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Mortality rates in the national bird ringing programme of Denmark and the Faroe Islands

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ABSTRACT

Capsule: Mortality varies across capture methods but remains overall low.
Aims: To investigate mortality associated with ringing operations in Denmark and the Faroe Islands, including the effects of species and capture methods.
Methods: We analyzed data for mortality rates of birds arising from ringing operations in Denmark and the Faroe Islands over a 20-year period. The data included a variety of capture methods and altogether the reports involve 1.8 million individuals.
Results: The overall mortality rate during ringing operations was 0.16%. The dominant form of capture, mist-netting, had a mortality rate of 0.21%, comparable to similar published studies. Capture methods with higher mortality rates were generally used in research aimed at informing management decisions. Predation was directly responsible for most deaths, with the Eurasian Sparrowhawk *Accipiter nisus* being the most common predator of birds captured in nets. Migrating passerines occurring in large numbers at bird observatories contributed most to the mortality rates in Denmark, with young birds on their first autumn migration being especially prevalent.
Conclusions: Overall, our study confirms that bird ringing remains an acceptable method of data collection and highlights the variation in mortality among species and methods. The results should be used to inform working practices to minimize any associated mortality, as far as possible.

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Methods for marking and recognizing individual birds are among the most important in the research and management of wild bird populations (Saino *et al.* 2011, du Feu *et al.* 2016, Jimenez-Munoz *et al.* 2019). National ringing schemes provide broad-scale data on the capture and handling of wild birds under systematic protocols, over a time series of several or many years.

Small fractions of captured individuals are inevitably harmed by the capturing device or during handling. Researchers are increasingly aware of the ethical principles of working with live animals, principles that have also entered the process of approval for individual science projects, as well as the funding for national ringing schemes (Wilson & McMahon 2006, Bodey *et al.* 2018).

Losses of individual birds during ringing operations have only been thoroughly quantified in a handful of studies. Earlier scientific field studies involving mist-netting have reported mortality rates of 0.8% or higher (Stamm *et al.* 1960, Recher *et al.* 1985, Colwell *et al.* 1988, Brooks 2000). However, in such studies the best practices for catching birds may, reasonably, have only been realized during the study period. National ringing schemes, especially ringing at bird observatories, which operate with permanent staff and a standardized capture programme that is repeated year after year, must be held to a higher standard.

Only two modern studies have collected and analyzed data for bird mortalities from ringing programmes on a national level. An evaluation of mist-netting captures from five ringing organizations in the USA found the average rate of mortality to be 0.23% (Spotswood *et al.* 2012). A high combined rate of injury and mortality (0.59%) in that study was driven by larger birds being more prone to incidents, such as wing injuries. More recently, Clewley *et al.* (2018) analyzed a large dataset of mist-net recaptures of passerines in the British Isles, covering the years 2005–2013. For these recaptured individuals, they

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found an overall mortality rate of 0.11%, with a higher risk for young birds and in the winter season.

Here, we investigate mortality rates from the Danish national bird-ringing scheme (covering Denmark and the Faroe Islands) over a period of 20 years (1999–2018), as the first study to include the entire ringing effort within a ringing scheme. The broad coverage is possible because of mandatory reporting of all causes of mortality from the beginning of the time series. The data cover any capture method used in the period, and all encounters of birds coming into contact with the ringing effort, whether primary ringing or recaptures. Our aim is to compare mortality rates for different types of capture method (for example mist-nets and traps), and for passerines or non-passerines, age and seasonality. Based on this, we provide a list of proposed measures for minimizing mortality rates in bird-ringing schemes.

Methods

The Copenhagen Bird Ringing Centre has collected information on injured and dead birds in Denmark and the Faroe Islands systematically since 1999, in an effort to assess and minimize the collateral mortality from ringing schemes. All ringers in Denmark and the Faroe Islands have been required to report circumstances of incidents on printed forms, and more recently as online reports.

Our stated aim is to measure rates of mortality within the ringing programme, but most dead birds are in fact not included in the standardized national ringing databases, due to never having been assigned a ring. Our overall dataset is therefore slightly larger than official data, as it is compiled from all ringing encounters, all recaptures of ringed birds and all recorded deaths (rings or no rings). For simplicity, we maintain the use of the term 'birds ringed' when referring to the totals.

Ringing effort increased gradually during the study period (Figure 1). However, the way of reporting bird mortality has changed slightly over the years. Until 2007, mortality was reported on a mandatory form together with other data on capture numbers and methods. After 2007, reporting of ringing data became electronic and the reporting of mortality relied on ringers uploading separate forms for each individual dead bird. Realizing that this may have resulted in lapses in reporting, since 2017 the ringing scheme has increased communication with ringers. However, in some years during the period 2008–2016 our data on mortality from individual ringers may not have been exhaustive.

We constructed datasets on capture methods, on the age of birds and the time of year from the national ringing database and individual reports from ringers. We also split the overall dataset for an analysis of

