Wybiórczość siedliskowa i strategia użytkowania tokowisk przez samce dubelta *Gallinago media* w okresie lęgowym

Habitat selection and lek use strategy of breeding male Great Snipes *Gallinago media*

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Spis treści

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Spis publikacji

1. Korniluk M., Białomyzy P., Grygoruk G., Kozub Ł., Sielezniew M., Świętochowski P., Tumiel T., Wereszczuk M., Chylarecki P. 2021. Habitat selection of foraging male Great Snipes on floodplain meadows: importance of proximity to the lek, vegetation cover and bare ground. Ibis 163: 486–506; DOI: 10.1111/ibi.12898

2. Korniluk M. & Chylarecki P. 2023. Intra-seasonal lek changes of Great Snipe males in the Northeast of Poland. Acta Ornithologica 58 (publikacja przyjęta do druku)

3. Korniluk M. & Chylarecki P. 2023. Factors influencing flight initiation distance in a cryptic bird species – the Great Snipe *Gallinago media*

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Streszczenie

Utrata siedlisk w wyniku antropogenicznych przekształceń środowiska jest postrzegana jako główna przyczyna wymierania gatunków ptaków oraz spadkowych trendów ich populacji w Europie i na świecie. Jedną z bardziej zagrożonych grup ekologicznych w europejskiej awifaunie są tzw. siewki łąkowe, do których należą m.in. czajka, rycyk, kulik wielki, czy dubelt. Wraz z osuszaniem terenów podmokłych oraz intensyfikacją rolnictwa ich siedliska znacznie się skurczyły, a niski sukces reprodukcyjny wynikający z drapieżnictwa i niszczenia lęgów na skutek prac agrotechnicznych znacząco pogarsza żywotność populacji. W efekcie, znalazły się one wśród 20% gatunków ptaków gniazdujących na terenie krajów Wspólnoty Europejskiej klasyfikowanych jako zagrożone wyginięciem. Ponieważ siedliska lęgowe łąkowych siewek są współcześnie w znacznym stopniu kształtowane przez użytkowanie rolnicze, przeciwdziałanie spadkowym trendom ich populacji polega dziś głównie na wdrażaniu odpowiednich systemów gospodarowania na użytkach zielonych. Spośród gatunków z tej grupy gniazdujących w Europie, jednym z najbardziej zagrożonych, a jednocześnie najmniej poznanych pod względem preferencji siedliskowych jest dubelt *Gallinago media*. Jego nizinna populacja, zasiedlająca wschodnią Europę, gniazduje w siedliskach zależnych od użytkowania rolniczego i pozostaje daleko słabiej zbadana niż populacja skandynawska zasiedlająca górskie torfowiska. Gatunek charakteryzuje się rzadko spotykanym systemem kojarzenia (*lekking*), w którym samce konkurują o dostęp do samic w trakcie gromadnych, nocnych toków. Ekologia gatunku jest więc w znacznej mierze kształtowana przez dobór płciowy działający w połączeniu z klasycznymi czynnikami doboru naturalnego.

Badania prowadzone w ramach dysertacji doktorskiej miały na celu określenie wybiórczości siedliskowej samców dubelta żerujących pomiędzy nocnymi sesjami toków na łąkach i pastwiskach położonych w dolinach rzek północno-wschodniej Polski. Preferencje siedliskowe były oceniane w dwóch skalach przestrzennych, a uzyskane wyniki miały posłużyć również znalezieniu związków pomiędzy preferowanymi przez samce cechami siedlisk, w tym zasobami pokarmowymi, a reżimem użytkowania rolniczego (**publikacja 1**). Chciałem również ustalić, jaką rolę w procesie wyboru siedlisk żerowiskowych odgrywa potrzeba minimalizacji ryzyka drapieżnictwa i w jakim stopniu może ona być rozbieżna z naciskami selekcyjnymi premiującymi efektywne żerowanie w celu szybkiej odbudowy zapasów energetycznych

(**publikacja 3**). Osobnym celem badań było też określenie czy i w jakim stopniu tokujące samce dubeltów mogą zmieniać tokowiska w trakcie sezonu lęgowego, wymuszając planowanie ochrony gatunku w skali wykraczającej daleko poza zasięg pojedynczych tokowisk (**publikacja 2**).

W latach 2013-2020, w trakcie 7 sezonów badawczych, oznakowałem nadajnikami telemetrycznymi 124 samce dubelta, schwytanych na 9 różnych tokowiskach we wschodniej Polsce. Pozyskane z nadajników dane, a także informacje o cechach siedliska zbierane w terenie w trakcie 4 sezonów lęgowych w miejscach żerowania samców w okolicy 6 tokowisk, zostały przeanalizowane przy użyciu modeli statystycznych (GLM, MARK) i narzędzi GIS.

Badania wykazały, że rozmieszczenie żerowisk samców było skupiskowe, a więc wyraźnie nielosowe (**publikacja 1**), a znacząca ich część zlokalizowana była w odległości do 500 m od tokowisk (**publikacja 1 i publikacja 2**). Wyraźna preferencja samców do żerowania bliżej tokowisk (**publikacja 1**) mogła wynikać z potrzeby oszczędności energii związanej z przemieszczaniem się między tokowiskiem a żerowiskami. Jest to spójne z wynikami wskazującymi, że w lokalizacjach bardziej oddalonych od tokowisk samce mniej chętnie podrywały się do lotu, dłużej zwlekając z ucieczką w obliczu zbliżającego się zagrożenia (**publikacja 3**). Elementy krajobrazu takie jak drzewa, krzewy czy bliskość lasu lub wody nie miały większego wpływu na wybór miejsc żerowania samców. Natomiast cechy siedliska oceniane w mikroskali, takie jak znaczna ilość odkrytej gleby, średnia zwartość i wysokość roślinności czy wysoka grząskość gruntu, silnie determinowały miejsca żerowania samców (**publikacja 1**). Wykształceniu tych cech siedliskowych najbardziej sprzyjało użytkowanie terenów jako dwukośne łąki z wypasem bydła następującym po koszeniu. W takich płatach siedliska stwierdziłem istotnie więcej dżdżownic (główny pokarm dubeltów), niż na gruntach użytkowanych w innych reżimach gospodarowania na użytkach zielonych. W takich miejscach prawdopodobieństwo stwierdzenia samców oceniane w szerszej skali przestrzennej było również najwyższe. Wykazałem przy tym, że proces wyboru siedlisk żerowiskowych jest w jakimś stopniu kompromisem ewolucyjnym, gdyż cechy siedliska najsilniej preferowane przez samce dubelta na żerowiskach, były nieco odmienne od cech siedliska zapewniających tym samym ptakom najwyższy poziom bezpieczeństwa podczas żerowania (**publikacja 1 i publikacja 3**). Badania ukierunkowane na wykrycie dalekodystansowych przemieszczeń wykazały, że 75% samców dubelta zmieniało tokowiska w okresie godowym

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(1 maja – 15 czerwca), odwiedzając do 9 tokowisk w trakcie sezonu. Średnie dzienne prawdopodobieństwo zmiany tokowiska wynosiło 0.12, przy istotnych różnicach pomiędzy kolejnymi latami badań. Przemieszczające się samce dokonywały średnio 9 tranzycji w trakcie sezonu lęgowego (maksymalnie do 43). Dominowały przemieszczenia do 50 km, a tylko około 10% samców odwiedzało tokowiska leżące w odległości większej niż 100 km od tokowisk na których zostały pierwotnie oznakowane (maksymalnie do 253 km). Przemieszczenia były niemal wyłącznie nocne, a w jednym spośród trzech analizowanych lat badań nasilały się wraz z postępem sezonu lęgowego. Silna korelacja maksymalnych dystansów przemieszczeń samców w sezonie z maksymalnym dystansem odwiedzanych przez nie tokowisk, sugeruje, że dalekodystansowa, wewnątrzsezonowa dyspersja samców ma na celu wyłącznie odwiedzanie innych tokowisk. Powszechność tego behawioru wskazuje na jego duże jego znaczenie dla funkcjonowania populacji i może być elementem alternatywnej strategii rozrodczej pozwalającej skompensować niektórym samcom niski sukces kojarzenia.

Relatywnie intensywne użytkowanie łąk preferowane przez samce dubelta może wiązać się z dużym ryzykiem niszczenia lęgów i prowadzić do powstania pułapki ekologicznej. Dlatego też, skuteczna ochrona siedlisk gatunku w skali krajobrazowej, wymaga by rejonie tokowisk dostępne były również płaty siedlisk koszone później, zapewniające bezpieczeństwo lęgów. Czynna ochrona mająca na celu utrzymanie wysokiej jakości siedliska dubelta powinna więc preferować utrzymanie mozaiki użytkowania zapewniającej występowanie zarówno cech preferowanych przez żerujące samce, jak i terenów stanowiących odpowiednie i bezpieczne miejsca lęgów dla samic. Tego typu działania ochronne powinny być priorytetowo wdrażane na terenach położonych bliżej tokowisk. Ochrona siedlisk powinna również obejmować większe fragmenty dolin rzecznych, obejmując przynajmniej kilka tokowisk, powiązanych regularnymi przemieszczeniami dyspergujących pomiędzy nimi samców i samic dubelta.

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Summary

Habitat loss caused by anthropogenic environmental transformation is considered as a major cause of bird extinction and their population declining trends in Europe and worldwide. One of the most endangered ecological groups in European birds species are the so-called meadow waders, which include the Lapwing, Black-tail Godwit, Eurasian Curlew and the Great Snipe. With the drainage of wetlands and the intensification of agriculture, their habitats have deteriorated considerably and their low reproductive success due to predation and agriculture practices on the breeding grounds does not allow to population recovery. As a result, they are among 20% of breeding bird species in the European Union countries classified as endangered. Given that breeding habitats of meadow waders are nowadays largely dependent on agricultural use, counteracting the declining trends of their populations nowadays mainly consists of implementing appropriate grassland management systems. Among the meadow waders breeding in Europe, one of the most threatened and yet least studied in terms of habitat preferences is the Great Snipe. Its lowland population, inhabiting eastern Europe, breeds in habitats dependent on agricultural use and remains far less studied than the Scandinavian one inhabiting mountain fens. The species is characterised by a rare mating system (lekking) in which males compete for access to females during clustered, nocturnal display. The ecology of the species is thus largely shaped by sexual selection acting in conjunction with classical natural selection factors. Research carried out as part of PhD dissertation was aimed to determine the habitat selection of male Great Snipe foraging between nocturnal display sessions on meadows and pastures located in river valleys in north-eastern Poland. Habitat preference was assessed at two spatial scales, and the results were also intended to find relationships between males' preferred habitat characteristics, including food resources, and agricultural use regime (**publication 1**). I also wanted to determine what role the need to minimise predation risk plays in the process of selecting foraging habitats and to what extent this may be at odds with selection pressures that reward efficient foraging for rapid recovery of energy reserves (**publication 3**). A separate aim of the study was also to determine whether and to what extent males Great Snipe may change leks during the breeding season, forcing conservation planning for the species on a scale far beyond the range of one breeding location (**publication 2**).

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Between 2013 and 2020, during 7 research seasons, I tagged with telemetry transmitters a total of 124 male Great Snipe that were captured at 9 different leks in eastern Poland. The data obtained from the transmitters, as well as information on habitat characteristics collected in the field during 4 breeding seasons at male foraging sites in the vicinity of 6 leks, were analysed using statistical models (GLM, MARK) and GIS tools.

I found that the distribution of male foraging sites was clustered and not random (**publication 1**), with a significant proportion located at a distance of 500 m from the leks (**publication 1 and publication 2**). The apparent preference of males to forage closer to the leks (**publication 1**) could be driven by the need to conserve energy associated with moving between the leks and foraging grounds. This is consistent with results indicating that in locations farther away from the leks, males were less likely to flush, delaying flight decision in the face of predation risk (**publication 3**). Landscape elements such as trees, shrubs or proximity to forest or water elements had no influence on the choice of foraging sites for Great Snipe males. On the other hand, micro-scale habitat characteristics such as a significant amount of bare ground, medium density and height of vegetation, or high soil penetrability strongly determined the foraging sites of males (**publication 1**). These characteristics were most strongly influenced by two-cut and grazed meadows, where the probability of finding males was highest and where we found significantly more earthworms, compared to the other land use types. The probability of finding males assessed on a broader spatial scale was also highest at such sites. The process of habitat selection was shown to be to some extent an evolutionary trade-off, as the habitat characteristics strongly preferred by Great Snipe males at foraging sites were in some extent different from the habitat features providing the highest level of safety (**publication 1 and publication 3**). The research aiming to detect long-distance movements revealed that 75% of Great Snipe males changed their leks during the mating season (1 May - 15 June), visiting up to 9 different leks (**publication 2**). The average daily probability of changing the lek by a male was 0.12, with significant differences between survey years. Moving males made an average of 9 transits during the breeding season (up to a maximum of 43). Movements of up to 50 km predominated, with only about 10% of males visiting leks located more than 100 km from the sites where they were originally tagged (up to a maximum of 253 km). Movements were almost exclusively nocturnal, and in one of the three study years they increased as the breeding season progressed.

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Strong correlation of the maximum distances of male movements between leks with the maximum foray, suggests that the long-distance, intra-seasonal dispersal of males was performed exclusively in order to join other leks. The prevalence of this behaviour indicates its major importance in the population and may be part of an alternative mating strategy to compensate for some males' low mating success.

The relatively intensively used grasslands preferred by male Great Snipes may be associated with a high risk of brood loss and lead to ecological trap, so patches of habitat mown later in the landscape should also be available to ensure breeding safety. Active protection aimed at maintaining a high quality habitat for the Great Snipe should therefore be a mosaic of land use, providing both habitat characteristics preferred by males for foraging and those providing suitable and safe breeding sites for females. In doing so, these activities should be prioritised in the vicinity to leks and encompass several leks in the landscape to ensure free movement of males and females between lekking sites. Such conservation measures should be implemented as a priority in areas closer to the leks. Habitat protection should also encompass larger sections of river valleys, covering at least several leks, to ensure regular movements of males and females dispersing between them.

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Wstęp

Spośród ok. 11 000 gatunków ptaków współcześnie żyjących na Ziemi, blisko połowa (48%) wykazuje spadkowe trendy liczebności populacji, a tylko 6% gatunków charakteryzuje się trendami rosnącymi (Lees *et al.* 2022). Niemal 1/5 gatunków ptaków gniazdujących na terenie 28 krajów Wspólnoty Europejskiej (82/451 gatunków) jest postrzegana jako zagrożona wyginięciem (EAA 2015). Co więcej, 13% gatunków ptaków jest zagrożonych przyspieszonym wymarciem w skali globalnej wg kryteriów IUCN (Lees *et al.* 2022). Wiodącą przyczyną spadków populacji i postępującego wymierania gatunków ptaków jest obecnie utrata siedlisk i ich degradacja (Lees *et al.* 2022). Utrata siedlisk jest przede wszystkim wynikiem antropogenicznych przekształceń środowiska, z intensyfikacją i industrializacją rolnictwa na czele, zaś zmiany klimatyczne dodatkowo potęgują skalę niekorzystnych oddziaływań (Donald *et al.* 2001, Julliard *et al.* 2004, Huntley *et al.* 2008, Kays *et al.* 2015, Powers & Jetz 2019). Dostępność odpowiednich siedlisk jest więc w Antropocenie jednym z najważniejszych czynników limitujących liczebność i zasięg występowania populacji biologicznych. W tej sytuacji, wiedza o wymaganiach siedliskowych poszczególnych gatunków jest kluczowym warunkiem ich skutecznej ochrony.

Przyjmuje się, że wybór miejsca bytowania przez ptaki jest kształtowany przez silne naciski selekcyjne pozwalające ocenić jakość siedliska (Levins 1968, Fretwell & Lucas 1969, Cody 1981), rozumianą jako dostępność niezbędnych (limitujących) zasobów kształtujących osobnicze dostosowanie (*fitness*), takich jak: pożywienie, schronienie, możliwość rozrodu czy bezpieczeństwo (Kristan 2006, Boulinier *et al.* 2008, Fuller 2012). Wybiórczość siedliskowa, czyli proces wyboru optymalnego siedliska przez poszczególne osobniki (Fretwell & Lucas 1969, Cody 1981, Hall *et al.* 1997) jest z reguły analizowana jako sekwencja decyzji zachodzących w różnej skali przestrzennej, począwszy od biomów, poprzez krajobrazy, a kończąc na fragmentach siedlisk bezpośrednio otaczających osobniki (Johnson 1980, Orians & Wittenberger 1991, Mayor *et al.* 2009, Fuller 2012). Zgodnie z teorią tzw. idealnego wyboru siedlisk, osobniki – używając szeregu przesłanek i informacji - potrafią ocenić jakość siedlisk i ostatecznie powinny dążyć do tego, by osiedlać się w miejscach zapewniających im najwyższe możliwe dostosowanie (Fretwell & Lucas 1969, Pulliam & Danielson 1991, Chalfoun & Schmidt 2012, Fuller 2012). W praktyce, wybór optymalnych osobniczo siedlisk jest na szereg sposobów ograniczany – choćby przez terytorialne zachowania innych osobników czy niepełną informacją odnośnie jakości siedliska. W szczególności, w środowiskach silnie przekształconych przez człowieka, wybierane przez zwierzęta siedliska mogą okazywać się suboptymalne z uwagi na obniżoną przeżywalność dorosłych osobników lub niższy sukces reprodukcyjny (Schlaepfer *et al.* 2002, Hale & Swearer 2016). Innymi słowy, jeżeli przesłanki (*cues*), na podstawie których zwierzę ocenia jakość siedliska rozmijają się na niekorzyść z rzeczywistą jego jakością, proces selekcji siedlisk staje się nieadaptacyjny (Gilroy & Sutherland 2007, Gilroy *et al.* 2011), co może prowadzić do powstania tzw. pułapki ekologicznej (Schlaepfer *et al.* 2002, Kristan 2003, Robertson & Hutto 2006). Zjawisko to w skrajnych sytuacjach, może nawet prowadzić do ekstynkcji lokalnych populacji, szczególnie tych których liczebność i zagęszczenie są niewielkie (Kokko & Sutherland 2001, Weegman *et al.* 2016).

Przy szybko postępujących zmianach w środowisku często najbardziej narażone na ekstynkcję są gatunki wyspecjalizowane (McKinney 1997, Julliard *et al.* 2004), definiowane jako te, które wykorzystują relatywnie ograniczone spektrum zasobów, a tym samym siedlisk, przy czym niejednokrotnie ich niskie możliwości adaptacyjne wynikają ze złożonych cyklów życiowych czy skomplikowanej biologii rozrodu (Colles *et al.* 2009). Przeciwdziałanie spadkowym trendom populacji gatunków zagrożonych, polega dziś głównie na poprawie jakości ich siedlisk lub ich odtwarzaniu oraz zapewnieniu w nich wszystkich niezbędnych funkcji życiowych. Dlatego też, poza fundamentalnym w ochronie przyrody rozumieniem ekologii gatunku, kluczowym celem w efektywnej czynnej ochronie gatunków jest optymalizacja jakości ich siedlisk (Johnson 2007, Eglington *et al.* 2009), przy czym powinna się ona opierać o jasno określone i mierzalne wskaźniki (Milsom *et al.* 2000, Mott *et al.* 2021) oraz uwzględniać uwarunkowania lokalne (Doherty *et al.* 2016). Ochrona siedlisk gatunków wyspecjalizowanych, szczególnie tych o skomplikowanej ekologii jest jednak dużym wyzwaniem, gdyż może okazać się nie tylko nieskuteczna, np. ze względu na trudność w kształtowaniu preferowanych cech siedliska lub nieobjęcia wystarczająco dużej części populacji dla zapewniania jej trwałości (Frankham 2015), ale co gorsza przeciwskuteczna w sytuacji, gdy odtworzone siedlisko jest preferowane, ale zapewnia niższe dostosowanie ewolucyjne (*fitness*) niż dotychczas wykorzystywane siedliska (Weegman *et al.* 2016, Hale & Swearer 2017, Seward *et al.* 2019). Przykładowo, Seward i in. (2019) na podstawie analizy dynamiki meta-populacji zagrożonej wyginięciem rybitwy różowej *Sterna dougallii*, wykazali, że jedna z trzech objętych intensywną ochroną czynną kolonii lęgowych, działa jako tzw. populacja ujściową (*sink*) dla całej meta-populacji, gdyż jej stabilna lub wzrostowa liczebność (co pozornie jest dobrym sygnałem w ochronie czynnej) zależna jest od imigracji z innych kolonii lęgowych. Co więcej, przewidywania modeli wskazywały, że populacja tego gatunku, mogłaby być o co najmniej 10% większa, gdyby dyspersja pomiędzy koloniami zasilającymi populację (*source*), a tymi tworzącymi „ujścia” (*sink*) nie miała miejsca. Innymi słowy, z punktu widzenia meta-populacji, korzystniejsze długoterminowo byłoby gdyby kolonia ta nie była chroniona i przestała istnieć.

Tzw. siewki łąkowe (*meadowbirds*) są we współczesnej Europie jedną z silniej zagrożonych grup ptaków o zbliżonych wymaganiach ekologicznych i historiach życiowych (*life histories*), odzwierciedlających w dużej mierze wspólną filogenezę. W ostatnich dekadach populacje wielu gatunków z tej grupy wykazują silne i powszechne trendy spadkowe, którym nierzadko towarzyszy postępująca redukcja zasięgów (BirdLife International 2015, 2021). Trzy gatunki z tej grupy (czajka *Vanellus vanellus,* krwawodziób *Tringa totanus*, kszyk *Gallinago gallinago*) zostały w 2021 roku sklasyfikowane w oparciu o kryteria IUCN jako narażone (*vulnerable*) w skali Europy, zaś kolejne trzy (rycyk *Limosa limosa*, kulik wielki *Numenius arquata*, batalion *Calidris pugnax*) jako bliskie zagrożenia (*near threatened*) w skali kontynentu (BirdLife International 2021). Jeszcze gorzej przedstawia się sytuacja siewek łąkowych w 28 krajach Unii Europejskiej (UE28), gdzie status rycyka jest oceniany jako zagrożony (*endangered*), a do taksonów narażonych zaliczono kolejny gatunek – dubelta *Gallinago media* (BirdLife International 2021). Pierwotną przyczyną spadkowych trendów populacji tych ptaków w Europie jest utrata i degradacja ich siedlisk lęgowych spowodowana postępującym, wielkoskalowym osuszaniem terenów mokradłowych (Zedler & Kercher 2005), w szczególności torfowisk i zalewowych łąk w dolinach rzek, połączonym intensyfikacją rolnictwa na użytkach zielonych (Donald *et al.* 2001, Wilson *et al.* 2004). W ostatnich dekadach, istotnym czynnikiem spadku liczebności ptaków z tej grupy był też niski sukces reprodukcyjny, powodowany głównie utratą lęgów na skutek drapieżnictwa (Schekkerman *et al.* 2009, Roodbergen *et al.* 2012, Madden *et al.* 2015, Plard *et al.* 2020). W Europie Środkowej i Wschodniej, utrata siedlisk siewek łąkowych była również lokalnie powodowana sukcesją wtórną zbiorowisk szuwarowych, następującą w rezultacie porzucenia tradycyjnego użytkowania rolniczego (Ławicki *et al.* 2011, Leito *et al.* 2014, Silva-Monteiro *et al.* 2021).

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Znaczenie tego ostatniego czynnika w pierwszej dekadzie XXI w. było najbardziej wyraźne na obszarze polski północnowschodniej i w krajach bałtyckich (Kuemmerle *et al.* 2016).

Negatywne trendy populacyjne obserwowane wśród europejskich ptaków siewkowych, znalazły odzwierciedlenie w rosnącej liczbie badań z zakresu ekologii aplikacyjnej (*applied ecology*) dotyczących tych gatunków, przeprowadzonych w ostatnich dekadach w Europie Zachodniej. Większość z nich dotyczyło lepszego rozpoznania preferencji siedliskowych (Berg 1992, 2008, Johansson & Blomqvist 1996, Milsom *et al.* 2002, Durant *et al.* 2008, Laursen & Hald 2012, Kentie *et al.* 2014), oceny zagrożeń lęgów (Green *et al.* 1987, Roodbergen *et al.* 2008, Kentie *et al.* 2015, Roos *et al.* 2018) oraz wypracowaniu metod służących kształtowaniu siedlisk i ochronie lęgów (Eglington *et al.* 2008, 2010, Malpas *et al.* 2013, Laidlaw *et al.* 2015, Franks *et al.* 2018, Mason *et al.* 2018, Verhoeven *et al.* 2022).

