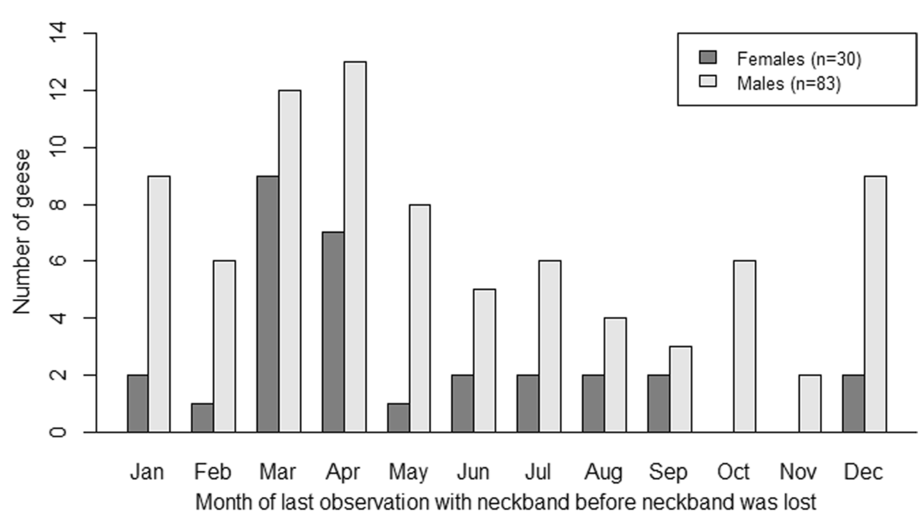
Among these 912 geese, neckband loss was seen in 113 geese (73 × type A, 35 × type B, 5 × type C). The last observations during which a goose still had its neckband before it was lost while the goose lived on, occurred in both sexes mainly in March and April and in males also often during December–January (Fig. 1). Neckbands were lost within 1 year ($n=23$ geese), or after 1 (15), 2 (16), 3 (13), 4 (10), 5 (10), 6 (10), 7 (6), 8 (4), 9 (2), 10 (1), 11 (1), 12 (0), 13 (2) or 14–16 years (0), i.e. on average 3.9 years after marking (± SD 3.0, range 1.5 months–13.8 years). For 30 geese, loss of leg rings was recorded (24 × coded plastic leg ring, 7 × metal ring, i.e. one individual lost both but retained neckband). However, only 3 out of 912 geese had lost all leg rings by the time of their last neckband observation, as far as was known. We therefore believe our calculations to give a good representation of real neckband loss probabilities.

To assess the effect of the neckband on survival, the survival of geese with a neckband was compared with the survival of the 113 geese that had lost their neckband. As by definition, geese aged while losing their neckband, it was important to account for the number of years since marking (see "Mark-recapture models"). Although we did not have a classic control group, this comparison of survival is expected to give a reliable impression of the effect of neckbands on survival, given the large range in the moment at which the neckbands were lost (see above). The geese that were ringed with only leg rings were not included, because the ring types were not assigned randomly (see "Capture and marking"): geese ringed without neckbands were ringed as small goslings which can be expected to have different survival than geese ringed as adults, which would distort the comparison.

Mark-recapture models

To estimate neckband loss probabilities, we used 'multistate mark-recapture models with recaptures only' in Program MARK version 6.2 (White and Burnham 1999; Cooch and White 2019) which we parameterized using RMark (Laake 2013). Multistate models estimate, apart from survival and recapture probabilities, the transition probabilities between states. We defined states here as the ring type with which the goose was reported: neckband (state N), if present, and

Fig. 1 Distribution of months in which geese were last seen with their neckband, before their neckband was lost while the goose lived on, for males and females. Because of high resighting probabilities (per year 0.974 for neckbands and 0.639 for leg rings, metal and plastic combined) this is expected to give a good indication of when geese lose their neckbands



otherwise leg rings (state L). An assumption of this model is that leg rings are not lost. If a goose had a neckband, in addition to other marks, it was always reported based on the neckband, as this was the most clearly visible mark. For simplification, the state of leg rings combined the sightings of the coded plastic ring and the metal ring, although the resighting probability of both ring types differed slightly. In this way, the transition probability from the neckband state to the leg rings state (Psi N→L) gave the neckband loss probability, while the transition from leg rings to neckband (Psi L→N) was fixed at 0. We performed multistate models to evaluate: (1) neckband loss in relation to the number of years since marking, age at marking, sex, and neckband type, thus showing between-year patterns; and (2) neckband loss in relation to season and sex, thus showing within-year patterns; and (3) in both cases, an assessment of a potential difference in survival between geese with and without neckbands.

