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Body condition in relation to environmental factors on the breeding grounds and given stages of the annual cycle of adult Great Snipes *Gallinago media* from Eastern-European, lowland population

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Związek między kondycją a czynnikami środowiskowymi panującymi na terenach lęgowych oraz wybranymi etapami cyklu rocznego dorosłych dubeltów Gallinago media ze wschodnioeuropejskiej populacji nizinnej

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Table of contents

Summaries

English summary

Introduction:

Great Snipe *Gallinago media* is a lekking wader, conducting a long-distance migration, covering a majority of its distance in one non-stop flight towards sub-Saharan wintering grounds (Cramp & Simmons 1983, Lindström *et al.* 2016). Adult females and males differ in the timing of performed tasks in reproduction, with females still wading chicks after males finish displaying at leks (Lemnell 1978, Cramp & Simmons 1983). After the breeding period, but still on their breeding grounds, adult Great Snipes initiate moult of flight feathers (Debayle *et al.* 2017) and undertake fuelling for a non-stop migratory flight. In this species, there are two breeding populations distinguished (Kålås *et al.* 1997, Ekblom *et al.* 2007), with the Eastern-European, lowland population being more numerous and habituating larger area, compared to the Scandinavian population (Birdlife International 2022). At the same time, the latter is more extensively studied in terms of breeding behaviour, migration, and demography.

Different studies pointed out to the importance of body condition on birds' performance in relevant stages of an annual cycle, such as breeding and migratory performance (Milenkaya *et al.* 2015, Duijns *et al.* 2017, Anderson *et al.* 2019, Gajdošová *et al.* 2023). One of the approaches is to describe body condition using morphometric indices, aiming to describe the amount of energy resources gathered by an individual. Elevated body condition can also be translated into the increased quality of an individual, positively projecting onto its fitness. However, those commonly used measures of body condition have their limitations, as they tend to be context-specific and depend on various factors e.g. organism hydration and structural size of an individual (Labocha & Hayes 2012, Labocha *et al.* 2014).

In the case of Great Snipe, body condition may significantly affect male performance on the lek, due to their high energy expenditure during competitive displays (Höglund *et al.* 1992). Therefore, in their breeding season, male Great Snipes rely on the presence of abundant prey, especially earthworms, in the vicinity of leks, which allows for replenishing resources lost during lekking (Løfaldli *et al.* 1992). Environmental factors that affect the availability of prey may indirectly influence their body condition, potentially altering the intensity of their display and further their fitness.

Breeding, migration, and moult are considered life events in the annual cycle of migratory waders, which are costly in terms of the energetic resources needed for their completion. To prevent a trade-off in energy allocation, birds should schedule those processes to avoid their coinciding. While the timing of breeding and migration is often environmentally constrained (Wingfield 2008), there is more flexibility in fitting moulting into the annual cycle (Conklin *et al.* 2013). Great Snipes initiate moulting of their flight feathers at their breeding grounds, which is an unusual strategy for a long-distance migratory wader (Remisiewicz 2011). The completion of this process is conducted on their wintering grounds, as this species suspends the moult of flight feathers before departure towards sub-Saharan Africa (Debayle *et al.* 2017). Among all three stages of the annual cycle performed on their European breeding grounds, adult Great Snipes should prioritize investing energy in their breeding performance and migratory fuelling, since completing moult on breeding grounds is possibly less tied to their fitness. However, the strategy of moult of flight feathers and fuelling conducted on breeding grounds, as well as the influence intra-sexual differences in reproductive roles and of body condition on those processes were not yet described in this species.

Studying demographic parameters, such as the survival of adult individuals and its relation to their body condition, can provide valuable information about population dynamics, as well as the importance of the environmental conditions, influencing the nutrition state of birds during certain parts of the annual cycle (Zöckler *et al.* 2010, Péron *et al.* 2013). Body condition, reflecting the quality of an individual measured in a given moment of the annual cycle, might influence individual survival and its performance in different life-history events, due to the carry-over effect between subsequent stages of an annual cycle (Bergan & Smith 1993, Møller & Szép 2002). Great Snipe is a declining species, with individuals from the Eastern-European, lowland population constituting the majority of the global population (Birdlife International 2022). At the same time, this population is understudied, and obtaining its demographic parameters, including the survival of adults could not only improve our understanding of life-history traits of this species but also be useful in its conservation.

Aims and hypotheses

Here I investigated body condition, reflecting an amount of gathered energetical resources, in relation to hydrological factors influencing food availability during the lekking period. Moreover, I aimed to describe a link between body condition and progression of moult, fuelling for migratory flight, and annual survival in adult individuals of the lekking, long-distance migratory species – the Great Snipe. Below I state my specific objectives:

First Objective

I investigated how the water level in the river (Pripyat River) flowing through the breeding site indirectly influenced the body condition of lekking Great Snipe males. This hydrological parameter alters the moisture content and penetrability of the floodplain meadow's soil in the vicinity of the river, which in turn determines the availability of Great Snipes' major prey – the earthworms (Milsom *et al.* 2002, Onrust *et al.* 2019). I hypothesized that rising water in the river changes the hydrological properties of the soil, causing its higher moisture content, which forces the movement of the earthworms in the direction of the surface of the ground. Great Snipes feed by probing the soil with their long bills, and a higher concentration of prey in the upper layer of the ground, as well as increased penetrability of moist soil, would increase their availability to foraging birds. This in turn could increase their body condition.

Second Objective

Secondly, I focused on two events of the Great Snipe's annual cycle taking place after the lekking period, yet still on their European breeding grounds: moult of flight feathers and fuelling for southward migratory flight. I aimed to describe the progression of moult, taking into account intrasexual differences, as well as the effect of the individual body condition on this process. Moreover, I investigated changes in body condition over time for both female and male Great Snipes, illustrating fuelling before departure towards wintering grounds. Both moult and fuelling require a surplus of resources to be fulfilled (Lindström *et al.* 1994, Rubolini *et al.* 2002), thus conducting them at the same time would create a trade-off in energy allocation. I hypothesized that Great Snipes fit both of those events of the annual cycle together on a temporal scale avoiding or at least minimising an overlap between them. Out of those two events, migratory fuelling possibly acts as a stronger bottleneck, as gathering sufficient stores for fuelling a long-distance, non-stop flight, as well as the right timing of departure puts larger constraints on an individual's survival (Buehler & Piersma 2008). Therefore, Great Snipes should prioritize fuelling over moulting of flight feathers, especially since flying with missing or actively growing wing feathers would further increase the costs of migration. This, however, could reduce the time available for moult. Therefore, I hypothesized that Great Snipes are unable to complete this process on their breeding grounds, which leads to suspending their moult of flight feathers before departure towards Africa. Investing resources in flight feather exchange should be related to decrease in gathered energetic resources, therefore I hypothesised that birds with more advanced moult would have a reduced body condition. I expected that females and males vary in the flight feathers moult progression and fuelling and that those differences stem from female-only parental care found in this lekking species. Males finish displaying at leks when females still rear chicks, which allows them to initiate moult and fuelling sooner than females, resulting in them being more advanced in either of those processes at a similar time of the studied period.

Third Objective

Lastly, I used a long series of mark-recapture data to investigate the apparent annual survival of adult males of Great Snipe and how individual traits such as body size and body condition may influence this parameter. Body condition measured at a given moment may reflect the general quality of an individual (Labocha & Hayes 2012). Therefore, chances of surviving and performing well at challenging moments of an annual cycle should be increased in individuals with higher body condition. Natural selection is an ongoing evolutionary mechanism, that can cause shits of the phenotypic responses in the life history and morphology of animals, under the pressure of changing environmental factors. Indeed, differences in mortality of individuals with diverse morphological traits were previously described in other bird species (Verhulst *et al.* 2004, Van Buskirk *et al.* 2010). In the Great Snipe males, I expected an increased survival of larger birds, due to their potentially broader foraging niche, which could be crucial to survival in critical stages of the annual cycle requiring increased energy intake.

Methods

The majority of data used in this doctoral thesis project came from the long-term monitoring program of breeding Great Snipe, organized since the year 2000 by the Turov Ringing Station, located in Turov Gomel Region, Belarus (52° 05′ N, 27° 46′ E). Work of this field station conducted in the Pripyat River Valley focuses on waders using this area as their breeding grounds and stopover sites both during autumn and spring migration. My contribution to the data collection included fieldwork conducted in the spring of 2019 and 2020. Moreover, to complete the analysis of moult and fuelling, required for investigating the Third Objective, I used additional data from eastern Poland, that was gathered during the work of the Nature Association Dubelt Society, participating in the implementation of the National Action Plan for Great Snipe in Poland (Korniluk & Piec 2016). Data collection consisted of capturing individuals on leks or feeding sites. In the case of capturing conducted on leks, we aimed to reduce the disturbance of displaying birds, by reducing time spent on fieldwork to a maximum of four hours per catching session and separating subsequent catching sessions by minimum five-day long breaks. All captured birds were marked with metal rings with a unique, alphanumeric code, allowing for future recognition of a given individual, which allowed for investigation of the Second Objective. Moreover, birds' body mass, together with their linear body measurements, and their primary and secondary moult scores were recorded. To investigate the First Objective of my doctoral thesis project, data on the water levels in the Pripyat River were collected from a gauging station in Chernichi, located approximately 3.5 kilometres from the studied lek. In this work, I defined the body condition of an individual as an amount of gathered energetic resources, using two morphometric parameters: body mass and scaled mass index, in which the body mass is corrected for the structural size of an individual (Peig & Green 2009). All three objectives were tested with different statistical methods, which are described in detail in the corresponding chapters of this thesis. Statistical analyses were performed in R environment (R Core Team 2022) and program MARK (White & Burnham 1999).

Results and discussion

Chapter 1: Effect of environmental factors on the body condition of lekking males of Great Snipe

Body condition of lekking male Great Snipes declined over the breeding season, with birds losing on average 3% of their initial body mass throughout May, considered a period of intensive lekking in this species. This decline was caused by the high energy expenditure of displaying males (Höglund *et al.* 1992). The water level in the river significantly influenced changes in the body condition of the studied birds. High water levels were linked to an increase in their body condition, as earthworms moved closer to the surface in search of optimal conditions (Onrust *et al.* 2019), which created more foraging options for Great Snipes. However, a further rise in the water level flooded the meadow, reducing the body condition of lekking males of this species. This decline can be explained by the deterioration of the feeding conditions, as earthworms abandon flooded areas (Zorn *et al.* 2005). Additionally, the enlarging of the flooded areas created an inaccessible foraging site for birds, necessitating movements to more distinct areas and potentially increasing competition between individuals, which requires increased energy expenditure.

Chapter 2: Moult of flight feather and fuelling for southward migratory flight in Great Snipe

Males initiated primary moult earlier and moulted faster, leading to a broader range of renewed primaries compared to females. Males do not partake in parental duties and therefore can start this process sooner, when females are still rearing chicks (Cramp & Simmons 1983, Höglund & Alatalo 1995). Both males and females were unable to complete their primary moult on their breeding grounds, which lead to suspension of this process long before the timing of departure towards wintering grounds (a strategy detected in all males and half of the females), or postponement of conducting moult of flight feather on breeding grounds (a strategy detected in the other half of females). Females possibly undertake different strategies of moult depending on their breeding success, as females with failed broods could start this process sooner and exchange more primaries compared to successful females. The body condition of individuals did not influence the start date and duration of flight feathers' moult. Great Snipes are able to quickly utilize their fat stores and lean body mass can change significantly during moult (Höglund *et al.* 1992), including changes in the size of the pectoral muscle relative to the body mass (Lind & Jakobsson 2001). This could explain a limited impact of the body condition index, relying on body mass, on moult parameters observed in this study. Moult of secondaries was a rare phenomenon in Great Snipe, which was detected in less than 1% of birds, and only in males that were able to renew a large number of their primary feathers.

Body condition reflecting the amount of gathered energetical resources showed a non-linear increase over the studied period. A period with the stable and low body condition of birds overlapped with the timing of the primary moult and/or chick-rearing period, indicating a trade-off in resource allocation between feather growth and fuelling before the departure. Later an increase in the body condition was noted, with a fuelling rate of approximately 1% of the lean body mass increase per day. Males were able to increase their energetic stores at a faster pace compared to females. Males begin their migration sooner than females (Debayle *et al.* 2017), and maximizing their fuelling rate would allow for advanced departure and increase the overall speed of migration. Obtained fuelling rate is relatively low compared to other long-distance migratory waders of similar size (Kvist & Lindström 2003, Piersma *et al.* 2005). However, it is possible that this rate of fuel accumulation further intensifies closer to departure (Lindström *et al.* 2019).

Chapter 3: Annual apparent survival of Great Snipe males

Obtained annual apparent survival of male Great Snipes was relatively low ($\Phi(.) = 0.43$), compared to other waders with similar body size (Méndez *et al.* 2018), but stable over the 22 years of data collection. Great Snipe males face high energetic costs due to their lekking behaviour and long-distance, non-stop migratory flights, indicating a 'fast pace of life'. This aligns with the rate-of-living theory, which suggests that animals with elevated metabolic rates tend to have lower survival and decreased longevity (Pearl 1928, Vágási *et al.* 2019). Long-distance migration is not uncommon among waders, however, the rarity of lekking as a breeding system may contribute to the lower survival of Great Snipe males compared to other wader species. Apparent survival increased with body size, possibly due to limited foraging options available for smaller males with shorter bills (Alves *et al.* 2013, Duijns *et al.* 2015), which could cause malnutrition at stages of annual cycles acting as bottlenecks. I did not find a significant influence of body condition on the apparent survival of male Great Snipes, as the used index of body condition reflects the amount of energetic stores, which can change considerably during a single night of lekking or the whole breeding season, and therefore fails to serve as an indicator of overall quality of an individual.

Conclusions

The presented results of my doctoral thesis indicate that:

1. The level of the water in the river, which is an environmental factor affecting the availability of prey, indirectly influences the body condition reflecting the amount of energetic resources of lekking male Great Snipes.
2. Differences in parental duties between sexes affect the processes of moult of flight feather and fuelling in the studied species, with females solely providing parental care being delayed in both processes.

3. Great Snipe males are characterized by relatively low apparent survival, possibly due to elevated costs of life, related to their lekking behaviour. Males with smaller body size have decreased chances of survival, possibly due to their limited foraging options.
4. Although body condition indexes such as body mass and scaled mass index may be used as a simple measure of energetic stores gathered in a given moment by a bird, their appliance as a measure of the general quality of the individual is questionable.

Streszczenie po Polsku

Wstęp

Dubelt *Gallinago media* jest tokującym ptakiem siewkowym, który pokonuje dużą część długodystansowej wędrówki nieprzerwanym lotem w stronę subsaharyjskich zimowisk (Cramp & Simmons 1983, Lindström *et al.* 2016). Rola dorosłych samic i samców tego gatunku w okresie lęgowym jest zupełnie odmienna (Lemnell 1978, Cramp & Simmons 1983). Budową gniazda, wysiadywaniem jaj i opieką nad pisklętami zajmuje się wyłącznie samica. Samce w tym okresie intensywnie tokują na zbiorowych tokowiskach. Po sezonie lęgowym, na terenach lęgowych w Europie, dorosłe dubelty zaczynają pierzyć lotki (Debayle *et al.* 2017) oraz otłuszczać się przed długodystansowym lotem na południe. U tego gatunku wyróżnia się dwie populacje lęgowe (Kålås *et al.* 1997, Ekblom *et al.* 2007), z których skandynawska jest znacznie lepiej zbadana pod względem lęgów, wędrówki i demografii. Nasza wiedza o nizinnej, wschodnioeuropejskiej populacji jest wciąż ograniczona pomimo że jest ona liczniejsza i zajmuje większy areał lęgowy (Birdlife International 2022).

Różne opracowania naukowe wskazują na duży wpływ kondycji ciała osobnika na jego udział w kluczowych momentach cyklu rocznego, takich jak rozród i wędrówka (Milenkaya *et al.* 2015, Duijns *et al.* 2017, Anderson *et al.* 2019, Gajdošová *et al.* 2023). Jednym ze sposobów opisu kondycji ciała osobnika jest użycie morfometrycznych wskaźników, opisujących ilość zgromadzonych przez organizm zasobów energetycznych. Zwiększona kondycja ciała może być też rozumiana jako lepsza jakość osobnika, która pozytywnie wpływa na jego dostosowanie ewolucyjne. Jednakże użyteczność wspomnianych wskaźników kondycji jest ograniczona ze względu na ich zależność od kontekstu ekologicznego a także różnych czynników osobniczych, takich jak nawodnienie organizmu czy jego wielkość (Labocha & Hayes 2012, Labocha *et al.* 2014).

W przypadku dubelta, kondycja ciała może znacząco wpływać na tokowanie samców ze względu na wysoki wydatek energetyczny związany z ich zachowaniem godowym (Höglund *et al.* 1992). Aby uzupełnić zasoby stracone podczas tokowania, samce muszą polegać na wysokiej dostępności ich pokarmu, głównie dżdżownic, w pobliżu tokowisk (Løfaldli *et al.* 1992). Dlatego czynniki środowiskowe, które są w stanie wpłynąć na dostępność dżdżownic w glebie mogą pośrednio przekładać się na kondycję ptaków, a co za tym idzie intensywność ich tokowania i późniejszą przeżywalność.