Dubelt jest jednym spośród tych gatunków ptaków siewkowych, które mają za sobą długą historię redukcji europejskiego zasięgu występowania i których współczesna sytuacja pogarsza się szczególnie szybko. W ostatnich latach (już po ocenie BirdLife International 2021) jego status został oceniony jako bliski zagrożenia (*near threatended*) w skali globalnej (BirdLife International 2023), a w krajach EU28 uznawany jest obecnie za gatunek narażony na wyginięcie. W skali Polski jego status (oceniany na podstawie kryteriów IUCN) został określony w czerwonej liście ptaków Polski (Wilk et al. 2020) jako zagrożony (*endangered*). Wiodące znaczenie dla tej oceny miała niewielka populacja lęgowa licząca zaledwie 400-550 samców (Chodkiewicz *et al.* 2015) oraz spadkowy trend krajowej populacji sięgający -53% na przestrzeni 10 lat (Wilk et al. 2020). Osuszanie terenów bagiennych oraz intensyfikacja rolnictwa, jak również polowania są postrzegane jako pierwotne przyczyny ekstynkcji dubelta na nizinach centralnej i północnej Europy (Løfaldli *et al.* 1989). We wczesnych dekadach XX wieku, gatunek wyginął zupełnie w północnych Niemczech, Danii oraz na obszarach nizinnych Szwecji i Norwegii (Løfaldli *et al.* 1989, Kålås *et al.* 1997, Gedeon *et al.* 2014, Berndt 2018). Pod koniec XX wieku zanikły ostatnie stanowiska gatunku w zachodniej i środkowej Polsce. Wycofywanie się gatunku z rozległych obszarów środkowej Europy doprowadziło do rozerwania ciągłości kontynentalnego zasięgu dubelta i było prawdopodobną przyczyną powstania dwóch izolowanych genetycznie (Ekblom *et al.* 2007) i nieco odmiennych morfologicznie populacji (Kålås *et al.* 1997a), postrzeganych obecnie jako niezależne jednostki konserwatorskie (Sæther *et al.* 2007). Tak zwana populacja zachodnia, występująca w górach Skandynawii na terenach stabilnych, dobrze zachowanych torfowisk niskich i w niskich zaroślach wierzbowych powyżej górnej granicy lasu, wykazuje brak spadkowego trendu (Ekblom & Carlsson 2007, Østnes *et al.* 2014). Tymczasem populacja wschodnia (zwana również nizinną), której zasięg rozciąga się od Polski Wschodniej, poprzez kraje bałtyckie, Białoruś, Ukrainę aż po rzekę Jenisej, wykazuje znaczący regres liczebności (Mongin 2002, Chylarecki *et al.* 2018, Artemyev 2022, Shydlovskyy *et al.* 2022), przyczyniając się do spadkowego trendu i pogłębiającego się zagrożenia globalnej populacji gatunku (Kålås 2004, BirdLife International 2023). W ostatnich dekadach skandynawskie populacje dubelta były obiektem licznych badań z zakresu ekologii behawioralnej (e.g. Løfaldli 1989, Höglund & Robertson 1990, Höglund et al. 1992, Løfaldli *et al.* 1992, Ekblom et al. 2007, Sæther *et al.* 2007), gdyż jest on jednym z nielicznych w Europie gatunków ptaków wykazujących specyficzny, promiskuityczny system kojarzenia (Kempenaers 2022), określany jako tokowiskowy (*lek mating system*; Bradbury 1981, Höglund & Alatalo 1995). W odróżnieniu od stosunkowo dobrze zbadanych populacji skandynawskich, nizinna populacja dubelta była przedmiotem stosunkowo nielicznych badań (Kuresoo & Luigujõe 2001, Mongin 2002, Sviridova *et al.* 2018), mimo tego, iż stanowi ona około 90% globalnej populacji tego gatunku (Birdlife International 2023). Co więcej, inaczej niż w przypadku populacji zachodniej, siedliska lęgowe dubelta na nizinach wschodniej Europy, przede wszystkim torfowiska niskie, ekstensywnie użytkowane łąki na równinach zalewowych oraz osuszone torfowiska, są obecnie habitatami narażonymi na znaczącą i rosnącą antropopresję. W rezultacie, długoterminowe utrzymanie tych siedlisk jest obecnie w pełni zależne od użytkowania rolniczego (Kålås 2004, Korniluk & Piec 2016).

Wśród przyczyn ekstynkcji dubelta w Zachodniej Europie oraz utrzymującego się spadkowego trendu populacji nizinnej, znaczącej roli można upatrywać w silnej specjalizacji ekologicznej tego gatunku, pozostającej w związku z jego systemem kojarzenia. Dubelty występują na obszarach wyróżniających się pod względem zasobności wierzchnich warstw gleby w dżdżownice (Lumbricidae), które stanowią około 90% diety gatunku na lęgowiskach (Kålås et al. 1997b, Løfaldli *et al.* 1992). Jednocześnie, żerujące w okresie lęgowym ptaki wykazują silne preferencje względem wybranych cech strukturalnych siedliska w obrębie żerowisk zlokalizowanych na otwartych terenach porośniętych wysoką roślinnością zielną (Løfaldli *et al.* 1992, **publikacja 1, publikacja 3**). Przyjmuje się, że pierwsza z tych cech jest związana z kosztownym energetycznie behawiorem tokowym samców dubelta. Tokujące w nocy samce, w ciągu kilku godzin spędzonych na zrytualizowanych popisach godowych (Lemnell 1978) tracą nawet do 5-7% masy ciała (Höglund *et al.* 1992). Behawior ten wykształcił się prawdopodobnie pod silną presją doboru płciowego, gdyż samice preferują jako partnerów seksualnych te samce, które podczas toków wykazują się najwyższą aktywnością energochłonnych popisów, oraz, na przestrzeni sezonu lęgowego, spędzają najwięcej czasu na tokowisku (Höglund & Lundberg 1987, Höglund & Robertson 1990a, Fiske *et al.* 1994). Tym samym, istnieje silna presja selekcyjna na to, by żerując w ciągu dnia, w przerwie pomiędzy kolejnymi nocami poświęconymi na toki, samce były w stanie szybko uzupełnić uszczuplone zasoby energetyczne. Taka sytuacja jest możliwa jedynie, gdy w pobliżu tokowisk znajdują się zasobne żerowiska, pozwalające dubeltom na szczególnie efektywne żerowanie. W rezultacie, obecność siedlisk zasobnych w dżdżownice, łatwo dostępne w czasie całego sezonu lęgowego, jest czynnikiem limitującym rozmieszczenie tokowisk dubelta, a także występowanie gatunku w szerszej skali geograficznej, skutkując wybitnie wyspowym rozmieszczeniem tokowisk dubelta (Kålås *et al.* 1997b).

Z kolei silne preferencje względem wybranych cech strukturalnych siedlisk na żerowiskach wynikają po części z potrzeby zapewnienia efektywnego pobierania pokarmu. Dubelty żerują sondując długim dziobem w wierzchnich warstwach gleby i lokalizując tam z pomocą dotyku ukryte dżdżownice. Wysoką efektywność takiego żerowania zapewnia odpowiednia grząskość gruntu, mało zwarta roślinność (Løfaldli *et al.* 1992, **publikacja 1**) czy znaczny udział odkrytej gleby (**publikacja 1**). Jednocześnie jednak, intensywnie żerujące ptaki narażone są na atak drapieżnika, co stwarza presję selekcyjną na wykształcenie rozmaitych strategii antydrapieżniczych, w szczególności pozwalających na minimalizację wykrycia i uniknięcie ataku (Ruxton et al. 2004, Caro 2005).

Tokowiskowy system kojarzenia dubeltów wiąże się z silną konkurencją samców o partnerkę rozrodczą, zaś ze względu na brak udziału samców w budowie gniazda, wysiadywaniu jaj i opiece nad potomstwem - również z wysoką selektywnością samic przy wyborze samca o najlepszych cechach, powiązanych z jakością genetyczną partnera (Gibson & Bradbury 1985, Alatalo *et al.* 1992, Sæther *et al.* 1999, Luttbeg 2004). W konsekwencji, w systemie tym obserwuje się wybitnie skośny rozkład sukcesu kojarzenia samców na tokowisku (Wiley 1991, Höglund & Alatalo 1995). W przypadku dubelta, obserwacje na tokowiskach skandynawskich wykazały, że tylko około połowa samców ma szanse na kopulację w danym sezonie rozrodczym, a najbardziej preferowany samiec może uczestniczyć nawet w około 1/3 wszystkich kopulacji obserwowanych na pojedynczych tokowiskach (Höglund & Lundberg 1987, Fiske *et al.* 1994). Wysoka heterogenność prawdopodobieństwa kopulacji samców dubelta na jednym tokowisku w trakcie sezonu, jak również preferencja samic względem osobników starszych (Höglund & Lundberg 1987, Höglund *et al.* 1990, Fiske *et al.* 1994), wywierają silną presję selekcyjną na szereg cech samców, w ramach procesu doboru płciowego, co od dawna było przedmiotem zainteresowania badaczy strategii rozrodczych. Jednocześnie jednak, co było już przedmiotem mniejszego zainteresowania, przynajmniej w odniesieniu do dubelta, znaczne zróżnicowanie sukcesu reprodukcyjnego samców stwarza niszę do ewolucji alternatywnych zachowań rozrodczych (*alternative mating strategies or tactics*) pozwalających skompensować niski sukces reprodukcyjny (Dominey 1984, Gross 1996, Luttbeg 2004, Gibson *et al.* 2014).

Drapieżnictwo jest jednym z wiodących nacisków selekcyjnych działających w ramach doboru naturalnego. Jednak silny dobór płciowy (jak w przypadku gatunków kojarzących się na tokowiskach) często zwiększa podatność osobników na drapieżnictwo, stwarzając dodatkową presję na wykształcenie skutecznych adaptacji antydrapieżniczych (Andersson 1994, Ruxton et al. 2004, Caro 2005, Merilaita *et al.* 2017). W przypadku dubelta, za taką adaptację można uważać nocne toki (Lemnell 1978), gdyż pod osłoną ciemności, zarówno wykrywalność zdobyczy jaki i sprawność polowania wielu drapieżników są ograniczone (Ruxton et al. 2004). Wysokie koszty energetyczne toków samców dubelta (Höglund *et al.* 1992) trwających nieraz całą noc (Lemnell 1978), wymuszają tym samym szczególnie sprawną dzienną regenerację zasobów energetycznych samców. W ciągu dnia antydrapieżniczym przystosowaniem dubelta jest z pewnością kryptyczne ubarwienie. Przy czym, aby spełniało ona swoja funkcję, proces wyboru miejsc żerowania powinien być ukierunkowany na wybór mikrosiedlisk zapewniających jak najlepszy kamuflaż (*background matching*), gdyż wraz ze wzrostem kryptyczności maleje prawdopodobieństwo wykrycia przez drapieżniki, a tym samym ryzyko drapieżnictwa (Ruxton et al. 2004). Mikrosiedliska, w których żerują samce dubelta w ciągu dnia muszą więc zapewniać zarówno odpowiedni poziom regeneracji zasobów energetycznych jak również bezpieczeństwo żerujących intensywnie ptaków. Jednoczesne zapewnienie jednej i drugiej funkcji może być przedmiotem przeciwstawnych nacisków selekcyjnych i ewolucyjnych kompromisów (*trade-off*), gdyż cechy siedliska zapewniające najwyższy poziom

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kryptyczności mogą być w jakimś zakresie odmienne od tych, które zapewniają najwyższą jakość żerowisk.

Spodziewaną, alternatywną taktyką rozrodczą, odmienną od preferowanej przez samice dubelta dużej wytrwałości samców w spędzaniu dostępnego czasu na tokowisku (Höglund & Lundberg 1987, Fiske *et al.* 1994) może być zmiana tokowiska lub wręcz wielokrotne zmiany i odwiedzanie wielu tokowisk w trakcie sezonu lęgowego. Samce, którym nie udaje się zdobyć partnerki na określonym tokowisku mogą teoretycznie zwiększać szanse kojarzenia przemieszczając się na inne tokowiska w poszukiwaniu miejsc o mniejszej liczbie konkurujących samców, mniejszej liczbie bardziej atrakcyjnych samców lub większej liczbie receptywnych samic. Teoretyczne modele optymalnej wielkości tokowisk (Widemo & Owens 1999, Hoglund & Alatalo 1995) przewidują, że zmiana tokowiska może być korzystna dla samców, szczególnie w przypadku dużych tokowisk. Tymczasem mimo intensywnie prowadzonych badań behawioralnych na dubeltach w Skandynawii, przemieszczania samców nie były raportowane (choć sugerowano, że występują, patrz: Höglund & Robertson 1990; Sæther et al. 2005). Jednocześnie, obecność takich zachowań wśród samców była wykazywana w populacji nizinnej na podstawie obrączkowanych ptaków, przemieszczających się pomiędzy tokowiskami odległymi od siebie do 10 km (Karpowich 1962). Przyczyną braku informacji na temat wewnątrz-sezonowych przemieszczeń samców dubelta między tokowiskami były z pewnością brak dostępności odpowiedniej wielkości nadajników telemetrycznych służących śledzeniu przemieszczeń w dużej skali i rozdzielczości (nadajniki VHF mają ograniczony zasięg i wymagają obecności w terenie co ogranicza częstość i zasięg próbkowania) oraz zmniejszenie zainteresowania tym gatunkiem wśród badaczy w Szwecji i Norwegii. Wzrost powszechnej dostępności nadajników telemetrycznych, zwłaszcza działających w systemie GPS (Bouten *et al.* 2013, Geen *et al.* 2019), umożliwił śledzenie przemieszczeń z dużą rozdzielczością odkrywając przed naukowcami nowy wymiar w badaniach ekologicznych i behawioralnych (Nathan et al. 2022), nierzadko wpływając na obalenie klasycznych paradygmatów w ekologii, w tym postrzegania funkcjonowania ptasich systemów kojarzenia (Baldassarre et al. 2019, Lislevand et al. 2020). Użycie nadajników tego typu w badaniach przemieszczeń wewnątrz-sezonowych innych gatunków o tokowiskowym systemie kojarzenia wykazało większą niż przypuszczano skalę przemieszczania się samców między tokowiskami (Borecha *et al.* 2017, Fremgen *et al.* 2017, Wann *et al.* 2019). w tym spektakularne odkrycie dyspersji wewnątrzsezonowej samców biegusów arktycznych *Calidris melanotos* z sukcesywnym odwiedzaniem kolejnych stanowisk lęgowych (do 23 potencjalnych tokowisk; >13 000 km łącznych przemieszczeń w trakcie czterech tygodni) rozsianych na rozległych obszarach globalnego zasięgu gatunku (Kempenaers & Valcu 2017).

Obecnie, wewnątrzsezonowe przemieszczanie się samców między tokowiskami jest postrzegane jako ważny elementem ewolucji i funkcjonowania tokowiskowego systemu kojarzenia (Gibson *et al.* 2014, Fremgen *et al.* 2017, Kempenaers & Valcu 2017, Wann *et al.* 2019). Ponadto, ze względu na to, że mają one istotny wpływ w przepływie genów wewnątrz populacji (Fremgen *et al.* 2017), przyczyniają się do utrzymania wysokiego zróżnicowania genetycznego, a tym samym dobrej kondycji genetycznej populacji, zapewniającej odporność (*resilience*) na zaburzenia środowiska (Frankham 2005). Jest to szczególnie istotne w populacjach izolowanych i mało licznych, gdyż niskie zróżnicowanie genetyczne może potęgować ryzyko ekstynkcji populacji (Frankham 2015, Griffiths *et al.* 2020). Dane dotyczące przemieszczeń między tokowiskami wspierają też inne narzędzia służące ochrony gatunków. Takim jest z pewnością monitoring dynamiki populacji, będący podstawą wnioskowania o stanie jej zachowania (Burgman 2005). W przypadku gatunków tokujących, indeksem liczebności populacji lęgowej, na podstawie którego określany jest trend populacji, jest liczba samców na tokowisku (Cayford *et al.* 1991, Walsh *et al.* 2004, Korniluk *et. al* 2015). Jednakże bez informacji na temat skali przemieszczeń między tokowiskami, jej częstości oraz zmienności w trakcie sezonu tokowego, wynik liczenia może być niewiarygodny, np. ze względu na wielokrotne liczenie tych samych samców (Gibson *et al.* 2014, Fremgen *et al.* 2017). Przykładowo, w przypadku preriokurów ostrosternych *Centrocercus urophasianus*, tymczasowa nieobecność samców, wynikająca między innymi z przemieszczeń między tokowiskami w trakcie sezonu wyjaśniała 40% rocznej zmienności w wynikach liczeń ptaków (Blomberg *et al.* 2013). Dlatego też dynamika przemieszczeń między tokowiskami została uwzględniona w metodach prowadzenia monitoringu tego gatunku i planowaniu jego ochrony w skali krajobrazu (O'Donnell *et al.* 2019, Monroe *et al.* 2022). Dane o zasięgu dyspersji wewnątrzsezonowej samców dubelta mogą ponadto dostarczyć cennych informacji na temat zasięgu potencjalnej kolonizacji lub rekolonizacji siedlisk, a tym samym wskazywać obszary, w których odtwarzanie siedlisk gatunku może przynieść najlepsze rezultaty.

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Ochrona populacji dubelta w Polsce wymaga więc uzupełnienia elementarnej wiedzy na temat ekologii gatunku. W pierwszym rzędzie dotyczy to lepszego zrozumienia procesu wyboru siedlisk w różnych skalach przestrzennych, w szczególności z uwzględnieniem faktu rolniczego użytkowania tych siedlisk. Duże znaczenie ma również określenie faktycznego obszaru użytkowanego przez samce dubelta w trakcie sezonu lęgowego, z uwzględnieniem ignorowanego (a przynajmniej nie badanego dotąd) procesu dyspersji ptaków między tokowiskami.

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Cel badań

Nadrzędnym celem mojego doktoratu było poznanie wybranych aspektów ekologii samców dubelta *Gallinago media*, które dostarczą narzędzi w planowaniu skutecznej ochrony tego zagrożonego wyginięciem gatunku.

Szczegółowe cele badawcze skupiały się przede wszystkim na:

1. Określeniu wybiórczości siedliskowej samców dubelta na żerowiskach na poziomie mikrosiedlisk oraz w stosunku do otaczających elementów krajobrazu jak również użytkowania rolniczego (**publikacja 1, publikacja 3**).
2. Opracowaniu i ewaluacji uniwersalnego modelu pozwalającego ocenić jakość żerowisk dubelta w różnych jego siedliskach w oparciu o cechy mające największe znaczenie w procesie selekcji siedlisk (**publikacja 1**).
3. Określenie roli, jaką odgrywa w procesie selekcji siedlisk przez samce dubelta potrzeba zapewnienia bezpieczeństwa oraz zrozumienie interakcji pomiędzy selekcją mikrosiedlisk, a kryptycznością w kontekście antydrapieżniczych adaptacji.
4. Określenie zasięgu dyspersji wewnątrzsezonowej samców oraz sezonowej i dobowej dynamiki przemieszczeń się samców dubelta między tokowiskami (**publikacja 3**).
5. Sformułowaniu zaleceń dotyczących ochrony populacji i kształtowania siedlisk dubelta w oparciu o konfrontację uzyskanych wyników z dotychczasową wiedzą na temat biologii gatunku (**publikacja 1, publikacja 2, publikacja 3**).

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Metody

Badania prowadzone były na skraju zachodniego zasięgu nizinnej populacji dubelta *Gallinago media* na 9 stanowiskach gatunku, zlokalizowanych w północnowschodniej i wschodniej Polsce, w dolinach rzeki Narew (tokowiska Odrynki 1, Odrynki 2, Zajączki), Biebrza (tok. Lipsk, Gugny), Supraśl (tok. Gródek, Supraśl), Siniocha (tok. Perespa) oraz w kompleksie łąk Blota Serebryskie (tok. Błota, Ryc. 1). Tokowiska objęte badaniami zlokalizowane były na torfowiskach niskich w dolinach rzecznych (Lipsk, Gugny, Perespa), równinach zalewowych średniej wielkości rzek nizinnych (Odrynki 1, Odrynki 2, Zajączki, Supraśl), na łąkach potorfowiskowych (Gródek) oraz na pojeziernych torfowiskach alkalicznych (Błota). Charakteryzowały się one stałością pod względem wykorzystania przez dubelty areny tokowej (aktywne co roku w okresie co najmniej 5 lat) oraz liczby tokujących samców (w zależności od roku i tokowiska od 6 do 20 samców). Badania prowadzone były w głównym okresie trwania toków dubelta w Polsce (Korniluk i in. 2015) od początku maja do około połowy czerwca w trakcie siedmiu sezonów badawczych - na dwóch tokowiskach w latach 2013 i 2014 (**publikacja 1**), sześciu tokowiskach w latach 2013, 2014, 2015, 2017, 2018 (**publikacja 2**) oraz sześciu w latach 2013, 2014, 2020, 2021 (**publikacja 3**).

Danymi wyjściowymi, umożliwiającymi realizację zaplanowanych badań były miejsca żerowania samców w okolicy tokowisk (**publikacja 1 i publikacja 3**) oraz lokalizacje miejsc bytowania samców w trakcie trwania sezonu tokowego w całym zasięgu wykorzystywanej przez nie przestrzeni (**publikacja 2**). Dubelty były chwytane w nocy na tokowiskach na początku sezonu lęgowego przy użyciu sieci ornitologicznych, a część losowo wybranych samców otrzymała nadajniki telemetryczne, których rodzaj był dobierany do celów poszczególnych badań. Dotychczas badania prowadzone z użyciem nadajników telemetrycznych, wykazały brak ich wpływu na behawior samców dubelta (Kålås *et al.* 1989). W latach 2013 i 2014, odnalezienie miejsc dziennego bytowania samców dubelta, mające na celu scharakteryzowanie cech siedlisk na żerowiskach (**publikacja 1, publikacja 3**) zostało umożliwione dzięki wyposażeniu 23 samców (kolejno 13 i 10 samców w poszczególnych latach) w miniaturowe (1.1 – 1.3 g) radiowe nadajniki VHF. Oznakowane osobniki były lokalizowane w terenie przy użyciu anten kierunkowych typu Yagi namierzających sygnał radiowy nadajników. Ptaków poszukiwano w zespołach 2-3 osobowych w odstępach 1-3 dniowych,

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w zasięgu do około 2 km od tokowisk. W ciągu dnia samce dubelta spędzają większość czasu na żerowaniu (Höglund *et al*. 1992, Løfaldli *et al.* 1992), dlatego też założono, że większość miejsc (jeżeli nie wszystkie), z których płoszone były samce dubeltów w ciągu dnia było wykorzystywanych w celu żerowania. Niemniej, w celu uniknięcia próbkowania na tokowisku lub w miejscach wynikających z przemieszczania się samców w kierunku tokowiska (Lemnell 1978, Løfaldli *et al.* 1991), a tym samym ograniczenia ryzyka dokonywania pomiarów poza żerowiskami, ptaki były wyszukiwane od dwóch godzin po wschodzie słońca do dwóch godzin przed zachodem. Każdy samiec był namierzany maksymalnie raz dziennie, tym samym proces selekcji miejsc żerowania był każdego dnia niezależny, gdyż z założenia rozdzielony okresem nocnych toków. Zapewnienie możliwie najwyższego poziomu niezależności próbkowania, miało na celu redukcję autokorelacji obserwacji. Miejsca spłoszenia samców napotkanych w terenie przypadkiem (również w latach 2020,2021 – **publikacja 3**) były również uwzględnione w badaniach, przy czym stanowiły mniejszą część obserwacji. Dokładne lokalizacje wykrytych w terenie samców były zaznaczane przy użyciu ręcznego odbiornika GPS. W celu określenia miejsc żerowania samców w latach 2020-2021 (**publikacja 3**), część schwytanych na 4 tokowiskach ptaków (N=31) została wyposażona w nadajniki GPS-GSM (o masie około 5 g). Umożliwiały one rejestracje pozycji samców przy użyciu satelitów GPS w interwale 0.5-1 h, które były następnie przesyłane za pośrednictwem sieci GSM. Podczas prac terenowych, mających na celu opis siedlisk w miejscach żerowania samców, dubelty były wyszukiwane przez obserwatorów na podstawie ostatnio zgranych pozycji GPS. Częstość i czas próbkowania były wykonywane zgodnie ze schematem opisanym dla lat 2013-2014 (**publikacja 1**).

Charakterystyka siedliska bezpośrednio otaczającego osobnika w miejscach żerowania samców dubelta została wykonana w oparciu o pomiary zmiennych środowiskowych, mające ekologiczne uzasadnienie w procesie selekcji siedlisk stanowiących żerowiska gatunku (Løfaldli *et al.* 1991). Opisywały one strukturę roślinności, grząskości gruntu, wilgotność, udział odkrytej gleby oraz ilość bezkręgowców glebowych (**publikacja 1 i publikacja 3**). Dodatkowo, opisywano w terenie czynniki, mogące mieć wpływ na poczucie strachu wśród samców (Stankowich & Blumstein 2005), jak również poziom ich kryptyczności (Ruxton *et al.* 2004), niezależne od cech siedliska. Były to: odległość od tokowiska, miejsce prowadzenia badań, zachmurzenie,

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temperatura otoczenia, data i godzina płoszenia, liczba obserwatorów oraz liczba spłoszonych osobników (**publikacja 3**).

