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ORIGINAL ARTICLE

Body size constrains the annual apparent survival of lekking Great Snipe *Gallinago media* males of eastern, lowland population

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Abstract

Survival of adult individuals is a key demographic parameter, that is critical for conservation programs of species and evolutionary research focused on life-history traits. Here, we present the estimates of the apparent annual survival of lekking male Great Snipes of the lowland population, breeding in wet meadow habitats in the valley of the Pripyat River. We also investigate individual traits such as body size and body condition, that may influence birds' survival. The annual apparent survival in the studied population was low (Φ (.) = 0.43), but no change in this parameter was found over the period of 22 years. The chances for survival increased with the body size of an individual. We hypothesize that smaller individuals with shorter bills might face limited foraging options compared to larger birds, which may result in insufficient nutrition during challenging life cycle events such as moulting of primaries combined with preparation for long-distance migration conducted in one non-stop flight. Additionally, the presented results indicate that the wet meadow in the Pripyat River Valley provides suitable breeding habitat for this species with sufficient conservation practices held there, and the low annual apparent survival is probably a life-history trait of this species resulting from a "high pace of life" and elevated metabolic rate. To our knowledge, this study provides the first estimates of the long-term population characteristic for the eastern, lowland population of this species, which could prove helpful in the assessment of population viability for this globally declining species.

Keywords Body size · Body condition · Floodplain meadow · MARK · Pripyat river

Zusammenfassung

In östlichen Tieflandpopulationen beeinflusst die Körpergröße die jährliche Überlebensrate areana-balzender Doppelschnepfen (*Gallinago media*)

Das Überleben adulter Tiere ist ein wichtiger demografischer Parameter, der für Artenschutzprogramme und für die Evolutionsforschung speziell zu Eigenschaften über die gesamte Lebenszeit hinweg von entscheidender Bedeutung ist. Wir berichten hier über festgestellte jährliche Überlebensraten arena-balzender männlicher Doppelschnepfen in Tieflandpopulation, die in feuchten Wiesenbiotopen im Tal des Prypjat (Belarus) brüten. Wir schauten auch auf individuelle Merkmale wie Körpergröße und allgemeiner Körperzustand, die beide einen Einfluss auf das Überleben der Vögel haben könnten. Die jährliche, feststellbare Überlebensrate in der untersuchten Population war niedrig (Φ (.) = 0.43), wobei über den Zeitraum von 22 Jahren hinweg keine Veränderung dieses Parameters festgestellt wurde. Die Überlebenschancen stiegen

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mit der Körpergröße eines Individuums. Wir stellen die Hypothese auf, dass kleinere Tiere mit kürzeren Schnäbeln im Vergleich zu größeren Vögeln begrenztere Möglichkeiten zur Nahrungssuche und –aufnahme haben, was eventuell zu einer Mangelernährung während besonders anstrengender Abschnitte in ihrem Leben führt, wie z. B. der Mauser der Jungvögel in Kombination mit den Vorbereitungen für den Langstreckenzug, der in einem einzigen Non-Stop-Flug absolviert wird. Die hier vorgestellten Ergebnisse deuten außerdem darauf hin, dass, mit ausreichenden Schutzmaßnahmen, die Feuchtwiesen in den Niederungen des Prypjat den Doppelschnepfen ein geeignetes Brutgebiet bieten und dass die festgestellte geringe jährliche Überlebensrate wahrscheinlich ein Life History-Kennzeichen dieser Art als Resultat eines „hohen Lebenstempos “ und einer erhöhten Stoffwechselrate ist. Soweit wir wissen, liefert diese Studie für die östliche Tieflandpopulation der Doppelschnepfen eine erste Langfrist-Einschätzung eines Populationsmerkmals; dies könnte sich für die Bewertung der Populations-Lebensfähigkeit dieser weltweit rückläufigen Art als hilfreich erweisen.