Lęgi, wędrówka i pierzenie to etapy cyklu rocznego, które u migracyjnych gatunków siewkowców są uznawane za kosztowne, biorąc pod uwagę ilość zasobów energetycznych, które muszą zostać na nie przeznaczone. Aby nie dopuścić do kompromisu w wydatkowaniu energii, ptaki najczęściej rozkładają te procesy w czasie tak, aby nie nachodziły na siebie. Czas odbywania lęgów i wędrówki uznaje się za silnie ograniczony przez warunki środowiskowe (Wingfield 2008), istnieje jednak większa elastyczność we wpasowaniu czasu pierzenia w cykl roczny (Conklin *et al.* 2013). Pierzenie lotek rozpoczyna się u dubelta na jego lęgowiskach, co jest nietypową strategią pierzenia u gatunków siewkowców odbywających długodystansową migrację (Remisiewicz 2011). U tego gatunku stwierdzono zatrzymanie pierzenia lotek przed odlotem do Afryki, które jest wznawiane później po przylocie na zimowiska (Debayle *et al.* 2017). Wydaje się, że dorosłe osobniki dubelta powinny w pierwszej kolejności zapewnić zasoby potrzebne do odbycia lęgów i otłuszczenia przed dalekodystansowym lotem, jako że dokończenie pierzenia lotek na lęgowiskach ma prawdopodobnie mniejszy wpływ na dostosowanie ewolucyjne danego osobnika. Strategia pierzenia i przygotowania do lotu na zimowiska, jak również wpływ kondycji ciała i międzypłciowych różnic w opiece rodzicielskiej na te procesy nie zostały jak dotąd opisane dla tego gatunku.

Badania parametrów populacji, takich jak przeżywalność dorosłych osobników i jej związek z kondycją ciała mogą dostarczyć cennych informacji o dynamice populacji, jak również znaczeniu warunków środowiska wpływających na stopień odżywienia ptaków w czasie danego etapu cyklu rocznego (Zöckler *et al.* 2010, Péron *et al.* 2013). Odzwierciedlająca jakość danego osobnika kondycja ciała, która została zmierzona w danym momencie może przekładać się na jego przeżywalność ze względu na to, że postępujące po sobie wydarzenia cyklu rocznego mogą wzajemnie na siebie rzutować (ang. *carry-over effect;* Bergan and Smith 1993; Møller and Szép 2002). Dubelt jest gatunkiem, którego liczebność w ostatnich latach spada, a większość globalnej populacji stanowią osobniki należące do nizinnej, wschodnioeuropejskiej populacji lęgowej (Birdlife International 2022). Jednocześnie jest ona mało zbadana, a otrzymanie parametrów demograficznych, takich jak przeżywalność dorosłych osobników, mogłoby przyczynić się nie tylko do zrozumienia strategii życiowej gatunku, ale też do jego ochrony.

Cele i hipotezy

W mojej pracy doktorskiej zbadałam związek między kondycją osobnika, opisującą ilość zgromadzonych zasobów energetycznych, z hydrologicznymi parametrami środowiska wpływającymi na dostępność pokarmu w czasie trwania sezonu tokowania u dubelta. Co więcej, moim celem było opisanie wpływu kondycji ciała osobnika na przebieg pierzenia, proces gromadzenia zapasów energetycznych przed odlotem na zimowiska i roczną przeżywalność dorosłych osobników dubelta, będącego dalekodystansowym migrantem, którego samce w okresie lęgowym gromadzą się na zbiorowych tokowiskach. Poniżej przedstawiłam moje cele szczegółowe:

Cel pierwszy

Pierwszym celem było zbadanie wpływu poziomu wody w rzece (Prypeci) przepływającej przez tereny lęgowe. Ten parametr hydrologiczny może bowiem pośrednio wpływać na kondycję tokujących samców dubelta: kształtuje on wilgotność i przepuszczalność gleby łąk terenów zalewowych w pobliżu rzeki. Założyłam, że podnoszący się poziom wody w rzece zmieni hydrologiczne cechy gleby, tj. zwiększy jej wilgotność, co spowoduje poziome przemieszczanie się dżdżownic w stronę powierzchni gruntu (Milsom *et al.* 2002, Onrust *et al.* 2019). Dubelty żerują poprzez sondowanie gleby, dlatego zwiększone zagęszczenie dżdżownic, stanowiących główny składnik ich bazy pokarmowej przy powierzchni, jak również wyższa przepuszczalność wilgotnej gleby, przełoży się na łatwiejszą dostępność pokarmu dla ptaków z tego gatunku. To z kolei może wpłynąć na ich kondycję ciała.

Cel drugi

Następnie skupiłam się na dwóch etapach cyklu rocznego dubelta, które mają miejsce na terenach lęgowych po okresie intensywnego tokowania: pierzeniu lotek oraz gromadzeniu zapasów energetycznych (głównie w postaci tłuszczu) przed odlotem na zimowiska. Moim celem było opisanie strategii pierzenia lotek, z uwzględnieniem różnic między płciami, jak również wpływu kondycji osobnika na przebieg tego procesu. Ponadto zbadałam zmiany kondycji samic i samców dubelta zachodzące w czasie, które pokazują przebieg procesu gromadzenia zapasów energetycznych przed odlotem. Zarówno pierzenie jak i otłuszczanie wymagają nadwyżki zgromadzonych zasobów do ich przeprowadzenia, dlatego ich zachodzenie w tym samym czasie powoduje konieczność kompromisu w przydziale zasobów między tymi procesami (Lindström *et al.* 1994, Rubolini *et al.* 2002). Z tego względu postawiłam hipotezę, że dubelty rozkładają oba procesy w czasie tak, aby zminimalizować ich nakładanie na siebie. Spośród tych dwóch procesów, otłuszczanie powinno powodować tzw. efekt wąskiego gardła, ponieważ zgromadzenie odpowiednich zasobów energetycznych przed nieprzerwanym, dalekodystansowym lotem, jak również odpowiedni termin rozpoczęcia wędrówki powinny w większym stopniu wpływać na przeżywalność osobników niż stopień zaawansowania wymiany lotek (Buehler & Piersma 2008). Dlatego przeznaczenie zasobów energetycznych na otłuszczanie powinno być dla tego gatunku priorytetem, zwłaszcza że lot z brakującymi lub rosnącymi lotkami dodatkowo zwiększa koszty energetyczne ponoszone w trakcie migracji. Wobec tego założyłam, że dubelty nie są w stanie wymienić wszystkich lotek na terenach lęgowych, co prowadzi do zatrzymania tego procesu przed odlotem do Afryki. Jako że proces wymiany piór wymaga zwiększonych nakładów energetycznych, powinien on być związany ze zużywaniem zgromadzonych przez organizm zapasów energetycznych. Z tego względu postawiłam hipotezę, że ptaki będące w bardziej zaawansowanym stadium pierzenia będą charakteryzować się obniżoną kondycją. Samice i samce powinny różnić się w przebiegu pierzenia lotek, co wynika z tego, że wyłącznie samice tego gatunku opiekują się potomstwem. Samce kończą toki w czasie kiedy samice nadal zajmują się pisklętami, co pozwala im na wcześniejsze rozpoczęcie pierzenia lotek i gromadzenia zapasów tłuszczowych przed odlotem w porównaniu do samic, w wyniku czego są one bardziej zaawansowane w przebiegu obu tych procesów w tym samym czasie.

Cel trzeci

Ostatnim celem mojej rozprawy doktorskiej było zbadanie względnej, rocznej przeżywalności dorosłych samców dubelta oraz wpływu cech osobniczych takich jak wielkość ciała i kondycja na ten parametr. Kondycja ciała zmierzona w danym momencie może obrazować ogólną jakość danego osobnika (Labocha & Hayes 2012). Z tego względu szansa na przeżycie powinna zwiększać się wraz ze wzrostem kondycji ciała. Dobór naturalny jest nieprzerwanie zachodzącym mechanizmem ewolucyjnym, który pod wpływem presji zmieniającego się środowiska może powodować odpowiedź fenotypową w zmianie strategii życia oraz morfologii zwierząt. Rzeczywiście, różnice w śmiertelności osobników o różnych cechach morfologicznych zostały uprzednio opisane u innych gatunków ptaków (Verhulst *et al.* 2004, Van Buskirk *et al.* 2010). Założyłam, że u samców dubelta zwiększone szanse na przeżycie będą związane z większym rozmiarem ciała ptaków, ze względu na ich potencjalnie szerszą niszę pokarmową. Może to być kluczowe dla przeżywalności w etapach cyklu rocznego wymagających gromadzenia zapasów energetycznych z pożywienia.

Metody

Większość danych użytych w mojej rozprawie doktorskiej pochodziła z długotrwałego programu monitorowania populacji lęgowej dubelta, organizowanego od roku 2000 przez Stację Obrączkowania

Ptaków Turov (Turov Ringing Station) zlokalizowanej w Turowie w obwodzie Homelskim na Białorusi (52° 05′ N, 27° 46′ E). Prace tej stacji terenowej prowadzone są w Dolinie Prypeci i skupiają się na badaniu siewkowców odbywających na tym terenie swoje lęgi, jak również używających tego terenu jako miejsca przystankowego zarówno podczas jesiennej, jak i wiosennej migracji. Mój wkład w zbieranie danych w terenie zawierał się w pracach terenowych przeprowadzonych wiosną 2019 i 2020 roku. Dodatkowo, aby zwiększyć liczbę danych potrzebnych do opracowania wyników związanych z pierzeniem i otłuszczaniem przed odlotem, niezbędnych do spełnienia Celu Trzeciego mojej pracy doktorskiej, wykorzystałam dane zebrane w czasie prac Towarzystwa Przyrodniczego Dubelt, biorącego udział we wprowadzaniu Krajowego Programu Ochrony Dubelta w Polsce (Korniluk & Piec 2016). Prace terenowe obejmowały chwytanie ptaków na tokowiskach lub żerowiskach. W przypadku odłowów prowadzonych na tokowiskach, w obu miejscach prowadzenia badań podjęto kroki w celu zminimalizowania wpływu na tokujące ptaki, poprzez ograniczenie aktywności badaczy do czterech godzin w czasie pojedynczego odłowu oraz ponawianie odłowów na danym tokowisku po przynajmniej pięciodniowej przerwie. Wszystkie złapane osobniki zostały oznakowane metalową obrączką zawierającą indywidualny, alfanumeryczny kod, umożliwiający późniejsze rozpoznanie danego osobnika przy ponownym stwierdzeniu, co było niezbędne do zrealizowania Celu Drugiego mojej pracy doktorskiej. Odnotowywano masę ciała i pomiary liniowe, jak również stopień przepierzenia poszczególnych lotek pierwszo- i drugorzędowych. Aby zrealizować Pierwszy Cel mojej rozprawy doktorskiej zgromadziłam dane dotyczące poziomów wody w Prypeci, pochodzące ze stacji pomiarowej w Czerniczy, położonej około 3.5 kilometra od badanego tokowiska. Na potrzeby mojej pracy doktorskiej zdefiniowałam kondycję ciała danego osobnika jako ilość zgromadzonych zasobów energetycznych. Do tego celu użyłam dwóch wskaźników morfometrycznych: masy ciała oraz przeskalowanego wskaźnika masy (ang. *scaled mass index*; Peig and Green 2009), który koryguje masę ciała osobnika o jego wielkość strukturalną. Do przetestowania postawionych hipotez użyłam różnych metod statystycznych, których dokładny opis zamieściłam w pozostałych rozdziałach tej pracy. Analizy statystyczne zostały wykonane w środowisku R (R Core Team 2022) i programie MARK (White & Burnham 1999).

Wyniki i dyskusja

Rozdział 1: Wpływ czynników środowiska na kondycję ciała tokujących samców dubelta

Kondycja ciała tokujących samców dubelta spadała wraz z postępowaniem sezonu lęgowego, gdzie ptaki traciły średnio 3% swojej masy w ciągu maja, uznawanego za okres intensywnego tokowania u badanego gatunku. Opisany spadek był spowodowany wysokim wydatkiem energetycznym samców podczas tokowania (Höglund *et al.* 1992). Poziom wody w rzece istotnie wpływał na kondycję ciała tokujących ptaków. Wysoki poziom wody w rzece został powiązany ze wzrostem kondycji ciała. Jest to najprawdopodobniej związane z przemieszczaniem się dżdżownic w stronę powierzchni gruntu w poszukiwaniu optymalnych warunków (Onrust *et al.* 2019), co prowadzi do polepszenia żerowisk dubelta. Dalszy wzrost poziomu wody w rzece spowodował spadek kondycji ciała tokujących ptaków, ponieważ dżdżownice opuszczają zalane tereny (Zorn *et al.* 2005). Dodatkowo, postępujące zalanie łąk prowadzi do zwiększenia się niedostępnego dla ptaków terenu, wymuszając ich przemieszczenie na dalsze żerowiska, jak również potencjalnie zwiększa konkurencję między osobnikami, podnosząc wydatkowanie energii.

Rozdział 2: Pierzenie lotek i otłuszczanie przed odlotem na południe u dubelta

Samce rozpoczynały proces pierzenia lotek wcześniej i pierzyły się szybciej, co prowadziło do większego zakresu wymienionych piór w skrzydle w porównaniu do samic. Samce nie biorą udziału w opiece rodzicielskiej, dlatego są w stanie rozpocząć proces pierzenia lotek szybciej, w czasie kiedy samice nadal opiekują się pisklętami (Cramp & Simmons 1983, Höglund & Alatalo 1995). Zarówno samice jak i samce dubelta nie były w stanie wymienić wszystkich lotek w czasie pobytu na terenach lęgowych, co prowadziło do zatrzymania tego procesu na długo przed odlotem na zimowiska (strategia odnotowana u wszystkich samców i połowy samic), lub do zaniechania tego procesu w całości (strategia odnotowana u drugiej połowy samic). Samice prawdopodobnie prezentują różne strategie pierzenia lotek w zależności od ich sukcesu lęgowego, gdzie samice po stracie lęgu są w stanie rozpocząć ten proces szybciej w porównaniu do samic z udanym lęgiem. Kondycja ciała nie wpływała na datę rozpoczęcia i czas pierzenia lotek pierwszorzędowych. Dubelty są w stanie szybko wykorzystywać swoje zapasy energetyczne (Höglund *et al.* 1992), a beztłuszczowa masa ciała może znacząco zmieniać się podczas pierzenia, np. poprzez zmiany wielkości mięśni piersiowych względem całkowitej masy ciała (Lind & Jakobsson 2001). Może to tłumaczyć niewielki wpływ wskaźnika kondycji ciała, silnie związanego z masą ciała, na odnotowane parametry pierzenia. Pierzenie lotek drugorzędowych było rzadko obserwowanym zjawiskiem u dubelta, które zostało stwierdzone u mniej niż 1% wszystkich zbadanych osobników i tylko u samców z dużą liczbą wymienionych lotek pierwszorzędowych.

Kondycja ciała odzwierciedlająca zgromadzone zasoby energetyczne zwiększała się nieliniowo w badanym okresie. Faza stabilnej i niskiej kondycji ciała pokrywała się w czasie z aktywną wymianą lotek pierwszorzędowych i/lub wychowywaniem potomstwa, co wskazuje na istnienie kompromisu w inwestowaniu zasobów energetycznych między pierzeniem a otłuszczaniem. W późniejszej części badanego okresu zaobserwowano wzrost kondycji ciała, gdzie tempo zwiększania masy osiągnęło przyrost około 1% beztłuszczowej masy ciała dziennie. Stwierdziłam szybsze tempo otłuszczania u samców w porównaniu do samic. Samce rozpoczynają migrację wcześniej niż samice (Debayle *et al.* 2017), stąd przyspieszone tempo otłuszczania pozwala na przyspieszenie odlotu na zimowiska i całościowe skrócenie czasu migracji. Opisane tempo otłuszczania jest względnie niskie w porównaniu do innych gatunków siewkowców o zbliżonych do dubelta wymiarach ciała i odbywających dalekodystansową wędrówkę (Kvist & Lindström 2003, Piersma *et al.* 2005). Możliwe, że tempo gromadzenia zasobów energetycznych potrzebnych do zrealizowania lotu migracyjnego zwiększa się w późniejszym czasie, bliżej terminu odlotu (Lindström *et al.* 2019).

Rozdział 3: Względna roczna przeżywalność samców dubelta

Uzyskane wartości względnej rocznej przeżywalności u dubelta były stosunkowo niskie (Φ(.) = 0.43), w porównaniu do innych gatunków siewkowców o podobnej wielkości ciała (Méndez *et al.* 2018), jednak nie wykryto trendu zmian tego parametru na przestrzeni badanych 22 lat. Samce dubelta ponoszą wysokie koszty związane z tokowaniem oraz długodystansowym, nieprzerwanym lotem migracyjnym, co wskazuje na 'szybkie tempo życia' u tego gatunku. Jest to zgodne z teorią tempa życia (ang. *rate-of-living theory*), która sugeruje że zwierzęta z podwyższonym tempem metabolizmu charakteryzuje obniżona przeżywalność i skrócona długość życia (Pearl 1928, Vágási *et al.* 2019). Dalekodystansowa migracja nie jest nietypowa dla siewkowców, jednak tokowanie jest rzadko spotykaną strategią rozrodczą, co może przyczyniać się do zmniejszonej przeżywalności samców dubelta w porównaniu do pokrewnych gatunków. Względna przeżywalność zwiększała się z wraz z wielkością ciała danego osobnika, prawdopodobnie ze względu na zmniejszoną dowolność wyboru miejsc żerowania dla samców o krótszych dziobach, co może przekładać się na utrudniony dostęp do pokarmu w kluczowych etapach cyklu rocznego (Alves *et al.* 2013, Duijns *et al.* 2015). Nie stwierdziłam istotnego wpływu kondycji ciała na przeżywalność badanych osobników, ponieważ użyty wskaźnik kondycji ciała objaśnia ilość zgromadzonych zapasów energetycznych, która u dubelta może znacząco zmienić się na przestrzeni pojedynczej nocy na tokowisku, jak również w czasie całego sezonu lęgowego. Z tego względu wskaźnik ten nie obrazuje ogólnej jakości danego osobnika.

Wnioski

Opisane wyniki mojej rozprawy doktorskiej wskazują, że:

1. Poziom wody w rzece, będący warunkiem środowiska określającym dostępność pokarmu, może pośrednio wpływać na kondycję ciała odzwierciedlającą ilość zgromadzonych zasobów energetycznych u tokujących samców dubelta.