For the between-year analysis, subsequent encounters after ringing (state N) gave the state during the following calendar year (January–December), and so on. That state was defined as the last observed state before the end of the calendar year. Thus, state L was noted if a goose was observed with the leg rings during this year. The years since marking (hereafter YSM) were partly grouped after the first five years, to maintain a suitable sample size of observed geese per group: 1 (767 individuals), 2 (653), 3 (551), 4 (459), 5 (364), 6–7 (268 + 210 = 478) and 8–16 (respectively 160 + 122 + 101 + 75 + 51 + 25 + 15 + 9 + 3 = 561) YSM. YSM was entered as a continuous variable ('year classes' 1–7) in the functions of transition probability to test if neckband loss increased over time since marking. We evaluated visually whether the linear trend accurately described the change in neckband loss probabilities over YSM, by plotting in addition to the obtained parameter estimates and SE also those obtained when taking YSM as a categorical variable. In the functions of survival, YSM was entered as categorical variable. All other explanatory variables were entered as categorical variables. In our models, we let the survival (S) and transition (Psi) probabilities depend on the same set of variables, to allow for a good assessment of the importance of accounting for neckband loss on survival estimates of different ages and sexes, when compared to models that do not account for neckband loss (see last paragraph of Methods). In all models, an effect of state (N or L) on survival was included, to see whether neckbands increased mortality, and the resighting probability (p) depended on the sex and interactive effects of state (N or L) and year. We performed a set of models to quantify specific effects: the overall annual neckband loss (model 1: S(state), p(state × year, sex), Psi(.)), the neckband loss per sex (model 2: S(state + sex), p(state × year + sex), Psi(sex)), the overall neckband loss over years since marking (model 3: S(state + YSM), p(state × year + sex), Psi(YSM)), which was also differentiated per sex (model 4: S(state + sex × YSM), p(state × year + sex), Psi(sex × YSM)) and per age at marking (henceforth AAM; model 5: S(state + AAM × YSM), p(state × year + sex), Psi(AAM × YSM)), and per sex and AAM simultaneously in a three-way interaction [model 6: S(state + sex × AAM × YSM), p(state × year + sex), Psi(sex × AAM × YSM)]. Further, we tested whether neckband loss probabilities differed between neckband types (model 7: S(state + type), p(state × year + sex), Psi(type)) which was also differentiated per sex [model 8: S(state + type × sex), p(state × year + sex), Psi(type × sex)]. The significance of each effect was calculated based on a z score using the logit-transformed estimate and its standard error.

For the analysis of within-year variation in neckband loss, years were split into two seasons, June–November and December–May, based on Fig. 1. The periods June–November and December–May were each combined for all years. Due to limited computational power, it was not possible to split up the year in more than two periods. The subsequent encounters after ringing (state N) gave the state during the following half year (December–May), and so on. That state was defined as the last observed state before the end of that half year, i.e. state L if a goose was observed with leg rings during that half year. All explanatory variables were entered as categorical variables, and a model was defined to test whether the transition probability differed between seasons and sexes (model 9: S(state + season × sex), p(sex + season + state × year), Psi(season × sex)). We further tested whether an effect of neckbands on survival differed between seasons, corrected for years since marking and age at marking [model 10: S(state × season + season × sex + YSM × AAM), p(sex + season + state × year), Psi(season × sex + YSM × AAM)]. Again, the significance of each effect was calculated based on a z score using the logit-transformed estimate and its standard error.

To assess the importance of neckband loss for survival estimates, we compared the survival estimates of neckbanded birds from annual models (model 1, 2, 6) as well as the seasonal model (model 9) with survival estimates from models which included the same independent variables, but did not account for neckband loss. For this, we used Cormack-Jolly-Seber (CJS) live-recapture models (Cooch and White 2019), and used the same encounter histories as for the multistate models, but adapted by replacing all encounters in state N by "1" and those in state L by "0", thus ignoring the resightings of leg rings. Using the annual encounter history, we thus applied CJS models where survival (Phi) depended on the same variables as S did in models 1, 2 and 6, while the resighting probability depended on additive effects of sex and year. Using the half-year encounter history, we applied a CJS-model where survival (Phi) depended on an interaction of season and sex (as in model 9), while the resighting probability depended on additive effects of sex, season and year. The discrepancy, if present, in survival estimates between the models accounting (multistate) or not accounting (CJS) for neckband loss, gave the effect of neckband loss on survival estimates. We tested the significance of these discrepancies by calculating z-scores based on the logit-transformed estimates of survival probabilities and their standard errors: $z = (\text{estimate}_{CJS} - \text{estimate}_{Multistate}) / (SE_{CJS}^2 + SE_{Multistate}^2)^{0.5}$. Estimates ± standard error (SE) are given.