Introduction

Demographic characteristics are essential estimates for monitoring the dynamics of animal populations, creating effective conservation programs, as well as evaluating their outcomes (Lebreton et al. 1992; Zöckler et al. 2010). They can provide useful information not only for one species but also for whole ecosystems as indicators of their state (Péron et al. 2013). Among such characteristics, the survival of adults and their fecundity are listed as highly important ones, as the population's persistence results in a dynamic balance between losses of individuals by mortality and recruitment of new individuals by reproduction (Sandercock 2003). Although most conservation programs focus on increasing the size of a population by improving its reproductive success (i.e., van Heezik et al. 2009; Collins et al. 2016), the survival of breeding adults is a key demographic parameter determining the growth rate of the population, especially in long-living species of animals (Sæther and Bakke 2000; Sandercock 2003). In waders, such estimates may be relevant to species conservation, as many recent studies show concerning population declines (Zöckler et al. 2010; Pearce-Higgins et al. 2017; Plard et al. 2020). Whereas the number of studies providing demographic characteristics for this group has grown considerably, still ~ 75% of wader species lack such estimates (Sandercock 2003; Méndez et al. 2018).

The Great Snipe Gallinago media is a long-distance migratory wader known for its lekking behaviour (Cramp and Simmons 1983; Lindström et al. 2016). In this species, there are two genetically distinct populations (Ekblom et al. 2007), where the majority of individuals of the global population account for the lowland eastern population, which occupies grassland habitats of north-eastern Europe as breeding grounds (Kålås 2004). Despite the considerably higher number of individuals and larger inhabited breeding area of this population compared to the Scandinavian one, the latter is a better studied one, with annual, perennial counts of lekking males conducted (Kölzsch et al. 2007). Yet, the estimates of adult survival or productivity were made in neither of those populations. The need for such characteristics is considerable, as the Great Snipe suffers a loss in numbers of the global population (Birdlife International 2022) which is most probably caused by the degradation of nesting habitats due to climate change, agriculture, and aquaculture practices that distress vulnerable ecosystem of wet meadows, marshes, and other grasslands habitats (Shydlovskyy et al. 2023). Currently, this species is considered as near threatened (NT category) by IUCN Red List, and many countries are undertaking conservation actions for their breeding population (Kålås 2004, IUCN 2022).

Lekking is a relatively rare mating strategy, where males gather to engage in intensive competitive displays and courtship rituals to gain a partner (Höglund and Alatalo 1995; Fiske et al. 1998). Such behaviour generates high energetic costs for breeding males, linked to the development of secondary sexual traits and/or display, as males do not participate in parental care (Yang et al. 2013; Jiguet and Bretagnolle 2014). Females of lekking species visit leks for copulation limited to a few, most attractive males at the site. They acquire only the gametes from mates, because males do not hold any resources useful for incubation or chick-rearing (Höglund and Alatalo 1995). Leks are characterized by stability in space and time on a populational level. For a single individual, such stability means strong site fidelity for a particular lek (Höglund and Alatalo 1995; Gibson et al. 2014). This high site fidelity makes lekking males a great example to study the annual survival on breeding grounds with mark-capture recapture methods and apparent survival models (Sandercock 2003) and also provide information on the life history of species in evolutionary research (Székely et al. 2014). Here, we used 22 years of capture-recapture data to obtain estimates of the apparent annual survival for lekking males of Great Snipe and determine whether individual traits such as body size and body condition on the breeding site may influence this parameter, as some evidence points to their importance in this matter (Brown and Brown 1998; Verhulst et al. 2004; Van Buskirk et al. 2010).

Methods

Fieldwork

Data collection took place on a single lek of Great Snipe located in the floodplain meadow in the valley of Pripyat River near Turov, Gomel Region, Belarus (52° 05′ N, 27° 46′ E). Trapping was conducted in Great Snipe's breeding season (April–June) (Cramp and Simmons 1983) for 22 consecutive seasons since the year 2000. We captured birds using mist-nets in the night during the time of lekking. The single capturing event did not last longer than 4 h and such events were separated with a minimum 5-day break in between, to minimize the disturbance of courting birds. Each year the procedure included the ringing of unmarked birds with uniquely numbered steel leg bands provided by the Belarus Bird Ringing Centre as well as noting down recaptured birds that had been ringed in previous seasons. This enabled us to create the history of reencounters for each individual, which was later used in survival analysis. At every capture of a given individual, we measured the total head length (measured with callipers to the nearest 0.1 mm), wing length, tarsus plus toe length (all measured with a ruler to the nearest 1 mm), and weight (measured with an electronic balance to the nearest 0.1 g), according to standard procedure (Busse and Meissner 2015). We did not distinguish between adults and second-year birds, as there is no certain method to differentiate between those two age categories (Sæther et al. 1994). Although second-year individuals may be taking part in courtship display, their lek attendance is probably low, similar to other lekking species (Alonso et al. 2010; Vernasco et al. 2021), which makes the chances of capturing them relatively small. After the release, birds were sexed based on bill measurements according to Höglund et al. (1990). As we caught only a few females at the lek, further we report on data from males only.