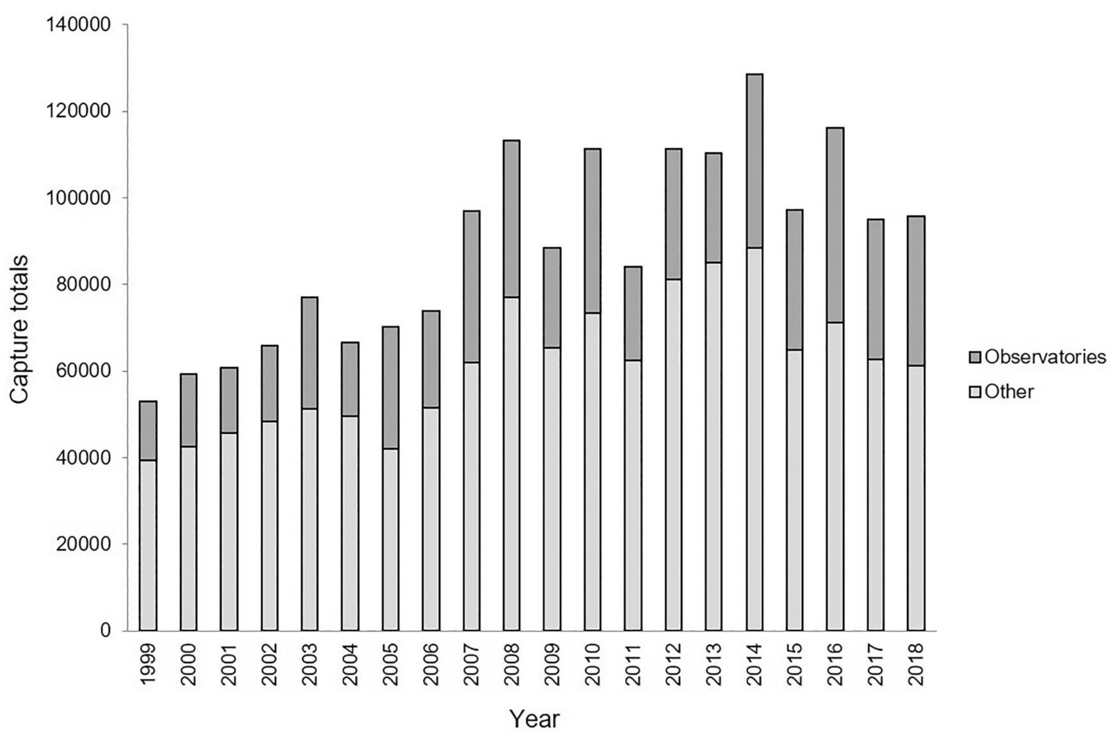

Figure 1. Time series of bird ringing totals in Denmark during the period 1999–2018. The columns show an aggregate of the ringing in observatories and ringing elsewhere ('other').

passerines versus non-passerines. Some of our secondary datasets varied in time series covered or the amount of data in certain years. This is because for some early years, especially 1999–2004, we do not have digitized records of the attributes and locality of individual birds. Supplementary Table S1 lists the size of each of the primary and secondary dataset.

For capture methods, we condensed the many types of data into the most distinct capture methods that have been used in Denmark. These are mist nets, clap nets, cannon nets and fleyg nets. Furthermore, any kind of mechanical trap was lumped in the category 'trap', and any capture method that involves direct contact between the ringer and the bird was lumped into capture 'by hand'. Appendix S1 gives more details on the categories. We ran an additional analysis focused on mist nets, comparing captures from the four national bird observatories (five since 2016) with captures in all other settings across the country. We repeated the same comparison but lumped all capture methods, other than mist-netting, with the caveat that 99% of the ringing at observatories is in fact by mist-netting.

Our analysis on bird age was restricted to the period 2005–2018, for which all ringing data have been computerized. For some species, it is difficult to assign an age or the age has been imprecisely recorded by the ringers, leaving a dataset of 1.26 million birds ringed (71% of our overall dataset). We separated age into three classes: nestlings (captured by hand), first calendar-year birds (first-year), and birds older than the first calendar year (adult). The primary comparison was between first-year and adult birds. We chose to categorize all second calendar-year birds as adults. Since we are mainly dealing with migratory birds, the assumption is that young birds already having undergone a migration to winter quarters and back are more similar to adult birds. The calculated mortality rates for age classes should be used only for relative comparisons among classes, because far from all birds in the mortality dataset were aged by the ringer, and thus mortality is certain to be underestimated.

The seasonality dataset was also based on the 2005–2018 period. We defined spring as March–May, summer as June–August, autumn as September–November and winter as December–February. Many species are not distinguishable by sex when in the hand, so we did not attempt to analyze differences between sexes. We expected no systematic bias in the data series for age, season or capture methods.

The Danish ringers also reported the presumed or known causes of each mortality since 1999. In the report form, the cause of death is condensed into categories including predators, being stuck in the nets/traps, the bird being in poor condition, or death from handling by the ringer. We have also tallied the species of predators as they have been reported by the ringers.

Finally, we looked at patterns of vulnerability at the species level, as well as among the broad groups of passerines and non-passerines. We tallied the mortality rate for each species, but, given our prior knowledge that nestlings and other birds caught by hand show near-zero mortality, we differentiated the mortality for each species according to the distinct capture methods. For this analysis, we only included data for more than 500 individuals caught by a particular method (54 species, 65 combinations of species/method). The analysis of passerine birds versus non-passerines was done for the whole 1999–2018 series. Most of the birds ringed in Denmark are passerines (1.4 out of 1.7 million birds). Because the study on American data (Spotswood *et al.* 2012) found larger birds in nets or traps were more prone to injuries, we made an additional analysis for *Turdus* thrushes alone. Similarly, because there was a significant difference between mortality rates in mist nets at bird observatories and among other ringing, we also performed secondary analyses separately for each on seasonality, age and on passerines/non-passerines.

All statistical analyses were performed in R version 4.1.2 (R Core Team 2021). Trends in ringing numbers were tested with simple linear regression, and trends in mortality rates were tested with logistic regression on the annual numbers of dead versus live birds in the period 1999–2018. Comparative analyses of capture methods, age, season and passerine birds were done with simple χ^2 tests on raw numbers of all dead and live birds within e.g. each capture method category. Binomial confidence intervals of mortality rates for individual species were calculated with the prop.test function in R (1-sample proportions test).

To investigate whether the proportion of birds reported dead at the bird observatories was affected by the number of birds captured, we applied both a simple quartile test as well as Poisson and negative binomial regressions (including a zero-inflated model) on deaths per capture in relation to birds captured. The quartiles were defined based on days with the fewest captures until days with the most captures, each quartile holding approximately 115,000 birds caught at the observatories. Differences among quartiles were tested with a χ^2 test. For Poisson, negative binomial and zero-inflated negative binomial regressions, we investigated the relationship with numbers caught by including both first- and second-order terms in the regression. Negative binomial models were fitted in R using the MASS package (Venables & Ripley 2002) and zero-inflated models using the pscl package (Vers 1.5.5.1; Jackman 2020). For models with the same parameters, the zero-inflated model had far better support ($\Delta AIC > 100$) and so we report only results of the zero-inflated models.