Results

Resighting probability

The frequent sightings resulted in a high resighting probability. On average, this was 0.974 per year for neckbands and 0.639 for leg rings (model 6), and the resighting probabilities did not differ between the two seasons (model 9, $z = -0.3734$, $p = 0.709$). The resighting probability decreased slightly over the study period for neckbands (linear model: $\beta = -0.00348$, $t = -7.379$, $p < 0.001$) and leg rings ($\beta = -0.0288$, $t = -3.991$, $p < 0.001$, Supplement Figure S1–2).

Variation in neckband loss probability over the years

Overall, the neckband loss probability was 0.0383 ± 0.0037 per year ($z = -32.53$, $p < 0.001$, model 1) and differed significantly between the sexes, with a loss probability of 0.0206 ± 0.0038 in females and 0.0560 ± 0.0061 in males ($z = 4.781$, $p < 0.001$, model 2, see also Supplement Table S1). The neckband loss probability increased with years since marking (logit-transformed effect size: 0.1338 ± 0.0460 increase, i.e. an increase of 0.0038–0.0069 per year class, model 3, $z = 2.909$, $p = 0.0036$, see also Fig. 2). This effect of years since marking did not differ significantly between the sexes ($z = 0.164$, $p = 0.870$, model 4), nor between different ages at marking ($z = 0.817$, $p = 0.414$, model 5). However, when comparing specific estimates in the full model (model 6), the neckband loss probability of males ringed as juveniles was, during the first year after marking, not significantly different from females ringed as juveniles (difference = 0.0138 ± 0.0098, $z = 1.413$, $p = 0.158$) or from females ringed as adults (difference = 0.0099 ± 0.0108, $z = 0.916$, $p = 0.360$), but tended to be lower than in males ringed as adults during the first 3 years after marking; YSM1: difference = − 0.0255 ± 0.01.46, $z = -1.746$, $p = 0.081$; YSM2: difference = − 0.0257 ± 0.0132, $z = -1.954$, $p = 0.051$;