Statistical analysis

Body size and condition

For each individual, we established body size using the First Principal Component (PC1) of the Principle Component Analysis (PCA) on log-transformed data of total head length, tarsus plus toe length, and wing length. The PC1 values explained 60.3% of the variance of the body measurements data. Although the biometrics in waders may change over time (van de Pol and Wright 2009), we did not account for the variability of the body size of individuals, and we used the PC1 value calculated based on body measurements taken from the first time the bird was captured.

We estimated the body condition of each individual using the scaled mass index (SMI; Peig and Green 2009), which is a measure of gathered energetic stores corrected for the structural size of an individual. To obtain this parameter from studied male Great Snipes, we used the following equation:

$$\mathrm{SMI} = W* \left(\frac{93.78}{\mathrm{THL}}\right)^{3.197},$$

where W is the weight of an individual, THL is the total head length of an individual, the value of 93.78 is the mean total head length for the studied population, and the value of 3.197 is the slope derived from OLS regression line demonstrating the relationship between the ln-transformed weight and ln-transformed total head length. As body condition in birds can vary between seasons (Piersma et al. 2003; Campo-Celada et al. 2022) and in lekking Great Snipe males, it depends on environmental conditions likely changing between years (Witkowska et al. 2022), this parameter was calculated for every single encounter of an individual and used as a time-dependent factor in our survival analysis.

Survival analysis

To assess the apparent annual survival of adult males of Great Snipe we used Cormack-Jolly-Saber models (CJS) calculated in the MARK program (White and Burnham 1999). Such models provide an estimation of two parameters: the apparent survival (Φ), which reflects the probability that an individual survives from year_i to the year_{i+1}, and the probability of reencounter (p), which reflects the chance that a given individual is present in the population in the year_i and will be encountered (e.g. by recapture or resighting) in the same year_i.

Our basic, starting model included constant Φ and constant p values (Φ(.), p(.)), which we subsequently expanded by testing models assuming constant or time-dependent Φ and p values and the individuals' covariates such as body size and body condition. As there is no goodness of fit analysis suitable for the survival models incorporating individual covariates (Cooch and White 2019), we established our basic, starting model as a global model for further analysis. We used two approaches available in MARK for assessing the goodness of fit of our global model and obtaining the variance inflation factor ($\hat{c}$): (1) the median $\hat{c}$ procedure with 1000 run simulations and (2) the parametric bootstrap goodness of fit test with 1000 run simulations, which calculated $\hat{c}$ as observed $\hat{c}$ divided by the mean $\hat{c}$ from simulations. Both approaches indicated slight overdispersion of the global model fitting the survival data (median $\hat{c}$ procedure:

Table 1 Ranking of Cormack–Jolly–Saber models for estimates of annual apparent survival of lekking adult males of Great Snipe

No	Model	*k*	$QAIC_c$	Δ $QAIC_c$	w_i	Dev.
1	Φ (.), *p* (t)	22	646.67	0.00	0.48	597.78
2	Φ (size), *p* (t)	23	647.52	0.85	0.31	596.38
3	Φ (*t* × (size + SMI)), *p* (.)	64	649.17	2.50	0.14	494.01
4	Φ (.), *p* (.)	2	651.24	4.57	0.05	647.21
5	Φ (*t*), *p* (.)	22	653.01	6.33	0.02	604.12
6	Φ (*t*), *p* (*t*)	42	675.47	28.79	< 0.01	584.03
7	Φ (size + SMI), *p* (*t*)	25	686.90	40.22	< 0.01	468.13
8	Φ (SMI), *p* (.)	3	649.89	48.50	< 0.01	598.75
9	Φ (SMI), *p* (t)	23	650.51	54.41	< 0.01	551.57

