"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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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 (Φ(.) = 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.

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