Określenia lokalizacji miejsc bytowania samców w trakcie trwania sezonu tokowego, mającego na celu zbadanie dyspersji wewnątrzsezonowej i dynamiki przemieszczeń między tokowiskami (**publikacja 2**), dokonano na podstawie odczytów z nadajników GPS-UHF. Pozwalają one domyślnie rejestrować pozycje GPS w interwale 0.5-2 h, przy czym przesłanie zebranych danych następowało za pośrednictwem sygnału radiowego w interwale 10 minutowym do stacji bazowych w zasięgu około 100-200 m. W celu zgrania danych GPS z nadajników, zainstalowano w okresie badań stacje bazowe na wszystkich tokowiskach, na których zakładano nadajniki. Ograniczeniem tej technologii jest więc to, że zgranie zebranych przez nadajnik pozycji GPS było uzależnione od przynajmniej około 10 minutowej obecności samca na jednym z tokowisk, na którym zainstalowana była stacja bazowa. W pierwszych latach (2013, 2014, 2015) na 4 tokowiskach wyposażono w sumie 50 samców w nadajnik o masie około 5 g (kolejno 7, 21, 22), zaś w latach 2017-2018 na dwóch tokowiskach 20 samców (kolejno 9 i 11) w nadajniki o masie 3.5 g.

Publikacja 1.

Określenia wybiórczości siedliskowej samców dubelta względem miejsc żerowania dokonano w tzw. schemacie *„use–availability”* (Manly et al. 2002) w skali płatu siedliska bezpośrednio otaczającego osobnika (model mikrosiedliskowy) oraz na poziomie krajobrazu (model makrosiedliskowy). Jego ogólnym założeniem była konfrontacja cech siedlisk dostępnych dla dubeltów w zasięgu potencjalnych żerowisk (*„available”*) z cechami siedlisk w miejscach dziennego stwierdzenia dubeltów (*„used”*). Analizy wykonano przy użyciu dwóch, niezależnych dla każdej ze skal modeli regresji logistycznej z użyciem uogólnionych modeli liniowych (GLM) powszechnie nazywanych modelami selekcji zasobów (*resource selection function*). W celu scharakteryzowania cech siedlisk dostępnych dla dubeltów, w buforze 500 m od dwóch badanych tokowisk (w tej odległości stwierdzono większość miejsc dziennego bytowania dubeltów z nadajnikami GPS-UHF - **publikacja 3**, oraz 97% wszystkich stwierdzeń samców z nadajnikami VHF - **publikacja 1**), w wylosowanych 383 lokalizacjach znajdujących się w siedliskach potencjalnych gatunku dokonano pomiaru zmiennych środowiskowych, tożsamych z tymi, określanymi w miejscach żerowania. Zmienne wyjaśniające, użyte w modelu makrosiedliskowym stanowiły relacje przestrzenne wyrażone odległością pomiędzy miejscami

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żerowania i lokalizacjami losowymi a elementami krajobrazu (lustro wody, krzewy, las, pojedyncze drzewa), jak również wysokość nad poziomem morza (na podstawie modelu NMT) oraz sposób użytkowania łąk (nieużytkowane, jednokośne, dwukośne, wypasane, dwukośne i wypasane). Lokalizacja elementów krajobrazu, jak również sposób użytkowania rolniczego zostały określone przy użyciu narzędzi GIS na podstawie ortofotomap RGB i CIR o rozdzielczości 2 cm, opracowanych w trakcie sezonu badań w oparciu o dwa naloty fotogrametryczne. Do modeli dodano ponadto zmienną będącą średnią odległością do tokowisk. W modelu mikrosiedliskowym wprowadzono interakcję zmiennych wyjaśniających z datą próbkowania, gdyż wartości tych zmiennych były zależne od czasu w jakim były mierzone. Rankingu i selekcji modeli w obu skalach dokonano na podstawie kryterium AIC (Burnham & Anderson 2002). Oceny sprawności predykcji wyselekcjonowanych modeli, dokonano metodą walidacji krzyżowej (*cross-validation*) na podstawie średniej z trzydziestu wyliczeń pola pod krzywą ROC (niezależnie losowanych zbiorów testowych i uczących porównując dane z dwóch tokowisk), określanego jako AUC (*area under curve*). Do oceny różnicy w zasobach pokarmowych (biomasy bezkręgowców glebowych i niezależnie dżdżownic) w miejscach żerowania i lokalizacjach losowych, jak również porównania zasobów pokarmowych w różnych typach użytkowania rolniczego, wykorzystano modele GLM dostosowane do ujemnych rozkładów dwumianowych z zawyżoną frekwencją zer (*zero-inflated negative binomial models*).

Publikacja 2

Kwantyfikacja użytkowania przestrzeni samców dubelta w trakcie sezonu tokowego, zwłaszcza pod względem sezonowej i dziennej dynamiki przemieszczeń między tokowiskami oraz zasięgu dyspersji wewnątrzsezonowej, została dokonana na podstawie zaklasyfikowania poszczególnych lokalizacji GPS samców do wymienionych poniżej kategorii. „Tokowisko”, jeżeli pozycja samca była zarejestrowana w buforze 500 m od znanych i potencjalnych tokowisk. Lokalizacja tych pierwszych była znana na podstawie prowadzonego monitoringu dubelta w ramach Monitoring Ptaków Polski (http://monitoringptakow.gios.gov.pl/) lub potwierdzonych nowych tokowisk w trakcie prowadzonych badań. Za tokowiska potencjalne, uznano lokalizacje oddalone co najmniej kilometr od znanych tokowisk, odwiedzane przez tego samego osobnika przynajmniej podczas dwóch nocnych wizyt lub lokalizacje odwiedzane w nocy przez co najmniej dwa różne samce. Kategorię „lot”, przypisano do pozycji GPS gdzie prędkość zarejestrowana przez nadajniki była większa niż 3 m/s. Ze względu na stwierdzania pojedynczych tokujących samców, poza znanymi obszarami tokowania, podjęto również próbę opisania skali tego zjawiska. W tym celu, poza już sklasyfikowanymi pozycjami, stacjonarne pozycje nocne zostały przypisane do kategorii „*solo nocturnal presence*". Pozostałe pozycje GPS zostały przypisane do kategorii „niesklasyfikowane". Na podstawie przypisanych w ten sposób kategorii, wyliczono liczbę odwiedzanych przez samce tokowisk oraz dzienny i sezonowy rozkład przemieszczeń między tokowiskami, jak również czas spędzany przez samce w rejonie poszczególnych tokowisk oraz w pozostałych kategoriach behawioralnych (dla danych z lat 2015, 2017 i 2018 gdzie uzyskano lepszą jakość danych pod względem stałości zbieranych pozycji GPS). Zmienność w liczbie odwiedzanych przez samce tokowisk w poszczególnych latach obliczono przy pomocy uogólnionych modeli liniowych (GLM). Prawdopodobieństwo zmiany tokowiska przez samca wraz z postępem sezonu tokowego wyliczono przy użyciu modeli MSMR (*multi-state mark-recapture*, tylko dla danych z lat 2015, 2017 i 2018). Zasięg dyspersji wewnątrzsezonowej samców dubelta określono na podstawie: (i) najdalej zarejestrowanych pozycji GPS od tokowisk (*max foray*), (ii) maksymalnych odległość pomiędzy odwiedzanymi przez samce tokowiskami, oraz (iii) maksymalnej odległości od tokowisk, na których nałożono samcom nadajnik do pozycji w kategorii „*solo nocturnal presence*".

Publikacja 3

Rolę, jaką w procesie wyboru siedlisk przez samce dubelta odgrywa potrzeba zapewnienia bezpieczeństwa (a więc minimalizacji ryzyka drapieżnictwa) badano poprzez analizę zależności pomiędzy dystansem płoszenia samców (FID – *flight initiation distance*), a cechami siedliska oraz innymi czynnikami mogącymi mieć wpływ na decyzję poderwania się do lotu. FID jest powszechnie stosowanym wskaźnikiem poczucia strachu (Weston *et al.* 2012) jak również, w przypadku gatunków o kryptycznym ubarwieniu, postrzeganego („odczuwanego") poziomu kamuflażu ofiary (Ruxton *et al.* 2004). Założono, że decyzja poderwania się do lotu następuje w momencie zrównania kosztów i zysków wynikających z jej podjęcia, zgodnie z tzw. ekonomicznym modelem dystansu ucieczki (Ydenberg & Dill 1986) oraz, że wraz ze wzrostem poczucia bezpieczeństwa samców dubelta na żerowisku (wynikającym głównie z zapewnienia kryptyczności) dystans płoszenia będzie się zmniejszał. FID mierzono podczas wyszukiwania dubeltów i stanowił on odległość między dokładnym miejscem, z którego samiec poderwał się do lotu, a najbliżej przebywającym obserwatorem w momencie spłoszenia.

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Zależności te badano przy użyciu uogólnionych modeli liniowych z rozkładem błędu zgodnym z rozkładem Poissona (*Poisson GLM*). Zmienną objaśnianą był FID, zaś zmiennymi objaśniającymi (predyktorami) były cechy siedliska bezpośrednio otaczającego żerujące osobniki (zmienne opisane w **publikacji 1**) oraz pozostałe czynniki mogące wpływać na decyzję o poderwaniu się do lotu (odległość od tokowiska, miejsce prowadzenia badań, zachmurzenie, data i godzina płoszenia, liczba obserwatorów oraz liczba spłoszonych osobników). Selekcję zmiennych w modelu, najlepiej wyjaśniających zmienność w dystansie płoszenia samców dubelta dokonano przy użyciu kryterium AIC (Burnham & Anderson 2002).

Analizy statystyczne we wszystkich wymienionych publikacjach wykonano za pomocą programu R i R-studio zaś analizy przestrzenne w programie ArcMap.

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Wyniki

Publikacja 1.

Średni dystans miejsc żerowania samców dubelta od tokowiska wyniósł w przypadku pierwszego 484 m (sd = 247.0, n = 85) zaś w przypadku drugiego 294 m (sd = 163.4, n = 41). Prawdopodobieństwo stwierdzenia samców istotnie spadało wraz ze wzrostem odległości od tokowisk. Rozmieszczenie miejsc dziennego bytowania samców miało charakter wyraźnie wyspowy i było zmienne na przestrzeni dwóch sezonów badawczych. Predykcja modelu makrosiedliskowego wykazała, że użytkowanie łąk było głównym czynnikiem wyjaśniającym zmienność wyboru przez samce dubelta miejsc żerowania w skali krajobrazu. Najsilniej preferowane były łąki wypasane oraz kośno-pastwiskowe (z dwoma pokosami), w których prawdopodobieństwo stwierdzenia dubelta wynosiło kolejno około 0.9 oraz 0.6. Najniższe zaś (około 0.1 i 0.2) model przewidywał dla łąk nieużytkowanych i koszonych raz w roku. Oprócz unikania bliskości zwartych połaci krzewów, nie stwierdzono wyraźnych zależności między miejscami dziennego bytowania dubeltów, a pozostałymi elementami krajobrazu. Stąd też zdolności predykcyjne modelu makrosiedliskowego były relatywnie ograniczone (AUC = 0.64 oraz 0.72). Najlepszy model mikrosiedliskowy, przewidujący miejsca żerowania dubelta w skali płatu siedliska zawierał udział odkrytej gleby, będącej najsilniejszym z predyktorów i której znaczenie (duży udział) wzrastało wraz z postępem sezonu. Kolejnymi czynnikami mającymi znaczenie w procesie wyboru siedlisk były grząskość gruntu, wysokość roślinności oraz jej gęstość, wyrażona w odległości z jakiej obserwator nie dostrzegał sylwetki dubelta w miejscu z którego spłoszony był samiec. Model przewidywał wzrost prawdopodobieństwa stwierdzenia dubelta wraz ze wzrostem grząskości gruntu (będącą proxy jej wilgotności) oraz największą szansę (~0.3) stwierdzenia samców w średniej wysokości roślinności (30 - 60 cm). Pod względem gęstości roślinności, prawdopodobieństwo stwierdzenia samców dubelta było najwyższe (około 0.8) gdy obserwator mógł dostrzec sylwetkę ptaka z odległości około 10-15 m, zaś jej wartość szybko malała zarówno wraz ze wzrostem gęstości roślinności jak również jej spadkiem. W miejscach żerowania (n = 161) stwierdzono nieznacznie, choć istotnie większą ilość bezkręgowców glebowych (x = 23.9 g/m2, se = 2.58) w stosunku do miejsc losowych (x= 19.3 g/m2, se = 1.48; p = 0.046, n = 297). Różnice te nie były jednak istotne przy porównaniu wyłącznie biomasy dżdżownic, stanowiących około 75% masy wszystkich bezkręgowców glebowych (średnia z miejsc żerowania = 15.3 g/m2, se = 1.7; średnia z miejsc losowych = 15.8 g/m2, se =1.36; p = 0.926). Najwyższą biomasę bezkręgowców (średnia = 36.5 g/m2, se = 5.60), w tym dżdżownic (średnia = 32.5 g/m2, se = 5.89) stwierdzono na łąkach kośno-pastwiskowych i były one istotnie większe niż na łąkach jednokośnych, gdzie zasoby pokarmowe dubeltów były najmniejsze (bezkręgowce: średnia = 15.3 g/m2, se = 2.21; dżdżownice: średnia = 10.4 g/m2, se = 1.75; kolejno p = 0.010 oraz p = 0.003). Zasoby pokarmowe w pozostałych typach użytkowania łąk nie różniły się od siebie w sposób istotny. Zdolność predykcyjna modelu mikrosiedliskowego była bardzo wysoka (AUC = 0.89 i 0.91) co wskazuje zarówno na właściwy dobór zmiennych opisujących proces selekcji dubelta jak również silną specjalizację gatunku względem cech siedliska bezpośrednio otaczającego żerujące osobniki. Predykcja prawdopodobieństwa stwierdzenia dubelta przy użyciu tego modelu dla różnych typów użytkowania rolniczego w oparciu o zmienne środowiskowe z losowych lokalizacji, była zbieżna z predykcją preferencji samców dubeltów w stosunku do typów użytkowania łąk przewidywanej przez model makrosiedliskowy.

Publikacja 2.

Przemieszczenia wewnątrz-sezonowe dubeltów między tokowiskami (uwzględniając również te potencjalne) stwierdzono u 75% samców (43/57). Połowa z nich odwiedzała dwa tokowiska w trakcie sezonu (21/43), trzy do sześciu tokowisk odwiedzało 15 samców (35%), zaś 15% (7/43) odwiedzało w trakcie sezonu od 7 do 9 tokowisk. Biorąc pod uwagę wyłącznie potwierdzone tokowiska, 61% samców (35/57) odwiedziło więcej niż jedno tokowisko w trakcie sezonu, a pojedyncze osobniki zarejestrowano na 5 i 6 różnych tokowiskach. W okresie pięciu lat badań, w trakcie jednego sezonu tokowego, samce dubelta odwiedzały średnio 3.1 tokowisk (sd = 2.21, n = 57). Zmienność w liczbie odwiedzanych tokowisk między latami była znacząca i wynosiła średnio od 1.9 tokowiska (sd=1.2, n=16) w 2015 r. do 6 tokowisk (sd=2.4, n=9) w 2018 r. Wśród samców, które przemieszczały się między tokowiskami, dominowały (35/43) maksymalne przemieszczenia do 50 km, a tylko około 10% samców (n=4) odwiedzało tokowiska leżące w odległości większej niż 100 km od tokowisk, na których były one schwytane (zakres 136 - 253 km). Największe odległość w jakich stwierdzono samce od tokowisk (max foray) były silnie skorelowane (r=0.94, P<0.01) z odległością najdalej odwiedzanych przez nie tokowisk. W ciągu 5 lat badań, stwierdziliśmy w sumie 362 tranzycje wewnątrz-sezonowe samców między tokowiskami. Wśród tych, które odwiedziły co najmniej raz inne tokowisko (n=43), około połowa (53%; N=23) dokonała zmiany tokowiska do 5 razy w trakcie sezonu, 37% samców (N=16) zmieniała tokowiska od 5 do 17 razy a 4 samce dokonały zmiany tokowiska więcej niż 20 razy z rekordzistą, który zmieniał miejsce toków (przemieszczając się głównie między tokowiskiem w Polsce i odległym o 21 km tok. na Białorusi) 43 razy w trakcie jednego sezonu w okresie od 4 maja do 15 czerwca. Przemieszczenia między tokowiskami odbywały się niemal wyłącznie w okresie nocy (poza dwoma przypadkami odpowiadającymi 0.02 % przemieszczeń), ze szczytem między godziną 21.00 a 22.00 (26% przemieszczeń, n=73) i większością (66%, n=183) w godzinach między zachodem słońca a północą. Odwiedzanie przez samce więcej niż jednego tokowiska w ciągu jednej nocy było częste, obecne w 54% nocy, w których dochodziło do przemieszczeń. Wśród tych, 36% przypadków (n=55) dotyczyło dwukrotnej zmiany tokowisk, trzy zmiany tokowiska w ciągu nocy były obecne w 10% przypadków, zaś cztero- i pięciokrotne zmiany tokowisk przez samca w ciągu jednej nocy były stwierdzone kolejno w dziesięciu (7%) i dwóch (1%) przypadkach. Dzienne prawdopodobieństwo, że samiec dokona zmiany tokowiska przynajmniej raz w ciągu nocy wyniosło dla wszystkich lat średnio 0.12, przy czym zmienność między sezonami była znacząca. Jedynie w 2015 była tendencja wzrostu prawdopodobieństwa przemieszczania się samców między tokowiskami wraz z postępem sezonu lęgowego, podczas gdy w pozostałych latach zaobserwowano jego pik w połowie maja (2017) lub znaczną fluktuację (2018). Średnio 84% czasu (zakres: 51 – 100%, sd=12.75, n=36) w trakcie sezonu tokowego samce dubeltów przebywały w zasięgu 500 m od sklasyfikowanych tokowisk, a tylko przeciętnie 1% czasu (zakres: 0 – 5.3%, sd = 1.4) przeznaczały na lot poza tymi obszarami. Średnio 3.7 % czasu (zakres: 0.2 - 17.8%) samce dubeltów przebywały nocą poza zaklasyfikowanymi obszarami tokowisk („solo nocturnal presence”), zaś miejsca najdalej zarejestrowanych w tej kategorii, były oddalane średnio o 38 km (zakres: 0.6 – 247 km, sd = 62.7, N=36) od tokowisk, na których samce były schwytane. Biorąc pod uwagę samce, które odwiedzały więcej niż jedno tokowisko w trakcie sezonu (n=27 dla ptaków z lat 2015, 2017 i 2018), około 75% samców (n=20) spędzało większość czasu (zakres: 53-99 %) w rejonie jednego tokowiska, a tylko 11% (n=3) spędzało w rejonie jednego tokowiska mniej niż 40% czasu (zakres: 25-40%).

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Publikacja 3.

Analiza zależności pomiędzy dystansem płoszenia samców dubelta (n=517), a cechami siedliska w miejscu żerowania oraz pozostałymi czynnikami mogących mieć wpływ na decyzję poderwania się ptaków do lotu wykazała, że decyzja ta jest kształtowana przez wiele czynników działających jednocześnie. Wśród zmiennych opisujących cechy siedliska, największe znaczenie miały: (i) gęstość roślinności wyrażona dystansem z jakiego przestawała być widoczna dla obserwatora kukła dubelta z miejsca spłoszenia, (ii) wysokość roślinności jak również (iii) potencjalne zasoby pokarmowe wyrażone ilością dżdżownic w wierzchniej warstwie gleby. Pozostałe zmienne opisujące siedlisko bezpośrednio w miejscach żerowania samców takie jak udział odkrytej gleby, pokrycie wertykalne roślinnością oraz wysokość kęp turzycowych, nie miały natomiast wpływu na podjęcie przez samce decyzji o poderwaniu się do lotu. Wśród czynników nieśrodowiskowych, mających wpływ na dystans płoszenia samców największe znaczenie miały: liczba płoszonych osobników, liczba obserwatorów, zachmurzenie jak również data i godzina płoszenia. Istotne znaczenie miał też dystans w jakim spłoszone samce znajdowały się w stosunku do tokowisk. Mniejsze, choć w przypadku jednej powierzchni istotne, znaczenie miało też miejsce prowadzenia badań. Dystans płoszenia samców zwiększał się wraz ze spadkiem gęstości roślinności ocenianej w płaszczyźnie horyzontalnej zaś jego wartość malała wraz ze wzrostem wysokości roślinności. Model wykazał też, pozytywną zależność pomiędzy ilością dżdżownic w glebie, a dystansem płoszenia samców. Dystans płoszenia samców był najmniejszy (około 10 m), gdy płoszył się jeden osobnik i wzrastał sukcesywnie wraz ze wzrostem liczby osobników osiągając wartość około 15 m, gdy z miejsca żerowania płoszyły się trzy lub cztery osobniki. Największy dystans płoszenia oscylujący wokół wartości 32 m miał miejsce w sytuacjach, gdy do lotu podrywało się 7 samców. Dubelty płoszyły się w istotnej, niemal dwukrotnie większej odległości, gdy były podchodzone przez dwóch lub trzech obserwatorów, w stosunku do sytuacji, gdy spłoszone były przez jednego obserwatora. Wzrost dystansu płoszenia odnotowano też wraz ze wzrostem poziomu zachmurzenia, przy czym był on najbardziej wyraźny (8 a 13 m), gdy chmury pokrywały od 40 do 100% nieba. Stwierdzono też, że samce dubelta nieznacznie wcześniej (kolejno około 2 i 3 m różnicy) płoszą się w godzinach porannych i wieczornych, w stosunku do godzin okołopołudniowych, gdzie dystans ten wynosił około 9 m. Podobną, u-kształtną zależność

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w zbliżonych wartościach FID stwierdziliśmy też w przypadku okresu w jakim płoszone były samce, przy czym większy dystans płoszenia model przewidywał dla końca okresu tokowego przypadającego na dwie ostatnie dekady czerwca. Przeprowadzone analizy, wykazały też wyraźną zależność spadku dystansu płoszenia samców (z około 9 do 6 metrów) wraz ze wzrostem odległości miejsca żerowania od tokowiska.

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Wnioski i aplikacyjność wyników

Przeprowadzone badania dostarczają brakującej wiedzy na temat preferencji siedliskowych i wykorzystania przestrzeni samców dubelta w okolicy tokowisk (**publikacja 1, publikacja 2, publikacja 3**), fundamentalnej w planowaniu ochrony populacji nizinnej tego zagrożonego gatunku. Prezentują one również szczegółową charakterystykę użytkowania przestrzeni samców dubelta w szerszej skali, odkrywając zasięg i dynamikę przemieszczeń samców dubelta między tokowiskami, rzucając w ten sposób nowe światło na rozumienie tokowiskowego systemu kojarzenia (**publikacja 2**).

Uzyskane wyniki wskazują na niewielkie znaczenie elementów krajobrazu w procesie selekcji siedlisk stanowiących żerowiska samców dubelta (**publikacja 1**) oraz na bardzo silne znaczenie cech siedliska bezpośrednio otaczającego miejsca bytowania ptaków (**publikacja 1 i publikacja 3**). Wykazano, że silna specjalizację siedliskową samców dubelta na poziomie mikrosiedlisk, jest efektem zarówno potrzeby zapewnienia wysokiej efektywności żerowania (**publikacja 1**), jak również redukcji ryzyka drapieżnictwa, odzwierciedlających dążenie samców do żerowania w miejscach, ale i okolicznościach zapewniających im najwyższy poziom kryptyczności (**publikacja 3**). Wykazano przy tym, że proces wyboru siedlisk jest kompromisem ewolucyjnym gdyż, cechy siedliska najsilniej preferowane przez samce dubelta na żerowiskach, były różne od cech siedliska zapewniających najwyższy poziom bezpieczeństwa podczas żerowania (**publikacja 1 i publikacja 3**). Ponadto, wykazano, że decyzja samców o poderwaniu się do lotu zależy od bardzo wielu czynników działających równocześnie, i choć próba ekologicznego wyjaśnienia zmienności tego behawioru była dużym wyzwaniem (**publikacja 3**), uzyskane wyniki wskazują, że zapewnienie bezpieczeństwa podczas żerowania jest dla samców dubelta bardzo ważna. Tym samym, zmniejszenie presji drapieżników, szczególnie w bliskiej okolicy tokowisk, gdzie prawdopodobieństwo żerowania samców jest największe (**publikacja 1 i publikacja 2**) może się przyczynić nie tylko do oczywistego efektu jakim jest zwiększenie przeżywalności samców, ale również do znaczącej poprawy efektywności ich żerowania a tym samym poprawy jakości wybieranych przez ptaki siedlisk. Poprawa wynika bezpośrednio ze zmniejszenia częstości płoszenia (zwiększenie zasobów czasowych na żerowanie), ale też pośrednio, w sytuacji procesu selekcji w układzie kompromisu (**publikacja 1 i publikacja 3**), poprzez potencjalną modyfikację procesu selekcji w kierunku siedlisk o cechach zapewniających wyższą efektywność żerowania aniżeli redukcji poziomu drapieżnictwa (**publikacja 3**).