Results

The total of birds ringed in Denmark and the Faroe Islands in 1999–2018 was 1,776,038 (rounded to 1.8 million), across 307 species. The overall number of dead birds recorded during ringing operations in this period was 2812 across 88 species, corresponding to 0.16% of the ringed birds.

The annual number of birds ringed increased towards the later part of the study period (Figure 1). The majority of ringing throughout the time series (69%) was outside of the bird observatories. For the observatories, for other sites and for the total, the increase in ringing numbers was statistically significant (Table S2).

The yearly mortality rate was lower in the latter half of our time series (Figure 2), in particular, the mortality from non-observatory sites was markedly lower after around 2008. Logistic regression showed a highly significant decrease in mortality over the years in the total ringing series, the bird observatories and among other ringing (Table S2). Due to possible under-reporting of deaths in ringing outside of observatories in 2008–2016, we additionally tested the mortality trends when specifically excluding those years, for other ringing and totals. These two extra tests still showed a significant decrease in mortality over the reduced time series.

Capture methods

The mortality among the seven capture methods was significantly different ($\chi^2 = 764$, df = 5, $p < 0.001$). Since the 1960s, mist-netting was by far the most common capture method in Denmark and made up 71% of the total captures in our project period (Table 1). It was also the method that had the largest number of bird fatalities, with 94% of all cases being associated with

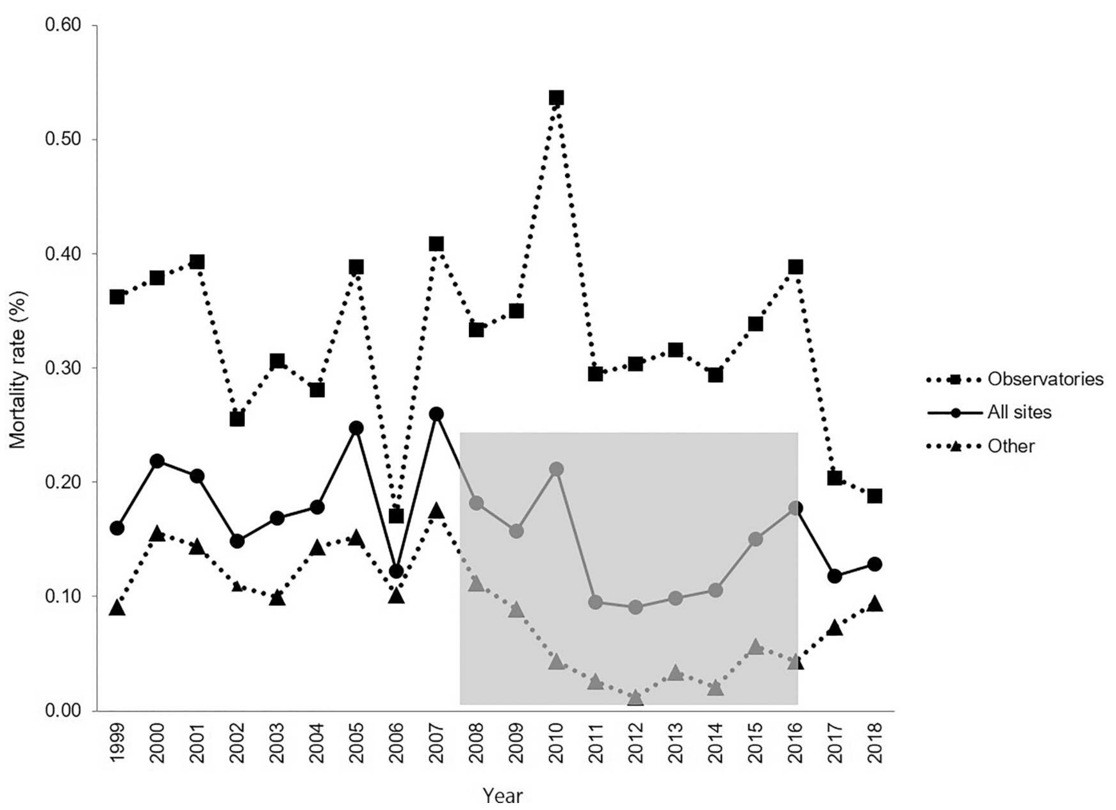

Figure 2. Time series of mortality rates in Denmark during the period 1999–2018. Mortality rates are the percentage of ringed birds that died in each year. Separate line graphs are shown for all sites, for the observatories alone, and for ringing outside observatories ('other'). The shaded area represents the years where reporting on deaths from 'other' ringing was not optimal.

Table 1. Comparison of mortality rates for each capture method in the period 1999–2018.

Method	Birds ringed	Deaths	Mortality rate
Mist-net	1,219,177	2,605	0.21%
By hand	341,734	40	0.01%
Traps	120,881	96	0.08%
Fleyg net	14,341	4	0.03%
Clap net	7,139	14	0.20%
Cannon net	2,338	13	0.56%

The methods are ordered by ringing totals for each. Mortality rates are the number of dead birds per number of birds ringed for the specific method. For further details see Appendix S1.

mist nets, resulting in a mortality rate of 0.21%. In contrast, the second-most frequent capture method, hand capture, had the lowest mortality rate with just 40 fatalities out of 340,000 birds (0.01%).

However, mist-netting was not the method with the highest mortality rate. The cannon net method, used in research projects on geese, had a very high mortality rate (0.56%), but this method is seldom used and represented only 0.1% of ringing totals in Denmark. The clap net had a high mortality ratio of 0.20%, but this is also a rarely used method, involving only 0.4% of all ringing. Both of these methods have become less used over time, having their most frequent use in the first five years of our survey period.