2. Odmienna rola samic i samców dubelta w sezonie lęgowym i różny wkład w opiekę rodzicielską wpływają na różnice w przebiegu procesu pierzenia i otłuszczania przed odlotem w kierunku zimowisk. U samic samodzielnie opiekującymi się pisklętami obserwuje się opóźnienie obu tych procesów.
3. Samce dubelta charakteryzują się stosunkowo niską względną przeżywalnością, prawdopodobnie spowodowaną wysokimi kosztami życia związanymi z tokowaniem. Mniejsze samce mają obniżoną przeżywalność, prawdopodobnie ze względu na ograniczone możliwości żerowania.
4. Choć wskaźniki kondycji ciała, takie jak masa ciała i przeskalowany wskaźnik masy (ang. *scaled mass index*) mogą być użyte jako proste miary obrazujące zgromadzone zasoby energetyczne organizmu, ich użyteczność jako miary jakości danego osobnika jest wątpliwa.

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General Introduction

Great Snipe *Gallinago media* is a wader species of the family Scolopacidae, known for its lekking, which is a relatively rare breeding strategy that entails a communal courtship display of males competing for copulation with females visiting lekking arenas (Lemnell 1978, Cramp & Simmons 1983). Females select a mate from displaying males based on their performance and secondary sexual traits, which serve as a proxy for the male's overall quality (Höglund & Alatalo 1995). Indeed, a number of studies indicated increased attractiveness of lekking males with higher body condition, which enables for higher energy expenditure in the development of secondary sexual traits and displaying, as males of lekking species do not invest their resources in parental care (Morales *et al.* 2003, Yang *et al.* 2013, Jiguet & Bretagnolle 2014). Female Great Snipes favour males with a high intensity of display performance (Höglund & Lundberg 1987), which comes at high energy costs for lekking males, causing a substantial decrease in body mass both during a single night of lekking, as well as during the period of intense lekking (Höglund *et al.* 1992). Therefore, males must rely on a source of abundant prey, which is crucial for replenishing their energy reserves and allows for participation in lekking. Indeed, leks are situated in the vicinity of rich feeding sites, specifically those with easily available and abundant earthworms (Lumbricidae), that constitute the majority of the Great Snipes diet (Løfaldli *et al.* 1992). Their availability for foraging birds can be affected by both moisture and the penetrability of the soil (Milsom *et al.* 2002, Onrust *et al.* 2019), which in floodplain meadows is influenced by the level of water in the river.

Breeding is costly and requires substantial resources to be conducted. As in other lekking species, the energy expenditure of females and males of Great Snipe stems from different breeding behaviours (Lemnell 1978, Höglund & Alatalo 1995), where males' investment in displaying has been to some extend studied (Höglund *et al.* 1992). We lack knowledge on reproduction costs for females of this species, however, they are assumed to be significant, since incubation and chick rearing are solely the female's responsibility. Differences in breeding investment and parental duties between sexes can project on other life history events of the annual cycle, resulting in intrasexual variation in a strategy of moult and migration (Summers *et al.* 2004, Meissner 2005, Machín *et al.* 2018, Mazur *et al.* 2021). In the Great Snipe, evidence from sub-Saharan wintering grounds indicates that moult of flight feathers is initiated still on their breeding grounds, and presumably follows the end of the lekking and chick-rearing period (Debayle *et al.* 2017). The process of exchanging feathers in birds is energetically demanding, as resources are used to produce feathers (Rubolini et al., 2002), but also because missing feathers may impair flight ability and thermoregulation, creating additional costs (Swaddle & Witter 1997, Buttemer *et al.* 2020). Great Snipe is a long-distance migrant, which covers a large portion of their migration in one non-stop flight from European breeding grounds to sub-Saharan Africa (Lindström *et al.* 2016). The ability to conduct such migratory flight requires a deposition of a large amount of energetic stores, which Great Snipe convey on their European breeding grounds. All three events of the Great Snipe's annual cycle conducted on their breeding grounds require elevated energy investment, therefore birds should schedule them in a way that avoids overlap, in order to minimize potential trade-offs in resource allocation. At the same time, stages of Great Snipe's annual cycle between breeding and southward migration have not yet been studied in terms of their timing and energy expenditure.

The performance of an individual in a given event of the annual cycle may project onto other, following stages (Harrisom *et al.* 2011, Conklin & Battley 2012, Fayet *et al.* 2016). Indeed, in some bird species, a connection between high body condition measured in one moment of the annual cycle and increased chanced of survival throughout the year was described (Bergan & Smith 1993, Møller & Szép 2002). Survival of adults in an animal population is one of the basic demographic characteristics, which provides important information about the state of the whole population as well as its habitat (Zöckler *et al.* 2010, Péron *et al.* 2013). Therefore, obtaining this metric can be relevant to species conservation, as well as evolutionary studies devoted to their life history traits. In Great Snipe there are two breeding populations, distinguished based on the genetical differentiation in the major histocompatibility complex (MHC) genes (Ekblom *et al.* 2007), morphological differences in body size and plumage traits (Kålås et al., 1997), and their disjunct geographical locations, with different environmental conditions shaping their habitat (Kålås 2004): 1) Western-European, Scandinavian population breeding in sub-alpine habitat at the edge of tree line of the mountain slope, and 2) Eastern-European, lowland population, occupying floodplain meadows, pastures and marshes. Demographic estimates for the global population of Great Snipes indicate that the lowland population constitutes the majority of the global population and occupies a larger habitat in comparison to the Scandinavian population (Birdlife International 2022). However, there is an existing bias in scientific work conducted on both of the breeding populations, with the lowland population being less studied in terms of breeding behaviour and migration. Both populations are considered separate management units for conservation (Kålås 2004), due to major differences in occupied breeding habitat and limited gene flow between populations (Ekblom *et al.* 2007). The decline of global population is associated with loss of individuals resulting from degradation of vulnerable grasslands ecosystems due to climate change, agriculture, as well as wetlands and rivers intensive management (Kålås 2004, Østnes *et al.* 2014, Shydlovskyy *et al.* 2023). Currently Great Snipe is listed as a Near Threatened, with nearly meeting the requirements for being listed as Threatened by the International Union for Conservation of Nature (IUCN 2023), with several action planes created for protection of this species (Kålås 2004, Pinchuk & Mongin 2012, Korniluk & Piec 2016).

Body condition is widely used as a characteristic describing the health and quality of an individual (Peig & Green 2009, Labocha & Hayes 2012, Labocha *et al.* 2014). It is usually measured indirectly, as a parameter assessed based physiological and biochemical metrics, such as haematological and plasma parameters (Masello & Quillfeldt 2004, Minias 2015). Common approach found in birds studies is to identify body condition based on morphometric indices, aiming to reflect the state of nutrition or gathered energetic resources of a given individual (Labocha & Hayes 2012, Labocha *et al.* 2014). As such, they usually rely on body mass of an individual as a sole measure of bird's energy reserves or correct body mass for structural size of an individual, using its linear body measurements. Whether morphometric body condition is a meaningful predictor for individual quality and fitness is still being tested. An underlying assumption is that individual fitness is positively related to body condition, as a surplus of resources may be allocated towards improving bird's performance in different stages of an annual cycle. Indeed, there is an existing evidence of improved survival (Bergan & Smith 1993, Moller & Szep 2002), advanced departure (Schmaljohann & Naef-Daenzer 2011), faster migration (Duijns *et al.* 2017) and fewer stopovers (Anderson *et al.* 2019), as well as lower asymmetry of moult of flight feathers (Pérez-Arteaga *et al.* 2019) and improved aspects of breeding performance (Wendeln & Becker 1999, Milenkaya *et al.* 2015, Gajdošová *et al.* 2023) in individuals with higher body condition reflecting energy reserves. At the same time, existing limitations for using morphometric body conditions indices put in question their utility as predictors for quality of individuals. First of all, as they rely on body mass, they may be affected by other factors influencing this parameters, such a hydration state of an organism and structural size of an individual, in case of lacking of or insufficient correction for its effect (Peig & Green 2009, Labocha & Hayes 2012). Second off all, the assumption that individuals of better quality accumulate more energy stores in a given moment of an annual cycle is not always true. If there is no reason for gathering energetic resources enforced by the costly event of an annual cycle, it is often more advantageous for birds to be as light as possible, especially if the environment ensures easily available and plentiful food resources (Piersma & Gils 2011). Lastly, morphometric body condition indices are highly context-specific as they vary between stages of the annual cycle and are relative to sex and age, which not always is related to the true quality of an individual (Milenkaya *et al.* 2013). Therefore, interpreting body condition as a surrogate for individual quality and fitness should be done with caution and taking stated limitations into account.

In this doctoral thesis project, I examined the concept of body condition as an indicator of energy reserves and its relationship with environmental factors affecting prey availability during the breeding season. Moreover, I investigated the connections between body condition and the progression of moult, fuel accumulation for migratory flights, as well as the annual apparent survival of adult individuals of the lekking, long-distance migratory species, the Great Snipe.

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Chapter 1

Effect of environmental factors on the body condition of lekking males of Great Snipe

Research Paper no. 1

The level of water in the river flowing through the breeding site shapes the body condition of a lekking bird – the Great Snipe *Gallinago media*

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ORIGINAL ARTICLE

The level of water in the river flowing through the breeding site shapes the body condition of a lekking bird—the Great Snipe *Gallinago media*

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Abstract

The display of lekking Great Snipe males is an energetically demanding activity and therefore, access to the rich feeding sites in the proximity of their leks is essential. During the breeding season, Great Snipes mostly prey on earthworms, whose availability is affected by moisture and penetrability of the soil. In this study, we investigated the relation between the body condition of displaying Great Snipe males and the water level of the river flowing through their breeding grounds, which can affect soil characteristics. We found that the body condition of males decreased over the course of the lekking period in May, showing the great energetic expenditure of their advertising display in courtship. The high water level in the river resulted in the increase in body condition of birds, probably due to improved prey availability, as earthworms moved closer to the ground surface in search of optimal conditions. Further rise in the water level caused flooding of the meadow and a decrease in the body condition of lekking Great Snipes, possibly because of the deterioration of feeding condition, as earthworms tend to leave flooded areas. Moreover, as the flooded area enlarged, the floodplain became inaccessible for foraging Great Snipes, due to their relatively short legs restricting them from wading in deep water. Our results show that for the lowland leks of the Great Snipe to be preserved it is advisable to allow for the natural water level fluctuations in the river shaping the hydrological conditions of the floodplains.

Keywords Communal courtship · Body mass · Floodplains · Wet meadow · Wader

Zusammenfassung

Der Wasserstand eines Flusses durch das Brutareal beeinflusst die physische Verfassung balzender Doppelschnepfen *Gallinago media*

Das Balzen der Doppelschnepfe ist eine energetisch anspruchsvolle Tätigkeit, weshalb die Verfügbarkeit naher, ergiebiger Futterplätze von wesentlicher Bedeutung ist. Während der Brutzeit ernähren sich die Doppelschnepfen hauptsächlich von Regenwürmern, deren Verfügbarkeit wiederum von der Feuchte und Durchlässigkeit des Bodens abhängt. In dieser Studie untersuchten wir den Zusammenhang zwischen der physischen Verfassung balzender Doppelschnepfenmännchen und dem Wasserstand des Flusses, der durch ihr Brutgebiet fließt und möglicherweise die Bodenbeschaffenheit beeinflusst. Wir stellten fest, dass die physische Verfassung der Männchen im Laufe der Balzzeit im Mai abnahm, was auf den hohen Energieaufwand für ihre Balz-Aktivitäten hinweist. Ein hoher Wasserstand des Flusses führte zu einer Verbesserung der physischen Verfassung der Vögel, was wahrscheinlich an der besseren Verfügbarkeit von Beute lag, da dann die Regenwürmer auf der Suche nach besseren Bedingungen näher an die Bodenoberfläche kommen. Ein weiterer Anstieg des Wasserspiegels

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führte zur Überflutung der Wiese und zu einer Verschlechterung der physischen Verfassung der balzenden Doppelschnepfen, möglicherweise wegen der Verschlechterung der Nahrungsbedingungen, weil Regenwürmer dazu neigen, überflutete Gebiete zu verlassen. Mit der Vergrößerung des Überschwemmungsgebiets und steigendem Wasserspiegel wurde das Gebiet außerdem für die Doppelschnepfen unzugänglich, da sie aufgrund ihrer relativ kurzen Beine nicht in tieferem Wasser waten können. Unsere Ergebnisse zeigen, dass es für den Erhalt tiefer liegender Balzplätze von Doppelschnepfen ratsam ist, die natürlichen Wasserstandsschwankungen von Flüssen, die die hydrologischen Bedingungen von Hochwassergebieten prägen, zuzulassen.

Introduction

The lekking behaviour is relatively rare among species, yet it is present in a great number of taxa, e.g., insects, amphibians, mammals and birds (Höglund and Alatalo 1995; Fiske et al. 1998). Lekking is a communal, competitive courtship display of males aiming to draw females to the lekking site. Females choose a mate among displaying males based on their performance along with secondary sexual traits and then engage in courtship. When it comes to breeding performance, lekking males invest resources mainly in their secondary sexual traits, as they do not participate in parental care (Höglund and Alatalo 1995). A number of those traits, ranging from the quality of ornaments to the intensity of the display are related to the body condition of an individual. Generally, males with higher body condition, which allows for a higher amount of energy expenditure on lekking, are more attractive to females visiting the lekking site (Carranza and Hidalgo de Trucios 1993; Andersson 1994; Morales et al. 2003; Sardà-Palomera et al. 2011; Yang et al. 2013; Jiguet and Bretagnolle 2014). The evolutionary rule is that females rely on the condition-dependent traits as indicators of the general quality of a mate, not only in terms of the mating performance but also other biological aspects. This allows for an indirect increase in the fitness of the female, as traits of a high-quality male may be inherited by a female's offspring (Höglund and Alatalo 1995; Ryder et al. 2010).

The Great Snipe *Gallinago media* is a lekking wader species, whose eastern, lowland population occurs in grassland habitats, such as pastures, marshes, and floodplain meadows of river valleys (Lemnell 1978; Cramp and Simmons 1983). Among a number of the secondary sexual traits hypothesised to influence the attractiveness of a displaying male, the high rate of the display performance was proved to be favoured by females (Höglund and Lundberg 1987; Höglund et al. 1992; Sæther et al. 2000; Ekblom et al. 2004). Such performance is energetically costly for displaying males, as their daily energy expenditure during a breeding period reaches four times the basal metabolic rate, which is considered to be almost the maximum sustainable work rate for birds. Great Snipe males lose approximately 5% of their body mass during a single night of active lekking (Höglund et al. 1992). Therefore, males must rely on abundant prey available at feeding sites on their breeding grounds, as breeding display constrains the replenishment of energetic resources by foraging during the day. The location of the Great Snipe leks is determined by the proximity of such rich feeding sites, especially with easily accessible and abundant earthworms *Lumbricidae* that compose 90% of the diet in this species (Løfaldli et al. 1992; Kålås et al. 1997; Korniluk et al. 2020). Hence, it is possible, that the availability of high quality food such as earthworms determines the body condition of lekking birds.

Terrestrial earthworms constitute the majority of soil animal biomass in grasslands (Zorn et al. 2005; Hamer et al. 2006) and their availability often determines the richness of the feeding sites for birds (Green et al. 1990; Vickery et al. 2001; Atkinson et al. 2004; Davis et al. 2006). Their vertical distribution in the soil is mainly determined by the soil moisture (Rundgren 1975; Jiménez and Decaëns 2000), as earthworms require the optimal moisture content for maintaining their body hydrostatic pressure and respiration (Bohlen and Edwards 1995). Although the preference for soil moisture is species-specific and may differ with the type of inhabited soil, in most studies the greatest abundance of earthworms was reported at approximately 30% soil moisture content (Grant 1955; Berry and Jordan 2001; Wever et al. 2001; Onrust et al. 2019). This indicates that optimal living conditions for earthworms is neither too dry nor too moist soil and many species of grassland earthworms abandon flooded soil (Plum and Filser 2005; Zorn et al. 2005), even though laboratory studies have shown their ability to survive long periods (14–23 weeks) immersed in the water (Roots 1956; Zorn et al. 2008). The rising level of groundwater during the flooding events causes earthworms to migrate vertically to the soil layers with sufficient oxygen and moisture content (Mather and Christensen 1988; Onrust et al. 2019). Such conditions are favourable to vertebrate earthworms' predators such as gulls, thrushes, and waders, as the accessibility of prey increases with earthworms accumulating in the top layer of the soil (Macdonald 1983; Verhulst et al. 2007; Coulson and Coulson 2008). Hence, the eastern population of the Great Snipe which accounts for the majority of the global population of this species, occupies open grassland habitats, such as floodplains and wet meadows (Kålås 2004). The hydrological conditions on these floodplain meadows are shaped by the water level in the nearby river, which can indirectly affect the quality of feeding sites (Davis et al.

2006). Indeed, floodplain meadows are one of the world's most biologically productive areas (Ward et al. 1999; Tockner and Stanford 2002), that provide optimal feeding conditions for birds during the breeding season and enable refuelling, as they function as a stopover site for migrating birds (Verhulst et al. 2007; Rhymer et al. 2010; Pinchuk and Karlionova 2011), due to the high biomass of soil invertebrates, including earthworms (Zorn et al. 2005; Hamer et al. 2006).

We aimed to investigate the influence of the water level on the breeding site on the body condition of lekking Great Snipe males. We hypothesised that the water level in the Pripyat River flowing through the breeding site of the Great Snipe might have an indirect influence on the body condition of lekking males by affecting the soil hydrological conditions and therefore determining the availability of their prey. It is possible, that with the rise of the level of water in the river hydrological conditions of the soil in the proximate meadow changes towards higher moisture content, which can force the earthworms to move closer to the surface of the ground. This would make them more accessible for foraging Great Snipes which could result in an increase of the body condition of birds.