Użytkowanie rolnicze było jednym z głównych czynników, kształtujących preferowane przez samce dubelty cechy siedliska (**publikacja 1**). Ekstensywne użytkowanie sprzyjające ochronie siedlisk dubelta, jest jednak nieopłacalne ekonomicznie bez stosownych subwencji, co historycznie doprowadziło w Polsce do utraty wielu płatów dogodnych siedlisk w wyniku intensyfikacji rolnictwa lub – przeciwnie – w wyniku zarzucenia gospodarowania rolniczego. Dlatego też głównym narzędziem ochrony siedlisk dubelta w kraju są dziś tzw. „warianty ptasie", wdrażane obecnie poprzez Interwencje rolno-środowiskowo-klimatyczne ujęte w Planie Strategicznym Wspólnej Polityki Rolnej na lata 2023-2027. Warianty te muszą jednak wskazywać jaki typ użytkowania sprzyja zachowaniu funkcji życiowych gatunków, którym dedykowane są interwencje. Ponadto są one głównym narzędziem ochrony siedlisk gatunku w Planach Zadań Ochronnych sporządzanych dla obszarów Natura 2000. Tym samym, ważnym efektem niniejszej pracy było określenie użytkowania łąk sprzyjającego utrzymaniu cech siedliska preferowanych przez samce dubelta podczas żerowania (**publikacja 1**), niezmiernie istotnego dla behawioru samców ze względu na ich wysokie zapotrzebowanie energetyczne w trakcie toków (Höglund *et al.* 1992). Na badanych równinach zalewowych był to ekstensywny wypas oraz relatywnie intensywne użytkowanie łąki dwukośnych, połączone z wypasem. Wbrew oczekiwaniu odpowiadającym wiedzy w roku rozpoczęcia badań (2014), nie były to łąki koszone późno i raz do roku, a więc w reżimie, który wg wiedzy w tamtym okresie był w Polsce postrzegany jako korzystny dla dubelta, co znalazło odzwierciedlenie w programie rolno-środowiskowym przygotowanym między innymi specjalnie dla tego gatunku w Programie Rozwoju Obszarów Wiejskich na lata 2007-2013. Przyczyną preferencji samców do żerowania na relatywnie intensywnie użytkowanych łąkach, było to, że poprzez dwukrotne pozyskiwanie siana, usuwana jest z siedlisk znacząca część produkcji pierwotnej, zmniejszając tym samym trofię siedliska. W efekcie, łąki użytkowane w takim reżimie charakteryzują się mniej zwartą roślinnością zielną, oraz zmniejszonym tempem wzrostu roślinności (**publikacja 1**). Tym samym zapewniają one preferowaną przez samce dubelta niską i mało zwartą roślinność (**publikacja 1**). Wypasane zwierzęta, poprzez nierówne zgryzanie trawy jak również rozdeptywanie racicami darni, tworzą zaś urozmaiconą strukturę roślinności, kreując jednocześnie wiele płatów odkrytej gleby, będącej cechą siedliska najsilniej preferowaną przez samce dubelta na żerowiskach, i której znaczenie wzrastało wraz z postępem sezonu (**publikacja 1**). Odchody pasących się zwierząt, wpływają natomiast na lokalne zwiększenie wilgotności i trofii siedlisk, co sprzyja rozwojowi i dostępności dżdżownic, będących głównym pokarmem dubelta. Nasze badania wykazały, że łąki, na których był prowadzony wypas cechowały się największą zasobnością w bezkręgowce glebowe (w tym dżdżownice) spośród wszystkich typów użytkowania, natomiast w obrębie łąk, gdzie wdrożony był program rolno-środowiskowy zasobność dżdżownic była najniższa (**publikacja 1**). Zakładając, że samice preferują gniazdowanie w bliskiej okolicy tokowisk (Kålås *et al.* 1997b), co jest często stwierdzane w populacji nizinnej, najkorzystniejszy dla utrzymania żerowisk samców dubelta typ użytkowania może wiązać się z wysokim ryzykiem niszczenia lęgów (**publikacja 1**). Wynika to z faktu, że zarówno wypas prowadzony w maju i czerwcu (co jest typowym terminem wypasu na równinach zalewowych), jak również terminy pokosów łąk dwukośnych (rozpoczynające się w połowie maja) pokrywają się niemal w pełni z etapem wysiadywania lub wodzenia młodych (Mongin 2008; M. Korniluk, dane niepublikowane). Wynik ten wskazuje na istnienie u dubelta sprzecznych wymogów siedliskowe obu płci i sugeruje duże ryzyko wystąpienia pułapki ekologicznej, potencjalnie wzmacnianej wraz ze wzrostem jakości siedlisk dubelta (więcej dobrych żerowisk sprzyja większej liczbie samców na tokowisku i gniazdujących w okolicy samic). Dlatego też ochrona siedlisk tego gatunku, powinna zapewniać zarówno utrzymanie odpowiednich żerowisk jak i miejsc bezpiecznego gniazdowania. Na równinach zalewowych będących żyznymi siedliskami, taki kompromis może być osiągnięty poprzez utrzymanie mozaiki siedlisk użytkowanych mniej i bardziej intensywnie (**publikacja 1**), szczególnie, że samce dubelta zdają się preferować na lęgi, łąki koszone późno lub nawet użytkowane sporadycznie raz na kilka lat (M. Korniluk, dane niepublikowane). Wzrost prawdopodobieństwa stwierdzenia dubelta bliżej tokowisk (**publikacja 1**), co znalazło odzwierciedlenie w wysokim, średnio 84-procentowym udział czasu jaki samce spędzając w trakcie sezonu w zasięgu 500 m od tokowisk (**publikacja 2**), wskazuje zaś na zasięg implementacji takiego mozaikowego użytkowania oraz priorytetyzacji ochrony siedlisk gatunku jak najbliżej tokowisk. Druga z przytoczonych wskazówek, jest szczególnie istotna w sytuacji ograniczonych zasobów finansowych jak również ograniczeń wynikających z możliwości zarządzania terenem (własności gruntów). Należy przy tym zaznaczyć, że badania nasze wskazują, jakie jest korzystne dla dubelta użytkowanie łąk na równinach zalewowych. Są one jednak tylko jednym z czterech głównych typów siedlisk w jakich występują dubelty w Polsce

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(Korniluk i Piec 2016). Bezpośrednia wartość aplikacyjna naszych badań jest tym samym ograniczona. Przykładowo, torfowiska niskie czy łąki potorfowiskowe, w których również występują dubelty, cechują się niższą trofią a więc i mniejszą dynamiką wzrostu roślinności. Tym samym, w tych siedliskach mniej intensywny sposób użytkowania będzie prawdopodobnie zapewniał samcom dubelta preferowane przez nie cechy siedliska. Dlatego też pożądane jest narzędzie pozwalające ocenić, jak różne typy użytkowania rolniczego wpływają na cechy siedlisk, które są kluczowe dla zapewnienia dubeltom odpowiednich żerowisk także w pozostałych trzech typach siedlisk gatunku. Takim narzędziem może być opracowany przez nas model mikrosiedliskowy, gdyż cechuje się on bardzo wysoką zdolnością predykcyjną (wynikającą w dużej mierze z silnej specjalizacji siedliskowej gatunku i właściwego doboru zmiennych). Wykazał on predykcję prawdopodobieństwa wystąpienia dubelta na losowym zbiorze w różnych typach użytkowania rolniczego zbieżną z predykcją modelu w skali krajobrazu (**publikacja 1**). Tym samym, uzyskana przy jego użyciu wartość prawdopodobieństwa stwierdzenia dubelta obliczona na podstawie pomiaru zmiennych w reprezentatywnej liczbie losowych lokalizacjach siedliska, może być traktowana jako mierzalny indeks jakości siedliska dubelta, który nazwaliśmy „*habitat suitability index*" (**publikacja 1**). Reprezentuje on empiryczne narzędzie oceny jakości siedlisk gatunku. Zależność pomiędzy uzyskanymi wartości indeksu jakości siedliska dubelta a konkretnym typem użytkowania rolniczego, pozwoli zaś ocenić, który reżim użytkowania najbardziej sprzyja zachowaniu cech siedliska preferowanych przez samce dubelta na żerowiskach. Określenie uniwersalnego mierzalnego wskaźnika jakości siedliska dubelta, jest silnie pożądane w ocenie tzw. stanu zachowania siedlisk gatunków na obszarach Natura 2000, gdyż w przeciwieństwie do wielu rzadkich i zagrożonych gatunków ptaków w Polsce, ze względu na słabe rozpoznanie biologii gatunku nie został od dotychczas określony (Zawadzka i in. 2013, Korniluk i Piec 2016).

Oprócz cennych informacji na temat ekologii samców dubelta, mających fundamentalne znaczenie w ochronie jego populacji w Polsce i w obrębie zasięgu nizinnej populacji gatunku, badania dostarczyły też wiedzy na temat funkcjonowania tokowiskowego systemu kojarzenia (**publikacja 2**), jak również wykazały złożoność procesu unikania drapieżników i zarządzania decyzją o ucieczce u tego kryptycznie ubarwionego gatunku (**publikacja 3**). Częste zmiany tokowisk przez samce dubelta w trakcie sezonu, znacząca liczba odwiedzanych tokowisk przez większość osobników oraz relatywnie duży zasięg takich przemieszczeń wskazuje, że funkcjonowanie tokowiskowego system kojarzenia nie może być rozpatrywane wyłącznie przez pryzmat jednego tokowiska (**publikacja 2**). Silna korelacja maksymalnych dystansów przemieszczeń samców w sezonie, z maksymalnym dystansem odwiedzanych przez nie tokowisk, sugeruje, że dalekodystansowa, wewnątrz-sezonowa dyspersja samców ma na celu wyłącznie odwiedzanie innych tokowisk (**publikacja 2**). Jak sugerują nasze badania, behawior ten może stanowić alternatywną strategię rozrodczą części samców, pozwalającą skompensować niski sukces reprodukcyjny niektórych osobników. I chociaż nie badaliśmy sukcesu kojarzenia samców przemieszczających się na inne tokowiska, obserwacje prowadzone na innych tokujących gatunkach, jak również teoretyczne modele, pozwalają założyć, że dyspersja samców ma znaczenie adaptatywne. Przemieszczenia między tokowiskami dubeltów muszą mieć też znaczenie w przepływie genów w populacji, wpływając w efekcie na zwiększenie jej zróżnicowania genetycznego i skutkując wyższą odpornością populacji na zmiany w środowisku, zmniejszając tym samym ryzyko ich wymierania (Frankham 2005). Ponadto część zarejestrowanych w trakcie badań wzorców przemieszczeń, wyraźnie wskazywała, że samce znają lokalizację tokowisk odwiedzanych w danym sezonie po raz pierwszy lub odwiedzają lotem niemal bezpośrednim odległe tokowiska, nieaktywne w danym sezonie (**Publikacja 2**). Wiedza samców o lokalizacji innych tokowisk musiała więc wynikać z informacji zgromadzonej w trakcie ubiegłych sezonów, co może wskazywać, że zachowania dyspersyjne samców mają znaczenie dostosowawcze wykraczające poza jeden sezon lęgowy. Lepsze poznanie funkcji przemieszczeń samców dubelta między tokowiskami i jego znaczenie na poziomie populacji wymaga dalszych badań, w szczególności tych wyjaśniających czynniki wpływające na decyzje o zmianie tokowiska i zróżnicowanie strategii przemieszczeń między samcami oraz sukcesu kojarzenia przemieszczających się samców (**publikacja 2**). Niemniej, skala tego zjawiska (samice również odwiedzają wiele tokowisk w trakcie sezonu lęgowego, Höglund & Robertson 1990b) nie pozwala nie dostrzegać jego ważnej roli w prawidłowym funkcjonowania populacji. Wskazuje na to chociażby fakt, że nie istnieją żadne izolowane tokowiska dubelta poza zwartym zasięgiem gatunku. Tym samym, w planowaniu ochrony populacji dubelta, mocno uzasadniona wydaje się być potrzeba obejmowania ochroną nie tylko wyłącznie areału pojedynczych tokowisk (tokowisko i przyległe siedliska wykorzystywane przez ptaki), lecz przynajmniej kilku tokowisk w możliwie najbliższej jednostce krajobrazowej (**publikacja 2**). Ponadto, biorąc pod uwagę, że większość najdalszych przemieszczeń samców między tokowiskami nie przekraczała 50 km (**publikacja 2**), wymiana genetyczna między tzw. populacją podlaską a lubelską (około 160 km między stałymi tokowiskami), może być znacząco ograniczona. W szczególności, że zarówno wewnątrz sezonu (**publikacja 2**), jak i między nimi nie stwierdzono dotychczas żadnych przemieszczeń między tymi populacjami (M. Korniluk, dane niepublikowane), również w oparciu o obrączkowane ptaki. Dlatego też istnieje potrzeba zbadania różnic genetycznych między tymi populacjami, a w przypadku wykrycia zubożenia puli genowej będącej wynikiem izolacji, należy dążyć do odtwarzania siedlisk gatunku w miejscach historycznych (**publikacja 1**), zlokalizowanych pomiędzy znanymi tokowiskami w obu regionach, tworząc tym samym „pomost genetyczny" między populacjami.

Ponadto, biorąc pod uwagę, że liczenia samców na tokowiskach są u dubelta (Kålås 2000, Korniluk i in. 2015) powszechnie stosowanym indeksem służącym monitorowaniu trendów populacji, dynamika przemieszczania się samców między tokowiskami powinna być wzięta pod uwagę zarówno przy planowaniu liczeń, jak również analizie danych (**publikacja 2**).

Z punktu widzenia ekologii ewolucyjnej, behawior dubeltów, na który składa się badany przez nas proces wyboru siedlisk na żerowiskach (**publikacja 1, publikacja 3**), unikanie drapieżnictwa (**publikacja 3**), jak również wewnątrz-sezonowa dyspersja mająca na celu przemieszenia się między tokowiskami (**publikacja 2**), jest w dużym stopniu efektem silnej presji doboru płciowego oddziałującego łącznie z doborem naturalnym. Tym samym, ochrona gatunków charakteryzujących się specyficznymi systemami kojarzenia może być zadaniem trudniejszym niż ochrona gatunków charakteryzujących się powszechniej występującymi systemami kojarzenia.

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Załączniki

Publikacja 1 - Korniluk M., Białomyzy P., Grygoruk G., Kozub Ł., Sielezniew M., Świętochowski P., Tumiel T., Wereszczuk M., Chylarecki P. 2021. Habitat selection of foraging male Great Snipes on floodplain meadows: importance of proximity to the lek, vegetation cover and bare ground. Ibis 163: 486–506; DOI: 10.1111/ibi.12898

Publikacja 2 - Korniluk M. & Chylarecki P. 2023. Intra-seasonal lek changes of Great Snipe males in the Northeast of Poland. Acta Ornithologica 58 (publikacja przyjęta do druku)

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Habitat selection of foraging male Great Snipes on floodplain meadows: importance of proximity to the lek, vegetation cover and bare ground

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Drainage of wetlands and agricultural intensification has resulted in serious biodiversity loss in Europe, not least in grasslands. Consequently, many meadow birds have drastically declined, and the habitats they select for breeding currently rely on land management. However, the selection of habitats maintained by agriculture may contribute to reduced fitness and thus remain maladaptive for individuals, which makes conservation challenging. An understanding of the relationships between species' habitat selection, food supply and land management in the context of species' behaviour is therefore crucial for conservation. Lowland populations of Great Snipe *Gallinago media* are currently declining at a moderate rate, causing a conservation concern. We examined the daytime site selection (assumed as foraging sites) and food supply of radiotracked Great Snipe males breeding on a floodplain in NE Poland. Foraging sites were classified at micro- and macro-scale levels using the logistic regression in a use–availability design. On the micro-scale level, males selected moderate sward height and density, and a large amount of bare ground patches, and the importance of these increased as the breeding season progressed. On the macro-scale level, these conditions were associated with (1) meadows mown twice per season and grazed thereafter (associated with the most abundant food resources – earthworms) and (2) extensively managed pastures, suggesting the importance of grazing. Abandoned or late-mown meadows under agri-environmental schemes (AES) were avoided by foraging males. However, parcels with delayed mowing offer safe breeding sites for females nesting close to leks, unlike land-use types preferred by foraging males, which may act as an ecological trap. Effective conservation of Great Snipes on floodplain meadows requires precisely targeted AES schemes that will provide a mosaic of intensive and extensive land-use patches in the vicinity of identified leks.

Keywords: agri-environmental schemes, earthworms, ecological trap, floodplains, foraging, function, *Gallinago media*, habitat selection, lekking, resource selection.

Habitat loss, coupled with climate change, is widely recognized as the main driving force of avian declines in Europe and worldwide (EEA 2015, Powers & Jetz 2019). Knowledge of what constitutes a 'good' habitat for a species is thus a prerequisite for its effective protection. Therefore, studies of habitat selection in birds, although often

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purely descriptive, today provide the foundations for informed conservation strategies for threatened species. Here, habitat selection is best viewed as a hierarchical process occurring on different spatial scales, reflecting sequential decisions made by individual birds in search of places providing key resources, e.g. food, shelter, mates or safety (Kristan & Scott 2006, Boulinier *et al.* 2008, Fuller 2012). [Correction added on 24 November 2020, after first online publication: the above sentence has been modified.] Analysing multiple scales of variation in habitat suitability, using different spatial grains (Meyer & Thuiller 2006), should thus provide conservationists with a better understanding of observed patterns in habitat use by birds and assist in designing appropriate management for species threatened by habitat loss and alteration.

Grassland waders figure prominently among European bird species showing widespread and rapid population declines in recent decades (BirdLife International 2015). In fact, in 2015 three species of this group were classified as threatened in Europe according to the IUCN Red List criteria (IUCN 2020), including Lapwing *Vanellus vanellus* (up-listed to 'vulnerable' category), Black-tailed Godwit *Limosa limosa* (assessed as 'vulnerable' in Europe and 'endangered' in EU27) and Eurasian Curlew *Numenius arquata* ('vulnerable' both in EU27 and throughout Europe). These trends were primarily attributed to continued loss and degradation of breeding habitats due to drainage (Zedler & Kercher 2005) and intensification of agriculture (Wilson *et al.* 2004), which have further reduced the low reproductive success caused by predation on eggs and chicks (Roodbergen *et al.* 2012). In central-eastern Europe, the abandonment of land, and succession due to economically unprofitable traditional management, have also been identified as threats for meadow birds (Leito *et al.* 2014).

For over 30 years, agri-environmental schemes (AES) have been the main tool in EU countries to counteract biodiversity loss in agricultural habitats, including population declines of meadow waders (Wilson *et al.* 2004, Franks *et al.* 2018). Evaluations of their effectiveness for biodiversity conservation in Europe have provided mixed results (Batáry *et al.* 2011, Kleijn *et al.* 2011, Pe'er *et al.* 2014, Franks *et al.* 2018), although fine-tuned measures implemented at regional level may prove highly successful (Peach *et al.* 2001). For meadow waders, no positive effects of AES have been found in central Europe (Żmihorski *et al.* 2016); however, those schemes were not specifically targeted at achieving beneficial outcomes for waders. In contrast, a recent meta-analysis revealed that in western Europe, targeted, species-specific AES can be broadly effective for waders (Franks *et al.* 2018), especially when applied regionally (Whittingham *et al.* 2007).

The Great Snipe *Gallinago media* is a medium-sized (weight *c.* 150 g), cryptic wader species, known for its lekking behaviour (Lemnell 1978) and narrow diet specialization, with earthworms (Lumbricidae) constituting up to 90% of its prey (Løfaldli *et al.* 1992). Male Great Snipes perform nightly displays on traditional mating arenas, with females apparently favouring individuals with the highest display rate (Höglund & Lundberg 1987). Male displays are highly energy-demanding, causing birds to lose *c.* 5% of their body mass each night, necessitating the rebuilding of energy reserves the next day. This is indeed challenging, as migrating waders of this size are expected to refuel at the maximum rate of 4.2% of lean body mass per day (Lindström 2003). The species is thus heavily dependent on energy-rich foraging grounds located in the vicinity of leks. The presence of good feeding sites, with high availability of large-sized subsurface invertebrates (mostly earthworms), is thought to shape the distribution of leks in this species (Kålås *et al.* 1997a).

Widespread loss of extensive fens to rapidly developing agriculture ('second agricultural revolution') coupled with hunting have been implicated as the main factors governing the extinction of Great Snipe from the lowlands of central and northern Europe in the late 1800s (Løfaldli *et al.* 1989). By the early 20th century, the species disappeared completely from large areas of northern Germany, Denmark, lowland Sweden and Norway, and from the majority of western Poland (Løfaldli *et al.* 1989, Kålås *et al.* 1997a, Gedeon *et al.* 2014, Berndt 2018). As other grassland waders continued to breed there on human-transformed grasslands, regional extinction of the Great Snipe is likely to reflect its extreme reliance on very specific wet habitats, where patches suitable for lek display arenas and breeding adjoin patches offering both rich food and vegetation cover from predators (Løfaldli *et al.* 1992).

Today, the Great Snipe consists of two genetically isolated (Ekblom *et al.* 2007) and morphologically distinct breeding populations (Kålås *et al.* 1997b), considered separate conservation units

(Sæther *et al.* 2007). The western one occurs above the tree lines in Scandinavian mountains and shows no decline, whereas the eastern, lowland population inhabits floodplains, natural sedge and sedge-moss fens and drained post-peatland meadows, from Eastern Poland through Ukraine, Belarus and the Baltic States to central Russia (Kålås 2004, Birdlife International 2020). There are numerous studies of Great Snipe ecology and habitat requirements in Scandinavia (e.g. Løfaldli *et al.* 1989, 1992, Höglund & Robertson 1990, Höglund *et al.* 1992, Løfaldli *et al.* 1992, Ekblom *et al.* 2007, Sæther *et al.* 2007) but the lowland population has been poorly investigated so far (Kuresoo & Luigujõe 2001, Mongin 2002, Sviridova *et al.* 2018), despite it making up 90% of the total species population (Birdlife International 2020). The habitats occupied by the lowland population (mostly managed grasslands) are also more influenced by humans, and thus more vulnerable to changes (Kålås 2004), than those occupied by the mountain population. Importantly, the lowland population has experienced a long-term decline and is now listed as ‘near threatened’ (Birdlife International 2020), so improved knowledge about its habitat requirements is needed.

We studied Great Snipe male foraging habitats and food resources on floodplain meadows in Eastern Poland, the habitat type that supports up to 70% of the lowland population (Kuresoo & Luigujõe 2001, Kålås 2004, Mongin 2008). Habitat selection was investigated throughout two successive breeding seasons at two spatial scales, somewhat analogous to the third- and fourth-level selection of Johnson (1980). Using radiomarked birds, we sought to identify habitat preferences of males foraging during the daytime around their leks, both on the level of patches of diverse habitat types occurring on the floodplains (termed macro-scale here) and on the level of structural habitat features identified around exact feeding places within the habitat patch (micro-scale). We restricted our analyses to these two scales, as we were primarily interested in results that will inform the national Great Snipe conservation plan developed for the Polish population (Korniluk & Piec 2016).

First, we wanted to identify habitat features that are preferred by foraging males on a fine scale (micro-scale), using attributes deemed important for montane populations as a reference (Løfaldli *et al.* 1992), besides obvious application to the conservation plan, which would provide us with information on how much the habitat preferences found in Scandinavia are generalizable and transferable to the lowland population.

Secondly, we sought to identify habitat types preferred by foraging males on a coarse scale (macro-scale), in conjunction with the presence of habitat features identified at the micro-scale as habitat types reflected different agricultural practices (see below), which should translate into possible recommendations regarding optimal land use and agricultural practices in the species management plan. Here we also wanted to assess whether a ‘broad and shallow’ AES applied to a proportion of land parcels within our study area, designed to support breeding waders, is indeed beneficial for Great Snipes.

Finally, we expected that given the high energetic costs of Great Snipe male displays (Höglund *et al.* 1992) and that most males join the lek every night (Höglund & Robertson 1990), males should prefer to forage close to the lek, as this would lower their commuting costs and save a maximum amount of energy for lekking while providing more time to refuel.

Taken together, the results should extend our knowledge of Great Snipe habitat requirements beyond what is known for the montane population of Scandinavia, to inform conservation measures that should be designed for and applied to the declining lowland population of the species in eastern Europe.

METHODS

Study area

The study area was located in NE Poland in the upper Narew river valley (52°55′N, 23°39′E, 165 m a.s.l.), which is an important wader breeding site (BirdLife IBA PL048). Narew is a medium-sized, naturally flowing and meandering lowland river with hydrological characteristics typical for the continental climate, with highest discharge during snowmelt (March), when most of the valley is flooded, and water possibly remaining in the valley until May. The natural flooding regimen of the Narew river has been altered by the presence of an artificial reservoir (Siemianowka – 7 km upstream of the study area).