All models were corrected for overdispersion by variance inflation factor: $\hat{c} = 1.89$. Models' factors included: Φ apparent survival, *p* the probability of reencounter, (.) constant parameter, (*t*) time-dependent parameter, (*size*) individual's body size described by PC1 value; (*SMI*) individual's body condition obtained on breeding grounds described by scaled mass index, × interaction between factors in a factorial model. Models' statistics included: *k* number of parameters, $QAIC_c$ quasi-Akaike's information criterion, Δ $QAIC_c$ the difference in $QAIC_c$ between the given model and the model with the lowest $QAIC_c$ value, w_i quasi-Akaike weight, *Dev* deviance

$\hat{c} = 1.094$; parametric bootstrap procedure: $\hat{c} = 1.89$). They indicated that the global model is a good starting point as none of the $\hat{c}$ values were higher than 3 and the small overdispersion is common in apparent survival studies (Miller et al. 2003; Sandercock et al. 2005). We corrected for overdispersion using the $\hat{c}$ estimated by the parametric bootstrap procedure, as this value was higher compared to the one obtained by the median $\hat{c}$ procedure, and we decided to assume bigger overdispersion in the apparent survival model fitting as Cooch and White (2019) advised. Model selection was made based on the quasi-Akaike's information criterion ($QAIC_c$), which corrects for overdispersion and small sample size, and the quasi-Akaike weights (w_i) (Burnham and Anderson 2004). We used relative variable importance (RVI) to assess the effect of studied variables on apparent survival.

We used a Generalized Linear Model (GLM) (McCullagh and Nelder 1989) with a log link function and normal error distribution to establish the trend of annual variation of both apparent survival (Φ) and probability of reencounter (*p*) in the studied period. Moreover, a GLM was used to determine the reliance of reencounter probability on the number of capture events, representing capture effort in a given season.

Results

In each season, we were able to capture from 1 to 33 adult males of Great Snipe, with a total sample size of 314 birds ringed in the studied period. Of those birds, 73 (about 23%) were recaptured, with 50 individuals captured only once more in the following seasons, 18 individuals recaptured twice in the following seasons, 2 individuals recaptured 3 and 4 times in the following seasons, and 1 individual recaptured 6 times in following seasons.

The average life expectancy of an adult Great Snipe male was established as 3 calendar years. With an additional one year when birds are immatures, this gives an average life expectancy of 4 calendar years since the hatching of an individual. The maximal life expectancy of an adult was established at 7 calendar years, which means a minimum of 8 years from the hatching of an individual. Such life expectancy was distinctive for two individuals in the studied population.

The best fitting models of the apparent survival of Great Snipe males were the one with constant survival (model number 1; Table 1) and the one including the effect of the size of an individual on apparent survival (model number 2; Table 1). Although the prior model had a higher value of quasi-Akaike's weight, it was equally parsimonious to the second-mentioned model, as the difference in the QAICc value between those two models was smaller than 2 (Burnham and Anderson 2004). Moreover, the obtained values of w_i for both models were close to each other, indicating relatively high model selection uncertainty. Therefore, hereafter, we describe results estimated with both models.

The probability of reencounter of an individual was well described by both best-fitting models incorporating it as a time-depending factor (Table 1). Overall, the values of this parameter changed annually and ranged from 0.11 to 0.68, with a mean value of 0.34 (Fig. 1). The probability of reencounter was related to the number of capture events (GLM, $F_{1.19} = 12.65$, $P = 0.002$) (Fig. 2), and it did not change over the years (GLM, $F_{1.19} = 0.09$, $P = 0.49$) (Fig. 1). The preliminary analysis showed that incorporating the number of capture events in a given season, representing annual capture effort, as a factor determining the probability of reencounter in the survival models did not improve its fit to the encounter history data (GOF test for the global model incorporating