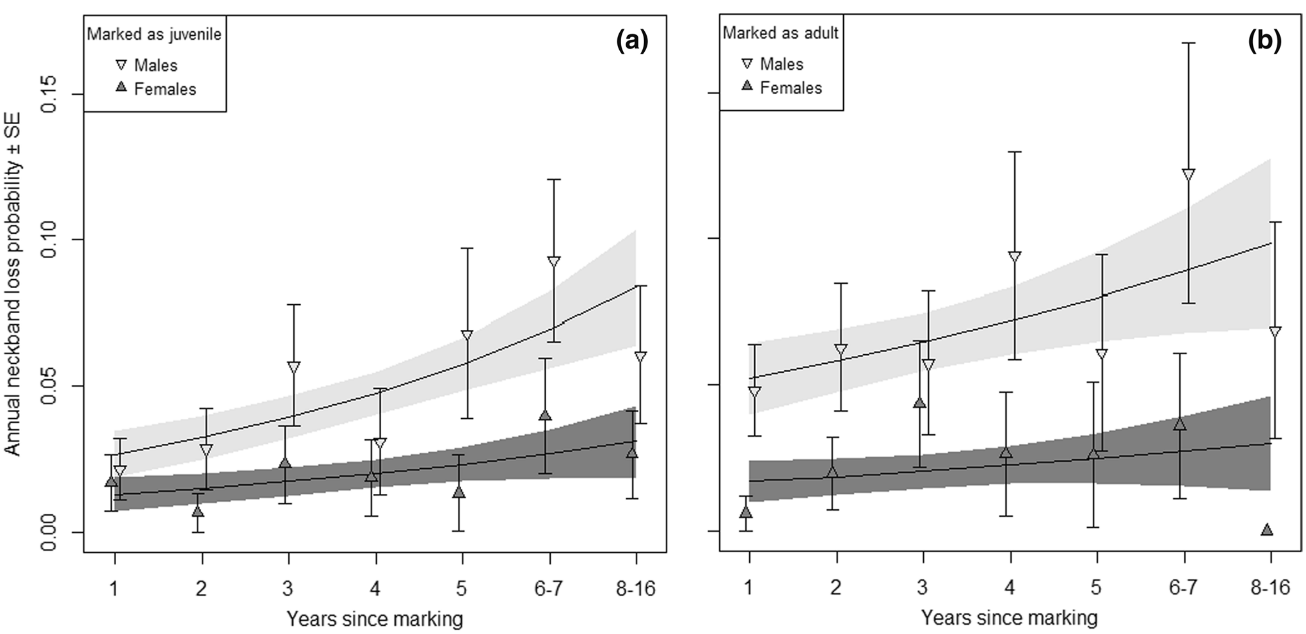


Fig. 2 Neckband loss probability in relation to years since marking (YSM), for geese marked as juveniles (**a**) and as adults (**b**). Results of model 6 (YSM as continuous variable with classes 1–7) are depicted as lines and shaded areas (model estimates ± standard error), whereas points are model results when taking YSM as categorical variable. Neckband loss was higher for males than females, and increased with YSM. Young males start with a neckband loss probability similar to females and lower than adult males

YSM3: difference = 0.0253 ± 0.0124, $z = -2.050$, $p = 0.040$, Fig. 2).

Neckband loss differed significantly between neckband types and was much higher for type B (0.1848 ± 0.0273) than for type A (0.0279 ± 0.0033, $z = -9.546$, $p < 0.001$, model 7) and type C (0.0212 ± 0.0096, $z = -4.775$, $p < 0.001$, model 7). The difference in neckband loss between types was similar in males and females (females: Type A: 0.0120 ± 0.0031, Type B: 0.1300 ± 0.0318, Type C: 0.0094 ± 0.0094; males: Type A: 0.0436 ± 0.0058, Type B: 0.2563 ± 0.0461, Type C: 0.0305 ± 0.0152) as the interaction of sex × Type A ($z = 1.030$, $p = 0.303$) and sex × Type C ($z = 0.300$, $p = 0.764$, model 8) were not significant.

Variation in neckband loss probability within a year

Neckband loss probabilities tended to be higher during December–May (females: 0.0148 ± 0.0034, males: 0.0302 ± 0.0051, total: 0.0221 ± 0.0030 per half year) than during June–November (females: 0.0067 ± 0.0022, males: 0.0276 ± 0.0045, total: 0.0168 ± 0.0025 per half year, $z = 1.933$, $p = 0.053$, model 9). The seasonal contrast did not differ between the sexes ($z = -1.469$, $p = 0.142$, model 9, see also Supplement Table S2).

Effect of neckband presence on survival

Corrected for the effects of sex, age at marking and years since marking, survival did not differ between geese with and without a neckband (neckbanded geese had 0.017–0.037 higher survival, not significant; logit-transformed effect size: $\beta_{\mathrm{State\ N-State\ L}} = 0.176 \pm 0.176$, $z = 0.999$, $p = 0.318$, model 6). This did not differ between the seasons ($z = 1.326$, $p = 0.185$, model 10).

Underestimation of survival when ignoring neckband loss

Because of significant neckband loss, the overall annual survival probabilities were underestimated, by 0.0342, when not accounting for neckband loss (CJS: 0.8024 ± 0.0061, multistate model 1: 0.8366 ± 0.0059, $z = -4.044$, $p < 0.001$). Split up per sex, the underestimation was larger and significant in males (i.e. 0.0483 underestimation, CJS: 0.7939 ± 0.0087, multistate model 2: 0.8422 ± 0.0082, $z = -4.046$, $p < 0.001$) than in females, where the underestimation was not significant (i.e. 0.0204 underestimation, CJS: 0.8108 ± 0.0084, multistate model 2: 0.8312 ± 0.0081, $z = -1.745$, $p = 0.081$). In line with the increasing neckband loss over years since marking, also the underestimation of survival probabilities in the CJS-model tended to increase with years since marking, but this was only significant for geese ringed as juveniles (linear models; females ringed as juvenile: $\beta = 0.00388$, $t = 3.160$, $p = 0.025$; females ringed as adult: $\beta = -0.00069$, $t = -0.283$, $p = 0.788$; males ringed as juvenile: $\beta = 0.00795$, $t = 3.350$, $p = 0.020$; males ringed as adult: $\beta = 0.00365$, $t = 0.995$, $p = 0.365$, model 6; Fig. 3, Supplement Figure S3). The largest underestimation was found 6–7 years after marking in males ringed as adults (0.096) and as juveniles (0.076).