As a result of fluvial processes, the valley bottom is a fine-scale mosaic of moulds and depressions (rarely exceeding 1–2 m), resulting in a sharp gradient of humidity and flooding duration.

The vegetation of the valley is related to the above-mentioned abiotic factors as well as to human activities, notably grassland management typical for floodplains. Since the 1990s, about 60–70% of the meadow area has been abandoned, leading to a succession of tall-herb communities, reedbeds and tall sedge beds, with a dominance of *Carex acuta* and *Glyceria maxima* stands.

The valley supports 40–60 Great Snipe males, distributed between seven to eight leks (M. Korniluk unpubl. data), and is the second most important breeding site in Poland (Polish population: 400–550 males, Chodkiewicz *et al.* 2015). Within the study area, two permanent leks and one satellite lek (active only in 2013, Fig. 1), were occupied by a total of 18–22 males in both years. We defined our 166-ha study area as an aggregated zone within a 500-m radius of the three Great Snipe leks (Fig. 1). Given that the diurnal locations of the male Great Snipe are distributed mostly up to a few hundred metres from the lek (rarely further than 800 m, M. Korniluk unpubl. GPS logger data) and that this aggregated buffer covered a majority of open landscape around the leks, we assumed all resources within this area are potentially available to the Great Snipe males.

Data collection methods

To examine habitat selection, we applied a use–availability design (Manly *et al.* 2002, Johnson *et al.* 2006) in two spatial scales (a micro-scale model and macro-scale model), where environmental characteristics at the male Great Snipe daytime presence sites ('used') were contrasted with characteristics at random sites ('available') within the study area. During the daytime, males spend most of their time foraging (Höglund *et al.* 1992, Løfaldli *et al.* 1992) and thus we assumed that most, if not all, of the sites where we found male Great Snipe during daytime were used by them for foraging. The models express the probabilities of foraging site selection as an index because our randomly selected set included both unused and potentially used sites (Manly *et al.* 2002, Johnson *et al.* 2006).

To localize foraging locations, we mist-netted birds at the two permanent leks during the peak of the displaying season in the first half of May 2013 and 2014 (leks are active from mid-April to late June) and attached VHF transmitters to 23 males (13 and 10 birds in 2013 and 2014, respectively; Holohill BD2 1.6–1.8 g, ~ 1.1% of the

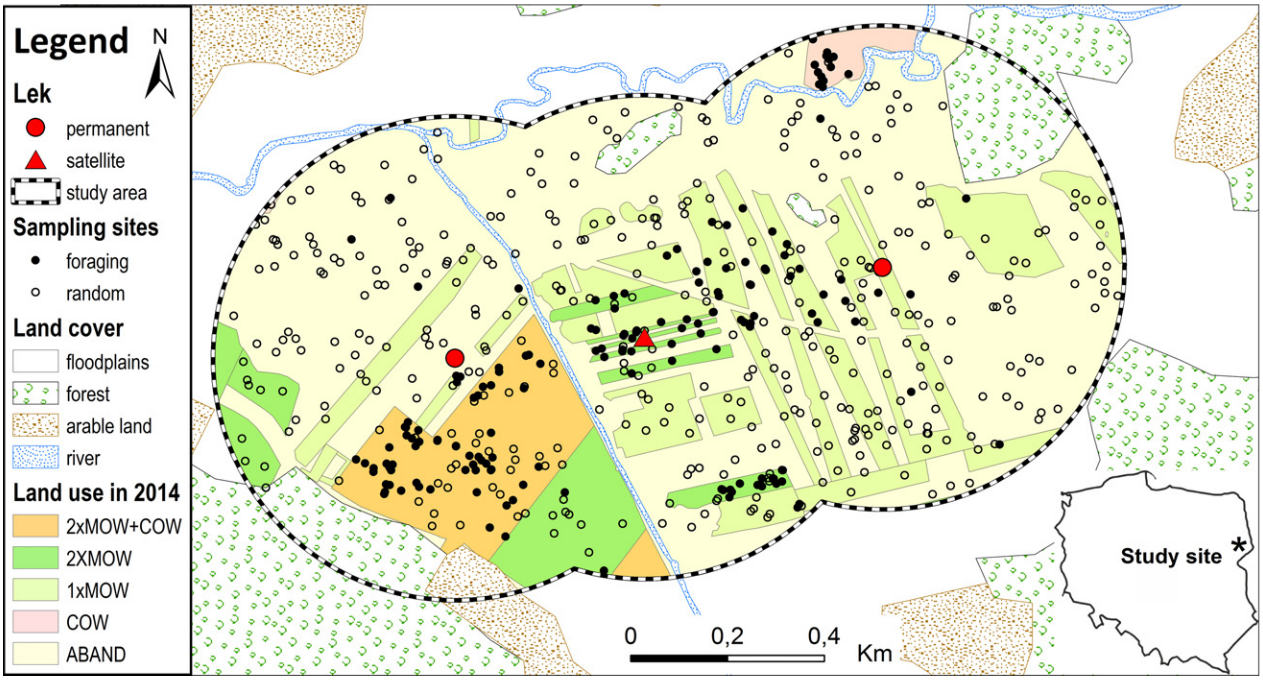

Figure 1. The study area (location within Poland indicated in the bottom right corner) where we examined Great Snipe foraging habitat selection in 2013 and 2014. Land use types in the legend are described in Table 2.

mean body mass of the studied birds (152.8 g)). Tags were attached to back feathers with cyanoacrylate glue or water-resistant black TESA tape. This method had been used on Great Snipes with no behavioural disturbance observed (Kålås *et al.* 1989). The usage of VHF transmitters excludes the potential bias of unequal detectability of individuals in different habitats. Two days after trapping, the birds were tracked with a Yagi directional antenna during daytime by groups of two or three persons every 1–2 days or occasionally with longer time gaps due to bad weather. After 5 days with no signal from any tagged birds (males left the study site permanently late in the breeding season or the VHF dropped off after 3–6 weeks), fieldwork was suspended, resulting in a sampling period from 12 May to 25 June in 2013 and 7 May to 19 June in 2014. We searched for birds within the study area and 500 m around it, to check whether males also forage outside the study area. When an individual was approached, we tried to locate the precise feeding site from where it was flushed and then sampled the attributes of the habitat (see Habitat variables below). If the foraging site was not precisely located, the sampling procedure was omitted. Some non-tagged birds were flushed by coincidence during fieldwork, and when their exact foraging site was detected (based on probing holes and fresh faeces), we applied the same sampling protocol and included the data in our analyses ($n = 41$). We assumed that most of those birds were males, as at that time in the season females spend ~ 90% of their time incubating (Løfaldli 1985) and thus the possible effect of a few samples from females is negligible. Foraging site positions were recorded with a GPS (Garmin 62sc) with an accuracy of ~ 3 m. We only tracked each tagged individual once a day to exclude sampling on non-foraging sites after disturbance. This time lag also reduced autocorrelation caused by non-independence of observations of the same individual (Muff *et al.* 2020). In total, we collected samples from 167 foraging sites (2013: $n = 77$, 2014: $n = 90$).

To determine available resources within the study area in 2013 and 2014, we generated 200 and 250 random locations, respectively (450 in total, using HAWTH'S TOOLS software, Beyer 2004). Random sites in dense bushes and forest were omitted as non-potential foraging sites (Løfaldli *et al.* 1992, our own data from GPS loggers). When the random sites were visited in the field (using a GPS device), a ball was thrown into the air and the precise place where it hit the ground was considered the random site that was sampled. Those sites were sampled roughly at the same time as foraging sites (12 May to 25 June in 2013 and 7 May to 19 June in 2014, see Fig. S1) with the same protocol (see Habitat variables below). In total, 383 random sites were sampled (2013: $n = 155$, 2014: $n = 228$).

Habitat variables

We chose habitat variables at the micro-scale that may have biological meaningfulness in Great Snipe habitat selection (ecological meanings of the chosen variables are described in Løfaldli *et al.* (1992) and Table 1). Additionally, we added the proportion of bare ground, as this habitat feature is important for ground-foraging waders (Smart *et al.* 2006, Chamberlain *et al.* 2009). To minimize observer bias, before each field season, we calibrated habitat variable assessment in the group of six observers who performed the fieldwork. For each of the foraging and random sites, we determined nine micro-scale habitat variables potentially important for foraging Great Snipes within 50 × 50-cm plots (Table 1). Mean vegetation (VegHeight) and tussock height (Tussok) were measured with a ruler to the nearest cm. Vertical vegetation cover (VegCovV), the percentage of vegetation that covers a blank piece of paper of 10 × 10 cm placed in the centre of the plot (site from where the Great Snipe was flushed), was assessed by the observer who looked at it from vertically above. Mean horizontal vegetation cover (VegCovH) was calculated as a mean of four distances (towards N, E, S, W) from where the observer could not see a Great Snipe decoy (brown ball of 8 cm diameter) placed where the birds were flushed; the denser the vegetation, the shorter the distance. We also estimated moisture (Moist) on a scale from 1 (dry) to 6 (flooded), where 1 = water table < 10 cm deep, 2 = water table 5–10 cm deep, 3 = water table 0–5 cm deep, 4 = water on soil surface (0–3 cm), 5 = water table 3–10 cm above the ground surface, 6 = flooded (> 10 cm of water above the ground). We estimated by eye the proportion of bare ground (BareGr) on the plot and mean soil penetrability (Penetr) as the mean penetration depth from three droppings of a pointed iron pin (8 mm in diameter, weight 180 g) from 1.5-m height at the centre of the plot. The above-mentioned variables were recorded at foraging and random sites on a 50 × 50-cm sampling square (delineated by the tape measure). The mean distance of each sample plot to the two permanent leks (LekDist) was added to the micro-scale model, as we expected that the distance to the lek might modify the resource selection behaviour similarly to that of central-place foragers (Orians & Pearson 1979). Using averaged lek distance, rather than distance to the lek where the male was caught, allowed us to include records of unmarked birds ($n = 41$) flushed opportunistically while locating marked males. This variable should be considered an index of preference to forage closer to the leks.

To assess subsurface invertebrates from the centre of the plot, we collected soil samples (15 × 15 × 10 cm deep, cut with a steel frame). All potential prey (> 0.5 mm) were searched within those samples in the lab, washed through a 1-mm mesh. Invertebrate abundance (total wet biomass of identified class, order or family weight, ± 0.001 g) was then analysed in the lab.

The macro-scale variables were obtained with the use of GIS software (ARCGIS 10.1, Redlands, CA, USA). Six continuous variables, concluded to be potentially important in habitat selection for the Great Snipe, were calculated (Table 1, see argument for ecological meaning of the chosen variables). Elevation (Elev), which can be understood as a proxy of wetness/flooding duration and depth, was obtained from the Digital Terrain Model (Project ISOK of Head Office of Geodesy and Cartography GUGIK – Poland) as a mean within a 3-m radius of focal points. Distances of foraging and random sites from the nearest

Table 1. Variables used to explain the male Great Snipe foraging habitat section on two levels – micro- and macro-scale

Scale	Variable code	Variable name and unit	Description and ecological meaning
Micro-scale variables	Date	Date of sampling (days)	Relative date within the breeding season, 1 = 01 May
	VegHeight	Vegetation height (cm)	Mean in a 50 × 50-cm plot, measured with a ruler[a]
	VegCovV	Vertical vegetation cover (%)	Vegetation coverage of 10 × 10-cm paper blank placed in the centre of the plot[a]
	VegCovH	Horizontal vegetation cover (m)	Mean of four perpendicular direction maximum distances from which we could not see a Great Snipe decoy[a]
	BareGr	Bare ground (%)	% of bare ground within the plot, an important feature for ground foraging waders (Smart *et al.,* 2006)
	Penetr	Soil penetrability (cm)	A mean measured in the centre of the plot by dropping three times a pointed iron pin (8 mm diameter, 180 g in weight) from 1.5 m height[a]
	Tussok	Tussock height (cm)	Mean for all tussocks in the 50 × 50-cm plot, measured with a ruler[a]
	Moist	Moisture (1–6)	On a scale from 1 (dry) to 6 (flooded)[a]
	DistLek	Mean distance to leks (m)	Mean distance to the two permanent leks, as we expected that the distance to the lek may modify the resource selection behaviour similarly to in central-place foraging theory (Orians & Pearson 1979)
Macro-scale variables	Elev	Elevation (m)	A mean 3-m radius based on Digital Terrain Model (Project ISOK of Head Office of Geodesy and Cartography GUGIK – Poland, 1 m resolution). The variable is a proxy for soil moisture gradient, given spring flooding of the study area[a]
	DistLek	Mean distance to leks (m)	As above
	DistTree	Distance to nearest single tree (m)	Distance between foraging and random sites to nearest landscape elements, those landscape characteristics are important for waders (Żmihorski *et al.* 2016)
	DistShrub	Distance to nearest shrubs (m)	
	DistForest	Distance to nearest forest (m)	
	DistWater	Distance to nearest water surface (m)	
	LandUse	Land use type	Land use regimen and type affects sward structure (Land use types listed in Table 2)

[a] Variables identified as biologically meaningful for Great Snipe according to Løfaldli *et al.* (1992).

landscape elements were identified with a 1-m accuracy in GIS based on aerial RGB and CIR cartometric images of the study area (FotoRaporty, Piaseczno, Poland) acquired on 14 May 2013 and 12 June 2014 with a UAV-based camera (resolution 2 cm): single trees (DistTree), shrubs (DistShrub), forest (DistForest) and permanent (oxbows and rivers) open water surface (DistWater). The mean distance to two permanent leks (LekDist) was also ascertained at the macro-scale, as the distance to the lek may also modify resource selection behaviour. Additionally, the land-use type for each of the used and available locations (five classes, Table 2) was defined based on an aerial-orthophoto from 2012 (open source aerial images form CODGiK) and aerial RGB and CIR cartometric images from 2013 (source described above); in some cases (late-mown meadows) the assignment was confirmed on the ground in October 2013. Land use from the previous year (rather than the year of the bird recording) was used in the analysis, as it had a stronger effect on vegetation structure experienced by the Great Snipe than in the study year. This is due to the general timing of grassland management relative to the period of Great Snipe tracking. Extensive grazing (~ 1 cow or bull/ha – COW) starts in mid/late May. On meadows mown twice a season (2xMOW, perceived as intensive on floodplains) the first mowing took place in early June and the second about 2 months later. Parts of such meadows (mown twice) are thereafter grazed extensively (1–2 cattle/ha – 2xMOW + COW). Extensively used meadows in AES (1xMOW) are mown once after 1 August. Given that sampling took place from the beginning of May to late June (lekking period starts from late April to late June) the birds experienced the vegetation structure that was created by the previous year's land management rather than the land management that took place in the study year. We also calculated mean invertebrate and earthworm biomass within each land use type (Table 2).

Statistical analyses

We analysed variables likely to influence daytime presence of male Great Snipes in the vicinity of their leks (presumed foraging sites), employing a use–availability design (Manly *et al.* 2002, Millspaugh *et al.* 2020). We coded sites where we found birds as 1 ('used') and randomly selected sites from within our study domain as 0 ('available') and used this as a binary response to model Great Snipe habitat selection as a function of candidate predictors measured at two spatial scales and listed in Table 1. We used generalized linear models (GLMs) with a binomial error structure and logit link function to model the relationship between the presence/absence of birds and candidate predictors at the micro- (GLM1) and the macro-scale (GLM2). We employed an information-theoretic approach (Burnham & Anderson 2002) to score multiple competing models for their fit to the data using Akaike's information criterion corrected for finite samples (AICc). Due to computational problems, we did not employ mixed models (binomial GLMMs) to account for the multiple records of the same individuals. Meaningful binomial GLMMs in habitat selection studies require random slopes to be fitted (Muff *et al.* 2020), which proved challenging, given the number of parameters to fit, the quadratic terms used and the still rather limited sample size. Our GLMMs constructed according to Muff *et al.* (2020), fitted with the *glmmTMB* package, notoriously failed to converge, prompting us to look for alternative ways (cross-validations; see section below) to examine possible effects of interindividual variation on habitat use in our sample.

For the micro-scale models, we considered nine candidate predictors (three of them in the squared form) as the main terms and also included interactions between those variables and the date, as micro-scale variables changed dynamically as the breeding season progressed (Fig. S1). All continuous variables (for both scale models) were checked for a possible non-linear effect on Great Snipe probability of occurrence by comparing the AIC of linear and squared terms in univariate GLMs for each covariate. We then analysed all possible subsets of this global model, which contained no more than seven predictors (both main terms and interactions). This was intended to avoid overfitting while sticking to the rule of having at least 10–20 data points per parameter to estimate (Harrell 2015). For a binomial GLM and 146 records of foraging sites (complete dataset with no missing values), we thus were bound to have 7–15 parameters, which translates into some six to eight predictors, which may show a few interactions and include squared terms. Thus, we screened 1226 candidate models containing one to seven predictors (plus intercept) and a null model.

Table 2. Land use types (a categorical variable used in the macro-scale model), their proportions within the study area in 2013 and 2014, and the number of foraging and random sites sampled within each class of land use with invertebrates and earthworm abundance in each class based on random soil samples

			Number of samples in sites		% of study area			Mean biomass, g/m^2 (sd)	
Variable code	Variable name	Variable class and code	Foraging (%)	Random (%)	2012	2013	No. of soil samples	Invertebrates	Earthworms
LandUse	Land use type	Meadows mowed twice and extensively grazed (2xMOW + COW)	53 (31.7)	21 (5.5)	0.4	8.4	20	36.5 (25.03)	32.5 (26.33)
		Meadows mowed twice a year (2xMOW)	41 (24.6)	40 (10.5)	14.6	7.2	36	25.4 (30.75)	18.0 (23.20)
		Meadows mowed once a year (1xMOW)	31 (18.6)	86 (22.5)	14.9	17.5	68	15.3 (18.26)	10.4 (14.43)
		Abandoned meadows (ABAND)	30 (18.0)	234 (61.1)	57.8	54.6	171	17.4 (25.92)	15.3 (25.10)
		Extensive pastures (COW)	12 (7.2)	2 (0.5)	1.1	1.1	2	39.7 (11.35)	39.6 (11.25)

At the landscape scale, we considered seven candidate predictors (four of them in the squared form) as the main terms to build a global model. Using the same logic explained above, we fitted and scored 128 candidate models, forming all possible subsets of the global model which have no more than seven predictors. We used the R environment (R Core Team 2019) to fit GLMs, with the *MuMin* package (Bartoń 2019) to run model selection. We refrained from model averaging, as the top models selected (for micro- and macro-scale) have relatively good support (as compared with the second-best models, see Results section) and given interpretability issues linked to model averaging (Cade 2015). Instead, we accepted the top selected models as the most informative models in the candidate sets and assessed their performance using a cross-validation approach (James *et al.* 2013). We also calculated the amount of deviance explained by the model with D-squared statistics (D2) in the *modEvA* package (Barbosa *et al.* 2016). Given that the top models were nested and simpler versions of the models were scored as second and third, we decided to accept the top model as the sole basis for our inference, based on the 'nesting rule' (Arnold 2010, Richards *et al.* 2011, Harrison *et al.* 2018).

We used cross-validation to assess the predictive ability of our most informative models, as measured by the area under the receiving operator characteristic curve (AUC) statistics, using the *caret* package (Kuhn, 2008). To assess possible bias introduced by individual lek features, we used a subset of our data including only marked birds with known lek affiliation (n = 127 records of 22 individual males) to cross-validate the top models between leks. Here, we used predictors from our top model to fit a training model on records pertaining to birds from the first lek and validated that model against birds from the second lek, with AUC as a measure of model performance. We then repeated that, with the birds from the second lek serving as a training subsample and birds from the first lek as a validation subsample. We used actual distances to the focal lek here, rather than averaged distance to the two leks. We repeated this procedure 30 times with random reallocation of background records ('available') to training vs. validation subsamples (50% vs. 50%), thus obtaining 30 AUC values for each of the two cross-validations.

Finally, to check for possible individual effects in the results, we performed a cross-validation of the selected binomial GLM using a leave-one-out cross-validation (LOOCV), with records belonging to the same individual being treated as cross-validation units. This involved 47 birds with one record each (including 41 records of unmarked birds) and 16 birds with 2–26 records each (average 7.5 records per bird in the latter group).

The biomass of food resources was not included in model selection because these variables were not assessed on all sampling sites (due to logistic constraints, biomass was available for only 83% of records). We therefore decided to model these variables independently, using separate GLMs (GLMs 3 and 4), to check for differences between foraging and random sites and differences between land use types (GLMs 5 and 6). Here, given the distribution of the two variables, we used zero-inflated GLMs with negative binomial error distribution and log-link, implemented in the *pscl* package (Jackman 2020).

For the most informative models, we used the *effects* package (Fox 2003) to estimate and visualize fixed-term effects (i.e. average model predictions) and their 95% confidence intervals.

Interplay between microhabitat variables and land use types

As land use type is one of the main factors creating vegetation structure and is a major conservation tool in AES, to investigate the interplay between habitat selection at the micro-scale and land use types (macro-scale), we calculated and compared some basic statistics for the top micro-scale model variables within each land use type used later in the Discussion section (Table 3).

Additionally, to check whether our micro-scale model can be considered as a tool to assess foraging conditions (for instance in Great Snipe habitat restoration) we used our top micro-scale model to predict probabilities of male Great Snipe occurrence within different land use types, based on the randomly selected points (available resources). The micro-scale model used here did not include the DistLek variable, as the distance to a lek is not a feature that describes the microhabitat conditions as such. Given that the predictions were made on the data subset used to describe available resources, these results should indicate a general Great Snipe microhabitat foraging suitability within different land use types (called below 'microhabitat suitability index').

RESULTS

Range and spatial pattern of foraging

Male foraging locations in the study area appeared to be clustered, suggesting active habitat selection (Fig. 1). The mean foraging distance to the lek where individuals were originally tagged was 484 m (sd = 247.0, *n* = 85) for Lek 1 and 294 m (sd = 163.4, *n* = 41) for Lek 2. Only on five occasions (3% of the foraging locations) were males detected outside the study area and these were excluded from the analyses.

Table 3. Mean, standard deviation (sd) and sample size (*n*) of the top model micro-scale habitat variables in foraging and random sites within land use types of the study area

		Random sites			Foraging sites		
Habitat variable	Land use type	Mean	sd	*n*	Mean	sd	*n*
VegHeight (cm)	1xMOW	62.0	25.22	83	54.4	24.96	31
	2xMOW	54.9	21.53	40	36.2	16.60	41
	2xMOW + COW	43.1	18.94	21	37.3	12.50	53
	ABAND	77.5	33.15	234	54.3	24.45	30
	COW	62.5	3.54	2	41.3	21.96	12
VegCovH (%)	1xMOW	3.6	3.42	85	5.5	3.05	31
	2xMOW	4.7	3.95	40	9.1	3.55	41
	2xMOW + COW	7.5	4.34	21	8.6	4.25	51
	ABAND	2.9	2.06	233	6.2	3.14	30
	COW	1.9	0.88	2	7.2	3.08	12
BareGr (%)	1xMOW	14.3	21.45	80	44.2	37.33	30
	2xMOW	13.1	19.68	40	42.4	31.11	41
	2xMOW + COW	20.0	25.30	21	42.5	30.37	51
	ABAND	10.0	20.08	222	44.3	33.00	30
	COW	5.0	7.07	2	60.0	29.54	12
Penetr (cm)	1xMOW	6.2	2.22	81	7.2	2.31	31
	2xMOW	5.0	1.38	39	5.6	1.42	40
	2xMOW + COW	4.9	1.34	21	5.5	1.21	50
	ABAND	7.4	2.86	214	8.7	3.57	29
	COW	5.3	0.00	2	8.2	1.96	11

Micro-scale habitat selection

The top selected model included distance to the lek, bare ground by date interaction, soil penetrability and two variables measuring vegetation cover as predictors of Snipe daytime occurrence. This model was about four times more likely to be a more informative model than the second model selected (evidence ratio = 4.24; Table 4), explaining 52.6% of the deviance. Cross-validations based on submodels fitted to data from one lek and tested on data from another lek revealed outstanding discriminatory ability ($AUC_1 = 0.91$ and $AUC_2 = 0.89$) and thus results were not biased due to lek-specific effects (Table 5). Model estimates were also not biased by multiple recordings of several individual males, as model coefficients obtained for 63 LOOCV subsamples were very similar to coefficients calculated using the whole sample, with none diverging more than 0.88 standard error units from the original estimate (results not shown). We therefore concluded that model estimates were not biased by inclusion of several individuals with multiple records.

Presence of male Great Snipe was strongly positively related to the share of bare ground and this relationship became stronger as the breeding season progressed (Fig. 2a). From June onwards, males could seldom be found in locations with less than 20% bare ground, preferring locations with over 60% ground with no vegetation.

The probability of male Great Snipe occurrence showed a quadratic relationship to horizontal vegetation cover (Fig. 2b). Our best model suggests relatively low probabilities of Snipe daytime occurrence when vegetation cover was very dense and enabled us to see the bird only from a distance of < 5 m. Snipes were most likely to be found at intermediate densities of vegetation, where birds could not be seen from a distance of 10–15 m, while apparently avoiding sites where they were already visible from around 20 m (Fig. 2b).