Materials and methods

Fieldwork

We collected the data in two closely located Great Snipe leks in the floodplain meadows of the Pripyat River near Turov, Gomel Region, Belarus (52° 05′ N, 27° 46′ E) for 20 consecutive years since 2001. In different years up to 70 males stayed in both lekking sites. Birds were captured in mist-nets in the night. To minimize the disturbance of lekking birds, capture events on a given lek did not last longer than 4 h and were separated by a minimum 5-day break. The lek of the Great Snipe starts at the end of April and may last until the end of July (Lemnell 1978; Cramp and Simmons 1983). At the studied site, birds arrived around mid-April and stayed there until the end of June (authors' unpublished data). The exact duration of the lekking period may vary between years and at its early and late stages, it may overlap with other life events of the annual cycle, such as fattening for autumn migration (Lemnell 1978). The floodplain meadows of the middle Pripyat River are an important stopover site for the wildfowl and waders during spring migration (Meissner et al. 2011; Pinchuk and Karlionova 2011; Pinchuk et al. 2016) and some Great Snipes may use this area as a stopover site. Moreover, Great Snipes start moult of primary feathers on their breeding grounds at the beginning of June (Cramp and Simmons 1983; Debayle et al. 2017). The earliest start of moult in the studied population was recorded on the 6th of June (authors' unpublished data). Consequently, we included into the analysis only data collected in May when birds have already established their leks, and moult and preparation for southward migration has not yet started.

The capture hour was noted of each individual. Since birds were captured during the whole month and the length of the night differs between the 1st of May (approximately 9 h of night) and the 31st of May (approximately 7.5 h of night), we defined the time of the capture as the time after the sunset on a given date with accuracy to the nearest half an hour. All birds were weighed with an electronic balance to the nearest 0.1 g and the following measurements were taken: total head length, bill length, nostril length, tarsus length; all these were measured with callipers to the nearest 0.1 mm. Moreover, wing length and tarsus plus toe length were measured with a ruler to the nearest 1 mm (Busse and Meissner 2015). The sex of an individual was identified based on bill measurements according to Höglund et al. (1990). Only males were included in further analyses. Each year the sample size ranged from 3 to 40 individuals, with a total number of 369 male Great Snipes captured and measured during 2001–2020 (additional information on sample size is given in Online Resource 1).

Body condition

The most common approach in studies is to identify individual's body condition as a measure of its state of nutrition and gathered energetic resources, that can be described as indices correcting for the structural size of an individual or as an uncorrected body mass (Labocha & Hayes 2012; Labocha et al. 2014). A preliminary analysis showed that using a body condition index—the scaled mass index (Peig and Green (2009), showed similar results as uncorrected body mass, as it did not remove much noise from the data (Online Resources 1). Moreover, as analyses of uncorrected body mass operates on units of mass, it provides results that are easily comparable between different studies. Therefore, we used the uncorrected body mass of each male Great Snipe as an indicator of body condition based on the amount of energetic resources of an individual.

Hydrological data

Levels of water in the Pripyat River were collected for each day of May at the gauging station in Chernichi, i.e., approximately 3.5 kms from the Great Snipe leks. This data were available for 16 years out of the 20-year study period. We analysed data on 236 individuals, for which the data on their body mass and water level at the breeding site were available (information on sample size and between year variation is available in Online Resources 1). To investigate the influence of the water level on the body condition of male Great Snipes, we took into the account three water levels defined by different periods in which they were measured: (1) the water level on the day of capture, (2) the water level averaged over 5 days preceding the day of the capture and (3) the water level averaged over 14 days preceding the day of the capture. The flooding of the meadow at the studied area started when the water level reached approximately 440 cm. When the water level was about 520 cm, the meadow was almost completely flooded.

We used the '*rtrim*' package in R (Bogaart et al. 2020) to describe the trend in the water level in the Pripyat River. For the TRIM model, we took into account daily water levels reported in 14 days preceding the date of each capture as this model requires long data series. We categorized the water level trend, based on an overall slope computed by the TRIM model, into two categories: increasing and decreasing water level. In three cases the water level was identified as stable. We decided to exclude the data collected over those capture events from further analysis, as the sample size of captured birds was too low and stable water level in rivers is rare during spring (Rawlins et al. 2009).

Statistical analysis

The body mass of lekking Great Snipe males was previously shown to decrease over a single night of lekking (Höglund et al. 1992). Therefore, we used data collected only in the first part of the night, up to 2.5 h hours after the time of the sunset, when we observed the nondecreasing body mass of birds (Fig. 1S) (additional information is given in Online Resource 1).

Generalized Linear Model (GLM) (McCullagh and Nelder 1989) with a log link function and normal error distribution was used to determine, whether the sampling date in the season (continuous, explanatory variable) influenced the body mass of male Great Snipes (continuous, response variable). The sampling date in the season was defined as the number of a day in May with the 1st of May being the 1st day of the season.

A preliminary analysis showed that the relationship between the body mass of male Great Snipes and the water level in the Pripyat River was not linear. Therefore, we applied the Generalized Additive Model (GAM), which is an extension of the Generalized Linear Model (GLM), widely used for analysing non-linear relations, in which the variable may be expanded as smooth functions of covariates (Hastie and Tibshirani 1986). With GAM we modelled the body mass (continuous, response variable) as a function of the water level (continuous, smoothing function of explanatory variable), the trend of the changes of the water level in the river (categorical, explanatory variable) and day of the season (continuous, explanatory variable). We computed GAM separately for each of three water levels defined by different periods. The penalized regression splines with the smoothing parameters selected by restricted maximum likelihood (REML) were used to fit the smooth function for the water level variable. The GAM was computed with the package "mgcv" in R (Wood 2020). We used adjusted R^2, the percentage of explained deviance and one-side ANOVA as a series of likelihood ratio tests to compare GAMs and select the best model describing the changes in the body mass of Great Snipes males. As we decided to use uncorrected body mass as an indicator of birds condition, we also checked if measurements of structural size of individual change with regard to the year and the water level. Since none of those relationships were significant, we did not include the linear measurements into the GAM models as a covariate (additional information is given in Online Resource 1).

Results

Changes of the body mass within a year

We found the decrease in the body mass of lekking males of Great Snipe over the breeding season according to Generalized Linear Model, with insignificant influence of a year as a cofactor (GLM, Wald's statistics = 14.75, $p = 0.01$; Fig. 1). In the first 3 days of May, the average body mass of birds was 156.5 g and by the end of the month, the body mass dropped to 152.2 g. On average, the body mass of birds

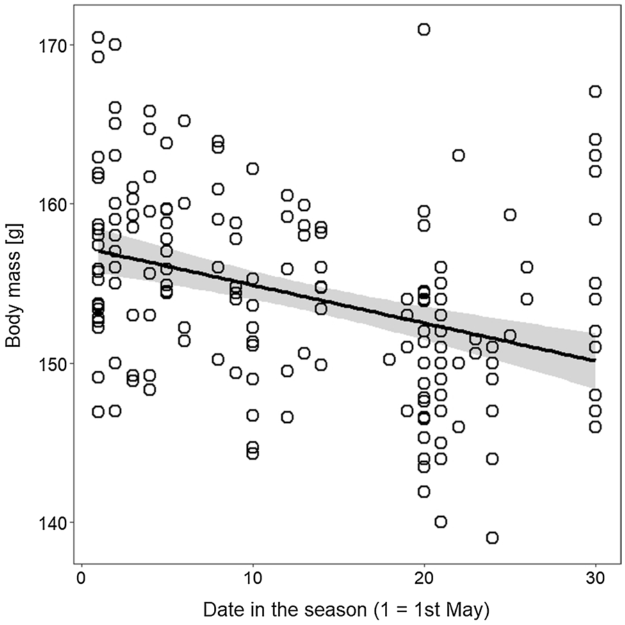

Fig. 1 Relationship between the body mass of lekking male Great Snipes and sampling date in the season. The black line represents a significant relationship estimated with the Generalized Linear Model (GLM, $p < 0.05$) and the grey area represents a 95% confidence interval

declined by approximately 3% over the whole month. Based on the regression function, during May lekking males of Great Snipe lose daily on average 0.15 g of the body mass.

Influence of the water level in the Pripyat River on the body mass

Among all variables incorporated into the proposed models, the date of the capture of an individual in the season had no significant influence on the body mass according to all nine computed Generalized Additive Models (Table 1). The water level and increasing trend in the water level had an effect on the body mass of birds, in contrast to the decreasing trend of water level, that did not influence this parameter (Table 1). Comparison of all nine GAMs showed significant differences (ANOVA, $F = 14.67$, $p = 0.003$), with only two GAMs being different from the rest of the proposed models: model 4, with the body mass explained by the mean water level from 5 days before the day of the capture as a single predictor (Tukey's post hoc test, $p < 0.05$) supported as the best model with the highest percentage of explained deviance and highest adjusted R^2 (Table 1). The second model shown to be different from the rest of proposed models was model 7 with the body mass explained by the mean water level from 14 days before the day of the capture, water level trend and date of the capture (Tukey's post hoc test, $p < 0.05$), presented as the worst fitting model with lowest percentage of explained deviance and lowest adjusted R^2. The remaining seven models did not differ from each other. Hence, only the best fitting model number 4 (Table 1) was used for further analyses.

The body mass of male Great Snipes was relatively stable when the water level in the river ranged from 210 to 440 cm as shown by the smoothed, conditional local means of this parameter (Fig. 2). A higher level of water was related to an increase in body mass until birds obtained the highest score of body mass when the water level was high and reached approximately 490 cm. Further increase in the water level was linked to the decrease in the body mass of lekking birds (Fig. 2).

Two opposing trends in the changes of the water level differently affected the body mass of male Great Snipes (Table 1). The decreasing trend in the water level did not influence the body mass of birds, whereas the increasing trend of changes in water level was linked to an increase in this parameter (Fig. 3). The increase of the body mass was observed until it had reached the maximum value for the available data set at the water level of 471 cm.

Table 1 Parameters of different generalized additive models used to model the body mass (BM) of lekking male Great Snipes

No	Model	Independent variables								Model parameters		
		Water level		Water trend				Day		edf	R^2 adj	Dev. exp
				Increasing		Decreasing						
		p	*F*	*p*	*t*	*p*	*t*	*p*	*t*			
	Water level measured on the day of the capture											
1	BM = s(WaterL1)	0.001	3.99	–		–		–		6.06	0.163	19.8%
2	BM = s(WaterL1) + WaterT	0.044	1.82	0.001	4.58	ns		–		1.26	0.145	16.4%
3	BM = s(WaterL1) + WaterT + Day	0.027	1.73	0.001	2.53	ns		ns		1.49	0.152	17.8%
	Water level averaged over 5 days preceding the day of the capture											
4	BM = s(WaterL5)	0.001	4.25	–		–		–		3.38	0.182	21.2%
5	BM = s(WaterL5) + WaterT	0.012	3.45	0.001	4.18	ns		–		3.39	0.176	20.6%
6	BM = s(WaterL5) + WaterT + Day	0.046	2.55	0.001	3.26	ns		ns		1.41	0.152	17.7%
	Water level averaged over 14 days preceding the day of the capture											
7	BM = s(WaterL14)	0.004	3.53	–		–		–		5.49	0.136	16.9%
8	BM = s(WaterL14) + WaterT	0.009	2.02	0.001	4.30	ns		–		6.05	0.170	20.4%
9	BM = s(WaterL14) + WaterT + Day	0.043	1.79	0.002	3.19	ns		ns		1.79	0.156	18.4%

Effective degrees of freedom, adjusted R^2 and the percentage of deviance explained is given. s() indicates the smooth term, WaterL1—water level measured in the day of the capture, WaterL5—the water level averaged over 5 days preceding the day of the capture, WaterL14—the water level averaged over 14 days preceding the day of the capture, WaterT—trend in the water level, Day—day of the capture in the season, ns—statistically non-significant result, '–'—lack of given parameter in the model

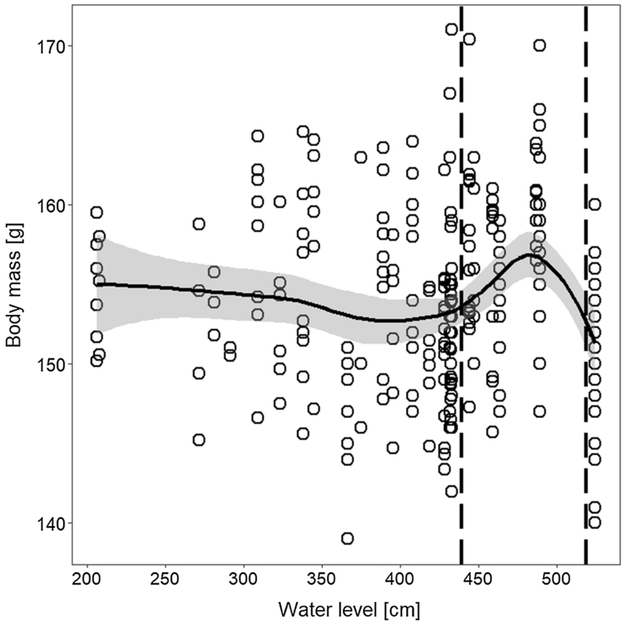

Fig. 2 Relationship between the body mass of lekking male Great Snipes and mean water level of Pripyat River from 5 days before the day of the birds' capture. The line represents smoothed conditional, local means along with the estimated 95% confidence intervals (grey area). The dashed lines indicates the water level at which the water enters the meadows and at which the meadows are totally flooded

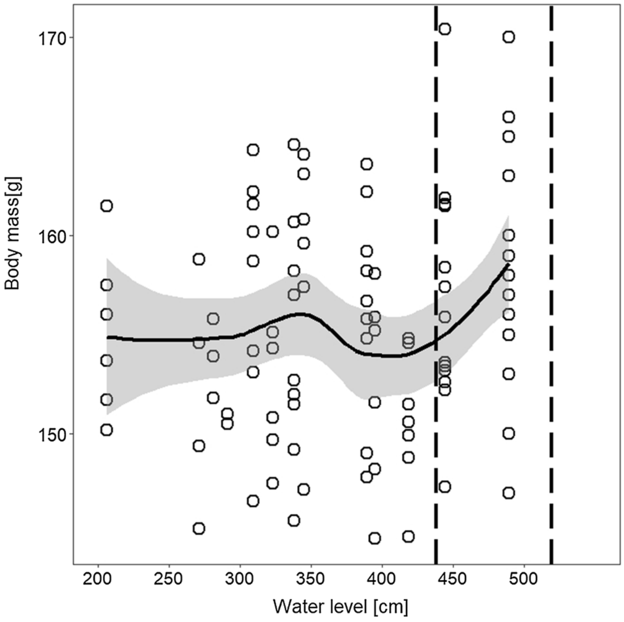

Fig. 3 Relationship between the body mass of lekking male Great Snipes and mean water level of Pripyat River from 5 days before the day of the birds' capture during the increasing trend of water level changes. The black line represents a significant relationship estimated with the smoothed conditional, local means and the grey shaded area represents a 95% confidence interval. The dashed lines indicates the water level at which the water enters the meadows and at which the meadows are flooded

Discussion

Advertising display of males of lekking species is considered energetically costly, leading to loss of energetic resources over the mating season. Such decrease in body condition was commonly observed also in other lekking bird species such as Jackson's Widowbird *Euplectes jacksoni* (Andersson 1994), Black Grouse *Tetrao tetrix* (Hämäläinen et al. 2012; Lebigre et al. 2013), Sage Grouse *Centrocercus urophasianus* (Vehrencamp et al. 1989) and Great Bustard *Otis tarda* (Carranza and Hidalgo de Trucios 1993). The males' constant ability to regain the lost resources is determined by the abundance of feeding sites on the breeding area, but also might reflect the quality of a given male. The body condition of lekking Great Snipes' males decreased over the studied period. Similarly, Höglund et al. (1992) described the loss of the body mass during the course of May in displaying Great Snipes. However, this relationship was significant only according to Generalized Linear Model analysis and was significant in none of the parameterised Generalized Additive Models. We think that the lack of significance of this factor is caused by smaller sample size, as for Generalized Linear Model we used data from 20 years and for Generalized Additive Model we limited the data set to years when data on Pripyat water levels were available. It can be also explained by uneven sampling effort in different years, as in some seasons there was only one capture event or capture events were not distributed evenly over the studied period.

Changes in the water level on the breeding site influenced the body condition of lekking Great Snipe males in our study area. Davis et al. (2006) showed that the water level of the river was responsible for the water-table depth and the soil moisture of adjacent wet meadows, which influenced the abundance of the earthworms in the top layer of the soil. It was hypothesised that hydrological changes in this region do not only influence the soli fauna itself, but as these invertebrates play an important part in the food chain of this ecosystem, it is likely that animals, such as birds are also influenced as they rely on the abundance and accessibility of these invertebrates. The relative stability of the body condition of lekking Great Snipes was observed for most of the range of studied water levels, indicating that the lower water levels (approximately from 220 to 420 cm) did not affect their body condition significantly. In these hydrological conditions, the water table is low and probably does not considerably change earthworms' accessibility for Great Snipes. The remaining, unflooded top layer of the soil is an area of a great thickness, that cannot be totally penetrated with the bill, as Great Snipes have access to maximally 6 cm depth of the top layer of the soil. The stability of the body condition of male Great Snipes at a large range of water levels of approximately two meters, might be an indicator of the high richness of the feeding sites in the proximity of the leks.

With the further rise of the water level beyond approximately 420 cm the body condition of males increased to the point of reaching the highest value at the water level of approximately 490 cm. This pattern was also observed in the trend of water level changes with the rise of the water level in the river. It appears that these hydrological conditions were the most favourable for male Great Snipes, allowing for an increase in the individual's body condition despite the high energetic costs of ongoing lekking. In such hydrological circumstances, the remaining unflooded soil layer is thin, and earthworms are bound to occupy it in great densities. The Great Snipe uses the tactile foraging strategy, probing the soil and mud with a bill in search for prey (Cramp and Simmons 1983), and prefers feeding sites with high soil penetrability (Korniluk et al. 2020). This parameter relies on the hydrological conditions of the meadow, as higher soil moisture can cause the top layer of the soil to become easier to penetrate (Armstrong 2000; Milsom et al. 2002). Therefore, the rise of the water level could not only improve the availability of prey by increasing the density of earthworms at the top layer of the soil, but also change the ground properties towards easier probing. In these circumstances, potentially more area becomes suitable feeding sites for Great Snipes, which might increase their body condition by lowering the need for more distant flights in search for a better feeding place as well as reducing the competition between individuals.