Within the capture 'by hand' category, more than 90% of the data were from the ringing of pulli in the nest. Given that such handling of pulli is known as widely unproblematic, we did a secondary calculation of mortality rates of 'by hand' captures separately for pulli and adults (possible only for the 2005–2018 period). This resulted in a mortality rate of 0.00% for the pulli and 0.04% for adults.

Overall, 31% of the mist-netted birds were from the national bird observatories, which ringed many thousands of birds during the migration seasons. These bird observatories accounted for 64% of all mortality in the study period 1999–2018. Figure 3 shows that the mortality rate in mist nets was much higher at the bird observatories (0.33%) than for mist nets at other sites (0.12%), where fewer birds were handled, and this was a significant difference ($\chi^2 = 637.6$, $df = 1$, $p < 0.001$). For methods other than mist-netting, the mortality rates for observatories and other sites were both low (0.07% and 0.04% respectively), but observatory data for those methods involved just 2875 birds ringed and two fatalities in total.

The mortality at bird observatories often occurred during specific events, typically when many birds were grounded on migration, in combination with adverse weather conditions. In our data, mortality events with more than five dead birds on one day were only reported from bird observatories, with a total of 45 such events. Those days with more than five dead birds constituted 17.4% of all mortality reported in Denmark and the Faroe Islands during 2004–2018. Figure 4 shows deaths on each day of mist-netting at the observatories in this period. For days with more

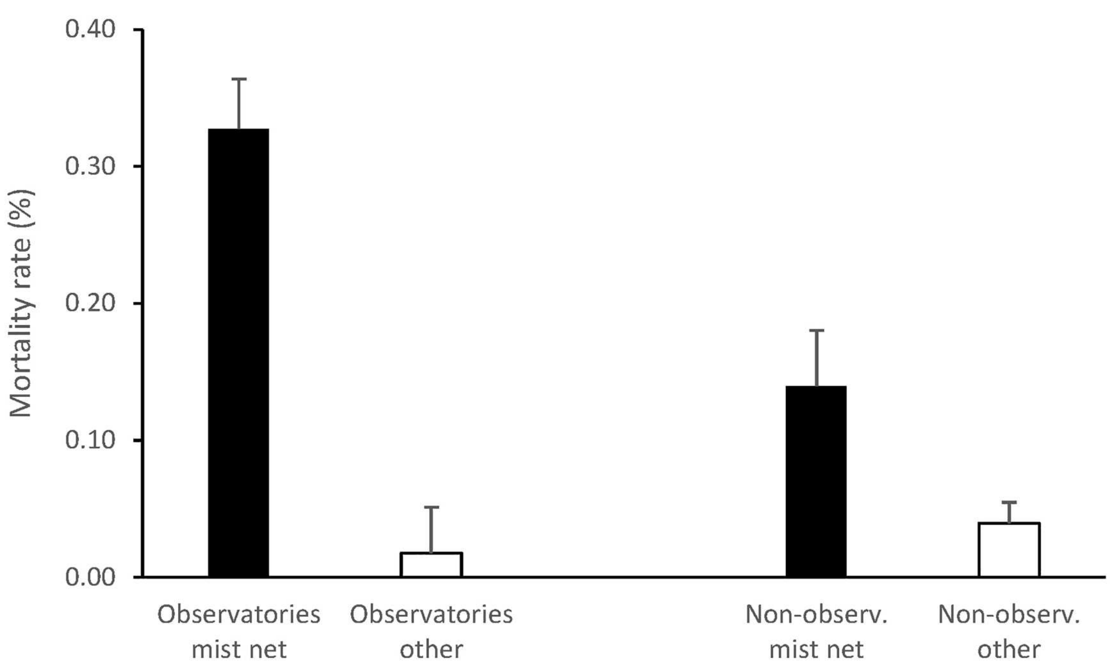

Figure 3. Average annual mortality rates at national bird observatories compared with mortality in all other sites throughout Denmark, in the period 1999–2018. The first two columns compile data from the observatories, the latter two columns compile data from all other sites. Black columns are mist-netting, white columns are all other methods. 95% confidence intervals are indicated.

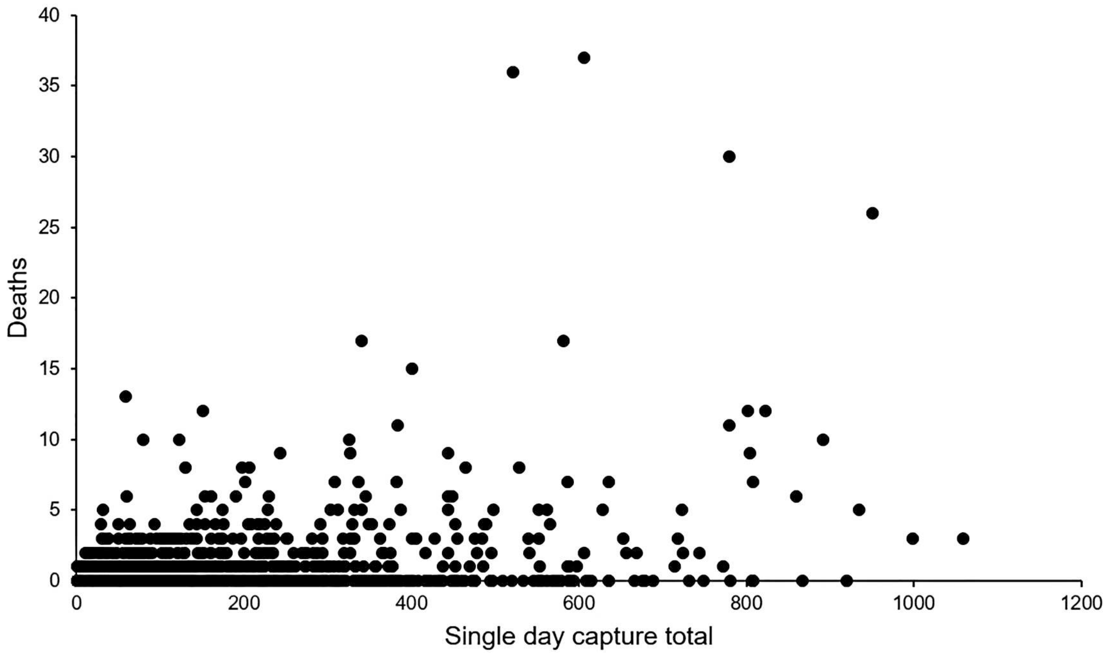

Figure 4. The number of recorded deaths on single days for all days with mist-netting at bird observatories 2004–2018. Number of days (*n*) is 8,292.