Our model showed an almost uniform increase of the probability of male Great Snipe presence with increasing soil penetrability, reaching a maximum level at a soil penetrability of 15 cm (Fig. 2c). The probability of male Great Snipe occurrence also showed a quadratic relationship with vegetation height (Fig. 2d), highest for vegetation 30–60 cm tall and distinctly lower for both shorter and still taller vegetation. There was a clear negative relationship between the likelihood of encountering a male Great Snipe and distance to the lek (as measured by averaged distance to two leks in the study area), with a five-fold decrease in use across 400 m of increasing distance (Fig. 2e).

Macro-scale habitat selection

Three models stood out as the best models (delta AICc < 2) to explain the probability of occurrence male Great Snipe during the day at the macro-scale level and each of them explained about 35% of the deviance (Table 4). While the AICc and the explained deviance of three models were very similar (Table 4), the top model was the best

Table 4. Ranking of the micro-scale and macro-scale models explaining the probability of male foraging Great Snipe occurrence

Model scale	Rank	Candidate model	AICc	Delta AICc	*w*	D^2
Micro-scale model	1	**VegCovH + BareGr + Penetr + LekDist + Date + Date*BareGr + VegHeight**	306.6	0.00	0.744	0.526
	2	VegCovH + BareGr + Penetr + LekDist + Date + Date*BareGr + Tussok	309.5	2.90	0.175	0.518
	3	VegCovH + BareGr + Penetr + LekDist + Date + Date*BareGr	311.8	5.26	0.052	0.495
	4	VegCovH + BareGr + Penetr + LekDist + Date + Date*BareGr + Date*Penetr	313.1	6.57	0.027	0.512
	5	VegCovH + BareGr + Penetr + LekDist + Date + Date*BareGr + Moist	313.7	7.18	0.020	0.511
Macro-scale model	1	**LandUse + DistShrub + Elev + LekDist + DistForest**	464.0	0.00	0.445	0.349
	2	**LandUse + DistShrub + Elev + LekDist + DistForest + DistTree**	465.3	1.29	0.233	0.351
	3	**LandUse + DistShrub + LekDist + DistForest + DistWater**	465.6	1.60	0.200	0.353
	4	LandUse + DistShrub + LekDist + DistForest	466.6	2.59	0.110	0.339
	5	LandUse + DistShrub + Elev + LekDist + DistWater	466.9	2.97	0.092	0.345

Shown are the five best models to give a better idea of the relative strength of the most informative model from the best model selected (models within 2 AICc units are given in bold). Variables VegCovH, VegHeight, DistShrub, Elev and DistForest are entered with a squared term. AICc, Akaike's information criterion corrected for small sample size; D^2, explained deviance; Delta AICc, difference in AICc between the focal model and the best model in the set; *w*, Akaike weight of the focal model.

Table 5. Results of the cross-validation of the top micro- and macro-scale model and a landscape model containing only the habitat variables concluded in the Discussion as being less specific to the study site

Model scale	Evaluated model	Mean AUC_1 (range)	Mean AUC_2 (range)
Micro-scale model	VegCovH + BareGr + Penetr + LekDist + Date + Date*BareGr + VegHeight	0.91 (0.89–0.93)	0.89 (0.87– 0.92)
Macro-scale model	LandUse + DistShrub + Elev + LekDist + DistForest	0.64 (0.57–0.74)	0.72 (0.68– 0.75)
	LandUse + LekDist	0.70 (0.61–0.79)	0.74 (0.57–0.80)

AUC_1: estimated mean area under the curve and the range of 30 times repeated cross-validations where models were fitted with the training data (a subset of males from Lek 1 and 50% of randomly selected random sites) and then evaluated on the testing data (males from Lek 2 and the remaining 50% of random sites). AUC_2: estimated mean AUC and the range of 30 times repeated cross-validations where models were fitted with the training data (a subset of males from Lek 2 and 50% of randomly selected random sites) and then evaluated on the testing data (males from Lek 1 and the remaining 50% of random sites).

supported (model weight = 0.445) and was twice as likely as the second-best model to be the most informative (evidence ratio = 1.9). Cross-validation revealed low to moderate discriminatory ability ($AUC_1 = 0.64$ and $AUC_2 = 0.72$, Table 5), indicating a lack of large lek-specific effects that could bias the results. Multiple recording of the same individuals did not bias the results either, as revealed by LOOCV (results not shown).

Land use type was the main factor explaining variation in Great Snipe male presence on the macro-scale. The grazed and twice-mown grazed meadows had the highest probability of bird presence (Fig. 3a), whereas abandoned meadows and once-mown meadows were several times less likely to support foraging Great Snipes (Fig. 3a). The probability of male Great Snipe occurrence decreased sharply with increasing mean distance to leks (Fig. 3b). Great Snipes were also less likely to forage close to shrubs (Fig. 3c). Modelled Snipe presence showed a weak quadratic relationship with elevation, with foraging birds avoiding the most elevated parts of the floodplain and being most likely to occur at intermediate elevation values. Apparent avoidance of sites located at the lowest elevation was associated with wide confidence bands (Fig. 3d). The model also predicted a U-shaped relationship between probability of Great Snipe presence and distance to the nearest forest (Fig. 3e).

Interplay between microhabitat preferences and land use types

The highest probability of the occurrence of Great Snipe males during the day, as predicted by the best micro-scale model applied to the set of randomly selected points in our sample, coincided with sites used as meadows that were mown twice and grazed thereafter (Fig. 4). This land management predicted a probability of the average occurrence of Great Snipe males that was 3.3 times higher than in abandoned meadows, 2.5 higher than on once-mown meadows and about 2.1 times higher than on meadows mown twice (Fig. 4). For the pastures, due to a low sample size ($n = 2$), the calculations were omitted.

Food abundance

We collected 458 soil samples from foraging ($n = 161$) and random sites ($n = 297$), of which 83% contained invertebrates. Lumbricidae earthworms constituted about 75% of the total biomass and were present in about 70% of all samples. The second most abundant group was Diptera larvae, which constituted 16% of the total biomass and were found in 39% of samples. The remaining biomass consisted of Hirudinea (leeches; 5%), Gastropoda (snails; 3%) and, in decreasing order (<1%): Coleoptera (beetles), Diplopoda (millipedes), Nematoda (roundworms), Chilopoda (centipedes) and Hymenoptera. Total invertebrate biomass was slightly but significantly higher on the Great Snipe foraging sites (mean = 23.9 g/m^2, se = 2.58) than on the random sites (mean = 19.3 g/m^2, se = 1.48; $P = 0.046$) but was not different for earthworm biomass ($\text{mean}_{\text{foraging}} = 15.3$ g/m^2, se = 1.7; $\text{mean}_{\text{random}} = 15.8$ g/m^2, se = 1.36; $P = 0.926$).

Across land use types, we found significantly higher invertebrate (mean = 36.5 g/m^2, se = 5.60)

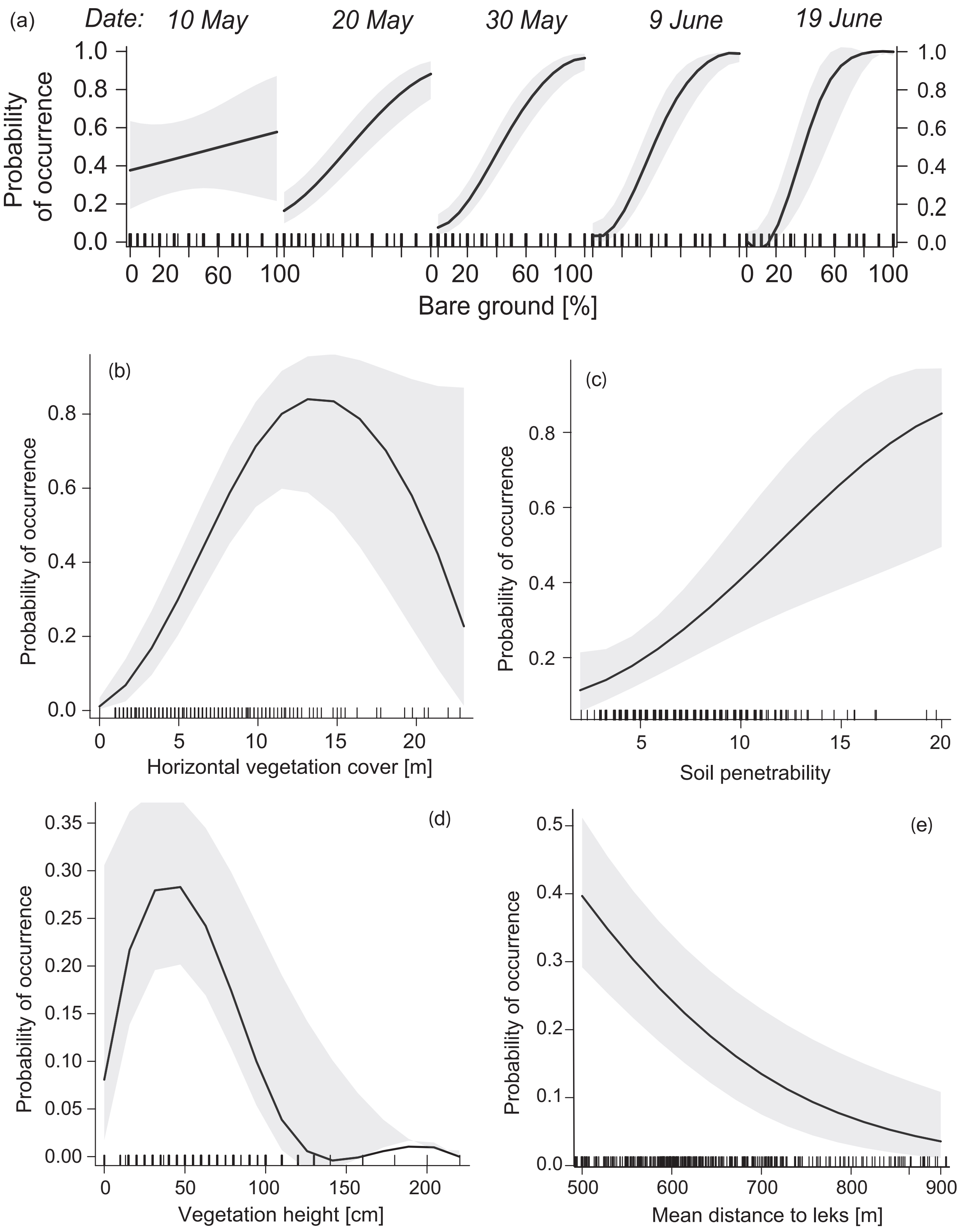

Figure 2. Predicted Great Snipe presence probability in relation to: (a) bare ground share, changing within the breeding season; (b) horizontal vegetation cover; (c) soil penetrability; (d) vegetation height; and (e) mean distance to leks within foraging sites. Predictions and 95% confidence intervals (grey polygons) are from the best micro-scale model selected (Table 3).

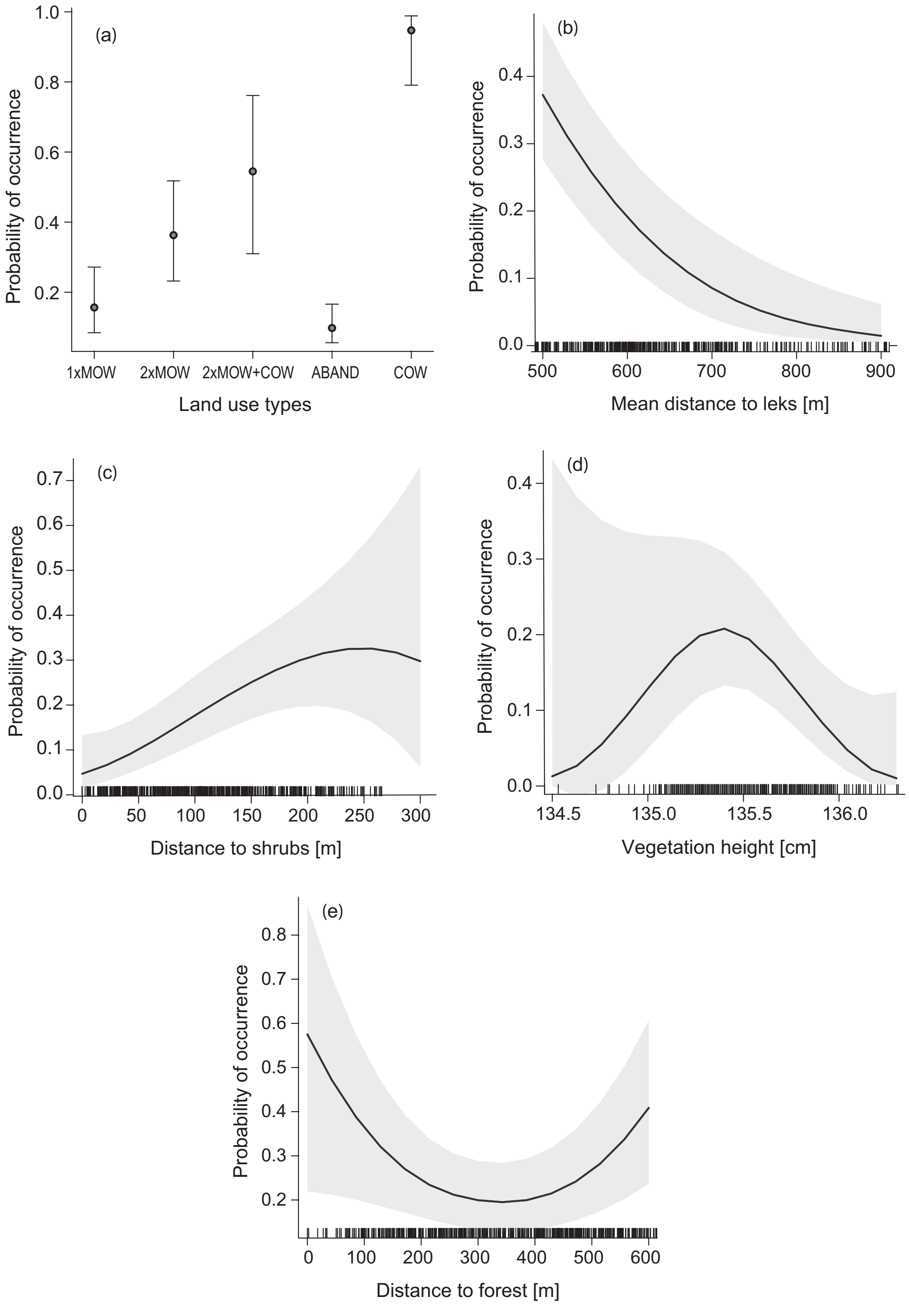

Figure 3. Predicted Great Snipe presence probability: (a) in four land use types (see Table 2, mean and 95% CIs), (b) with increasing mean distance to leks, (c) with increasing distance to shrubs, (d) with increasing elevation and (e) with distance to forest edge. Predictions and 95% CIs (whiskers and polygons) are from the best landscape scale model selected (Table 3).

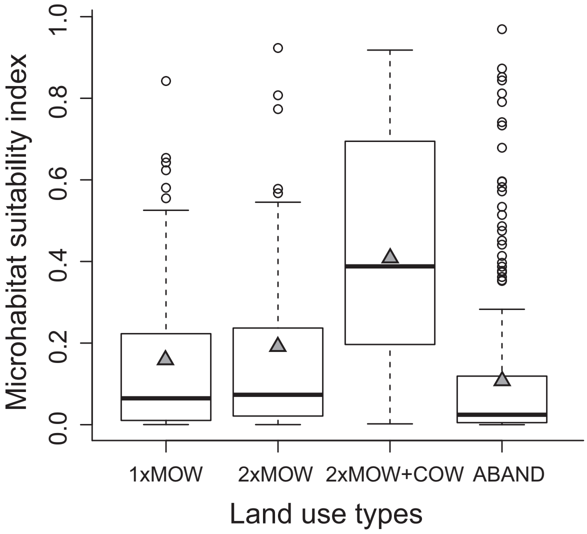

Figure 4. Male Great Snipe foraging habitat suitability in different land use types, based on predictions from the top micro-scale model applied to the randomly selected sites (sampled as available sites in micro-scale modelling). Boxes represent interquartile ranges (25–75%), thick horizontal lines within boxes show medians, grey triangles indicate mean values, and whiskers span from highest to lowest occurrence probabilities, excluding outliers (circles).

and earthworm biomass (mean = 32.5 g/m^2, se = 5.89) in twice-mown grazed meadows than in once-mown meadows (Table 2), where biomass was lowest (all invertebrates: mean = 15.3 g/m^2, se = 2.21; earthworms: mean = 10.4 g/m^2, se = 1.75; P = 0.010 and P = 0.003, respectively). The remaining land use types (grazed, twice-mown and abandoned meadows) were not significantly different from once-mown meadows in either invertebrate group (P = 0.077–0.401) or earthworm biomass (P = 0.116–0.408), except that abandoned meadows held significantly more earthworms (P = 0.040). However, more invertebrates (mean = 25.4 g/m^2, se = 5.12; P = 0.077) and earthworms (mean = 18.0 g/m^2, se = 3.87; P = 0.116) were found on twice-mown meadows than on once-mown meadows, suggesting a higher potential food resource in twice-mown meadows; however, the differences were not statistically significant.

DISCUSSION

We have found that male Great Snipes foraging around their leks on floodplain meadows prefer habitat patches maintained by relatively intense land management (meadows mown twice per season and grazed by cattle thereafter) and possibly located close to the leks. On a finer scale, male Great Snipes preferred sites with intermediate sward height and density, easily penetrable soil and extensive bare ground. Invertebrate biomass, but not earthworm biomass, was marginally higher in sites used for foraging. Male foraging preferences for intensively managed habitat patches offering ample food and preferred fine-scale features is noteworthy. If females prefer to nest close to leks, their preference for habitats offering good shelter and safety may conflict with the males' preferences for meadows mown twice and grazed. We discuss this issue in a separate section.

Micro-scale habitat selection

The Great Snipe males selected foraging habitat patches with moderate vegetation height and density, which is consistent with studies from floodplains in Belarus (Mongin 2002) and Estonia (Kuresoo & Luigujõe 2001). In Norway, Great Snipes were found at sites with vegetation cover similar to that in our study; however, they preferred lower vegetation height (around 20 cm, Løfaldli *et al.* 1992). Løfaldli *et al.* (1992) suggested that vegetation structure plays a role in ground predator avoidance. As the Great Snipe is a cryptic plumage species, the vegetation must provide some camouflage but also enable Great Snipes to be able to detect ground predators from a greater distance when vegetation is lower. The preferences towards higher vegetation at our sites may be specific for the lowland population. Here, in contrast to Norway, Great Snipe breeding sites overlap with those of the Marsh Harriers *Circus aeruginosus*, which are their potential predators. During this study we saw hunting Marsh Harriers every day and we found four Great Snipes that had probably been killed by this predator (Korniluk & Piec 2016). Higher vegetation may provide better camouflage for Great Snipes and also reduce the success of attacks by harriers (Collopy & Bildstein 1987). In Scandinavia, Hawk Owl *Surnia ulula* and Hen Harrier *Circus cyaneus* may also potentially predate Great Snipes (Höglund *et al.* 1992); however, the predator avoidance behaviour may be species-specific and dependent on predator densities.

Great Snipes also preferred high proportions of bare ground, and more so later in the season. Bare ground often provides favourable feeding conditions for ground-foraging waders (Smart *et al.* 2006, Chamberlain *et al.* 2009) because of a combination of higher prey abundance and detectability. For the Great Snipe, we suggest that foraging on bare ground may in addition be more efficient because of the lower root density (due to fewer plants), making probing for, locating and securing food items more efficient. The Great Snipe is a cryptic brownish species, and more bare ground within a foraging site may also play a role in possible background matching (Ruxton *et al.* 2018). Given that a choice of foraging site represents a trade-off between maximizing energy intake and predation risk (Lima 1985), the preferences of more extensive bare ground points toward possible seasonal changes of costs or benefits. This issue deserves further study.

Great Snipes preferred feeding sites with high soil penetrability, making foraging easier (Milsom *et al.* 2002) and ultimately enabling more efficient foraging. In other studies, soil penetrability was positively related to soil moisture (Armstrong 2000, Milsom *et al.* 2002) and earthworm abundance (Lee 1985), making this variable important for the Great Snipe (Løfaldli *et al.* 1992, Kålås *et al.* 1997) and other probing waders (Green *et al.* 1990, Groen *et al.* 2012). However, in our study we found no significant differences in earthworm abundance between sites available to birds and those actually used for foraging, in contrast to findings from a Scandinavian population (Løfaldli *et al.* 1992). This may be explained by earthworms being generally most abundant within the preferred land use type (twice-mown grazed meadows and pastures, Table 2). Great Snipe males also preferred to forage closer to the lek, which suggests they may face some costs connected with commuting between the lek and foraging sites, similar to those incurred by central-place foragers (Orians & Pearson 1979). Alternatively, males may prefer to stay close to the lek to control mating opportunity and competition on the display arenas. For instance, males that forage close to the lek may hear other males start to display (and join the lek at that time to protect their territory), which will maximize their foraging time and minimize the risk of missing a mating opportunity. We find this topic worthy of further study. The VHF tracking was done systematically only up to 500 m around the study sites, and thus potentially we could have missed some foraging sites outside this range. However, given that only on five occasions across two field seasons did we find male Great Snipe outside the study site, we think it is unlikely that this may bias the general trends that we found.

Macro-scale habitat selection and micro-scale habitat characteristics

We found that extensive pastures and twice-mown grazed meadows were selected by the Great Snipe males for foraging and the remaining land use types were less frequently used (twice-mown meadows) or avoided (once-mown and abandoned meadows, Fig. 2). We confirmed this by mapping predictions from a micro-scale model on land use types in a subsample of points we drew at random to measure available habitats (Fig. 4). This indicates a general match between our two models and confirmed that male Great Snipe prefer land use types which provide the best foraging conditions at the micro-scale. The vegetation within once-mown and abandoned meadows was on average taller and had a denser sward compared with remaining land use types (Table 3). Given Great Snipe preference for intermediate sward density and height, these land use types were probably already unsuitable for foraging Great Snipes early in the season, with the situation becoming worse with vegetation growth over the breeding season (Table 3). Alternatively, patches of once-mown and abandoned meadows might not be selected due to their lower food resources (Table 2). For the remaining micro-scale habitat characteristics, i.e. horizontal vegetation cover, proportion of bare ground and soil penetrability, we see no obvious reasons why Great Snipes should choose extensive pastures and twice-mown grazed meadows over other land use types (Table 3). We therefore see the sward structure (medium density and height) as the key micro-scale factor shaping the selection of foraging sites across land use types in our study area. Birds eventually choosing these sites ultimately benefit from rich food supplies and safety from predators. Løfaldli *et al.* (1992) also suggested that sward structure is important for foraging Great Snipes and found that males select medium vegetation density regardless of vegetation community. This suggests very narrow habitat specialization of the Great Snipe despite the differences in vegetation communities that occur in lowlands and above the treeline in mountains. We conclude that the Great Snipe preference for pastures and twice-mown grazed meadows is due to the larger proportion of bare ground (probably trampled by cattle), moderately dense sward structure, and high invertebrate and earthworm biomass found in these habitats. This strongly suggests that livestock presence is crucial for favourable feeding conditions for the Great Snipe on floodplains by creating a preferred sward structure and providing bare ground patches. In addition, the sward heterogeneity and mosaic of microhabitats present on pastures (Sharps *et al.* 2016) may be important factors, given that the micro-scale model explains more deviance and has a higher prediction ability than the macro-scale model (Table 5).

Microhabitat suitability index assessed across land use types using predictions from the micro-scale model shows that twice-mown grazed meadows offer, on average, two to three times more preferred foraging conditions than the other habitats analysed (Fig. 4). Despite extensive variation in this index, meadows that were first mown twice and thereafter grazed support more sites attractive for foraging Great Snipes than meadows mown only once a season. This result is of particular importance, as the latter meadows were managed with low intensity because they are contracted to do so under the concurrent AES scheme. Thus, the AES that decreases the intensity of grassland use by simply delaying biomass harvest until late summer or autumn obviously does not benefit Great Snipes, an EU Bird Directive Annex I species. We feel that these results are robust and call for a critical re-assessment of the AES in question, which is claimed to benefit grassland waders.

Additionally, given the described matching of our two spatial scale models (in terms of land management), coupled with high predictive abilities of our best micro-scale model (Table 5), we think the latter can be a useful tool for conservationists and could be used, for example, to assess relative foraging habitat suitability in restored habitats. Consistent with the results from the micro-scale model, the macro-scale model also indicates that the male Great Snipe preferred to forage closer to the lek (Fig. 2e). These results suggest that the choice of lek location may be influenced by foraging conditions close to potential lek sites, in agreement with Kålås *et al.* (1997b).