At very high water levels, when meadows are gradually flooded, we observed a decline of the body condition of lekking Great Snipes. At these very high water levels, the feeding conditions probably start to deteriorate, as the earthworms tend to leave the flooded soil (Ausden et al. 2001). There is a strong dependence of the length of wading species' legs and the depth of the water they prefer to forage, with short-legged species preferring shallower water (Baker 1979; Ntiamoa-Baidu et al. 1998). The bill length of Great Snipe males is considerably long, but their legs are relatively short. Therefore, the flooded area gradually stops being attractive for birds, as more possible feeding sites are submerged under water, which is too deep for their relatively short legs, despite Great Snipes' ability to reach the earthworms in the flooded meadow with their long bill. Therefore, individuals face limited access to food resources and the necessity of compensating for the worsening feeding condition, possibly by longer flights in search of higher positioned parts of the meadow. Such flights and increased competition between birds in a limited area of the feeding sites increase the energy demand, which causes an observed decline in the body condition of male Great Snipes. It is also possible that at the high water level states, with rising water level trends, the increase of body condition of male Great Snipes can be caused by the birds accumulating body energetic storages, as a preparation for the threat of worsening feeding conditions due to the approaching flooding event. During such an event, the accumulated energy stores can ensure males' undisturbed mating activity and attendance to the lek, that for many lekking birds was proved to be a factor related to the higher number of copulations and therefore higher mating success (Fiske et al. 1994; Lesku et al. 2012; Jiguet and Bretagnolle 2014). Similar phenomenon was also described in wintering Dunlins *Calidris alpina* during deteriorating thermal and foraging conditions (Kelly et al. 2002).

Changes in the water level of the river may have an indirect impact on the body condition of lekking Great Snipe males by determining the richness of feeding sites. However, it is worth mentioning that the presented models incorporating studied hydrological conditions are characterised by relatively weak statistical support. Therefore, we think that there is a number of other unstudied factors that influence the body condition of displaying Great Snipes, that would require further studies. In other lekking species of birds, it has been proved that more attractive males had higher body condition and that they bear greater energetic costs of producing the attractive secondary sexual trait as well as displaying and maintaining their position at the lek, compared to less attractive or nonbreeding individuals (Andersson 1994; Lebigre et al. 2013; Vehrencamp et al. 1989). For Great Snipes such detailed studies on individual costs of lekking have not yet been investigated, but we think that similarly to other lekking species, individual's changes in the body condition depend on energetic investment in the displaying of a male. Long lasting unfavourable weather conditions may result in decrease of body condition and lowering the lek attendance of lekking males (Vehrencamp et al. 1989; Fremgen et al. 2018). In our study, we were unable to incorporate other environmental factors that could alter the body condition such as ambient temperature, precipitation and wind conditions that can cause variation in body condition of individuals (Gardner et al. 2018). Nonetheless, according to our findings the right hydrological management of grasslands in river valleys is especially important not only for Great Snipes, but possibly also for other earthworm-feeding species and should allow the natural regime of water in the river with its water level fluctuations in spring. Unfortunately, only 37% of long rivers of the world remain free flowing, with dams, reservoirs, water extraction, and sediment trapping disrupting the natural flow of the rest of them (Grill et al. 2019). Those practices, along with diverting wet meadows of river valleys into intensively used agricultural land with excessive fertilization and drainage diches created to lower the level of groundwater, are the main reasons for losing the suitable breeding habitat for wader species of such ecosystems, among other negative effects causing the deterioration of the feeding conditions. Therefore, recently the wader species habituating wet meadows of river valleys suffered a decline in number (Vickery et al. 2001; Verhulst et al. 2007; Onrust and Piersma 2017; Onrust et al. 2019).

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Author contributions MW, PP, WM, NK carried out the fieldwork. MW and ZM statistically analysed the data with MW taking a lead in writing the manuscript.

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

Code availability Not applicable.

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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Supplementary materials for the Research Paper no. 1

1. Sample size and between year variation of body mass

Due to uneven sampling effort in different years the sample size in each year varied. On average we captured approximately 15 birds each year for which the water levels were known (SD = 8.61). The minimal sample size obtained in 2016 was 3 individuals and maximal sample size obtained in 2019 was 36 birds (Table 1S).

Table 1S. The sample size in each year with data on water level available.

Year	Date of capture event	Number of birds captured in a given capture event	Total number of birds captured in a given year
2001	1 V 7 V	11 5	16
2002	22 V 24 V	4 7	11
2003	10 V	10	10
2005	3 V 23 V	7 5	12
2006	8 V	4	4
2008	2 V	12	12
2009	20 V 30 V	11 6	17
2010	21 V	18	18
2011	19 V 26 V 30 V	6 2 8	16
2012	1 V	11	11
2013	14 V 18 V 20 V	6 2 10	18
2014	1 V 9 V	11 6	17
2015	1 V 4 V 6 V 12 V 14 V 25 V	2 6 9 4 5 2	31
2016	4 V	3	3

2019	11 V	2	36
	13 V	4	
	18 V	6	
	19 V	6	
	23 V	9	
	30 V	9	
2020	8 V	2	4
	14 V	2	
Total			236

The Kruskal–Wallis test showed the significant differences in body mass between years ($\chi^2 = 46.852$, $p < 0.001$) (Fig. 1S). The pairwise comparison of body mass in different years showed an among year variation with more than one year responsible for the presented effect (Table 2S).

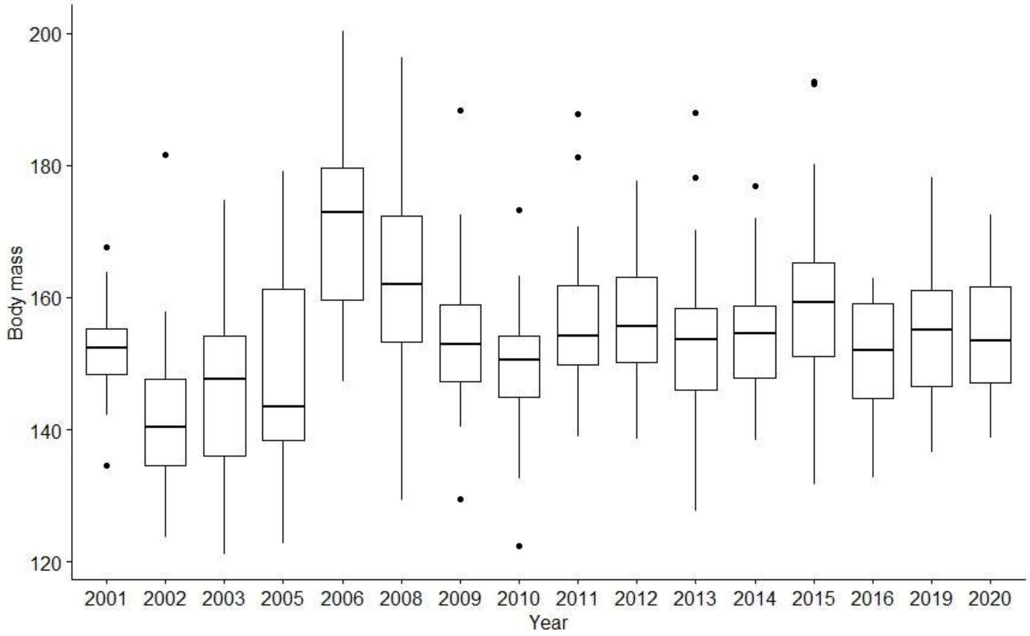

Fig. 1S. Differences in the body mass between years for which the data on water level were available. Line – median, box – 1Q and 3Q, whiskers – minimal and maximal value, dot – outlaying value.

Table 2S. p – values of pairwise comparisons of SMI in different years for which the data on water level were available according to Dunn post-hoc test. * <0.05 ** <0.01 *** <0.001 ns – non significant relationship

	2001	2002	2003	2005	2006	2008	2009	2010	2011	2012	2013	2014	2015	2016	2019	2020
2001	-	ns	ns	ns	**	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
2002	ns	-	ns	ns	***	**	ns	ns	**	**	ns	ns	***	ns	**	ns
2003	ns	ns	-	ns	***	ns	**	ns	**	*	ns	ns	**	ns	*	ns
2005	ns	ns	ns	-	**	*	ns	ns	ns	ns	ns	ns	*	ns	ns	ns
2006	**	***	***	**	-	ns	*	**	ns	ns	**	*	ns	**	*	**
2008	ns	**	ns	*	ns	-	ns	*	ns	ns	ns	ns	ns	**	ns	**
2009	ns	ns	**	ns	*	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	ns
2010	ns	ns	ns	ns	**	*	ns	-	*	ns	ns	ns	*	ns	ns	ns
2011	ns	**	**	ns	ns	ns	ns	*	-	ns	ns	ns	ns	*	na	ns
2012	ns	**	**	ns	ns	ns	ns	ns	ns	-	ns	ns	ns	*	ns	ns
2013	ns	ns	ns	ns	**	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	ns
2014	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	-	ns	ns	ns	ns
2015	ns	***	**	*	ns	ns	ns	*	ns	ns	ns	ns	-	*	ns	*
2016	ns	ns	ns	ns	**	**	ns	ns	*	*	ns	ns	*	-	*	ns
2019	ns	**	*	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	*	-	ns
2020	ns	ns	ns	ns	**	*	ns	ns	ns	ns	ns	ns	*	ns	ns	-

2. Changes of body mass within a night of lekking

Generalized Linear Model (GLM) (McCullagh and Nelder 1989) with a log link function and normal error distribution were used to determine, whether a time of capture (continuous factor, explanatory variable) influenced the body mass of male Great Snipes (continuous factor, response variable).

The body mass decreased over the duration of the night during the lekking season, during the 4.5 hours from the sunset (GLM, Wald's statistic = 6.532, p = 0.011) (Fig. 2SA). In order to obtain the data set collected in the period of a nondecreasing body mass of male Great Snipes, we subsequently repeated the GLM several times, each time excluding the data collected in the last half an hour of the late-night period, until there was no relationship between the body mass and the duration of the night of lekking. The analyses conducted on the data collected from the sunset till the 2.5th hour after the time of the sunset), revealed a lack of relationship between the body mass of birds and the time after the sunset (GLM, Wald's statistics = 1.85, p = 0.174) (Fig. 2SB). Therefore, we decided to exclude data from 11 birds collected from the 3rd to 5th hour after the time of the sunset, which constituted 4.3% of all sampled individuals.

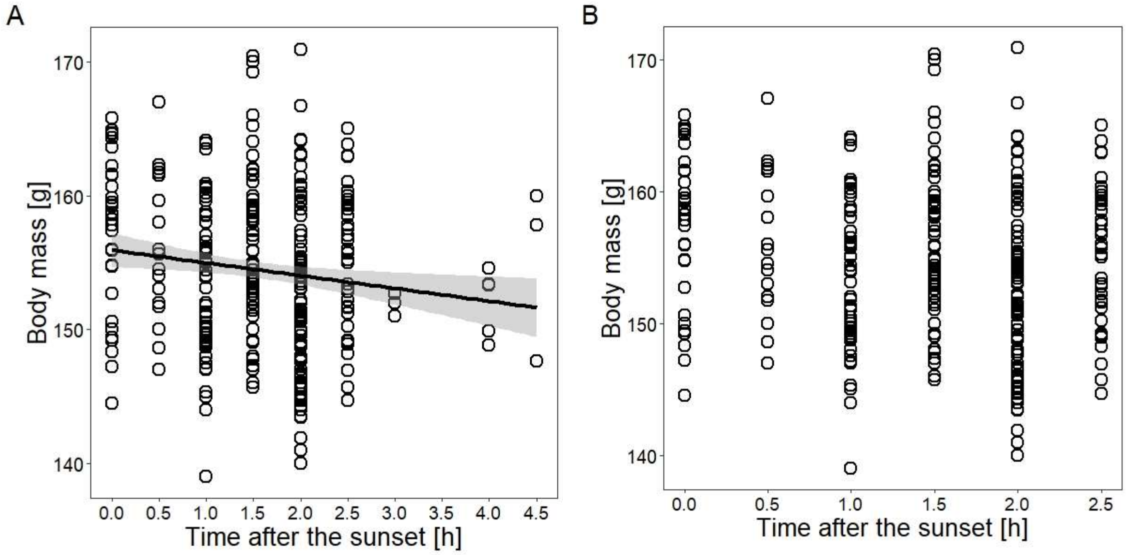

Fig. 2S. Relationship between the scaled mass index of lekking male Great Snipes and the time after the sunset, where 0 = time of the sunset to. Graph A displays a 4.5 hour period after the sunset and graph B displays a 2.5 hour period after the sunset. The black line represents a significant relationship estimated with a generalized linear model (GLM, $p < 0.05$) and the grey area represents a 95% confidence interval for the predicted relationship.

3. The scaled mass index analysis

3.1 The fitting between scaled body mass index and uncorrected body mass

In contrast to other widely used condition indices relying on measures of body mass and linear measures of body size, the SMI is not biased towards larger individuals by taking the true slope of the relationship between mass and length. SMI was calculated as follows:

$$\mathrm{SMI} = \mathrm{M_i} \times \left(\frac{\mathrm{L_0}}{\mathrm{L_i}}\right)^{\mathrm{b_{SMA}}} \quad (1)$$

where $\mathrm{M_i}$ is the body mass, $\mathrm{L_i}$ is a linear body measurement of an individual and $\mathrm{L_0}$ is a mean of the linear body measurement calculated based on data from the studied population. To calculate the $\mathrm{L_i}$ and $\mathrm{L_0}$ values we applied the Pearson correlation on ln-transformed data to check which linear body measurements had the strongest correlation with body mass. Among all linear body measurements, the total head length displayed the strongest correlation (Pearson correlation, $r = 0.378$, $p < 0.005$). The $\mathrm{b_{SMA}}$ value was calculated by dividing the regression line slope by the Pearson correlation coefficient of the linear regression of ln-transformed body mass and total head length.

There was a positive, strong relationship between uncorrected body mass and a scaled mass index of an individual (Pearson's correlation coefficient r = 0.711, p = 0.01, adjusted R^2 = 0.502,) (Fig. 3S), which indicates that SMI does not correct noise in the data to agreat extent.

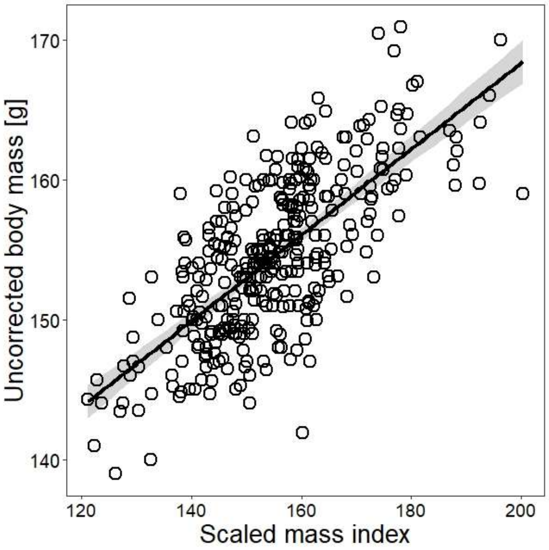

Fig. 3S. Relationship between the scaled mass index and uncorrected body mass of lekking male Great Snipes. The black line represents a significant relationship estimated with the generalized linear model (GLM, p <0.05) and the grey area represents a 95% confidence interval.

4. Variation in linear measurements

4.1 Changes of linear body measurements within years

Linear body measurements did not differ between year according to GLM:

Total Head Length ~ Year (GLM, F = 2.837, p = 0.09)

Bill length ~ Year (GLM, F = 1.701, p = 0.243)

Nostril Length ~ Year (GLM, F = 1.575, p = 0.21)

Tarsus Length ~ Year (GLM, F = 0.065, p = 0.725)

Tarsus plus toe Length ~ Year (GLM, F = 0.055, p = 0.815)

Wing Length ~ Year (GLM, F = 0.004, p = 0.949)

4.2 Changes of linear body measurements with water level in the river

Linear body measurements did not change with changes of water level in the river according to both GLM and GAM with water level stated as a smoothing function.

Total Head Length ~ WaterLvL (GLM, F = 1.541, p = 0.22)

Total Head Length ~ s(WaterLvL) (GAM, F = 3.735, p = 0.0546)

Bill length ~ WaterLvL (GLM, F = 0.701, p = 0.403)

Bill length ~ s(WaterLvL) (GAM, F = 3.753, p = 0.0546)

Nostril Length ~ WaterLvL (GLM, F = 2.618, p = 0.11)

Nostril Length ~ s(WaterLvL) (GAM, F = 1.618, p = 0.24)

Tarsus Length ~ WaterLvL (GLM, F = 0.012, p =0.914)

Tarsus Length ~ s(WaterLvL) (GAM, F = 0.152, p = 0.7)

Tarsus plus toe Length ~ WaterLvL (GLM, F = 3.14, p = 0.78)

Tarsus plus toe Length ~ s(WaterLvL) (GAM, F = 2.08, p = 0.151)

Wing Length ~ WaterLvL (GLM, F = 0.932, p = 0.335)

Wing Length ~ s(WaterLvL) (GAM, F = 0.004, p = 0.949)

Chapter 2

Moult of flight feather and fuelling for southward migratory flight in Great Snipe

Manuscript prepared for publication

The interplay between moult of flight feathers and fuelling conducted on the breeding grounds of the Great Snipe *Gallinago media* from the eastern European, lowland population

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Abstract

The Great Snipe as a long-distant migrant wintering in Africa, faces the challenge of accumulating sufficient energy reserves before the departure from European breeding grounds. Despite possible trade-offs in resource allocation, this species additionally initiates moult of flight feathers before southward migration. Here we discuss the strategy of flight feather moult and fuelling, exploring their scheduling, constrained by the timing of breeding and departure for female and male Great Snipes from the European lowland population. We found significant intrasexual differences in both moult initiation and its duration. Males start moulting more than two weeks earlier and moult faster compared to females. However, neither sex completed this process on breeding grounds before the migration, as late in the season all males and half of the females had suspended their primary moult, with the remaining females not moulting at all. Moult of secondaries occurred exceptionally in the studied population. We observed a non-linear energetic stores gain in the studied period, where both sexes maintained a stable and low body condition until the end of July, coinciding with the primary moulting period. Subsequently, there was an increase in body condition, of approximately 1% of the lean body mass per day, indicating a shift towards fuelling for migratory flight. The overlap between stages of maintaining a stable and low body condition and moulting suggests a resource allocation towards feather growth before initiating fuelling. Our study describes moult strategy in Great Snipe conducted on their breeding grounds, highlighting the intrasexual differences, resulting from different parental duties of males and females of this lekking species.