Within years, the underestimation in survival probability varied between seasons. During December-May it was 0.0267 for males (CJS: 0.8901 ± 0.0082, multistate model 9: 0.9168 ± 0.0076, $z = -2.389$, $p = 0.017$) and 0.0157 for females (non-significant, CJS: 0.8879 ± 0.0079, multistate model 9: 0.9036 ± 0.0074, $z = -1.441$, $p = 0.150$), whereas during June-November it was smaller, i.e. 0.0220 for males (CJS: 0.8763 ± 0.0079, multistate model 9: 0.8983 ± 0.0074, $z = -2.040$, $p = 0.041$) and 0.0058 for females (non-significant, CJS: 0.8951 ± 0.0073, multistate model 9: 0.9008 ± 0.0070, $z = -0.574$, $p = 567$, Fig. 4).

Discussion

We found that neckband loss was 0.038 annually, was higher in males than females, was higher in December–May than in June–November, increased with years since marking and depended on the type of neckband used. We also found that annual survival is underestimated by up to 0.096, when not accounting for neckband loss. Wearing a neckband appeared to have no effect on goose survival.

The overall annual neckband loss of 0.02–0.05 is similar to what previous studies in geese have found (0.007–0.045, Hestbeck and Malecki 1989; Schmutz and Ely 1999; Menu et al. 2000; Persson 2000; Wiebe et al. 2000; Coluccy et al. 2002; Reed et al. 2005; Juillet et al. 2010; Clausen et al. 2015). However, other, mostly older studies report higher overall neckband loss probabilities (0.072–0.317, Ballou and Martin 1964; Fjetland 1973; Craven 1979; Zicus and Pace 1986; Johnson and Sibly 1989; Samuel et al. 1990; Campbell and Becker 1991; Johnson et al. 1995; Wiebe et al. 2000; Samuel et al. 2001; Alisauskas and Lindberg 2002; Conn et al. 2004). The neckband loss probabilities tend to have decreased in studies over the past decades (linear model: $\beta = -0.00273$ per year, $t = -1.983$, $p = 0.061$, Fig. 5) and this may reflect improving practices when using neckbands, such as more durable material, larger overlap, the use of glue, or better glue. For example, early studies used flexible plastic neckbands produced by a rubber company (Sherwood 1966) and did not use glue, to allow the goose to escape from the neckband if it would get stuck in the environment (Fjetland 1973). Also in our study one neckband type was lost more often than the other two, thus care should be taken when comparing survival between cohorts marked with different type of neckbands.