Male Great Snipe apparently preferred to feed at sites a considerable distance from shrubs. This may relate to predator avoidance, as shrubs may offer a hide or a perch for avian predators (Żmihorski *et al.* 2018). However, we suggest that this may be a spurious correlation, as there are generally fewer shrubs in the more intensively used meadows selected by Great Snipes. The best macro-scale model also shows that male Great Snipe apparently prefer to feed either close to or far from the forest edge (Fig. 3e). However, we feel those relationships (distances to shrubs and forest) reflect the idiosyncrasy of our study area, rather than real preferences. That was supported by the cross-validations, in which we used the model fitted to birds from one lek to predict choices of birds from the second lek. Here, models that did not include distance to forest edge and shrubs performed better ($AUC_1 = 0.70$ and $AUC_2 = 0.74$) than our best model containing this predictor ($AUC_1 = 0.64$ and $AUC_2 = 0.72$, Table 5).

Males also prefer to forage on sites with a mid-position along the elevation gradient within the studied floodplain. As on floodplains the water table is relatively close to ground level, this finding seems related to Great Snipe preferences for moderate soil moisture (Løfaldli *et al.* 1992), correlating with higher earthworm abundance (Lee 1985) and high penetrability (Armstrong 2000). However, on floodplains, where the water table changes dynamically, elevation per se is not as important as small-scale diversity in the elevation of the river valley bottom. The presence of numerous fine-scale moulds and depressions close to a lek will ensure a high number of potential feeding sites, regardless of water table level in a particular year and its within-season dynamics. A foraging strategy mirroring that of central-place foragers, coupled with a preference for a diverse valley bottom relief, may explain why Great Snipe leks on floodplains often occur in the wider sections of the river valley or at confluences of tributaries (M. Korniluk unpubl. data). This fact may be a good predictor of lek occurrence on floodplain meadows, not least for selecting key sites for habitat restoration.

Have floodplains become an ecological trap triggered by the mating system?

Great Snipe males have high energy demands when lekking that have evolved under strong sexual selection pressure (Höglund *et al.* 1992). In such conditions, lek locations are restricted to habitats with high food abundance and availability (Kålås *et al.* 1997). Generally, nutrient-rich floodplains (Wassen 1995) may provide the necessary high food abundance and the earthworm biomass (main Great Snipe food, Løfaldli *et al.* 1992) increases with productivity (Lee 1985). This may explain why about 70% of leks in lowland populations occur on floodplains. On the other hand, high nutrient levels are associated with fast vegetation growth and high primary productivity, which may constrain food availability, as Great Snipes prefer to feed in sward which is moderately high and not too dense. Therefore, we expect that only floodplains with relatively intensive land use (early mowing with two cuts and grazing), which removes part of the primary production and maintains shorter vegetation in early spring, can currently provide favourable conditions for breeding Great Snipe males. This is exactly what we found in our study site.

Female Great Snipe start breeding in spring at a later date than most other meadow waders in Europe (Cramp 1985) and the majority of nests are located in the vicinity of leks (0.1–0.6 km, Dyrcz *et al.* 1972; 0.05–1 km, Mongin 2002), which is beneficial for females, as they use sites with high food abundance selected by males (Kålås *et al.* 1997). At our study site, the nests were also placed in the vicinity of leks at a mean distance of 276 m and a range of 50–550 m (three nests found and five nesting sites determined by VHF triangulation to 2–3 m accuracy; M. Korniluk unpubl. data). The breeding phenology data from Belarus show that none of the juveniles fledged before 11 June, and only 15% of young birds had reached fledging age before 21 June (Mongin 2008). Therefore, mowing at the beginning of June – a management practice used to create habitats strongly preferred by males, as we found – will probably destroy a significant part, if not all, of the broods. As found in Belarus (Mongin 2002), extensive grazing carried out during the Great Snipe breeding season may also markedly reduce nesting success (four of 10 clutches were destroyed by cattle). We therefore suggest that, historically, with the introduction of machine mowing and increased grazing intensity, which additionally lowers brood survival compared with traditional mowing by hand (Newton 2004), in many places selection for floodplains has become maladaptive for the Great Snipe. Many individuals may be falling into an ecological trap (Kristan 2003) manifested by reduced productivity caused by the reduced suitability of the habitat for brood survival. Such a scenario fits the conceptual model of ecological traps called ‘severe trap’ (Robertson & Hutto 2006), where an animal habitat simultaneously increases in attractiveness and decreases in suitability. Moreover, grassland management intensification in the vicinity of a lek increases the number of preferred foraging sites, which may attract prospecting males (at least 66% of males visited more than one lek within a season, Korniluk *et al.* 2014), leading eventually to larger leks. Given that larger leks are preferred by females (Queller 1987, Alatalo *et al.* 1992, Lank *et al.* 1995), more Great Snipe males on a lek may then attract more females (Höglund & Robertson 1990), presumably encouraging them to breed nearby. In such a scenario, a lek with a high number of displaying males, which is paradoxically considered an index of species habitat quality, will functionally be a sink for the Great Snipe population and may potentially lead to population decline or even extinction (Kokko & Sutherland 2001). Such a hidden relationship between a cue and the effect can easily escape the ecologist’s attention and indicates the need for further consideration in other species and the Great Snipe. We suggest that such a mechanism (simultaneously enhanced by hunting and habitat loss) could be responsible for the rapid and total extinction of the Great Snipe population in Western European lowlands. A plausible explanation of why, at some sites, Great Snipes have survived on floodplains is that such sites may have been partly mown comparatively late or have contributed to abandoned meadows in the early stages of succession (as in the case of our study site). The higher and denser vegetation there may have been preferred by some of the nesting females (in a number that enables population recovery), as they also built nests in denser (Løfaldli *et al.* 1992, Mongin 2002) and higher vegetation (Korniluk & Piec 2016) compared with that found in male foraging sites. Nesting sites located in our study site were placed in the following land management: twice-mown grazed meadows ($n = 3$), once-mown meadows ($n = 2$) and abandoned meadows in an early stage of succession ($n = 3$, M. Korniluk unpubl. data).

Implications for management

In the EU, reduced or delayed mowing is frequently applied in AES designed for wader protection (Franks *et al.* 2018). The AES implemented currently in sites where the Great Snipe occur in Poland (package called '4.10 A protection of the breeding birds' habitats: Great Snipe or Curlew') also includes delayed mowing until 10 July and allows one harvest per year to protect nests and broods from destruction. On floodplains, this may at the same time have failed to provide favourable foraging conditions for Great Snipes, given that we found that males prefer more intensively used meadows and avoid meadows mown once a year, as they had an unsuitable vegetation structure and the lowest food resources. On the other hand, under the potential maladaptive habitat selection we outlined as applying to floodplains, the delayed land management partly present in the vicinity of leks seems crucial for providing safe nesting sites, and thus may prevent the creation of a double ecological trap. We therefore suggest that the best management scenario on floodplain meadows that will provide both foraging sites and safe nesting habitats may be achieved by maintaining a mosaic of different land management types in the vicinity of leks, including a large share of grazed areas, which seem to be highly preferred by Great Snipe males. This management strategy can be also beneficial for other meadow waders (Oosterveld *et al.* 2011), although grazing during the breeding season should be introduced with caution (Mongin 2002, Sharps *et al.* 2016). Moreover, the land use heterogeneity that we recommend may substantially reduce nest predation rates (Laidlaw *et al.* 2017) and lead to higher invertebrate abundance (Vickery *et al.* 2001), which could benefit the feeding of both adults and chicks. Further studies on the best management scenario, specifying optimal land use proportions, management patch size and lek range size, are needed, as well as more information on nest locations and the habitat requirements of females and chicks.

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AUTHOR CONTRIBUTION

Michał Korniluk: Conceptualization (lead); Formal analysis (lead); Investigation (equal); Methodology (equal); Project administration (lead); Writing-original draft (lead); Writing-review & editing (equal). **Paweł Białomyzy:** Investigation (equal); Writing-review & editing (equal). **Grzegorz Grygoruk:** Investigation (equal); Writing-review & editing (equal). **Łukasz Kozub:** Conceptualization (supporting); Investigation (equal); Writing-review & editing (equal). **Marcin Sielezniew:** Investigation (equal); Writing-review & editing (equal). **Piotr Świętochowski:** Investigation (equal); Writing-review & editing (equal). **Tomasz Tumiel:** Investigation (equal); Writing-review & editing (equal). **Marcin Wereszczuk:** Investigation (equal); Writing-review & editing (equal). **Przemek Chylarecki:** Conceptualization (supporting); Formal analysis (supporting); Methodology (equal); Writing-review & editing (equal).

Data Availability Statement

We intend to archive data at the Dryad Digital Repository.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Fig. S1. Seasonal dynamics of main habitat features recorded in micro-scale, as measured in 2013 and 2014 (both years pooled). For Date 0 = 1 May (study period from 7 May to 25 of June). Grey dots indicate the values in the random sites and crossed symbols indicate foraging sites, respectively. Coloured lines show the linear regression fit.

Title

Intra-seasonal lek changes of Great Snipe males in the Northeast of Poland

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Abstract

In bird species with a lek mating system, male mating success is usually correlated with time spent at the lek, suggesting strong selection for lek attendance. We studied the lekking of Great Snipe males over 5 breeding seasons in Poland and found that, in apparent contradiction, 75% of males changed leks, often several times, within a single breeding season. GPS-tagged individuals tracked for an average of 31 days visited up to 9 different leks, often visiting 2-3 leks in quick succession within a few hours. Transitions between leks were entirely nocturnal, peaking before midnight. The majority of males that changed leks moved to sites within 50 km of the original lek, but 10% of males dispersed more than 100 km. Lek-switching males typically made several transitions between leks during the breeding season (median=4), with most mobile birds changing display sites more than 20 times. Lek-switching probabilities showed seasonal variation, with no males changing leks early in the breeding season and frequent changes thereafter.

The daily probability of lek change showed large inter-individual variation, allowing two groups of males to be distinguished, those who never or rarely changed leks (mean daily probability of lek change 0.02) and those who frequently changed leks (mean daily probability of lek change 0.23). This type of heterogeneity in male lekking behaviour is consistent with the hot-shot scenario of lek evolution. Here, lekking males with low mating chances should benefit from lek-switching - in contrast to top-ranking males - because changing display site may allow them to find leks with higher mating chances. Furthermore, regardless of its immediate success or failure, lek-switching can be seen as a form of prospecting behaviour that will pay off in future breeding seasons. Consistent with this, many of our lek-switching males moved in a way that suggests informed dispersal. The prevalence of intraseasonal lek switching in different Great Snipe populations across Europe should be assessed using the GPS-tagged birds, as this behaviour is likely to be much more widespread than reported in many previous studies.

Keywords: Great Snipe, lekking, dispersal, lek-switching, prospecting, individual quality, hotshot model

Introduction

Leks are aggregations of displaying males, visited by females for the primary purposes of mating and fertilization (Höglund & Alatalo 1995). Only about 1.5 % of bird species exhibit this special mating system, which is distinguished by several unique features indicative of a strong sexual selection, including elaborate male displays, extreme skew in male mating success, lack of male parental care and traditional use of many lekking sites (Wiley 1991, Höglund & Alatalo 1995, Jiguet et al. 2000). The spatial and temporal stability of leks was usually linked with high site-fidelity of displaying males that often use the same leks in subsequent years. More importantly, in many lekking species, male seasonal mating success is correlated with their lek attendance, exerting a strong selection on within-seasonal site fidelity and persistent use of lekking arenas throughout the whole breeding season (Andersson 1994; Fiske et al. 1994, 1998; Sæther et al. 2005).

On the other hand, given the strongly skewed mating success (mating skew) typically found among lekking males, males that fail to mate for a sufficiently long period of time may benefit from leaving the lek in question, in search of others that may offer better mating opportunities. Until recently, such movements have been rarely reported, but this may reflect difficulties in their detection rather than their actual rarity, per se. Early studies of lekking behaviour that focused on single or just a few leks, using colour rings in order to identify individuals, had an inherently low potential to detect male movements between leks (but see Karpovitch 1962, Gibson et al. 2014). Similarly, VHF tags required extensive tracking efforts to detect the switch using real-time recording (Borecha et al. 2017). It was only with the advent of tracking systems capable of storing location data that it became possible to record lek switching behaviour on larger spatial and temporal scales (Fremgen et al. 2017, Wann et al. 2019).

Theoretical models of optimal lek size (Widemo & Owens 1999) predict that males should benefit from switching leks once they exceed a certain size threshold, although the decision to switch should be constrained by several factors. As with any dispersal event, lek switching could be costly in terms of time, energy and risk factors (Bonte et al. 2012, Clobert et al. 2001, Clobert et al. 2012). In particular, searching for new leks should come at a price due to information constraints, i.e. limited knowledge of the location and quality of alternative leks. However, dispersing males may be able to reduce these potential burdens by utilising information on the location of alternative leks gathered during similar forays in previous years (or earlier in the season). They may also reduce the predation risk associated with dispersal movements by relocating during periods of low predator activity. Furthermore, among the approximately 150 lekking bird species (Jiguet et al. 2000), the energetic cost of inter-lek movements should be lower for species adapted to long, sustained flights (e.g., obligatory long-distance migrants) than for, say, species adapted to sedentary life in the forest or equipped with extensive flight-impairing ornamentation. Therefore, the prevalence and extent of male inter-lek movements may vary between species and taxonomic groups, in line with their long-distance dispersal abilities and degree of male ornamentation.

Whatever the reason, potential male movements between leks have tended to be neglected or, at best, underexplored in discussions of the evolution of lek systems (Höglund & Robertson 1990, Wiley 1991, Andersson 1994, Ligon 1999; but see Höglund & Alatalo 1995). This is unfortunate because undetected lek switching can lead to biased estimates of male variance in mating success. Males judged unsuccessful on the basis of single lek studies may in fact be able to mate at other leks visited in the same season, thereby mitigating the apparently strong mating skew that typifies the lekking system (Lanctot et al. 1997). Similarly, possible non-random dispersal between leks will represent another level of lek organisation not accounted for in the main models of lek evolution currently analysed (Höglund & Alatalo 1995).

Great Snipe *Gallinago media* is a medium-sized shorebird known for its lek breeding system, which has been extensively studied in the Scandinavian population of the species (Lemnell 1978, Höglund & Lundberg 1987, Fiske et al. 1994, Sæther et al. 2001). It currently consists of two geographically disjunct, genetically and morphologically distinct breeding populations (Kålås et al. 1997a, Ekblom et al. 2007), which are considered separate conservation units (Sæther et al. 2007). The western population occurs above the tree line in the Scandinavian mountains, while the eastern, lowland population inhabits floodplains and fens (peatlands) and extends from eastern Poland through Ukraine, Belarus and the Baltic States to central Russia and the Yenisei River (Kålås 2004). Unlike most lekking species, Great Snipes do not exhibit a clear sexual dimorphism, with both sexes having cryptic plumage. In addition, and in contrast to many other lekking species, Great Snipes are strong fliers, making non-stop flights of 4000-7000 km during their migratory journeys to sub-Saharan Africa (Klaassen et al. 2011, Lindström et al. 2016, 2021).

Great Snipe leks are usually comprised of several to 20 males, who engage in vocal and visual ground displays throughout the night (Lemnell 1978). Females apparently prefer to mate with those few males with the highest display rate, a high lek attendance, that are older and often occupy a central position in the leks (Höglund & Lundberg 1987; Höglund & Robertson 1990; Fiske et al. 1994). The majority of males, with lower dominance scores, apparently do not obtain a single mating in the observed leks

(Höglund & Lundberg 1987; Höglund & Robertson 1990; Fiske et al. 1994). Of several theories of lek evolution, the lekking displays of the Great Snipe are probably closest to what is called the hotshot model (Beehler & Foster 1988), where successful, attractive displaying males (“hotshots”) are joined by less attractive males trying to parasitize on their attractiveness (Höglund & Alatalo 1995).

Compared to other lekking bird species, Great Snipes seem predisposed to relatively frequent lek switching, due to strong dispersal abilities and lack of ornaments impairing flight performance – features shared with two other, closely related lekking shorebird species, the Ruff *Calidris pugnax* and the Buff-breasted sandpiper *Calidris subruficollis*, already known for their relatively frequent lek switches (Lanctot & Weatherhead 1997). Additionally, lowland Great Snipe populations living in river valleys experience extensive spatial and temporal variation in the quality of available leks and adjacent foraging habitats, driven by spring floods that vary in extent and duration. Thus, despite the paucity of information on lek-switching in the extensively studied Scandinavian Great Snipe populations, we have reason to believe that males of this species inhabiting the floodplains of northeastern Poland may exhibit more regular intra-seasonal lek-switching.

In this paper, we analyse the movement data of lekking male Great Snipes equipped with GPS transmitters and tracked throughout the breeding season in a lowland population breeding in NE Poland. We hypothesised that the use of telemetry devices would allow us to demonstrate that birds from our study population do indeed exhibit regular inter-lek movement, contrary to what is known from studies conducted in Scandinavia prior to the biologging era. Furthermore, given the strong mating skew described for the species, we proposed that possible lek-switching behaviour should be limited to a subset of males (presumably of lower quality), while other males should remain and reap the known benefits of lekking site fidelity. We also expected that if some males do switch leks in search of better mating opportunities, the prevalence of this behaviour should increase as the season progresses. This should reflect individual males' increasing knowledge of their ability to mate in a focal lek given the quality of competitors, coupled with a decreasing number of fertile females. In addition to testing these predictions, we report annual and diel variations in male lek-switching behaviour and quantify the inter-individual variation in the time allocated to attendance at different leks by individual males.

Methods

Study area and GPS tagging

The study was conducted in NE Poland, at the western edge of the breeding range of the lowland population of the Great Snipe in Europe. We trapped and tagged displaying males at 6 leks located in valleys of the Biebrza, Supraśl and Narew rivers. In order to track Great Snipe male movement within the lekking season, in May individuals were trapped at night at one of the leks by the use of mist nets (for details of the trapping method see Lindström *et al.* 2016) and equipped with a GPS-UHF solar powered logger attached to the bird's rump with a 2 mm Teflon tape (2013-2015 Ecotone ~5 g tags) or a flexible 1 mm thick (2017-2018 Milsar ~3.5 g tags) leg-loop harness (Rappole & Tipton, 1991). An Individual's sex was determined based on bilhead length, bodymass and tail coloration (Höglund et al., 1990). In 2013 we attached 7 tags at two leks (3 and 4 per each) in the Narew river valley (52°55 N, 23°39 E, for more details see Korniluk *et al.* 2021), 21 loggers were attached in 2014; 10 at the above two leks (4 and 6 units respectively), 4 on a lek also located in the Narew river valley (52°54' N, 23°11' E) and 7 tags in the upper Biebrza valley (53°42'N 23°20'E). In 2015 research was continued on the above leks where in total 22 loggers were attached, 13 tags were deployed at the study sites in the Narew river valley described in Korniluk *et al.* 2021 and 9 in the Biebrza river valley. In 2017 and 2018 another 9 and 11 loggers were attached respectively at two leks (53°03'N, 23°40'E; 53°12'N, 23°21'E) in the Supraśl river valley. In total, from 2013 to 2018, 70 Great Snipe males were equipped with the tags at 6 different leks. The technological limitation of the GPS-UHF devices we used is that the collected GPS data can only be downloaded from within about a 100 m range from the receiving stations. Thus, we permanently installed the data receivers at all leks where males were trapped and set the attempt to collect data at 10 min intervals. This means however, that if the bird doesn't return to the lek again within 10 min, we do not receive the data back. Loggers were set to collect GPS fix every 1 h (in the years 2017-2018 on some days every 10 and 30 min at night), however occasionally the interval could be longer in the case of long periods without sunny weather.

Lek classification

Great Snipe lek locations were determined by the information obtained from the local ornithologists who marked leks in the field using a handled GPS device with an accuracy of about 20-30 m. Part of the data was also obtained during the Great Snipe National Monitoring Scheme (https://monitoringptakow.gios.gov.pl/). Such leks were then attributed to the category of confirmed leks when the lek was active in a particular study year or a previous season. Additionally, based on nocturnal GPS fixes (from 8.30 PM to 5 AM local time) obtained during the study year, we classified a category of potential leks based on a visually determined cluster of male GPS positions (~50 m radius) that were at a distance greater than 1 km from the known leks, and males were registered there on at least two different nights (same or different individuals). The final location of a potential lek was at the centre of the cluster. Given that during the night males should spend time attracting female, such nocturnally visited sites were likely to be leks or sites where particular males at least displayed. To confirm our expectation, potential leks were checked at night during the lekking season and if the lek was confirmed (at least 2 males displaying), we changed the category of such a site from 'potential' lek to 'confirmed' lek. We chose a distance of 1 km, which is about the minimum distance between permanent and independent leks known from the Great Snipe Polish Monitoring Scheme (M. Korniluk data unp.). However, given that part of the mals tracking data was downloaded after the lekking season (see methods discretion of data downloading) and due to logistical constraints, we could not check all the potential leks within a lekking season or at the time when tagged males were present (see results).

GPS data pre-processing

The lekking period of the Great Snipe in Poland starts in late April and ends in late June, while occasionally leks that host a large number of males are still active at the beginning of July (Korniluk et al. 2015). However, some males in late June abandon the leks and move to foraging sites where they preassemble fuel for migration, and such sites are often found far outside the lekking areas (M. Korniluk, unpublished data). Therefore, to avoid analysis of intraseasonal male dispersal that is not attributed to lekking behaviour we decided to exclude from analysis data collected after the 15th of June. We then removed unrealistic GPS positions (errors) using a speed filter, deleting those positions that indicated a movement with a speed greater than 27 m/s calculated based on the distance between successive positions, which resulted in 0.1 % of GPS fixes being removed. For the data collected in 2014, a big discrepancy between successive GPS positions was present due to low tag efficiency (mean = 3.2 h, sd = 8.58). We used tag registration events at the receiving station to create a fix on the lek (where there is low tag battery voltage, GPS positions are not sampled, however the connection with the receiving station still takes place and is registered with date and time of connection) and included this data in the analysis. This resulted in 3131 additional positions of male presence in the leks and reduced variations between successive positions (mean = 2.1 h, sd = 7.45). To reduce bias of inferencing about Great Snipe male movement based on a very short tracking period, we considered only those tags that collected data for at least 10 days. This resulted in 57 tags used in later analysis with a mean Great Snipe male tracking duration of 31 days (SD=10.36 days, range: 11-46 days) and mean 35 fixes/day (SD=12.6, range: 5 - 54 fixes/day, N=40 - excluding the year 2014).

Analysis of movement between leks

In order to quantify Great Snipe male movement between leks during the lekking period we assigned nocturnal GPS fixes to confirmed leks and potential leks when they were located within a radius of 500 of each other. This buffer was used because in some years lek location can change within a particular season due to vegetation growth or a change in the water level (M. Korniluk data unpubl.). A distance of 500 m is also considered as a core area utilized by the Great Snipe males that join a particular lek during the breeding season (Korniluk et al. 2021). For the data collected in 2014, when the tags often failed to register nocturnal positions due to low battery voltage (3.2: 1 ratio day to night fixes), we also considered diurnal positions (assuming that a male was also present there during the lekking time at night). For each male, we then calculated the number of transition events among confirmed and potential leks and the number of confirmed and potential leks visited by particular males within the lekking season. Additionally, in order to strictly check whether males join other lekking arenas, we also investigated whether male GPS fixes were registered at night in a buffer zone of 50 m from the confirmed leks. Those results should be interpreted with caution however, as underestimation likelly occur due to frequent unstable lek location and inaccurate lek marking.

Intraseasonal dispersal parameters

During the first two study years (2013 and 2014) the tracking period was short and big variations between successive GPS positions of tagged males were noted in the collected data, which largely restricted their use in terms of more systematic analyses. Therefore, only very basic analyses were possible for the whole data set (57 males in years from five breeding seasons; 2013-2015, 2017-2018), while more detailed information could be obtained from a restricted data set involving 36 males studied in the last three seasons (2015, 2017 and 2018).

For all males (N=57 tagged individuals; average start date 10 May, tracked for 30.6 days on average) we have calculated the maximum distance between visited leks and the maximum foray. The first metric was calculated based on distances between the lek where a male was trapped (initial lek) and the male’s furthermost position assigned to a confirmed or potential lek. The maximum foray was a distance between the initial lek and the furthermost male’s position registered within a season (including those not assigned to leks).

For the data obtained in the years 2015, 2017 & 2018 (N=36) where a more stable interval between successive positions was maintained, we could present more precise summaries of male movement between leks. We have assigned all GPS fixes to the following three categories: (1) lekking site – when a position was within a 500 m radius from the confirmed or potential lek (leks S1 and S2 were merged into one category as they were located about 500 m apart); (2) flight - when the GPS speed was >3m/s and was outside a confirmed or potential lek; (3) solo nocturnal presence - a nocturnal position that was not assigned to the above categories. We created this category as we expected that when a male was not present at known or potential leks and was not flying during the night, it is very likely that at least to some extent displaying took place. We then calculated time taken to reach successive positions, which allowed us to quantify the proportion of time a male spent in the above category. This resulted on average in the classification of 88.8 % of a male's tracking period (sd=10.95, range = 54 - 100%). Based on the above assignment we also calculated the percentage of time a male spent at the main lek (the lekking site where a male spent the most of its time, later called "main lek") and the time a male spent at other leks (confirmed and potential leks, later called "other leks"). We decided to make those calculations based on time progression, which provides a robust quantification of a male's time allocation during the lekking period, insensitive to the unequal interval between successive GPS fixes. To present the dispersal range of males to sites that they occupy at night outside the classified leks we have calculated a maximum distance from the initial lek to fixes classified as "solo nocturnal presence".