Key words: primary moult, flight feathers, fattening, wader

Introduction

In the annual cycle of most bird species of the temperate zone, there are crucial life-history events distinguished, such as breeding, migration, and moulting. As all of those are considered energetically demanding processes, which require a large amount of available resources to be fulfilled, birds tend to avoid overlapping them, and by that evade possible trade-offs in energy allocation (Ricklefs 1996, Hemborg & Lundberg 1998, Stutchbury *et al.* 2011). The timing of breeding and migration is for many species environmentally constrained (Wingfield 2008), but there is usually some more flexibility in fitting moult into the annual cycle (McNamara *et al.* 1998, Helm & Gwinner 2006, Conklin *et al.* 2013), which is reflected in a large variety of moulting strategies in birds (Kjellén 1994). For small and medium-sized bird species annual replacement of worn feathers is crucial for their survival and performance in life-history events, due to their functions in a wide range of processes in birds, including but not limited to locomotion, thermoregulation and communication (Terrill & Shultz 2022). Migratory species, and especially those that conduct long-distance flights, should benefit from extending the time of moult, as the structural quality of feather increases with the time it takes for it to grow, which makes them more resistant to wear and could improve the migratory performance (Dawson *et al.* 2000a, Serra 2001a, Vágási *et al.* 2012). On the other hand, most bird species separate active moult and migration, as it compromises fuelling for flight (Swaddle & Witter 1997, Stutchbury *et al.* 2011), and the occurrence of the wing-gap impairs flight, additionally increasing energetical demands (Swaddle & Witter 1997).

Reviewing moult strategies in relation to migration revealed that most wader species that are long-distance migrants do not complete their primary moult on their breeding grounds before the departure (Remisiewicz 2011). Their most common strategies are to conduct moult on stopover sites, or wintering grounds (Kjellén 1994). It is thought to be caused by a longer time available for moulting on wintering grounds, where migrants usually spend a larger portion of the year, with migratory fuelling being the main temporal limitation for the timing of moulting. Moreover, availability of sufficient food resources further constrains scheduling of moult, and for long-distance migratory waders such predicable and rich resources are usually present on their southern, non-breeding grounds (Remisiewicz 2011). In comparison, reproduction carried out on breeding grounds together with the preparation for the southward migratory flight constrains time and resources available for moulting to a greater extent. Therefore, in those few wader species whose strategy is to begin moult on breeding grounds, prior to southward migration, both processes of feather growth and fuelling for a flight might overlap, and since both are energetically costly, birds should compromise resource allocation between them (Lindström *et al.* 1994, Rubolini *et al.* 2002, Bonier *et al.* 2007).

The deposition of fat and protein stores as fuel for flight is a key part of migration, that affects the speed and distance of the flight (Alerstam & Lindström 1990). It is also considered to be a determinant of the whole migration speed, as it takes longer than the migratory flight itself (Lindström *et al.* 2019). Since faster fuelling imposes increased migration speed, long-distance migrants covering a large range in non-stop flights, ought to maximize fuel deposition rates, because arriving sooner to the destination is considered advantageous (Faaborq *et al.* 2010, Morrison *et al.* 2019). However, this process can be limited by ecological factors such as insufficient food availability, or birds' physiological constraints (Lindström 2003). Moreover, other life events may project on fuel deposition, for example in species with females and males having different parental duties, strategies for fuelling may differ between sexes (Mazur *et al.* 2021).

The Great Snipe *Gallinago media* is a wader species known for its lekking behaviour and long-distance migration (Cramp & Simmons 1983). Unlike the majority of waders, the primary moult of adult females and males in this species is initiated on breeding grounds, followed by birds suspending it before the departure, and later completing the process in sub-Saharan Africa (Debayle *et al.* 2017). Studies on migration revealed that males of this species are able to cover a large portion of the migratory distance with one, nonstop flight, with a high speed achieved. After trans-Saharan flight birds stay in the Sahel zone for approximately three weeks before making a second flight further sought to their final wintering grounds (Lindström *et al.* 2016). Moreover, their migration follows a diel cycle, with birds considerably changing their flight altitude between day and night (Lindström *et al.* 2021). Unfortunately, we lack knowledge about similar details of migration strategy and other biological aspects in females, as there is an existing disproportion of research, with most studies focused on males' biology (Klaassen *et al.* 2011, Lindström *et al.* 2016, Korniluk *et al.* 2020, Witkowska *et al.* 2022, 2023). The pre-migratory processes conducted before departure to wintering grounds, such as initiation of moult of flight feathers and fuelling for long-distance, southward migratory flight were not yet investigated both in females and males of this species. Studying those processes would improve our understanding of migration strategy and the completion of moult achieved in Africa. In this work, we aimed to describe the strategy of moulting flight feathers on breeding grounds and fuelling for southward migratory flight for adult Great Snipe of the Eastern European, lowland population. We investigated intrasexual differences in both processes and how they fit together on a temporal scale limited by breeding and departure for wintering grounds.

Materials & Methods

Fieldwork

Data were collected between the year 2000 and 2023 in two locations occupied by the lowland population of Great Snipe (Cramp & Simmons 1983): 1) in the floodplain meadow in the valley of Pripyat River near Turov, Gomel Region, Belarus (52° 05′ N, 27° 46′ E), which is an important breeding and stopover site for waders during both spring and autumn migrations (Meissner *et al.* 2011, Pinchuk *et al.* 2016) and 2) valley of the upper Narew river (52° 55′ N, 23° 39′ E), being an important area for breeding waders. In both sites adult Great Snipes, older than their second calendar year, were trapped with mist nets from June till the early September, corresponding to the late part of the breeding season and the period of preparation for migratory flight for the studied species (Cramp & Simmons 1983). Capturing was conducted on leks and feeding areas. To reduce the disturbance of lekking birds, capture events on leks were limited to 4 hours and were separated by at least 5-day break. In all captured individuals we measured the total head length, bill length and tarsus length (measured with callipers to the nearest 0.1 mm), wing length (all measured with a ruler to the nearest 1 mm), and weight (measured with an electronic balance to the nearest 0.1 gram), according to standard procedure (Busse & Meissner 2015). For each individual we recorded moult formula of primaries and secondaries, representing the stage of moulting of each feather as proposed by (Ginn & Melville 1983). Following this method, each bird's moult state was described as ten digits representing ten primaries and ten digits representing ten secondaries respectively, where old feathers were coded as 0; new, fully grown feathers were coded as 5, and scores 1 to 4 are intermediate stages of feather development. Later, birds were sexed based on body measurements according to Höglund et al., (1990). We did not assign sex to individuals with measurements lying in the intermediate range between females and males. Overall, our sample contained 79 females and 223 males.

Statistical analysis

Body condition

Body condition can be interpreted in various ways, however, in this work, we approached it as an amount of energetic resources gathered by the individual. To quantify it we used two morphometric variables: 1) scaled mass index as proposed in (Peig & Green 2009), where the body mass of an individual is corrected for its structural size and 2) body mass of individuals. The body mass of an individual is commonly interpreted by researchers as a measure of energetic resources gathered by the individual (Labocha & Hayes 2012). Although it may be biased in species with variety in size between individuals, e.g. in species with strong body size sexual dimorphism, using body mass as a predictor of condition may be advantageous, due to its easy interpretation and comparison between studies. Great Snipes exhibit reversed sexual size dimorphism, with females being larger than males (Hoglund *et al.* 1990). To account for differences in body size between sexes, in this study, we used scaled mass index as our primary estimate for body condition in our analysis of factors affecting moult of a primary feather, as well as the process of fuelling before departure. Additionally, we provided descriptive results of the analysis of the fuelling process using body mass, with the full results presented in the Supplementary Online Materials. We also established lean body mass for each of the sexes separately, as the mean body mass of 10% of the lightest individuals.

Moult

In Great Snipe, moult of primaries progresses from the innermost primary towards the outermost primary and generally two or three primaries are being moulted at the same time. In this species moult can be suspended on breeding grounds and later resumed on wintering grounds (Debayle *et al.* 2017).

Based on that knowledge, all birds were grouped into one of the three moult stage categories: 1) moult not started, where we assigned birds with all 10 primaries scored as 0; 2) active moult, where we assigned birds with a number of adjacent primaries actively growing (scored from 1 to 4) in characteristic gradual pattern; and 3) suspended moult, where we assigned birds with a number of fully grown primaries (scored as 5) with the rest of the adjacent primary feathers next in moulting sequence being old (scored as 0). We did not report any individuals with a completed moult, therefore we did not account for such moult stage category. We used Pearson's χ^2 test with p-values computed by Monte Carlo simulation based on the 2000 replicates test to analyse differences in the proportion of birds in three established moult stage categories in a given half-month period, from the first half of June up until the second half of August. Similarly, we used the same statistical test to investigate variation between both sexes among individuals with suspended moult regarding differences in the range of moult of primaries conducted before suspending this process. In that case the range of moult of primaries was described as number of the last, most outermost renewed primary. For each individual, we calculated the Percentage of Feather Mass Grown (later referred to as PFMG) following the method described by Underhill & Zucchini, (1988), based on moult score of each primary and its mass reported for this species (Meissner *et al.* 2018). We used the Underhill-Zucchini moult model (later referred to as UZ moult model), computed with the *moult* package (Erni *et al.* 2013) in R version 4.2.2 (R Core Team 2022), to estimate moult parameters, such as mean start date and mean end date of moult and their standard deviation, as well as the duration of moult. Due to the lack of birds with primary moult finished, we decided to fit the type 5 model (Underhill *et al.* 1990) to our data, using data on birds with not started moult and birds actively moulting, excluding birds with suspended moult. The date of capture of a particular individual was stated as a day of the season, with the 1st of June established as the first day of the season. To determine differences in moult strategy between both sexes and to check for the effect of body condition on this process, we also modelled mean start date, mean end date, and the duration of moult as a function of the sex of an individual and scaled mass index, separately in single-predictor models, as well as a global model including both predictors together. Later all three models with sex and/or body condition estimation as predictors and a starting model containing no predictors were ranked using Akaike Information Criterion corrected for small sample size (AIC_c) and Akaike weights (w_i) (Burnham & Anderson 2004).

As the moult of the secondaries was observed in very limited number of individuals, constituting less than 1% of the whole data set, we were unable to perform any statistical analysis on those. Therefore we chose a descriptive approach to present results concerning this process undertaken by adult Great Snipes.

Fuelling

We considered the same period for analysing fuelling before the southward migratory flight, as we did for moulting, with the 1st of June established as the first day of the season. Preliminary analysis revealed a non-linear change in scaled mass index in time, therefore we decided to use the Generalized Additive Model (GAM) (Hastie & Tibsgirani 1986) to analyse the process of fuelling before departure, where scaled mass index was used as a as a dependent variable. In the set of proposed models, we included a null model, with intercept as the sole factor, the global model with the day of the season as a smooth term, sex, and its interaction with the day of the season as independent variables. We also established two reduced, nested models: a model with the day of the season as a single independent variable, and a model with the day of the season as a smooth term and the sex of an individual as an independent variable. Simillar to the UZ moult models used to analyse primary moult, in case of GAM model selection was carried out based on the Akaike Information Criterion and Akaike weights. Model fit was also described using R^2 and the percentage of explained deviance. The models were fit using *gamm4* package (Wood *et al.* 2020), with model selection performed using *MuMIn* package (Bartoń 2023) in R version 4.2.2 (R Core Team 2022)

Results

During the studied period we captured 12 females and 41 males actively moulting their primaries, as well as 11 females and 24 males showing suspended moult of primary feathers. Only in 3 males we detected signs of secondary mount, with all of them having their moult suspended, where only the first, innermost secondary was renewed, together with 6 (2 males) or 7 (1 male) primaries. The proportion of individuals in a given moult stage category differed between six established half month periods during the studied period both in females (χ^2 test, $\chi^2 = 36.71$, $P < 0.001$) and males (χ^2 test, $\chi^2 = 186.5$, $P < 0.001$). The general pattern showed the increase in proportion of birds with active moult and later with suspended moult in time, combined with the proportion of birds with moult not started decreasing over the season (Fig. 1). In both sexes first birds with active moult were caught in the second half of June and were present in the studied site up until the second half of July. There was no difference in the proportion of birds in different moult stage categories between sexes in the first two established periods (the first and second half of June; Table 1). However, later in the season males had a larger proportion of birds in active and/or suspended moult and a lower proportion of birds with moult not started compared to females. The last males with no signs of moult were captured in the first half of July, whereas females with all old primaries were present until the end of the field study in the second half of August (Fig. 1).

Table 1. Comparison of frequencies of individuals in three moult categories between females and males in the half-month periods, based on the estimates of Pearson's χ^2 test with p-values computed by Monte Carlo simulation with the 2000 replicates. First half of June is excluded, due to only one level of variables (all birds were in the same moult stage category).

Period	χ^2	P
II June (16th June – 30th June)	0.577	0.567
I July (1st July – 15th July)	6.875	0.024
II July (16th July – 31st July)	5.651	0.046
I Aug (1st Aug – 15th Aug)	11.455	0.001
II Aug (16th Aug – 31st Aug)	12.245	<0.001

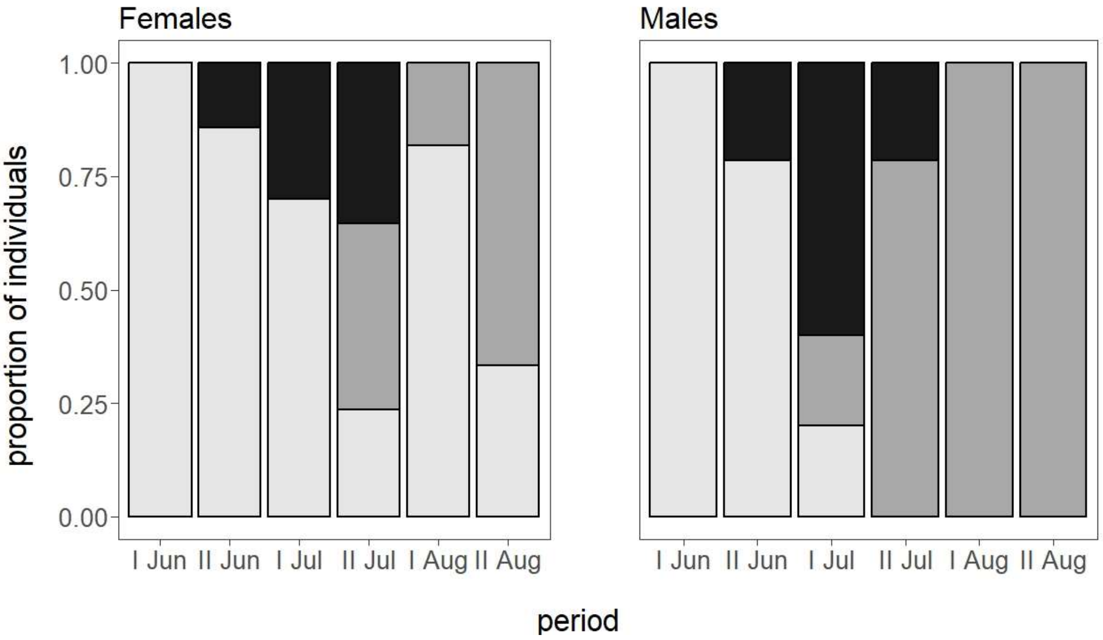

Fig. 1. Proportion of individuals in adult females and males in three different moult stage categories (light grey – moult not started, dark grey – suspended moult, black – active moult) in six consecutive half-month periods.

Females and males significantly differed in the acquired range of the suspended moult (χ^2 test, χ^2 = 26.915, P < 0.001), where majority of females suspended their moult either on the 1st, innermost primary or on the 2nd primary (respectably, 45% and 27% of all females with suspended moult). In males most individuals suspended their moult on the 5th or 6th primary (in both cases 48% of all males with suspended moult). No birds had moulted more than seven primaries before suspending their moult.

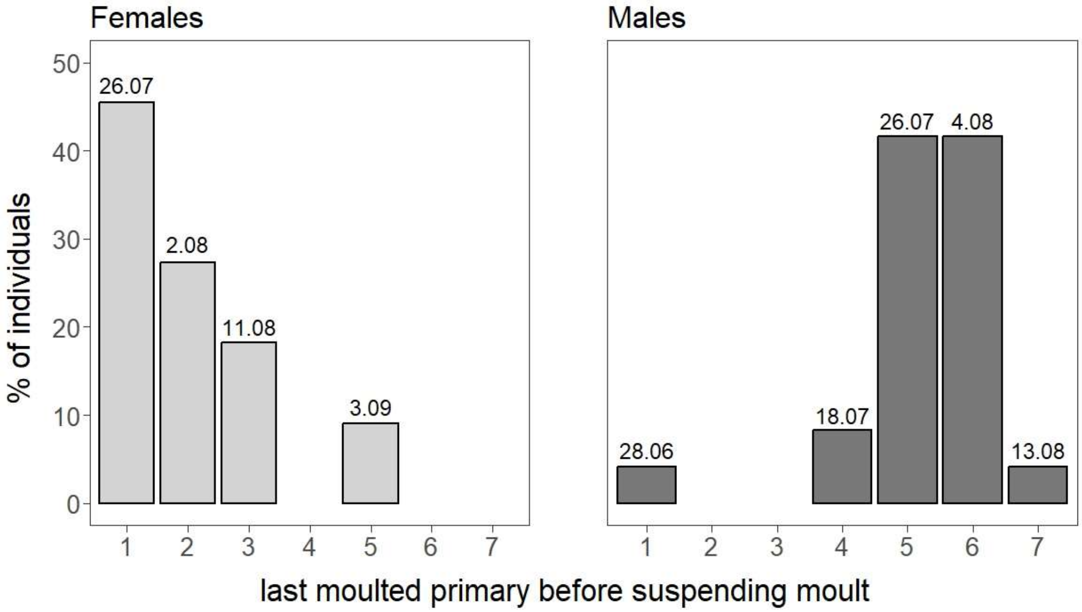

Fig. 2. Percentage of individuals in adult females and males suspending their moult on a given primary. Date of completing moult of a given primary, estimated with UZ moult model type 5 is give above each bar.