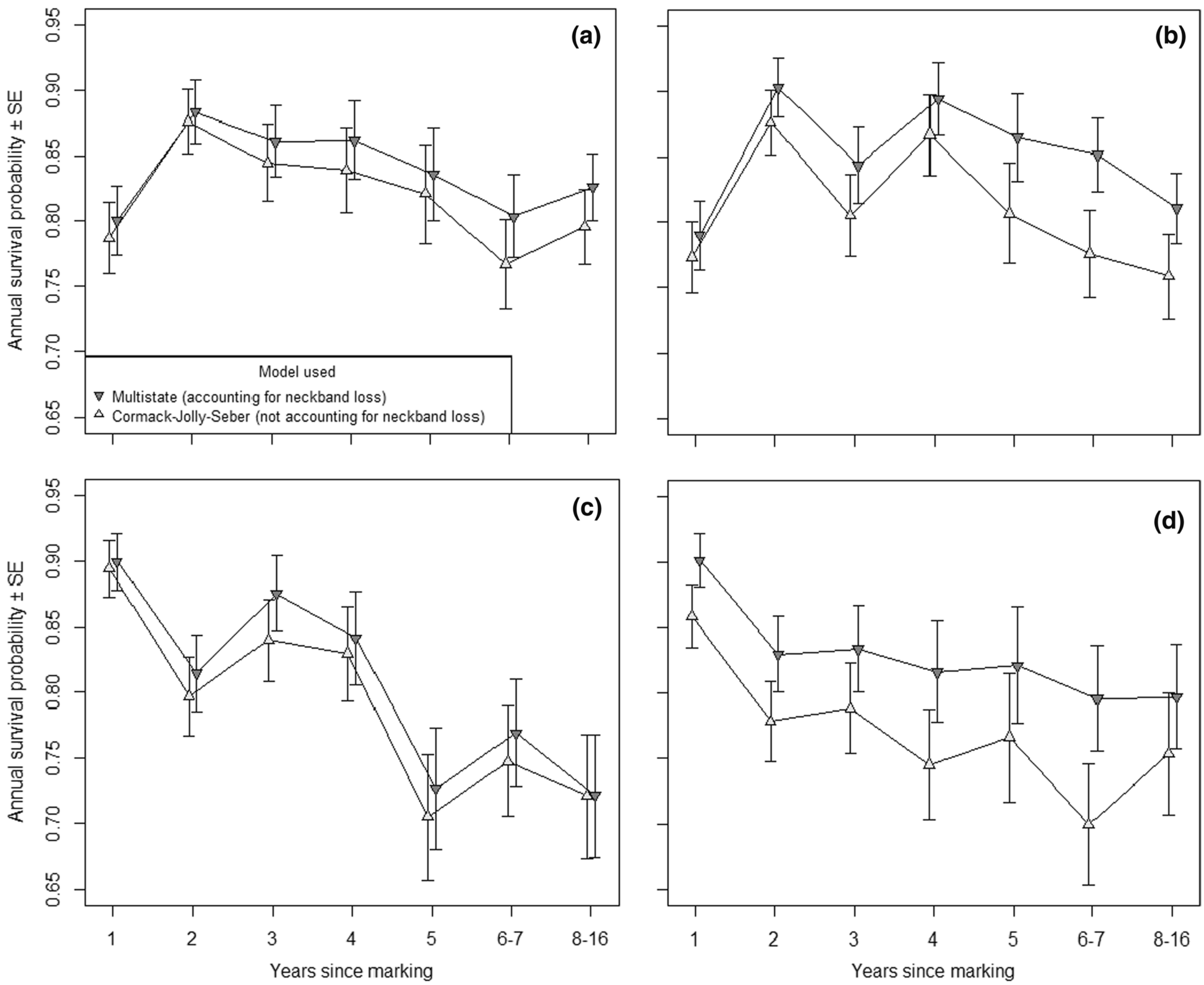


Fig. 3 Survival estimates in relation to years since marking (YSM), for geese ringed as juvenile females (**a**), juvenile males (**b**), adult females (**c**), and adult males (**d**). Because of significant neckband loss, survival was underestimated when not taking it into account (light grey pyramids, Cormack-Jolly-Seber model) as compared to multistate models (dark grey nablas). This underestimation generally increased over YSM, but only significantly in geese ringed as juveniles. Geese marked as juveniles show an initial increase in survival, after which survival decreases, as in adults. Geese marked as adult females show the steepest decline in survival over YSM

The larger neckband loss probability in males than females was also found in other studies in geese (Fjetland 1973; Johnson and Sibly, 1989; Samuel et al. 1990; Campbell and Becker 1991; Johnson et al. 1995; Persson 2000; Wiebe et al. 2000; Samuel et al. 2001; Alisauskas & Lindberg 2002; Coluccy et al. 2002; Conn et al. 2004) and in swans (Nichols et al. 1992). These authors explain this sex difference in loss probability as a result of (1) males being stronger and thus better able to damage or pull off their own neckband, (2) males being more territorial, aggressive and fighting more frequently, by which they may pull off each other's neckband, and (3) males receiving more damage from lead shot to their neckbands as hunters may target the larger individuals in a group. For neckband loss in Greylag Geese, we think that fighting is an important factor, which occurs mostly in males. During fighting, Greylag Geese bite and pull each other's neck while clapping the wings (Scheiber et al. 2013), and were also observed to pull the opponent's neckband if present (pers. obs. BV; also observed in other species by Campbell and Becker 1991; Johnson et al. 1995).