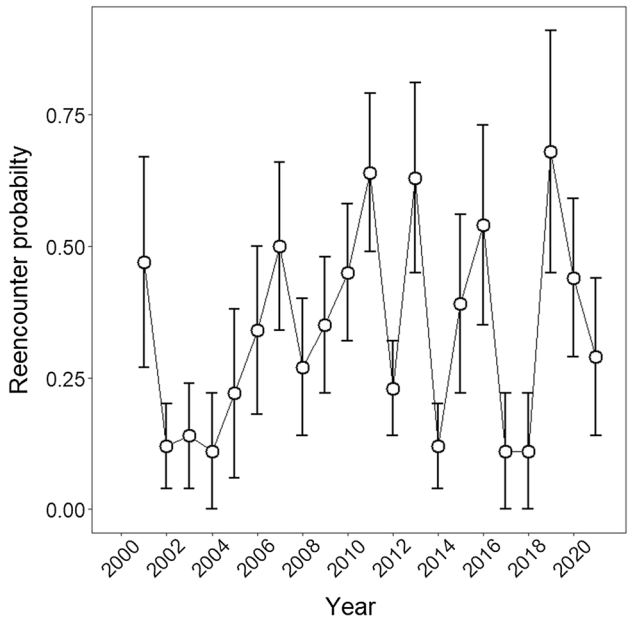

Fig. 1 Annual variation in reencounter probability of adult male Great Snipes. Estimates are made based on the best supported time-dependent model. White dot—mean reencounter probability in a given year (*p*), bars—standard error, black line—a link between subsequent seasons

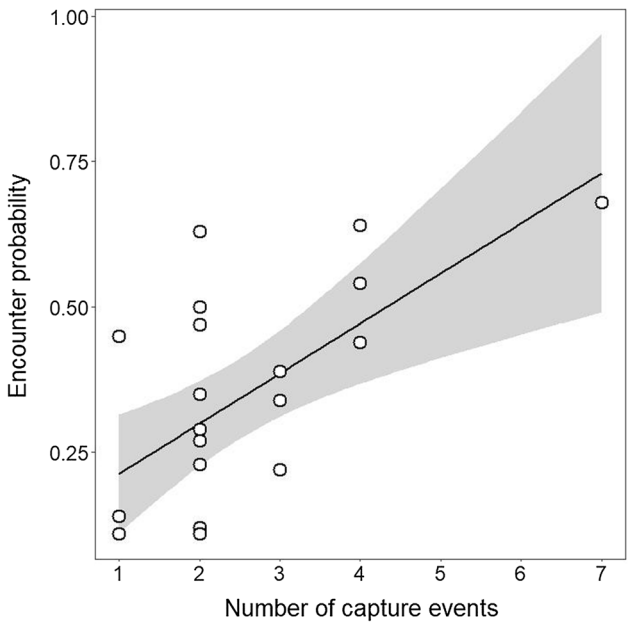

Fig. 2 Relationship between a number of capture events in given season and probability of reencounter. The 95% confidence interval is given

capture effort influencing the probability of reencounter $\chi^2 = 11.5$, $P = 0.66$, compared to the global model with

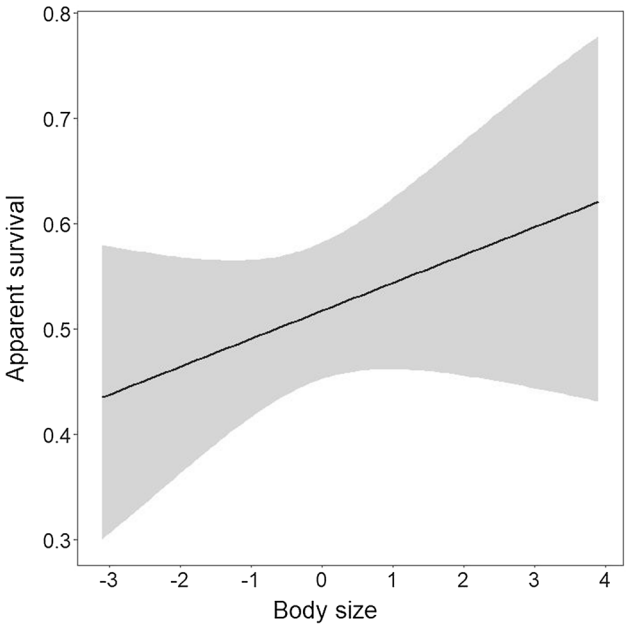

Fig. 3 Relationship between mean apparent survival estimated by the second-highest ranked model and the body size of an individual established as a PC1 value from linear body measurements. The 95% confidence interval is given