than 500 captures, we typically saw several deaths per day, and some days had more than 10 deaths. We found strong support for an increase in the proportion of deaths per capture with the numbers of birds caught (ΔAIC = 212 for a model with a second-order number caught term, compared to a first-order only). Similarly, the quartiles differed ($\chi^2 = 169.9$, df = 3, $p < 0.001$), with the lower quartile mortality rates of 0.23%, 0.24% and 0.28% respectively, and the quartile with the most captures per day having by far the highest mortality rate per capture of 0.49%.

Age and seasonality

We found virtually no mortality in the hand-captured pulli (Table S3). First-year birds had a slightly higher mortality rate than adult birds overall (0.11% and 0.08% respectively), which was significant when those two categories were tested directly ($\chi^2 = 27.03$, df = 1, $p < 0.001$). We repeated this test for observatories and other ringing, separately; in observatories, the first-year mortality was also higher (0.16% versus 0.08%; $\chi^2 = 42.02$, df = 1, $p < 0.001$), while in other ringing mortality was in fact higher for adults than first-years (0.08% and 0.06% respectively; $\chi^2 = 8.660$, df = 1, $p = 0.003$). As expected, all mortality rates were depressed because age, unfortunately, was not always recorded for dead birds (only 946 deaths in this dataset).

Regarding seasonality, most birds (38%) were ringed during autumn. There was significant variation among seasons in the overall data ($\chi^2 = 849.8$, df = 3, $p < 0.001$). The lowest mortality rates were in the summer and winter periods, while the autumn period had the highest rate (Table S4). Here, we also tested separately for observatories versus for other ringing. There was significant seasonal variation within observatories ($\chi^2 = 191.7$, df = 3, $p < 0.001$) as well as within other ringing ($\chi^2 = 125.1$, df = 3, $p < 0.001$), even though numbers for observatories in winter were quite small (4739 birds ringed and 10 deaths). For both observatories and other ringing, the highest mortality was in autumn. In all seasons the mortality was higher at the observatories (Table S4).

Passerines versus non-passerines

The mortality rate of passerines was 0.19%, whereas for non-passerines it was only 0.03% (Table S5), which was a significant difference ($\chi^2 = 445.3$, df = 1, $p < 0.001$). We further separated ringing at observatories from other ringing, and at the former, there was no difference between passerines and non-passerines ($\chi^2 = 1.86$, df = 1, $p = 0.17$), as the data held just five deaths among 3111 captures for non-passerines. For other ringing, away from observatories, the difference between passerines and non-passerines was significant ($\chi^2 = 224.4$, df = 1, $p < 0.001$), as deaths in non-passerines were virtually non-existent. For the 81,000 thrushes ringed, the mortality rate was 0.21%.

Predators and other causes of death

The dominant reported proximal cause of death was predators, which amounted to 55% of all cases of mortality (Figure 5). Entrapment (in the mechanism of the capture method) was the cause of 21% of fatalities. With 565 deaths, the Eurasian Sparrowhawk *Accipiter nisus* was the most important predator, mainly in mist nets (Figure 6). The Great Tit *Parus major* was recorded as responsible for many deaths, due to some events with mass captures, especially of tit species.

Vulnerable species

Eurasian Teals *Anas crecca*, Pink-footed Geese *Anser brachyrhynchus* and Eurasian Treecreepers *Certhia familiaris* had the highest mortality rates (Table 2), but only a moderate number of species showed mortality rates above the overall average of 0.16%. Our overall average rates were driven upwards by some of the species that are often caught in great numbers in mist nets while on migration, predominantly Goldcrest *Regulus regulus*, Eurasian Blue Tit *Cyanistes caeruleus*, Eurasian Wren *Troglodytes troglodytes* and European Robin *Erithacus rubecula*.

Discussion

We found an overall mortality rate of 0.16% for birds ringed in the national bird ringing programme for Denmark and the Faroe Islands. Most birds were caught in mist nets, with a mortality rate of 0.21%, and most deaths were caused by predation by Eurasian Sparrowhawks. Ringing of migrant passerines at bird observatories had the largest impact on mortality rates, and many reported deaths were of young birds on their first migration.

The overall mortality rate (0.16%) is similar to the 0.23% for 22 banding projects in the USA and Canada (Spotswood *et al.* 2012) and 0.11% from a recent analysis of British and Irish mist-net ringing (Clewley *et al.* 2018). The British and Irish data solely relate to recaptured birds, which are more likely to be local individuals, and possibly in better condition than transient birds that have just finished a leg of their migration route (Spotswood *et al.* 2012).