It is interesting to note that some studies reported that there was no significant sexual difference in neckband loss rate, for Pink-footed Geese (*Anser brachyrhynchus*, Clausen et al. 2015), Canada Geese (*Branta canadensis*, Craven 1979; Zicus and Pace 1986) and Greater Snow Geese (*Chen caerulescens atlantica*, Reed et al. 2005). Apart from potential lack of statistical power, an explanation could be, at least

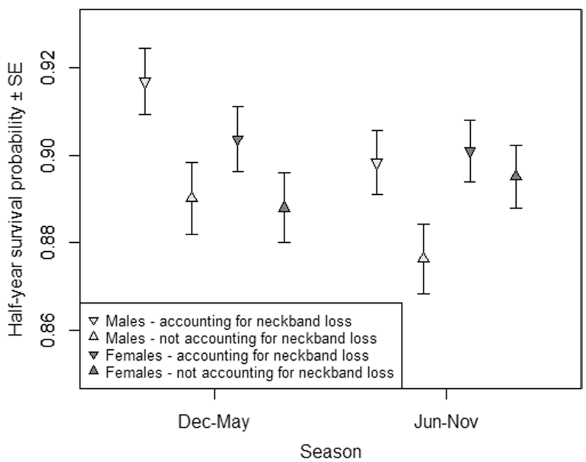


Fig. 4 Survival estimates in relation to season. When not accounting for neckband loss, survival probabilities were underestimated (pyramids, Cormack-Jolly-Seber model) as compared to multistate models (nablas). This underestimation tended to be larger in December–May than in June–November, in males (light grey) and females (dark grey)

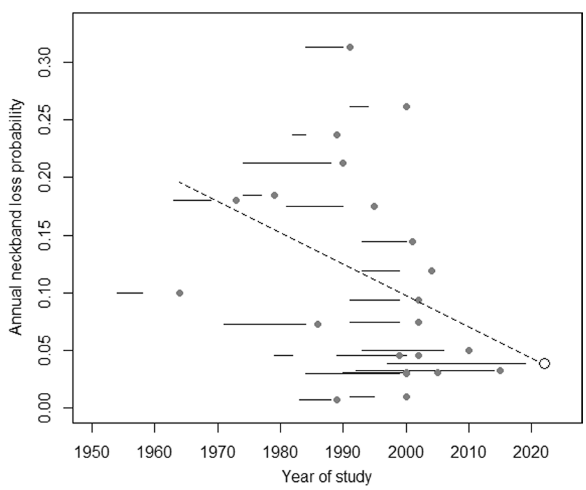


Fig. 5 Neckband loss in geese in historical perspective. Neckband loss probabilities are plotted over their publication date for 22 studies (grey filled circles) and the present study (open circle) and preceded by their study period (black lines from start to end of study). Neckband loss probabilities tend to have decreased over the past 60 years ($p=0.06$) and are recently generally below 0.05

for Pink-footed Geese, that these breed in small colonies and in low densities (Cramp and Simmons 1977), and thus presumably fight less on the breeding grounds than the species in which a sex difference was found: Canada Geese (*Branta canadensis* and subspecies *occidentalis, hutchinsi, parvipes, maxima*), Lesser Snow Goose (*Chen caerulescens caerulescens*), White-fronted Goose (*Anser albifrons* and subspecies *frontalis*), Greylag Goose. Also within species, neckband loss was found to covary with nest densities (Campbell and Becker 1991).

As fighting occurs mostly in spring, when nest sites are being occupied, one would expect that neckbands are mostly lost in spring. This seemed indeed the case, as loss probabilities tended to be higher in December–May than in June-November. Additionally, the last date on which a neckband was observed before it was lost (Fig. 1), is expected to give a good indication of the moment of neckband loss, because of the high resighting probabilities. Both sexes showed a peak in loss during March–April, and unlike males, females rarely lost neckbands in the remaining part of the year. This might indicate that females do fight, but only when it comes to nesting sites, whereas males fight also in remaining parts of the year, e.g. to obtain dominance (pers. obs. BV). This is in line with Johnson et al. (1995) reporting that for both sexes nearly 60% of lost neckbands of Lesser Snow Geese were found broken near nesting sites.

Another indication that fighting is important for neckband loss, is that males ringed as juveniles initially have neckband loss probabilities similar to females. Only as they become adult and start occupying territories after several years (Nilsson et al. 1997; Kampp and Preuss 2005), they show neckband loss probabilities that are similar to those of males ringed as adults, and higher than those of females. Also in Tundra Swans (*Cygnus columbianus*), Nichols et al. (1992) found lower neckband loss probabilities in immature than adult males.