constant probability reencounter $\chi^2 = 13.5$, $P = 0.78$). Hence, we use a simple time-dependent model instead.

Among both studied individual covariates, the body size described by the PC1 value could be considered to significantly alter the apparent survival of an individual (Table 1), with the RVI = 0.45. The apparent survival increased with the bird's body size (Fig. 3). The individual's body condition on the breeding grounds could only be used to model the apparent annual survival when interacting with time, together with the size of an individual (model number 3; Table 1). Such model had rather low support. However, based on quasi-Akaike's weight, had above 10% of support in the set of proposed models, and the RVI of body condition was 0.14.

Apparent survival estimated with the highest-ranking time-dependent model (model nr 3; Table 1) fluctuated considerably between seasons and ranged from 0.13 to 0.80 in the following years, with a mean value of 0.43 (Fig. 4). The RVI of the time as a variable was estimated to be equal to 0.16. Over the 22 years of data gathering, we did not observe a trend in apparent survival of adult male Great Snipes (GLM, $F_{1.19} = 0.06$, $P = 0.79$).

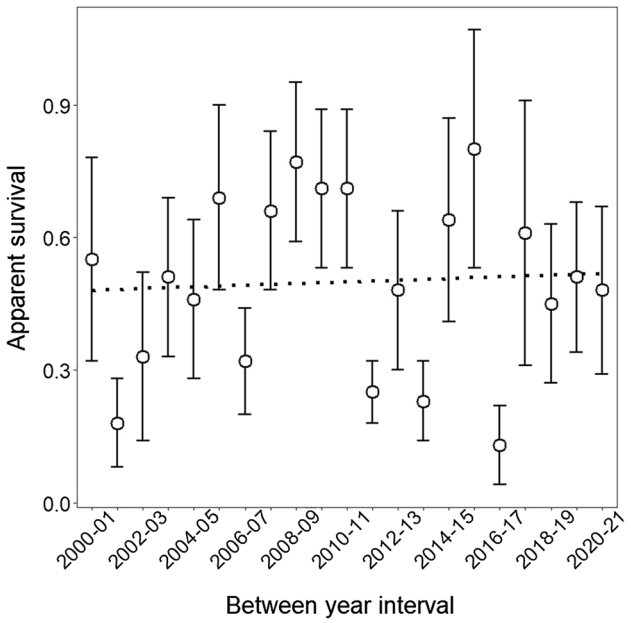

Fig. 4 Annual variation in apparent survival of adult male Great Snipes. Estimates are made based on the best supported time-dependent model. White dot—mean annual apparent survival (Φ) in a given time interval, bars—standard error, dotted line—a stable trend of apparent survival changes in the time estimated with the Generalized Linear Model (GLM, $p > 0.05$)

Discussion

The survival of males may be influenced by individual traits as well as seasonally changing environmental factors (Grisham and Boal 2015; Ryder and Sillett 2016). Therefore, for species conservation, the demographic characteristics of males alone, especially in polygenic species such as lekking birds, might not be as important as those of females. Nonetheless, they still could be useful in creating such conservation programs for species as some threats are similar for both sexes (Hovick et al. 2014; Lawrence et al. 2021).