The UZ moult model with included sex of individuals as a factor influencing all three moult parameters had the best fit and was the most parsimonious among the set of proposed models, due to the lowest AICc values and the highest w_i values (model UZ1, Table 2). Therefore, presented moult parameters obtained with UZ moult models were estimated based on this model. Including scaled mass index in UZ moult models did not improve their fit (models UZ3 and UZ4, Table 2).

Table 2. Ranking of UZ moult models used to estimate primary moult parameters for adult female and male Great Snipes. K – number of parameters, AICc – Akaike's Information Criterion for small sample size, ΔAICc – difference in AICc between the given model and model with the lowest AICc value, w_i – Akaike weight. Top ranking model with the ΔAICc = 0 and the highest w_i is bolded.

Model ID	Explanatory variables used to model a given parameter			K	AICc	ΔAICc	w_i
	Start date	SD in start date	Duration				
UZ1	**sex**	**sex**	**sex**	**6**	**342.15**	**0**	**0.972**
UZ2	sex	–	sex	5	349.97	7.82	0.020
UZ3	sex + SMI	–	sex + SMI	7	351.74	9.59	0.008
UZ4	SMI	–	SMI	5	363.92	21.77	< 0.001
UZ5	–	–	–	3	371.36	29.21	< 0.001

According to the best fitted UZ moult model (model UZ1, Table 2) males started their primary moult in the end of June (mean start date 24th June) and begin their primary moult on average 26 days earlier in comparison to females (Table 3). In females, the standard deviation of estimated start date was approximately 2.5 times larger than in males. Moreover, both sexes differed in primary moult duration, with males moulting their primaries approximately 1.4 times faster than females, resulting in their moult end date estimated to be on average 61 days earlier, assuming constant and uninterrupted progression of primary moult (Table 3, Fig. 3).

Table 3. Primary moult parameters estimated with the top ranking type 5 UZ moult model (UZ1; Table 1) and sample size of birds in two moult stage categories included in the model.

	Moult Parameters								Sample size	
Sex	Start Date		SD in start date		Duration in days		End Date		Moult stage category	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Moult not started	Active moult
Females	20th Jul	7.28	21.21	7.22	117.01	45.41	14th Nov	7.28	50	12
Males	24th Jun	7.38	8.45	1.02	85.04	46.41	17th Sep	7.38	138	41

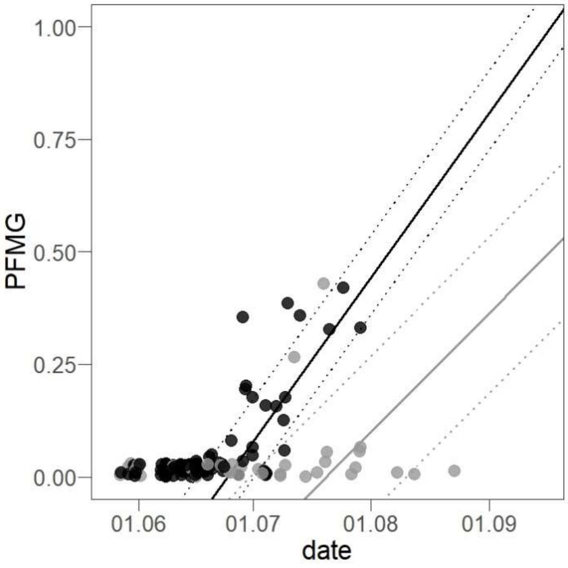

Fig. 3. Changes of the percentage of feather mass grown (PFMG) in the season form females (grey) and males (black). Dots – data points representing individuals with a given PFMG in particular day of the season, line – progression of moult estimated with the type 5 UZ model, dotted line – standard deviation of the moult start date

Ranking of GAM models used to describe fuelling before departure revealed that the global model including day of the season as a smooth term, sex and its interaction with day of the season performed better than other proposed models (model SM1, Table 4). In this model we detected significant influence of the day of the season as a smooth term on scaled mass index and significant interaction between sex of an individual and the day of the season, where stable scaled mass index was detected until approximately 54th day of the season (25th July) with later increase. More rapid increase of this parameter was detected in males than in females (Fig. 4, Table 5). Both sexes however did not differ in overall scaled mass index (Table 5). Analysis including body mass instead of the scaled body mass index yielded similar results (Table 1S, Table 2S, Fig. 1S), however presenting it Supplementary Online Materials allows for the comparison between previous studies using this parameter.

Table 4. Ranking of GAMs estimating the relationship of scaled mass index with sex and day of the season. 1 in model formula indicates null model with only intercept included as an independent variable. s() – independent variable used as a smooth factor, + - additive relationship, * - interaction between variables, edf – effective degrees of freedom, AICc – Akaike's Information Criterion for small sample size, ΔAICc – difference in AICc between the given model and model with the lowest AICc value, w_i – Akaike weight. Adjusted R^2 and percentage of explained deviance is given. Top ranking models with the ΔAICc < 2 are bolded.

Model ID	Model formula	edf	AICc	ΔAICc	w_i	adj. R^2	% Dev. Exp.
SMI1 (global)	**SMI = s(day) + sex + sex*day**	**9.07**	**2101.19**	**0**	**0.987**	**0.529**	**54.2%**
SMI2	SMI = s(day) + sex	8.23	2109.89	8.72	0.013	0.512	52.3%
SMI3	SMI = s(day)	6.22	2383.57	282.38	< 0.001	0.434	44.2%
SMI4 (null)	SMI = 1	2	2546.73	445.54	< 0.001	<0.001	0%

Table 5. Results of top ranking GAM (SMI1) explaining the relationship between scaled mass index and sex, interaction between sex and the day of the season and day of the season as a smooth factor.

Fixed effect	Estimate	SE	*z*	*P*
Intercept	47.57	3.87	12.29	<0.001
sex (M)	4.00	3.27	1.23	0.22
sex (M) * day	0.25	0.08	3.27	0.001
Smoothed term			*F*	*P*
s(day)			118.9	<0.001

We established the lean body mass of males as 142.5 g (SD = 3.06) and females as 148.5 g (SD = 3.93). The mean body mass obtained in first 49 days of the study period was higher than the estimated lean body mass, as in this period average mass of males was 154.0 g (SD = 7.13) and females was 178.0 g (SD = 18.7), with both sexes indicating having stored some fat and protein (Fig. 1S). Predictions for the mass gain made from the best fitted model (Table 1S) indicated an average body mass of 224.3 g for males and 245.6 g for females obtained on last, 91th day of the season (31st August). Assuming average mass from the period of stable body mass as a starting point for mass gain before the departure, males of Great Snipe accumulated 1.63 g per day corresponding to 1.12% of their lean body mass, and females gained 1.57 g per day corresponding to 1.06 % of their lean body mass (Fig. 1S, Table 2S)

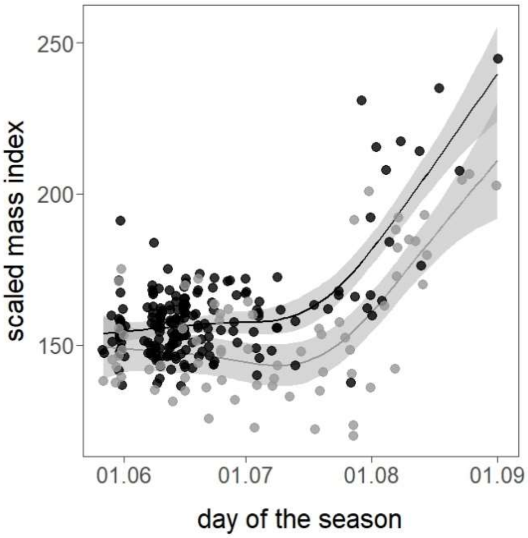

Fig. 4. Changes of scaled mass index during the season in adult females (grey) and males (black). Line – significant relationship estimated with the Generalized Additive Model, grey area – 95% confidence interval.

Discussion

Previously obtained results on the African wintering ground of the Great Snipe suggested that both females and males suspend their primary moult prior to departure from their breeding grounds (Debayle *et al.* 2017). Similarly, in our data we found a large proportion of individuals (all males and majority of females) suspending their primary moult, and no birds with active moult detected at the end of the studied period. Moreover, estimated end dates of the primary moult indicate that males should complete the exchange of their primaries in mid-September and females in mid-November. At this time both male and female Great Snipes already arrive at their wintering grounds (Lindström *et al.* 2016, Debayle *et al.* 2017), which means that Great Snipes are unable to conclude this process at their breeding grounds. Although the beginning of flight feathers moult on breeding grounds is rare in long distant migratory waders (Kjellén 1994, Remisiewicz 2011), this strategy may be advantageous, as migrants should benefit from expanding their flight feathers moult duration, since slowly grown feathers are of better quality (Dawson *et al.* 2000b, Serra 2001b). Great Snipes may exploit rich feeding sites at their breeding grounds and use resources still available there to partially moult their flight feathers. Than the moult is suspended to avoid migrating with actively growing feathers and with a gap in the wing area, which can generate additional costs for this already demanding process (Swaddle & Witter 1997). Great Snipes resume their flight feathers moult as soon as they reach sub-Saharan Africa in late August, and possibly finish this process before conducting their second, relatively short, intra-African flight. However, Debayle et al. (2017) suggested that some birds may be unable to conclude moult before this intra-African migration and are forced to again suspend their moult or fly with primaries still growing. Therefore advancing the process of flight feathers moult still on breeding grounds might be advantages, as it allows for reducing the amount of time and resources needed for completion of this process on their wintering grounds.

We detected a suspended moult of secondaries only in three males. Moult of secondaries usually starts later than moult of primaries and after reaching a certain threshold of a number of renewed primaries (Summers et al. 2004, Pinchuk & Meissner 2023 personal communication). Indeed, in all three cases birds with signs of started secondary moult were also advanced in their primary moult. It seems however, that moulting of secondaries on their breeding grounds is rather rare in Great Snipes, and majority of individuals conduct this process after reaching wintering grounds.

Female and male Great Snipes have different course of primary moult, with males starting moult earlier in the season and moulting faster compared to females. Moreover, males were characterized by a larger moult range, with a majority of males being able to renew far more primaries before suspending their moult than females. These results are consistent with findings reported by (Debayle *et al.* 2017), where females were less advanced in primary moult than males upon arrival to sub-Sharian Africa. Primary moult end dates given in this study for both sexes are estimated to be approximately one month ahead of dates reported in reality, as on wintering grounds a majority of males finish this process in November, and females in December (Debayle *et al.* 2017). This discrepancy can be explained by the fact that after suspending the moult on breeding grounds both sexes conduct migratory fuelling and later the migratory flight. This creates a temporal delay in the overall completion of moult. The sex-based differences in primary moult timing are most probably caused by the female-only parental care in this lekking species. In June males are still attending leks (Cramp & Simmons 1983), and displaying is an energetically demanding activity (Höglund *et al.* 1992), however, its intensity is possibly lower than in a peak lekking period in May, as suggested by the stable body mass of males at that time (Höglund *et al.* 1992, Witkowska *et al.* 2022). On the contrary in June females are still incubating, rearing the chicks, and investing resources in this process may constrain the initiation of moult. Similar pattern was found in the Purple Sandpiper *Calidris maritima*, where males that are responsible for chick rearing had delayed moult of flight feathers in comparison to females that finish their parental duties after the hatching of eggs (Summers *et al.* 2004). Even slight difference in breeding investment, caused by female producing the clutch may cause delay in the onset of moult. In wader species with parental duties being equally divided between females and males, females begin the process of moult later (Rogers *et al.* 2014, Machín *et al.* 2018).

In females, the standard deviation in the start date of primary moult was relatively large indicating the uncertainty of this estimate. Indeed, in our sample, we noted females with the timing and extent of primary moult resembling those of males, as well as females that did not yet start moulting very late in the studied period, and it is unlikely that they will initiate their moult of flight feathers on breeding grounds. We suggest that females may execute various strategies of primary moult, which possibly can be related to the breeding success of a particular individual. In birds underlying hormonal regulation of moult imposes that maintained breeding activity, causing elevated level of sex-hormones, delays the timing of moult (Dawson 2008). Females with lost broods may moult earlier in the season and at a faster pace, similar to males that are unburdened with parental duties. On the contrary, females with breeding success and therefore large energy expenditure in the chick-rearing period probably moult late in the season, or postpone the moult altogether, until the arrival to the wintering grounds. Indeed, in sub-Saharan Africa, there were some females recorded without any signs of moulting of the flight feathers upon their arrival (Debayle *et al.* 2017). Hence, provided estimates of the primary moult parameters for females based on the Underhill-Zucchini moult model, describe only a general tendency in the primary moult in females.

We found that the scaled body mass index of an individual did not significantly improve the fit of the Underhill-Zucchini moult models, indicating that body condition reflecting the amount of stored energetic resources was not a good predictor for variation in the primary moult parameters. Great Snipes can utilize their fat stores at a quick pace, resulting in large variations in their body mass within a single day (Höglund *et al.* 1992, Witkowska *et al.* 2022). It is possible, that the way of measuring body condition used in this study reflected a current nutritional state of an individual rather than its general quality, albeit a link between a progression of moult and stress caused by malnutrition was shown in other birds (DesRochers *et al.* 2009). Moreover, a negative relationship between moult and the amount of stored energetic resources was described in other bird species (Portugal *et al.* 2007, Alfaro *et al.* 2018), as the overall process of moulting is energetically demanding (Rubolini et al. 2002), with resources used not only for the sole purpose of producing the structure of the feather but also maintaining tissue responsible for the whole process, as well as additional costs related to impaired thermoregulation and flight ability (Buttemer *et al.* 2020). However, larger birds with the slow pace of feather exchange have a relatively low level of daily energetic expenditure devoted to the process of moulting (Lindström *et al.* 1993), that compromise neither flying nor thermoregulation (Hahn *et al.* 1992). Moreover, the lean body mass of birds during the moult changes considerably (Murphy & King 1992, Lind *et al.* 2004), including the ratio of pectoral muscle size to body mass (Lind & Jakobsson 2001), which). Hence, it may explain insignificant influence of the scaled body mass index on primary moult parameters.

In the studied period we detected a non-linear course of fuelling in both female and male Great Snipes. At the beginning of the studied period, birds of both sexes exhibited stable, low scaled mass index reflecting the amount of energetic stores corrected for body size of an individual. This period lasted until the approximately 54th day of the season (25th of July). The stable body mass of lekking males in this period was described in previous studies on the Scandinavian Great Snipe population. This stability, attributed to increased energy intake in late breeding stages, was linked to improved foraging opportunities resulting from snow melt and milder weather conditions (Höglund & Lundberg 1987).

However, the lowland population of the Great Snipe do not face such harsh environmental conditions as their Scandinavian conspecifics breeding in the mountains, therefore we think that this explanation is unlikely for birds studied in this work. Stable body condition may be caused by less intense displaying in the late breeding season combined with resource allocation toward the moulting of primary feathers. In females, we also did not find a decrease in those parameters, although chick rearing is considered energetically demanding (Tulp *et al.* 2009, Neubauer *et al.* 2017). We think that suitable conditions on the studied site, ensuring rich feeding sites in a wide range of environmental conditions, create environmental allowing females to maintain the stable body condition, while delaying the onset of their moult (Williams 2018). The period of stable, low body condition overlapped with the time of the moult for males Great Snipe and moult and/or chick rearing of females. The last birds, (two females and one male) with active moult were detected in our sample on the 58th day of the season (29th of July). Moreover, as most males suspend their moult on the 5th or 6th primary, and females on their 1st or 2nd primary, we could predict based on the modelled duration that the majority of males should suspend their moulting on breeding grounds on the 55nd to 64st day of the season (27th July and 4th August respectively) and females should do so from 55th to 62th day of the season (26th July and 2nd of August). This indicates that moulting and fuelling for migration do not overlap or overlap to a small extent, and indicates the trade-off in resource allocation between those two processes.

In the studied period both females and males had similar energetic resources stored, but significant interaction between sex and day of the season in the changes of the scaled mass index over time, indicates that males increase their energetic stores at a faster pace compared to females. Males end their breeding performance before females, as they do not participate in chick rearing, and are able to finish their moult sooner, despite having a larger range of exchanged primaries. This leads to effectively more time for males to exploit resources and fuel for migration, which could account for this effect. Moreover, males arrive sooner to sub-Saharan Africa compared to females, explaining their need for more rapid fuelling (Debayle *et al.* 2017). The overall rate of fuelling and maximum mass obtained in both sexes was similar to mass gain rates reported for fuelling on wintering grounds, before northward migratory flight (Debayle *et al.* 2017). Still, comparing the fuel load of other waders of a similar size (Gudmundsson *et al.* 1991, Kvist & Lindström 2003, Piersma *et al.* 2005), the fuelling rate presented in our study is relatively low for a long-distance migrant, covering 5000 km with a non-stop flight (Lindström *et al.* 2016). As Great Snipes begin moult of their wing feathers on breeding grounds prior to fuelling and as there is some plasticity in the extent of moult between individuals, it seems that gathering energetic stores for flight is not greatly time constrained. It is possible that we failed to detect fat Great Snipes ready for departure, although this would be the second attempt to describe the process of fuelling for migratory flight in this species that would do so (Debayle *et al.* 2017). Great Snipes reach Sub-Saharan Africa in late September (Debayle *et al.* 2017), and the last birds that we were able to measure in this study were caught on 1st of September. Time necessary for conducting trans-Sahara flight takes up to 3 days of non-stop flight (on average 64 hours) for Great Snipe males of Scandinavian population (Lindström *et al.* 2016). Therefore, there is still time left for Great Snipes to accumulate sufficient energetic stores before departure from European breeding grounds, especially that birds might increase their energy intake for more rapid migratory fuelling before departure (Meissner *et al.* 2011, Lindström *et al.* 2019).