An increasing neckband loss probability with years since marking was also found in several studies (Zicus and Pace 1986; Samuel et al. 1990; Campbell and Becker 1991; Johnson et al. 1995; Persson 2000). This is often explained as a result of accumulating damage and wear, and the breaking of glue, by which the neckband breaks or slips off more easily. However, this probably reflects a combined result of wear and fighting, as these effects enhance each other and also the fighting frequency itself might increase with age. Older males may occupy better nesting sites, in higher breeding densities, where geese are more aggressive (e.g. for Barnacle Geese *Branta leucopsis*, Black and Owen 1987).

Corrected for neckband loss, patterns in survival over YSM differed between sexes and ages. Geese marked as juvenile showed an increase in survival during their second year, which may indicate an increase in experience of the remaining individuals, or selective disappearance of the weaker individuals. Subsequently, survival decreased with YSM, as was also the case for geese ringed as adults already from their first year since marking. This decrease may reflect a worsening condition with age. The decrease was most prominent in females ringed as adults. The cause for this may be in a high nest predation by Red Fox (*Vulpes vulpes*) upon breeding adult females (see Scheiber et al. 2013). In the Gelderse Poort, a dead female was found at 12 (8.8%) out of 137 nests where all eggs were predated (pers. obs. BV). This predation pressure may also increase the cost of successful nest defense and therefore the survival cost of breeding.

We did not find evidence for a higher mortality in geese with a neckband than in geese with only leg rings. This may be due to a possibly insufficient statistical power: although the non-significant effect rather suggested a higher survival in neckbanded geese, only 113 geese could be included to assess the survival of geese without neckband, while correcting for effects of sex, age at marking and years since marking. Alternatively, the result may indicate that Greylag Geese in the Gelderse Poort are little influenced by wearing a neckband, or that they are able to compensate for negative effects. This population is almost exclusively residential and the area offers high quality food all year round (Voslamber et al. 2010). Also in other goose species, neckbands were found to have no effect on survival (e.g. Menu et al. 2000; Reed et al. 2005) whereas the effect was negative in others (e.g. Alisauskas and Lindberg 2002; Alisauskas et al. 2012; Caswell et al. 2012). However, the presence of the neckband might still affect other parameters than survival, as the effect of neckbands on geese may not only differ between species, but also between parameters of one species. For example, in Greater Snow Geese, neckbands did not affect survival, but still reduced clutch size and breeding propensity (Reed et al. 2005) and in Ross's Geese, neckbands reduced survival, but did not affect dispersal (Alisauskas et al. 2012).

Neckband loss was found to cause an underestimation of survival when it is not accounted for, i.e. in usual CJS models. We found on the annual level a maximum of 0.096 underestimation in the case of males ringed as adults, 6–7 years after marking. In general, the magnitude of the underestimation of survival was slightly smaller than the actual estimated neckband loss rate, which suggests that CJS models partially compensate for neckband loss in survival estimation. On average the underestimation of survival was 83% of the neckband loss probability (Supplement Figure S3). This can inform researchers that adjust survival probabilities for neckband loss post-hoc by dividing survival by neckband retention (e.g. Schmutz and Ely 1999).

By not accounting for neckband loss, misleading results may be obtained in three ways: (1) significant differences in survival (e.g. between seasons or sexes) might be in reality absent; (2) as the neckband loss increased with years since marking, also the survival underestimation increased with years since marking. This implies that studies of survival over age would overestimate the senescence, i.e. deteriorating survival of birds at old age, when neckband loss is not accounted for (see also Nichols et al. 1997; Crespin et al. 2006); (3) there might be apparent selective disappearance over time of certain 'personalities' of geese that are more likely to lose their neckband because of behavioural characteristics (see Kralj-Fišer et al. 2010). Thus, caution should be taken and correcting for neckband loss is important, especially in long-lived species and when using frequently resighted mark types that generate statistical power to detect small differences in parameters (whether real or not). To enable such a correction, it is important to collect data on mark loss from the beginning of a study onwards. For example, all ring types of an identified bird must be recorded systematically, and birds wearing only leg rings must be identified, even though this is more time-consuming. In any case, a mark type that survives longer than the bird, but with little effect on the bird, should be aimed for.

We conclude that neckband loss in Greylag Geese, even though lower than in studies of other geese decades ago, is significant and differed with sex, season, and years since marking. Although neckbands did not affect survival, neckband loss impacted survival estimates and therefore should be accounted for whenever possible to avoid making erroneous estimates and inferences.

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Declarations

Conflict of interest The authors declare that they have no competing interests.

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