The apparent annual survival of adult males of Great Snipe was low compared to other wader species of similar size, such as e.g. Common Snipe *Gallinago gallinago* with apparent survival values estimated at 0.76, and Red Knot *Calidris canutus* where different studies showed apparent survival values ranging from 0.56 to even 0.99 (Boyd 1962; Méndez et al. 2018). Great Snipe males excel in the energetic costs of different aspects of the annual life cycle, with lekking and long-distance, non-stop migratory flight being immensely demanding (Höglund et al. 1992; Lindström et al. 2016, 2021). Due to such life-history traits, this species might be considered to exhibit a 'fast pace of life', with a high metabolic rate needed to perform at all annual life cycle stages (Jetz et al. 2008). According to the rate-of-living theory (Pearl 1928) animals with elevated metabolic rates characterized by lower survival and, therefore, decreased longevity with some evidence for that proposed in other studies (Scholer et al. 2019; Vágási et al. 2019, but see: Stark et al. 2020). Although many wader species are long-distant migrants, the lekking behaviours is a rare in this group of birds (Cramp and Simmons 1983), and its additional cost might explain the lower survival of Great Snipe compared to other wader species.

As models calculating the apparent survival do not differentiate between mortality and permanent emigration from the studied site, the result obtained in this study may be understated, due to the relocation of males between the leks during the breeding season. For example, emigration from the breeding site resulting from unsuccessful breeding performance in the preceding season was previously proved to cause an underestimation of apparent survival in Spotted Sandpiper *Actitis macularia* (Reed and Oring 1993). However, the data from logger transmitters used on 13 male Great Snipes in the studied population showed no such movements within one season, and based on ring recoveries only 13 individuals among 314 ringed in 22 years had changed the lek between seasons (author's personal observation). Moreover, other lekking bird species are characterized by high fidelity to their lekking site (Gibson et al. 2014; Borecha et al. 2017). On the other hand, motivation to revisit the lek in Great Snipe males from the Scandinavian population depended on their copulation success, with unsuccessful males tending to relocate (Höglund and Robertson 1990), and recent studies on Great Snipe males in Poland show that movements between leks in some seasons are relatively frequent (Korniluk and Chylarecki 2023). Therefore, we think the real survival may be somewhat higher than estimates provided in this study. Nonetheless, such estimates are still valuable indicators of this parameter and can still be used to establish population demography dynamics and factors influencing them (Méndez et al. 2018). In the case of Great Snipe males, the established low values of apparent annual survival are probably a characteristic of this species. For instance, based on ring recoveries from the Scandinavian population, out of 90 marked males, only 30% were re-encounter again within 5 years of the study (Höglund and Robertson 1990).

The apparent annual survival fluctuated considerably during the study period, but the long-term trend of this parameter was stable. This fact is consistent with the results of annual, perennial counts of lekking males conducted in Central Norway, where between-year changes in population size, with a stable overall trend, were detected (Kölzsch et al. 2007), as the population size is strictly relying on the survival of adult individuals belonging to it (Sæther and Bakke 2000; Sandercock 2003). Such fluctuations might be caused by several stochastic environmental factors resulting from all stages of the annual cycle. For instance, as Great

Snipe is a food specialist feeding mainly on earthworms (Løfaldli et al. 1992), they choose a specific type of habitat to exploit their prey resources (Korniluk et al. 2020), the availability of which can be influenced by the changes of the hydrological conditions of the area (Witkowska et al. 2022). Furthermore, prolonged drought lowers the accessibility of the earthworms, which can contribute to reducing the body condition of an individual and its general fitness in other aspects of an annual cycle (Onrust et al. 2019). The predator pressure, which can vary between years due to seasonal changes in the available prey, was negatively related to the number of lekking males in the Scandinavian population of the Great Snipe (Kölzsch et al. 2007). Predators mostly influence the abundance of chicks, however, the elevated predation pressure might also affect the adult birds, especially lekking males that behave conspicuously while displaying. The lack of the decreasing tendency of the apparent annual survival in the studied 22 years lets us assume that the breeding population of Great Snipe, as well as the ecosystem of the floodplain meadows in the Pripyat Rivel Valley, are in a good overall state. Moreover, the preservation practices held there to ensure their welfare, such as maintaining the grassland habitat by reducing the overgrowing bushes and dry grass, or creating protective zones around leks, seem adequate.