The overall Danish bird ringing dataset also contains recaptured birds. For the period 2004–2018, there are c.37,000 overall (24,000 in mist-nets). In these data, we found a mortality rate of 0.07%, and for mist nets, it was 0.10%, almost identical to the result from

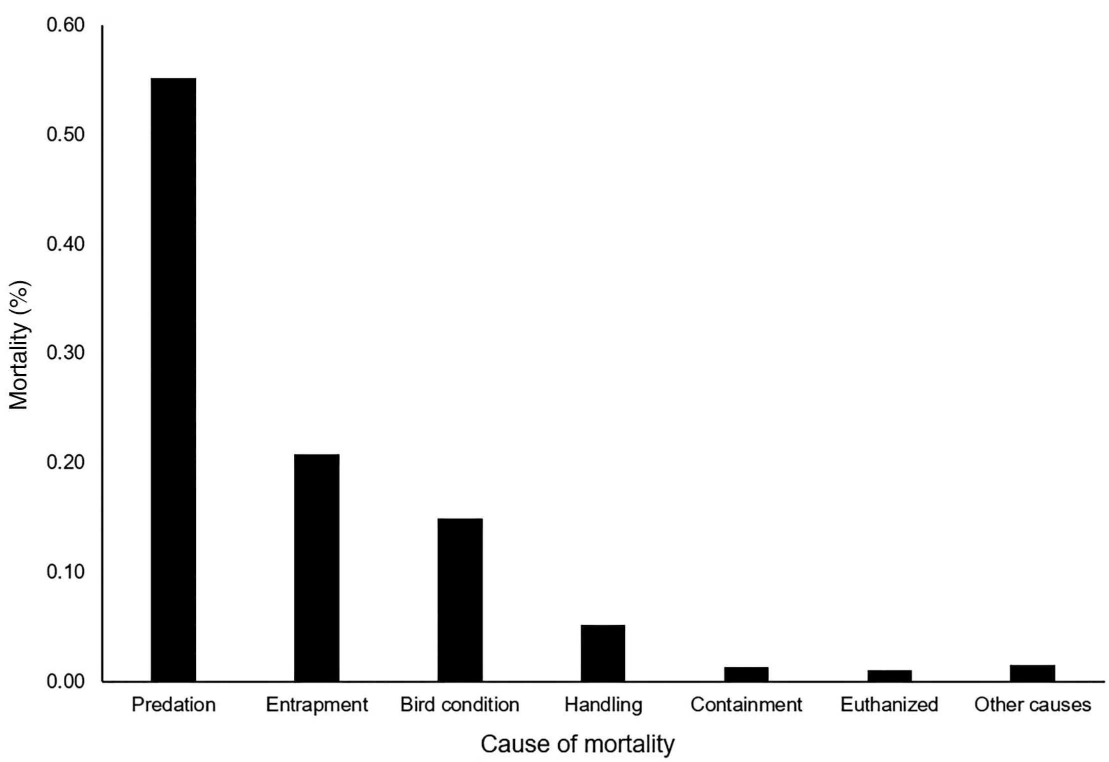

Figure 5. Causes of mortality observed for birds and recorded by the ringer. Entrapment relates to deaths from observable effects of being stuck in the net or other capture method (e.g. a trap). Handling refers to death at any time where the bird is held by the ringer. Containment refers to a bird that died while in a bag or a holding cage. Euthanized birds are those that were destroyed not because of injuries from nets or handling, but because they were observed to have debilitating illness such as bumblefoot. The *Y*-axis is proportion of all mortality for each in the period 1999–2018.

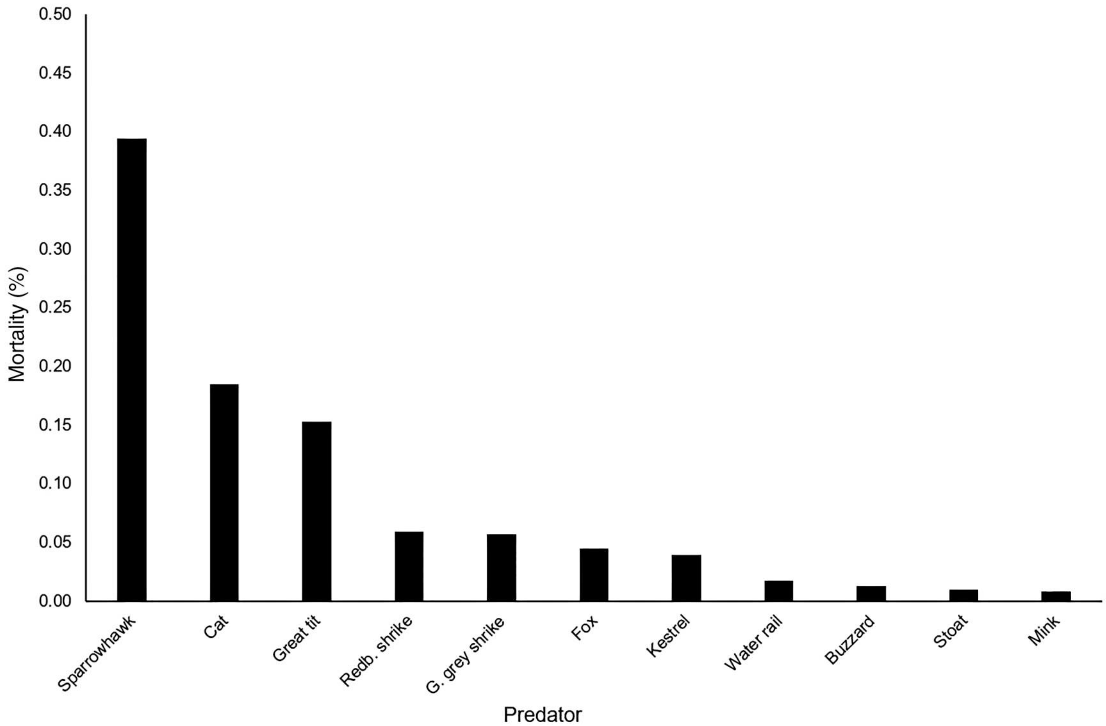

Figure 6. Ranked list of predator species that caused the most fatalities. Some birds were recorded as 'Shrike *Lanius* sp.', and these were divided equally between the two species displayed. The *Y*-axis is the proportion of mortality for each in the period 1999–2018.

Clewley *et al.* (2018), not considering minor differences in data collection. We also found a similar low mortality rate (0.12%) in birds captured in mist nets away from bird observatories, at other ringing sites throughout the country in scrubland, reedbeds or private gardens. Comparing this with the bird observatory mortality in mist nets (0.33%), we suggest that the mortality rate for birds on migration is more than twice as high as for local birds, mainly due to the difference in the condition of the birds.