Conclusion

In this study, we examined the primary moulting and fuelling strategies of Great Snipes, highlighting the balance between the reproductive efforts, moult, and migratory preparation for this species. Our research supported previous findings from wintering grounds, indicating that both females and males of this species suspend their primary moult before departing from their European breeding grounds. Males initiate primary moult earlier, moult faster resulting in a larger moult range of renewed primaries, compared to females. The intersexual differences in primary moult strategies stem from distinct parental roles within this lekking species. Females, responsible for incubation and chick rearing, might delay their moult, whereas males, unburdened with parental duties could begin moulting their flight feathers earlier. We observed a non-linear pattern of fuelling in both female and male Great Snipes. Stable and low body condition was maintained until late July overlapping with moult and/or chick-rearing period, suggesting a trade-off in resource allocation between these processes. Later in the season body condition increased, however, the fuelling rate of 1% of the lean body mass increase per day observed in Great Snipe appeared relatively low for a species undertaking a long-distance migration. It is possible that the accumulation rate of fat stores increases towards departure, similar to other wader species.

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Authors contribution

MW: Conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing – original draft, writing – review and editing

MK: Conceptualization, data curation, investigation, methodology, writing – review and editing

PP: Conceptualization, data curation, investigation, methodology, writing – review and editing

TT: Data curation, investigation, writing – review and editing

NK: Data curation, investigation, writing – review and editing

WM: Conceptualization, data curation, investigation, methodology, writing – review and editing

Ethical note

All conducted procedures were in accordance with Belarussian law. Capturing of Great Snipes in Poland was possible based on the permission from the General Directorate for Environmental Protection DOP-OZ.6401.03.337. 2012.dł.

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Conflict of interest

The authors declare there is no conflict of interest.

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Supplementary materials for the Manuscript prepared for publication

In this work to analyse the process of fuelling before departure, we decided to additionally present the second set of models using body mass instead of the scaled mass index as a dependent variable. We included a null model, with intercept as the sole factor, the global model with the day of the season as a smooth term, sex, and its interaction with the day of the season as independent variables. We also established two reduced, nested models: a model with the day of the season as a single independent variable, and a model with the day of the season as a smooth term and the sex of an individual as an independent variable. Model selection was carried out based on the Akaike Information Criterion and Akaike weights. In the case of models with delta AICc lower than 2, indicating their similar parsimony the estimates were derived from full model averaging (Burnham & Anderson 2004). Model fit was also described using R^2 and the percentage of explained deviance. The models were fit using *gamm4* package (Wood *et al.* 2020), with model selection and averaging performed using *MuMIn* package (Bartoń 2023) in R version 4.2.2 (R Core Team 2022)

Ranking of GAM models used to describe fuelling before departure revealed similar results in both sets of models with either body mass or scaled mass index as a depended variable. In case of the first set of models, two top ranking models were distinguished as similarly parsimonious based on their ΔAICc < 2 and approximate values of w_i, as well as having similar fit to the data (models BM1 and BM2, Table 1S). These models included day of the season as a smooth term, sex and/or interaction between sex and day of the season. Averaging their results indicated that the day of the season as smooth term significantly influenced body mass, where this parameter was stable till the approximately 49th day of the season (20th July) with later increase (Fig. 1S, Table 2S). Moreover, females had significantly higher body mass compared to males, with statistically insignificant interaction between sex and day of the season as an independent variable (Table 2S).

Table 1S. Ranking of GAMs estimating the relationship of body mass with sex and day of the season. 1 in model formula indicates null model with only intercept included as an independent variable. s() – independent variable used as a smooth factor, + - additive relationship, * - interaction between variables, edf – effective degrees of freedom, AICc – Akaike's Information Criterion for small sample size, ΔAICc – difference in AICc between the given model and model with the lowest AICc value, w_i – Akaike weight. Adjusted R^2 and percentage of explained deviance is given. Top ranking models with the ΔAICc < 2 are bolded.

Model ID	Model formula	edf	AICc	ΔAICc	w_i	adj. R^2	% Dev. Exp.
A) Body mass as a dependent variable							
BM1	**BM = s(day) + sex**	**9.13**	**2142.77**	**0**	**0.579**	**0.692**	**70.0%**
BM2 (global)	**BM = s(day) + sex + sex*day**	**10.08**	**2143.41**	**0.64**	**0.421**	**0.632**	**70.2%**
BM3	BM = s(day)	8.22	2463.71	320.94	< 0.001	0.568	57.7%
BM4 (null)	BM = 1	2	2705.30	562.53	< 0.001	0.000	0%

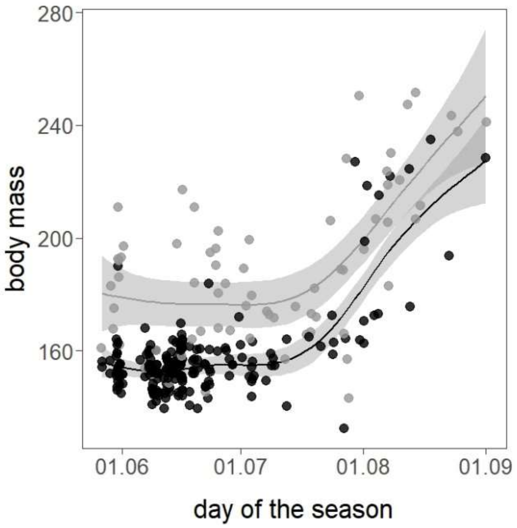

Fig. 1S. Changes of body mass during the season in adult females (grey) and males (black). Line – significant relationship estimated with the Generalized Additive Model, grey area – 95% confidence interval.

Table 2S. Results of top ranking GAMs (BM1 i BM2 averaged) explaining the relationship between body mass and sex, interaction between sex and the day of the season and day of the season as a smooth factor.

Fixed effect	Estimate	SE	*z*	*P*
intercept	134.67	56.85	2.37	0.018
sex (M)	-22.72	3.19	7.10	<0.001
sex (M) * day	0.04	0.07	0.56	0.57
Smoothed term			*F*	*P*
s(day)			60.51	<0.001

Overall using body mass instead of scaled mass index for describing the process of fuelling for the migratory flight in Great Snipes gave similar results. The two differences reported are:

- Sex was a significant factor influencing body mass, but not scaled mass index. This is caused by the sexual dimorphism in size in Great Snipes, where females are the bigger and, therefore heavier sex (Hoglund *et al.* 1990).
- Males increase their energetic stores at a faster pace compared to females, although this effect was detected only in model using the scaled mass index as a dependent variable. This is possibly due to the presence of one small male, with relatively small body mass caught late in the season, that resulted in insignificant interaction between sex and day of the season. We decided to not treat this record as an outlier, as this individual gathered sufficient energetic stores for this period, when its body mass was corrected by its body size

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Chapter 3

Annual apparent survival of Great Snipe males

Research Paper no. 2

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

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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 ($\Phi(.)$, $p(.)$), 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 ($t \times$ (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

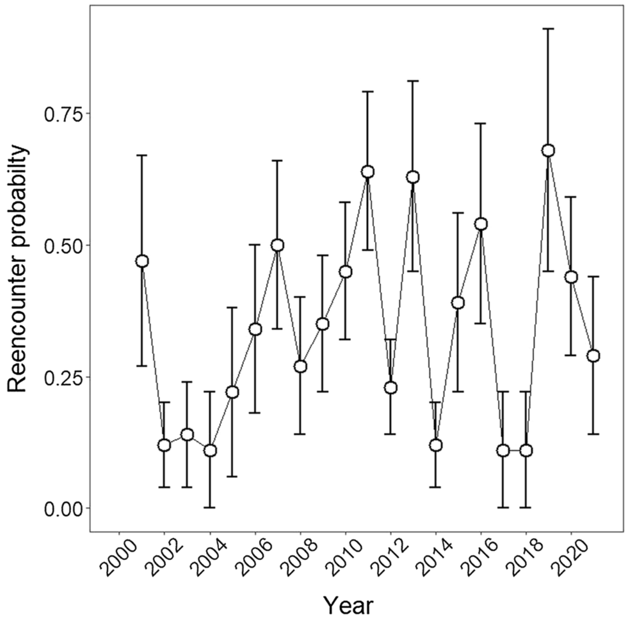

Fig. 1 Annual variation in reencounter probability of adult male Great Snipes. Estimates are made based on the best supported time-dependent model. White dot—mean reencounter probability in a given year (*p*), bars—standard error, black line—a link between subsequent seasons

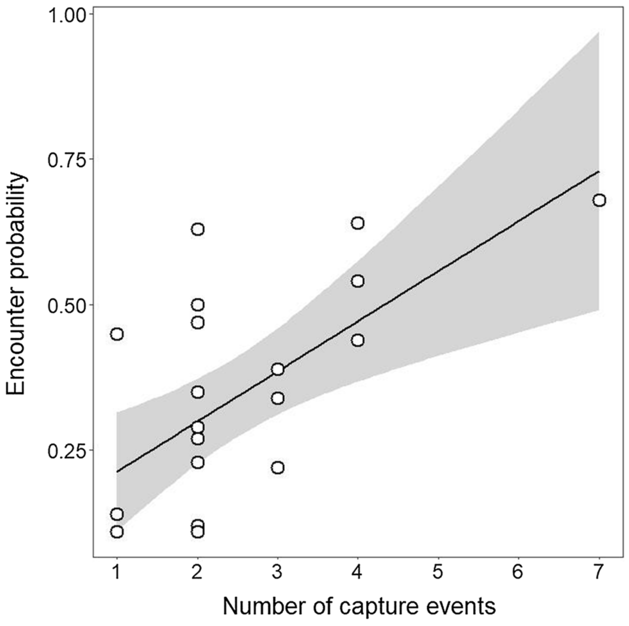

Fig. 2 Relationship between a number of capture events in given season and probability of reencounter. The 95% confidence interval is given

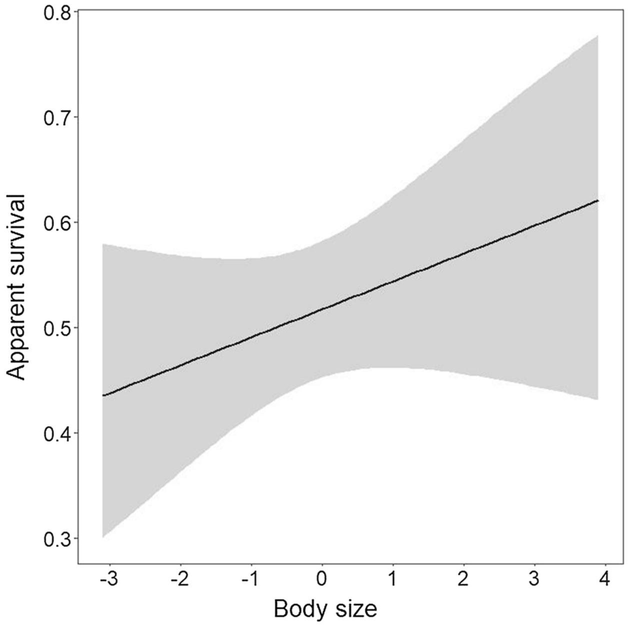

Fig. 3 Relationship between mean apparent survival estimated by the second-highest ranked model and the body size of an individual established as a PC1 value from linear body measurements. The 95% confidence interval is given

capture effort influencing the probability of reencounter $\chi^2 = 11.5$, $P = 0.66$, compared to the global model with 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, $F_{1.19} = 0.06$, $P = 0.79$).

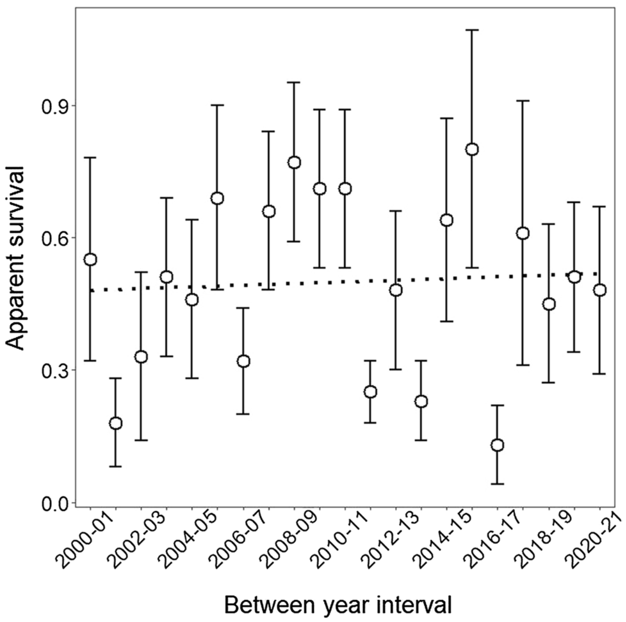

Fig. 4 Annual variation in apparent survival of adult male Great Snipes. Estimates are made based on the best supported time-dependent model. White dot—mean annual apparent survival (Φ) in a given time interval, bars—standard error, dotted line—a stable trend of apparent survival changes in the time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

In my doctoral thesis, I discussed the energetic costs of advertising displays, as well as a link between hydrological conditions, food availability, and body condition of lekking male Great Snipes. The observed decrease in the body condition over the studied period supports the previously described increased energy expenditure of lekking males. Changes in the river's water level on the breeding site indirectly influenced the body condition of studied birds, by affecting their prey availability. Stable body condition was observed within a certain range of the water levels, indicating suitable richness of feeding sites. High water levels in the river were linked to an increase in body condition, probably due to increased availability of food resources, as earthworms are forced to move the surface of the ground. Further increase in water caused a decrease in the body condition, likely due to deteriorating feeding conditions and increased competition between individuals. Obtained results emphasize the indirect impact of the river and soil hydrological parameters on the state of birds occupying floodplain meadows, and the importance of a natural water regime to support suitable breeding habitats for Great Snipes and other grassland bird species.

Studying the process of moult and fuelling of adult Great Snipes revealed sex-specific differences in both processes. Males exhibit earlier and faster moult of primaries, which enables them to exchange more primaries on their breeding grounds compared to females. Additionally, all studied males were able to initiate their moult on breeding grounds, in comparison to only half of all females. This delay of flight feather moult in females is related to female-only parental care characterizing this lekking species, with flexibility in this process being most probably related to their breeding success. Presented results support and complete the knowledge obtained on wintering grounds on moult of flight feathers in this species, indicating that Great Snipes are indeed unable to finish this process on breeding grounds, leading to its suspension. The non-linear course of fuelling is observed in both sexes, with minimal overlap between fuelling and moult, indicating their temporal separation, due to a trade-off in resource allocation. Intra-sexual differences in fuelling were identified, with males increasing their stores at a faster pace than females. Males finish breeding performance sooner and should depart earlier than females, explaining their faster fuelling for migratory flight. Obtained results suggest a relatively low fuelling rate for a long-distance migrant. However, I suspect that Great Snipes can increase their energy intake closer to departure, as they have more time to accumulate energy stores beyond the studied period.

The estimated apparent annual survival of adult male Great Snipes was relatively low ($\Phi(.) = 0.43$). This species exhibits energetically demanding life-history traits, including lekking and long-distance migratory flights and the metabolic costs associated with these activities could contribute to the lower survival rates. On the other hand, models used to estimate apparent survival do not difference between mortality and permanent emigration, therefore relocation of males between leks might have led to an underestimation of the apparent survival values. Large fluctuations of apparent annual survival are expected to be found in a food specialist, such as the Great Snipe, as stochastic environmental factors may largely change crucial prey availability between years. Despite the described variability in survival between years, the long-term trend in apparent survival remained stable, indicating the overall good state of the studied breeding population, and possibly the condition of its occupied habitat. Smaller males were observed to have a reduced apparent survival, possibly due to their limited foraging options. Although demographic characteristics obtained for males provide valuable information, in polygenic species like lekking birds, the survival of the adult females and chicks, as well as the recruitment rate is crucial for gaining knowledge on the stability of the population. As the global population of Great Snipes declines, the need for obtaining those estimates is more pressing.

Body condition did not significantly impact the survival of adult Great Snipe males, as well as moult parameters for both sexes. At the same time, the obtained results indicated an increase in body condition when birds were increasing their energetic stores, caused either by the increased availability of food resources or the context of an event of an annual cycle when birds undergo pre-migratory fuelling. I argue that although using morphometric indices of body condition may serve as meaningful indicators of the amount of energetic stores gathered by an individual, in case of the studied species it does not reflect an overall quality of a bird and therefore fail to predict its fitness.

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2. Witkowska M., Pinchuk P., Meissner M., Karlionova M. 2023. Body size constrains the annual apparent survival of lekking Great Snipe Gallinago media males of eastern, lowland population. Journal of Ornithology. https://doi.org/10.1007/s10336-023-02091-7

My role was: conceptualization, methodology, data collection, formal analysis, writing – original draft, review and editing, funding acquisition

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My role as co-author of these papers was to: participating in the conceptualization of the work, assisting in the field research, manuscript review and editing, and supervising.

I confirm also that Marta Witkowska was the leading author in both papers. She collected data in the field, carried out the formal analysis, developed the concept, wrote the manuscript and acted as correspondence author.

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My role as co-author consisted in: formal analysis

I confirm that Marta Witkowska was the leading author of this work. She collected data in the field, conducted formal analysis, conceived and wrote the manuscript and played the role of corresponding author.