In many bird species, the trade-off between survival and investment in the breeding of adults results in sex-biased mortality due to different costs of reproduction borne by males and females (Liker and Székely 2005). One of the hypotheses proposed to explain such bias states that the sex with elevated competition for a mate can suffer greater mortality due to the high cost of such behaviour and its conspicuousness resulting in an increased risk of being lost to predation. Males of lekking bird species are usually associated with extensive development of secondary sexual traits such as feather ornaments and/or body size compared to females. Contrary to other lekking birds, the Great Snipe is characterized by little pronounced sexual dimorphism both in size and the high intensity of lekking display is proved to improve the males' chances for copulation (Höglund and Lundberg 1987). Although the individual's body size was not a direct correlate of male mating success in the studied species (Höglund and Lundberg 1987), in our study, smaller males suffered reduced apparent survival. The body size may create constraints on other biological aspects of an annual cycle of male Great Snipes, for example, bigger individuals with longer bills might be able to access deeper buried prey, by that, extend their foraging niche compared to smaller birds as it was found in other wader species (Alves et al. 2013; Duijns et al. 2015). This fact might be crucial to survival in critical stages of the annual cycle that require elevated energetic resources, e.g., after the breeding season when Great Snipe moult their primary feathers and simultaneously gather fat stores before long-distance autumn migration (Cramp and Simmons 1983, authors' personal observation). It is worth mentioning that, including the size of the individual in used model gave a good fit to the data, however, the relative importance of this variable of rather at a medium level, with quite large confidence interval established for its relation with the apparent survival. Therefore, we would like to point out that this is result indicates a general tendency, to which in this study, we provided ecological explanations, rather than a rule for the studied species.

According to obtained results, the body condition of individuals had no significant impact on the survival of adult males of Great Snipe. This parameter was highly variable with a considerable decrease within a single night of lekking as well as a whole breeding season. Additionally, it changes in response to stochastic environmental conditions (Höglund et al. 1992; Witkowska et al. 2022). Hence, a single measurement of this parameter in a given moment might not reflect the overall quality of a bird, and body condition in the breeding period might not predict chances for further survival, but rather the temporary state of the lekking male (Andersson 1994; Lebigre et al. 2013). Furthermore, a rich ecosystem, such as the wet meadows of the Pripyat River Valley (Pinchuk and Karlionova 2011; Witkowska et al. 2022), might not create a highly demanding environment for birds and result in a more uniform condition state of different individuals compared to other, more challenging stages of an annual cycle. Kölzsch et al. (2007) suggested that environmental conditions on breeding grounds shape the population dynamics of the Great Snipes to a greater extent than those on the wintering grounds. However, this conclusion was made including the survival of chicks and first-year birds, not only lekking individuals. Perhaps, for adult individuals only, environmental conditions during migration and on wintering grounds create greater constraints on survival, than those on the breeding grounds.

Conclusion

In this study, we provided basic estimates of apparent annual survival of male Great Snipe studied on the breeding ground on wet meadows in Pripyat River Valley. We connected the chances of survival with body size of an individual, with smaller males having lower chances for survival, most probable due to constrains on foraging. To our knowledge, this is the first published attempt at obtaining such estimates, as well as long-term demographic parameters for the Great Snipe. Nevertheless, we would like to point out some of the gaps in research that are still remaining. Firstly, the analysis of males' survival should be re-evaluated with the inclusion of the possibility of movements between leks of individuals to obtain more accurate estimates. Secondly, whereas

estimates of the apparent annual survival of males are viable, we must stress the urgency of establishing those parameters for females, which survival and longevity are crucial for population persistence, especially in polygenic species with highly skewed copulations success of few, most attractive males, such as in lekking bird's species. Lastly, the proposed explanations for obtained results are mostly hypothetic, and they require proper testing with studies focusing on linking the body size with energetic expenditure during lekking and foraging limitations.

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Author contributions MW, WM, and PP: conceived the idea. All authors performed the experiments. MW: analyzed the data. MW and WM: wrote the paper. All read and approved the final draft of the manuscript.

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Data and code availability The data and code are available upon request to the corresponding author.

Declarations

Conflict of interest The authors declare there is no conflict of interest.

Ethical approval All conducted procedures were in accordance with Belarussian law.

Consent to participate Not applicable.

Consent for publication Not applicable.

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