Capture methods

The cannon net method had the highest mortality rate, but this is used in Denmark only for specific research projects on geese, and the actual number of fatalities was only 13 birds. Since the method involves firing out nets with great force over a large number of birds, there will be some risk of injury even when performed with great professionalism. The large majority of mortalities in Denmark were, however, among birds captured with mist-netting, especially at the bird observatories. In Denmark, these sites are associated with some of the greater European migration flyways, where tens of thousands of birds are handled each year in the spring or autumn seasons. Sometimes mass occurrences of birds happen with little notice, and if associated with sudden bad weather this can amplify the magnitude of these occurrences as well as the condition of the birds (Snell & Thorup 2019).

Captures by hand and capture of nestlings had the lowest mortality rates. However, some potential mortality associated with nestling capture, due to nestlings fleeing or otherwise disappearing or being predated, might be masked. Adult birds are rarely captured by hand, although some species, such as gulls and swans, have been captured this way.

Age and seasonality

While nestlings ringed in nestboxes or at breeding sites have little to no mortality recorded in connection with ringing activities, we found a higher mortality rate among our grouping of first-year birds. This is in accordance with the recent British and Irish study (Clewley *et al.* 2018). Younger birds are inexperienced, and this can result in, for example, their general condition being suboptimal compared to the more experienced adult birds. We speculate that the reason that sites other than observatories showed lower mortality in the first-year group could be a result of them being caught earlier in the summer, when they are in good condition, not far from where they hatched. Meanwhile, the observatories catch a large

Table 2. Mortality rates for individual species and capture methods.

Species	Method	Birds ringed	Deaths	Mortality (%)	Lower conf.	Upper conf.
Eurasian Teal *Anas crecca*	Traps	961	16	1.66	1.03	2.69
Pink-footed Goose *Anser brachyrhynchus*	Canon net	1,275	11	0.87	0.48	1.54
Eurasian Treecreeper *Certhia familiaris*	Mist-net	1,470	12	0.82	0.47	1.42
Goldcrest *Regulus regulus*	Mist-net	79,010	392	0.50	0.45	0.55
Fieldfare *Turdus pilaris*	Mist-net	1,089	5	0.46	0.20	1.07
Barnacle Goose *Branta leucopsis*	Canon net	506	2	0.40	0.11	1.43
Meadow Pipit *Anthus pratensis*	Mist-net	1,360	5	0.37	0.16	0.86
Spotted Flycatcher *Muscicapa striata*	Mist-net	3,144	11	0.35	0.20	0.63
Eurasian Blue Tit *Cyanistes caeruleus*	Mist-net	44,544	150	0.34	0.29	0.39
Eurasian Wren *Troglodytes troglodytes*	Mist-net	23,974	73	0.31	0.24	0.38
Eurasian Bullfinch *Pyrrhula pyrrhula*	Mist-net	11,175	30	0.27	0.19	0.38
European Robin *Erithacus rubecula*	Traps	827	2	0.24	0.07	0.87
Common Linnet *Linaria cannabina*	Mist-net	3,101	7	0.22	0.11	0.47
Tree Pipit *Anthus trivialis*	Mist-net	3,209	7	0.22	0.11	0.45
European Robin *Erithacus rubecula*	Mist-net	99,898	220	0.22	0.19	0.25
Song Thrush *Turdus philomelos*	Mist-net	16,735	36	0.22	0.16	0.30
Common Starling *Sturnus vulgaris*	Mist-net	3,286	7	0.21	0.10	0.44
Common Redpoll *Acanthis flammea*	Mist-net	28,842	60	0.21	0.16	0.27
Bearded Reedling *Panurus biarmicus*	Mist-net	4,219	8	0.19	0.10	0.37
Eurasian Siskin *Spinus spinus*	Traps	3,656	7	0.19	0.09	0.39
Common Redstart *Phoenicurus phoenicurus*	Mist-net	11,533	21	0.18	0.12	0.28
Eurasian Sparrowhawk *Accipiter nisus*	Mist-net	1,660	3	0.18	0.06	0.53
Common Chiffchaff *Phylloscopus collybita*	Mist-net	48,710	87	0.18	0.14	0.22
Dunnock *Prunella modularis*	Mist-net	33,531	56	0.17	0.13	0.22
Willow Warbler *Phylloscopus trochilus*	Mist-net	59,807	100	0.17	0.14	0.20
Lesser Whitethroat *Curruca curruca*	Mist-net	17,761	30	0.17	0.12	0.24
Red-backed Shrike *Lanius collurio*	Mist-net	1,220	2	0.16	0.04	0.60
Eurasian Tree Sparrow *Passer montanus*	Traps	2,618	4	0.15	0.06	0.39
European Greenfinch *Chloris chloris*	Mist-net	30,172	44	0.15	0.11	0.20
Common Whitethroat *Curruca communis*	Mist-net	24,210	36	0.15	0.11	0.21
Common Blackbird *Turdus merula*	Mist-net	36,428	56	0.15	0.12	0.20
Great Tit *Parus major*	Mist-net	48,421	66	0.14	0.11	0.17
Icterine Warbler *Hippolais icterina*	Mist-net	7,708	10	0.13	0.07	0.24
Eurasian Chaffinch *Fringilla coelebs*	Mist-net	27,872	36	0.13	0.09	0.18
European Pied Flycatcher *Ficedula hypoleuca*	Mist-net	6,744	8	0.12	0.06	0.23

Only species with the highest mortality rates are shown. The mortality % data are the mortality rates for the species only for the given method. This can be compared with the total number of birds ringed for that species using the same method. Only species with a ringing total of over 500 for the method are included.

proportion of first-year birds that have already crossed large distances during the autumn migration.

The same trend was mirrored in the results for seasonality. The summer period, when many nestlings are ringed, has the lowest mortality rate. In contrast, the autumn period has by far the highest rate. This is the period when most first-year birds have left the breeding grounds and are attempting their first migration, and many of them are caught at bird observatories.

Passerines

Our analysis of passerines versus non-passerines shows that the latter have remarkably low mortality rates from bird ringing in Denmark. This ties in with the capture methods used, as birds like gulls and swans are often caught by hand, and many ducks are caught using different kinds of traps or fleyg nets. Passerines are mainly caught in mist nets, and the mortality rate we found for them approaches the overall, higher rate found for mist nets. The separate analysis of *Turdus* thrushes did not show a higher mortality rate than for other passerines (0.21% compared to 0.19%), although the mortality of Fieldfares *Turdus pilaris* was high. We cannot confirm the notion that larger birds are more prone to incidents than smaller birds, but, as mentioned, for large non-passerines such as swans this result is conflated with the capture method.

Predators and other causes of death

It is difficult to disentangle what we may call 'proximal' causes of death (during capture and handling) from more 'distal' determinants, such as weather, which are not quantified. We did find that both the capturing action, as well as a bird's condition, were often reported as causes of death. Distinguishing proximal and distal elements would require multifactor modelling and collection of data hitherto not available (Clewley *et al.* 2018). We suggest that mortality report forms should include mandatory information on local weather conditions and changes in weather on the day, as these factors may then be included in future analyses.

When it comes to predator species, Eurasian Sparrowhawks can cause high mortality across sites and capture methodologies. Sparrowhawks that hunt at nets can be both local birds or themselves migrants that use a ringing site as a stopover source of food. We have anecdotal evidence of ringers having been able to capture and relocate some of the other predator species, e.g. cats and shrikes (*Lanius* spp.), and this intervention has had some success. In general, predators are unpredictable in their occurrence, and temporary closure of nets can be the only useful safeguard when several birds are taken.

Vulnerable species

When split into capture methods, the ringing totals for most species were only in the hundreds, and we excluded those with under 500 records. The outlier data point for the Eurasian Teal is from a specific avian flu project from around the year 2000, and the custom-built traps for that important project were since discarded. Both species of geese that were caught with cannon nets had high mortality rates, but mainly in studies particularly prudent to landscape management, such as researching the impact of grazing on agriculture. The Eurasian Treecreeper, at almost 1% mortality, is an unexpected result that is partially explained by eight of the 12 fatalities being the result of predation by Great Tits in a single migration event at a bird observatory. A couple of species confirming anecdotal reputations of not doing well in the nets are the Eurasian Bullfinch *Pyrrhula pyrrhula* and the Bearded Tit *Panurus biarmicus*.

Apart from these examples, there is a clear dominance of mortality among small species typically caught in large numbers in mist nets, in particular Goldcrests, Common Redpolls *Acanthis flammea* and Eurasian Blue Tits, but not for e.g. Great Tits and Eurasian Siskins *Spinus spinus*. In other words, it is not a given for all species that experience high numbers of captures to lead to increased rates of mortality, when compared with the day-to-day ringing numbers.

Implications

Being able to account for mortality is most useful for minimizing it during ringing operations. Therefore, we recommend that national ringing schemes develop robust methods of control for the reporting of incidences from all capture types and sites in their organization.

The method with the highest mortality in our study, the cannon-netting research method, had a mortality rate of 0.56%. It has been argued that any mortality rate under 1% is acceptable for scientific field studies (Spotswood *et al.* 2012). Relatively high losses are indeed often associated with scientific or management studies on target species. In our data, we saw the highest mortality rates in very few case studies, namely the impact studies of grazing by geese and avian influenza management, similar to rates in some pioneering scientific field studies (e.g. Recher *et al.* 1985, Brooks 2000). In contrast, we suggest that national background ringing, especially at bird observatories, must strive to achieve the lowest levels of mortality, given they often have years of refining the best daily practices, often with the same staff and at the same site.

Despite as much as a third of all migratory birds perishing every year (Dokter *et al.* 2018), it is essential that ringing programmes are perceived by society as minimizing losses of birds during their activities. We found that the days with the largest numbers of birds captured at bird observatories had more than twice the mortality rate than days with few birds, and a four-times higher mortality rate for mist-netting than at other sites. Often, such days are also associated with adverse weather, although we cannot quantify the exact effect with the data we have collected.

One obvious focus must, therefore, be on minimizing mortality at bird observatories at migratory hotspots, where days with large numbers of birds are stressful for the staff that must work at an increased tempo. If birds are left longer in the nets, they are also more prone to attacks by Eurasian Sparrowhawks, which can be migrating through the area on exactly the same days that have many passerines. Some specific measures can be employed to avoid high mortality events, including: (a) reducing the number of nets kept open under weather conditions that are known to cause mass events or increased mortality rates (certain wind directions, fog or rain showers), (b) increased frequency of tending the nets when such events can be expected, (c) closure of nets, and immediate release of birds without ringing them, in the face of severe weather events or an extreme number of birds. These are measures that ringers often apply on their own initiative, but it could be advantageous for any ringing scheme to formally implement such guidelines.

Another focus should be minimizing predation, which we have found to be the highest individual cause of death for captured birds, confirming other studies that have shown that predation is among the most important threats (Clewley *et al.* 2018, de Moura *et al.* 2023). The latter study suggests the shelf height of mist nets is important, suggesting that nets should be lifted higher away from the ground vegetation. The exact predator will, however, vary between countries;

in Denmark, it is the Eurasian Sparrowhawk, for which lifting of nets would have no effect. The height at which predation events occur could, however, be added to reports of fatalities, to increase knowledge of this particular aspect.

Even under current capture practices, the three national ringing datasets analyzed to date have all found mortality rates that are well below the historic rule-of-thumb for scientific studies (i.e. 1%). We have shown that some of our systematic and permanent ringing activities have reported losses closer to 0.1% of total captures, rather than the 1% rule-of-thumb. Higher ethical standards are expected in research projects today, compared with earlier decades, but with the additional cautionary measures mentioned here, combined with strict reporting of incidents and circumstances, bird ringing remains a commendable method for increasing our knowledge of birds.

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