Seasonal and diurnal dynamics of movement among leks

The raw lek-switching metrics, i.e. number of leks visited, number of lek switches, or number of nights with at least one lek switch, were influenced (or limited) by the length of the tracking period, which varied greatly between individual males. Birds with a longer history of recorded tracking are likely to have more lek changes. However, in our sample the actual correlations between these variables are rather low (correlation between the number of leks a male attended during the single breeding season and the number of days the bird was tracked: r=0.24, P=0.08, n=57; correlation between the number of nights with at least one interlek movement and the number of days a bird was tracked: r=0.20, P=0.16, n=37). This allowed us to use uncorrected values of lek-switching metrics for purely descriptive purposes. Nevertheless, in comparative analyses we used daily probabilities of lek switching, i.e. the number of switching events (nights with at least one lek switch) divided by the binomial denominator, i.e. the number of tracking days, to account for this individually variable exposure. To analyse inter-seasonal variation in lek switching behaviour, we used Poisson generalised linear model (GLM) with the raw number of lek attended as the response variable and the number of tracking days (log value) as the offset to correct for variable exposure. Here we tested for the importance of inter-seasonal variation by comparing models with and without the year effect using AIC as a criterion.

To further analyse temporal variation in lek-switching behaviour, we used a multi-state mark-recapture (MSMR) framework (Williams et al. 2002, Lebreton et al. 2009). and estimated daily probabilities of movement between leks from daily encounter histories of individual males. For each of the three years analysed (2015, 2017, 2018), encounter histories were generated for the 47-day window from 01 May to 15 June using location data retrieved from GPS tags of 16, 9 and 11 males, respectively (36 males in total). For this work, we shifted the daily time scale by 12 hours to centre the time units around midnight to account for the predominantly nocturnal transitions between leks (see Results). Consequently, days started at 12:00 and ended after 24 hours at 12:00 the next day. Encounter histories rarely covered the entire 47-day period, with the core 50% of birds providing daily location data for a series of 30-43 days (mean 34.6 days). Overall, 26.5% of the individual*day entries in the encounter history matrix had missing data.

We used a two-state live recapture model implemented in the program MARK 9.0 (White & Burnham 1999). The model has three parameters to estimate: survival (S), detectability (p) and the probability of transition between states (ψ). We defined state A as a male being present at the same lek as on the previous day, and state B as being present at a different lek than on the previous day (Fremgen et al. 2017). Each male was initially assigned state A. It remained at the same lek with a probability of $\psi_{A\rightarrow A}$ or moved to an alternative lek with a probability of $\psi_{A\rightarrow B}$. Birds that changed lek were then assigned to state B and stayed there with a probability of $\psi_{B\rightarrow B}$ or changed lek again (including going back to the previous one) with a probability of $\psi_{B\rightarrow A}$ to reach an alternative lek labelled (again) state A. The labelling of states was thus arbitrary and relative to the last lek change. Given such a definition of the states, we set $\psi_{A\rightarrow A} = \psi_{B\rightarrow B}$ and constrained the transition probabilities from A to B and from B to A to be equal ($\psi_{A\rightarrow B} = \psi_{B\rightarrow A}$). By similar reasoning we set $S_A = S_B$ and $p_A = p_B$. Note that transition probabilities that start from the same state are equal to 1 (e.g. $\psi_{A\rightarrow A} = 1 - \psi_{A\rightarrow B}$).

S in this setup measured the daily 'survival' of tags as retrieved by the receiving stations, rather than the apparent survival of birds, while p reflected the daily probability of retrieving data from tags. Thus, 'deaths' reflected tag failure or our inability to retrieve the relevant data in the field. Therefore, survival and detectability were treated as nuisance parameters and held constant across days and states. The daily probability of transition between states, or the daily probability of interlek movement, ψ, was therefore the only parameter of interest for the purposes of the study. ψ was modelled as a function of the year and time within the season, indexed by 9 consecutive 5-day periods, starting on 01 May and ending on 15 June (the last period being 6 days). We applied models with different combinations of ψ allowed to vary or held constant within years (between periods) and between years. Models were ranked using the Akaike Information Criterion (AIC, Burnham & Anderson 2002). The model with the highest AIC weight (or equivalently, the lowest AIC) was selected as the most parsimonious model in the dataset analysed.

The daily distribution of transitions between leks was summarised based on male departure hours from one lek to another (in 1 h intervals, range 0-24, local time: UTC+2). When more than one transition between leks was noted within an hour, such a record was duplicated accordingly to the number of transitions. All spatial and statistical analysis were made in ArcGIS software (ARCGIS 10.8, Redlands, CA, USA) and R environment (R Core Team 2022).

Results

Number of leks visited, dispersal distances and frequency of lek switches

75% of tagged Great Snipe males (43/57) moved between leks (including both confirmed and potential leks) within the single breeding season, visiting up to 9 different lekking sites, with half of these mobile males (21/43) visiting two different leks (Fig. 1). Taking into account only confirmed leks, 61% of all males (35/57) visited more than one lek within a season, with single individuals visiting 5 and 6 different leks, respectively (Fig. 1). Based on a subset of males that visited two or more confirmed leks (N=22, except males from the year 2013 and 2014) we found that of 44 visits to confirmed lekking sites, at least in 59.1% (26/44) of cases males joined the strict lekking arena (at least one nocturnal position was in a buffer zone of 50 m from a confirmed lek). We surveyed 13 sites classified as potential leks and visited earlier by dispersing birds. In 8 of them (61%) we found from 2 to 10 displaying males (mean = 5.3, sd = 2.90, Fig. 2) confirming their status as actual leks. The remaining potential leks were not controlled because the relevant tracking data were downloaded after 15 June or sites were located in Belarus or Russia (N=27). Given that many of those potential leks we checked in the field were surveyed in June when many small leks are no longer active (Korniluk 2016), we can expect that the majority of sites initially classified as potential leks, actually represented active leks, at least in the focal season. We thus assumed that all sites classified as potential leks visited by tagged males at night were in fact active leks and pooled both confirmed and potential leks (hereafter called collectively “leks”) in further analyses.

For males that moved between leks (N=43), the maximum distance between two leks visited during the single breeding season averaged 37.2 km (SD=58.32, range 0.5 – 253 km) and was closely correlated with the maximum foray recorded for the same birds (correlation r=0.94, P<0.01). The vast majority of dispersing males (81%, N=35) visited leks located up to 50 km from the lek where they were initially trapped, while only about 10% of males (N=4) visited leks that were located at a distance exceeding 100 km (136 - 253 km, Fig. 3).

During the 5 study years, we identified in total 362 interlek movements by Great Snipe males made within a single breeding season (1 May - 15 June). Of males that moved at least once among leks within a season (N=43) we found that about half (53%; N=23) made up to 5 transitions between leks, about 37% of males (N=16) made from 5 to 17 transitions between leks and 4 males made more than 20 interlek movements within a season (Table 1S.). The record-holding male switched its lekking site 43 times within the season, moving back and forth chiefly between the lek where he was trapped for the first time on 04 May and a lek located about 21 km away in Belarus (Fig. 4).

In a sample of 36 males that provided continuous tracking data for longer periods (1244 bird-days in total), we recorded 276 transitions between leks which occurred during 153 bird-days, including 84 bird-days when focal males made multiple switches during a single day. Daily probabilities of lek change calculated from this data varied widely among individual males (Fig. 5). Nine birds (25%) registered no change of lek at all, clustering with birds that changed lek only once per season and forming a distinct peak of values less than 0.05. On the other hand, many males showed higher probabilities of lek change, peaking at 0.20 per day and reaching up to 0.40 per day. The superposition of two binomial distributions fitted this data much better (AIC=185.31) than either a zero-added binomial (AIC=229.88) or a single binomial (AIC=280.83). Consequently, we concluded that the males in our sample consisted of two groups: birds that never or rarely changed leks (daily probability of change=0.02, 51% of the sample) and birds that changed leks every four to five days on average (daily probability of change=0.23, 49% of the sample, Fig. 5).

At the daily level, multiple lek switches were common, being recorded in 54% of bird-days with any lek change recorded. Albeit in 46% of instances (N=71) males changed lek just once during the course of the night, two transitions between leks were recorded in 36% of cases (N=55), and three changes between leks during the night were found in 10% of cases. Furthermore, males that switched leks 4 and 5 times during a single night was recorded ten (7%) and two times (1%) respectively.

Accounting for the variable tracking period, the number of leks attended per season averaged 3.1 but varied considerably between years (Fig. 6). The Poisson GLM assuming an inter-year variation in the number of leks visited by tagged males fitted the data much better than a model with the number of leks held constant across all study years (AIC=230.4 vs 244.3). For instance, in 2015, of 16 tracked individuals, 6 males were faithful to one lek, 9 individuals visited 2 leks, and one male joined six different leks, whereas in 2017 of 9 tracked males, only one was faithful to the lek where it was initially trapped, whereas remaining males visited between 4 to 9 leks within the season (Supplementary material Table S1).

Seasonal and diurnal dynamics of movement between leks

The vast majority of lek changes occurred during the night. Only in 2 instances (accounting for 0.2% of recorded switches) did Great Snipe males make a transition between leks during the daytime (at 7.45 AM and 6.05 PM, respectively; times of the last GPS fix on the lekking site before departure to another lek) while the remaining movements among leks were entirely nocturnal (Fig. 7). The highest intensity of departures (N=73, 26%) from one lek to another was recorded between 9 PM and 10 PM and the majority of switches (66%, N=183) took place between sunset and midnight.

The overall probability of switching lek at least once during a single night averaged 0.12 in a sample of 1244 bird-days. Seasonal variation in the daily probability of interlek movement, studied using multi-state mark-recapture (MSMR) modelling, revealed considerable differences between successive 5-day periods of the breeding season (Fig. 8). The top-ranked model (w_i=0.63; Table 1) indicated that interlek transition probability was changing across the breeding seasons in 2015 and 2017, though not considerably so in 2018. In all three study years, the probability of lek change was essentially zero in the first days of May but increased substantially thereafter. In both 2015 and 2017, the highest probability of lek switching occurred in the first days of June, although in 2017 a comparable peak occurred in mid-May (Fig. 8). Additionally, there was noticeable inter-year variation, with daily probabilities of lek switching being generally higher in 2017 (0.23 ± 0.02) than in 2015 and 2018 (0.09 ± 0.01 for both years; estimates from the second-best model from Tab. 1).

Proportion of time males spent at different activites

During the lekking season, Great Snipe males spent the majority of their time (mean 84%, range: 51 – 100%, N=36) in close proximity to the leks (within a 500 m radius from leks and potential leks) and on average 1% of the time (range: 0 – 5.3%, N=36) they spent on movement outside the classified leks (flight >3 m/s) whereas movement outside the classified lekking sites covered on average 42% of the time spent on movement (range: 1-99% SD=26.6%, Table 1S Supplementary materials). The proportion of time males spent solo at night outside the classified lekking sites covered on average 3.7 % of a male’s tracking period and *differ*s between individuals (Fig. 2S Suplementary materials) ranging between 0.2 % to 17.8%, which translates to 0.5 and 150 hours respectively (Table 1S Supplement materials). In another study where we tracked Great Snipe males with GPS-GSM loggers (which allow for obtaining data in 1 h intervals via GSM) we checked 7 sites where males stayed at night outside known leks and we confirmed in five instances (with thermal cameras) that males displayed there solo (M. Korniluk, unpublished data). The mean maximum distance from the initial lek to nocturnal solo position was 38 km (SD = 62.7, N=36) and varied substantially between individuals (range: 0.6 km – 247 km, Fig. 2S. Suplementary materials).

Taking into account only males that join more than one lek within the season (a subset of males from 2015, 2017 & 2018, N=27), about 74% of them (N=20) spent most of the time (range: 53-99 %) at one lekking site while only about 11 % of males (N=3) spent less than 40 % (range: 25-40%) of their time at one lekking site (Fig. 1S, Fig. 3S. Table 1S, Supplementary materials).

In the case of 6 males (22%), the lek where it was trapped was not the lek where a male spent most of its time over the course of the season (Table 1S. Supplementary materials). The time males spent at “other leks” varied substantially (Table 1S., Supplementary materials). On average males spent 14.9 % (range= 0.03–59.83 %) of their time at other leks, the majority (59%, N=16) spent up to 10 % of their time at other leks, whereas the rest (N=11) spent from 16 % to 60% of their time at other leks (Table 1 S., Supplementary material).

Discussion

Are lowland and montane populations different?

We found that among lekking Great Snipe males in northeastern Poland, intra-seasonal lek changes are common and involve the majority of individuals studied. Three quarters of the 57 tracked males changed leks at least once during the main breeding season lasting from May to mid-June. Males visited up to 9 different leks within a single breeding season, frequently switching between display sites and often visiting 2-3 leks in quick succession during a single night. The daily probability of lek change was quite high, averaging 12% across the three study years.

The high mobility of males found in Poland contrasts with the much more stable picture of Great Snipe leks found in the literature. Despite extensive studies of the lekking behaviour of Great Snipes in Sweden and Norway, frequent and extensive intraseasonal lek switching by males has not been reported from among the Scandinavian populations. However, males were not intensivlly radio-tracked in the Scandinavian studies, making it difficult to conclude to what extent these differences reflect limitations of the purely observational studies conducted in the past, rather than real differences in lek ecology between Great Snipes living in montane Scandinavia and those living in the floodplains of eastern Poland. Indeed, there is some indication that intra-seasonal lek changes are also not uncommon among males in Scandinavia. Detailed studies of male lekking behaviour have consistently shown a high degree of variation in the proportion of nights spent at the focal lek by individual males (Lemnell 1978; Höglund & Lundberg, 1987; Höglund & Robertson 1990; Fiske et al., 1994). A significant proportion of Scandinavian Great Snipe males did not show up at the study leks every night, although their temporal absences were left unexplained (or even attributed to migratory status; Lemnell 1978). Importantly, 40-50% of all males recorded at leks (referred to as "territorial subordinates") attended the display arenas on only <15% of nights (Höglund & Robertson 1990). Combined with a central tenet of Great Snipe lekking ecology, the extreme energetic cost of male displays (Höglund et al. 1992) these absences may be explained by differences in the ability of males to overcome these cost burdens, constituting reliable signals of their individual quality. Lower quality males may simply be unable to perform costly displays during their nights of absence, perhaps still foraging or engaging in some low cost activity. Our data clearly shows that this is not the case, at least in the Polish lowland population, where male absences from focal leks were associated with their presence at other leks, usually some 5-20 km away (but maximally up to 253 km). This may well be true of Scandinavian males - a possibility that some authors (Höglund & Robertson 1990 BES; Sæther et al. 2005) have considered, although without providing evidence. On the other hand, there is evidence that lek-switching is common in another lowland population breeding in western Russia (Karpovitch 1962), where at least 10% of males moved between leks up to 10 km apart (with more distant leks not being subjected to study). It is therefore possible that lowland populations living in more unpredictable conditions, driven by highly variable spring flood levels, are more likely to exhibit more exploratory behaviour, encouraging frequent lek switching. Clearly, further research, preferably using modern tracking technology, is needed to quantify the frequency and extent of this behaviour across the Great Snipe populations.

Why change leks? Benefits and costs of lek switching

As with many lekking species, the distribution of Great Snipe male mating success observed in the leks was skewed towards a few high ranking males, with about half of the males apparently failing to achieve a single mating (Höglund & Lundberg, 1987; Fiske et al., 1994). Mating success was related to male tenure on the lek, suggesting strong selection against lek switching (Fiske et al., 1994; Sæther et al., 2005). However, the selective forces shaping lek switching are likely to differ according to male status. High-ranking males who occupy central positions in the lek and obtain the most copulations during the breeding season should benefit from being faithful to the site where they are able to achieve predictably high mating success. However, if the mating success of low-ranking, peripheral males is consistently very low or zero, they will lose practically nothing by leaving the original lek and moving on to another. Obviously, for males, leks differ in their 'quality', indexed by the probability of mating, and an alternative lek may offer a higher mating chance due to a potentially lower quality (or number) of male competitors or a higher number of visiting females. Low-ranking males may thus follow a “win-stay, lose-switch” decision rule (Schmidt 2004), based either on actual matings or perhaps also on mating chances assessed on the basis of the available public information (Danchin et al. 2001). On the other hand, some models suggest that in a system where males tend to change leks frequently within a season, it is high ranking males, rather than low ranking ones, who should benefit most from lek switching as lek size increases (Widemo & Owens, 1999). In our study, we did not make behavioural observations on leks and were therefore unable to assess the dominance status of our lek-switching males. However, given the high prevalence of dispersing males in our sample (75%), we believe that they should be mostly low and middle ranking birds.

Reasons for lek switching may also incorporate factors operating outside the strict display arena. Male mating success is related to display intensity (Höglund & Lundberg, 1987; Höglund & Robertson, 1990) but mating displays are costly from an energy-expenditure point of view, with birds losing 5-7% of their body mass each night (Höglund et al., 1992) but also as the breeding season progressed (Witkowska et al. 2022). Males therefore need to replenish energy reserves during daily foraging, preferably in close proximity to the lek, with the vast majority of tracking records made within 500 m of the lek itself and a preference to forage close to the lek (Korniluk et al. 2021). Effective compensation for the nocturnal loss of energy reserves requires a high availability of abundant large prey, in this case consisting largely of earthworms found in the upper soil layer (Løfaldli et al. 1991). Foraging birds are also highly selective for the amount of bare ground and the structure and height of vegetation that likely provides camouflage from predators during daytime foraging (Løfaldli et al., 1991; Korniluk et al. 2021). It has therefore been hypothesised that the presence of suitable, rich foraging grounds in areas close to leks would limit the distribution of leks and perhaps the species in general (Kålås et al. 1997b). Resultantly, foraging conditions in areas adjacent to leks may also influence lek-switching decisions. Changes in water levels in Great Snipe habitats have been found to correlate with the number of males attending leks (Grygoruk et al. in press.) and changes in their body condition (Witkowska et al. 2022). Finding an alternative lek with better foraging grounds in close proximity, allowing more efficient replenishment of energy reserves, should therefore contribute to improved male mating success. If lowland breeding Great Snipes are indeed more likely to change leks within the breeding season than birds from montane populations in Scandinavia, then changing water levels on river floodplains and drained peatlands with cascading effects on foraging conditions close to leks may be a factor contributing to this difference.

Certainly, the potential decision to seek another lek should be influenced not only by the perceived chances of mating success at alternative leks, but also by the numerous costs of moving to a new site, which are relatively well recognized for animals involved in breeding dispersal (Bonte et al. 2012, Clobert et al. 2001, Clobert et al. 2012). Our results show that, on average, these costs are likely to be low for male Great Snipes moving between leks in NE Poland. While some of the dispersing males (presumably inexperienced) clearly exhibited searching behaviour, in many other cases birds moved to alternate leks in a directed, straight-line flight with no evidence of having searched for the new lek. Such transitions are rapid (mean flight speed c.55 km/h; M. Korniluk, unpublished information), directional and the location of the destination appears to be known in advance. This can be illustrated by the movement of one of our tagged males, which left the upper Biebrza basin and flew almost directly to reach a traditional lek 160 km SE in the floodplain of another lowland river, the Bug. Although this lek proved to be inactive this year, 3-4 displaying males were found there last year. We are certain that among the male Great Snipes studied, dispersal between leks was often informed by the birds' previously acquired knowledge of the whereabouts of lek locations. Therefore, the potential multiple costs of searching for a new lek should be highest for inexperienced males, whereas older males in our population may be able to disperse at relatively lower cost to themselves.

That given, any dispersal costs associated with male absence from the original lek and unavailability to females are short-lived and probably negligible. On the other hand, given the available data on the energetics of avian flight (Jehl et al. 2003, Butler 2016), the dispersal costs of flight are likely to be not insubstantial. Although high, the energy cost of flight is likely to be broadly comparable to that of sustained overnight lekking displays (5 * basal metabolic rate [BMR]; Hoglund et al. 1992), especially for a bird species adapted to long distance migratory flights (6-8 * BMR; Piersma & Jukema 1990, Hedenstrom 2010). As shown by Höglund et al. (1992), male Great Snipes are able to (almost) compensate for the costs of nocturnal displays by efficiently foraging at selected rich foraging sites. Thus, by replacing the cost of lekking displays with the cost of relatively short transit flights, males may not be overly increasing their energy expenditure in order to recover the following day. Furthermore, data from a related polygynous, migratory shorebird species, the Pectoral Sandpiper *Calidris melanotos*, show that males are able to bear the energetic costs of rather extreme dispersal flights - in addition to the non-trivial costs of mating displays - in pursuit of matings (Kempenaers & Valcu 2017).

On the other hand, dispersing males may incur costs by having to establish their position in a new dominance hierarchy at the new lek (Widemo 1998, Widemo & Owens 1999, Cayuela et al. 2019). However, this again should depend on the status and quality of the individual male. If the dispersers are high quality dominant males, then these costs may be substantial, at least in terms of time. Conversely, if dispersers are mostly low quality males, then they are likely to maintain their low status at the new lek at low cost as non-territorial, peripheral males attempting to steal copulations from high quality males present locally.

Although the costs and benefits of male lek change are best analysed in terms of maximising seasonal mating success, the adaptive role of this behaviour should also be considered on a longer time scale. Even if dispersing males fail to find a mate at a new site in a given year, they still gain knowledge about the location of traditional leks over some spatial extent. Obviously, this knowledge is of critical importance for young males attempting to breed for the first time. However, regardless of age and experience, this information would certainly be useful in subsequent breeding seasons, when the ability to quickly find a better lek than the one initially selected would be at a premium. In particular, if lek features indexing male mating chances (e.g. lek size, number of dominant males, female visitation rate) tend to be temporally autocorrelated (Schmidt 2004), informed dispersal should be a profitable strategy for lower ranking males. We therefore argue that, in addition to immediate mating success, lek-switching should also be seen as a form of prospecting for new leks which can be utilised in future seasons, with possible benefits (in terms of increased mating success) being reaped in later years. The phenomenon of prospecting for potential new breeding sites for use in subsequent years has been described in many bird population studies (Reed et al. 1999, Danchin et al. 2001, Davis et al. 2017, Oro et al. 2021), although – to our knowledge – not in the male lek-switching context (but see Gerber et al. 2019).

Temporal variation in lek switching

Male Great Snipes tracked in northeastern Poland moved to new leks almost exclusively at night, such a move probably arising as an anti-predator strategy. At least two local raptor species (Goshawk *Accipiter gentilis* and Peregrine falcon *Falco peregrinus*) are able to prey on flying snipes during the day, but we are not aware of any aerial predators that are able to do so at night, at least in non-urbanised areas. In addition to avoiding predators, nocturnal transits between leks should be beneficial for male Great Snipes, as they allow flying birds to easily locate previously unknown leks using acoustic cues provided by displaying males. Similarly, nocturnal arrival at a lek allows the male to quickly assess the situation at the lek, chiefly the number and quality of displaying males. This would be impossible during the day when birds are foraging outside the lekking arena. Consistent with this interpretation are our observations of males frequently changing leks several times during a single night (up to 5 times), which can be interpreted as a result of departure from leks that proved unattractive propositions. Interestingly, dispersing males moved between leks mainly in the first two hours after sunset, which coincides with the period of highest vocal activity of displaying males (Auniņš 2001) allowing dispersers to maximise the information gained when arriving at a new lek. Similarly, males are less likely to disperse around midnight, perhaps to avoid missing the period of highest lek visitation by females (Kålås et al. 1995).

Seasonal variation in lek switching did not show a consistent pattern across the three study years, with the exception of virtually no switching recorded during the first five days of May. In one study year (2015), there was a tendency for lek switching to become more frequent towards the end of the season, but this was not supported in the other two seasons, when the probability of lek switching either peaked twice per season, starting before mid-May (2017), or showed no significant differences throughout the season (2018). We would expect males to be increasingly likely to search for new leks as the season progresses, in line with decreasing chances of finding fertile females and deteriorating foraging conditions, but this was not the case in two of the three study years. We see no obvious explanations for the observed temporal patterns, except perhaps our inability to detect meaningful signals in the data due to the low precision of the estimates.

Similarly, we have no clue as to why the frequency of lek changes was twice as high in 2017 as in the other two study years. However, the numbers of males tagged in the three main study sites (Narew, Biebrza, Supraśl) in the particular study years were far from balanced, with 2017 represented only by birds captured at a single lek in Supraśl. Therefore, the effect of year is confounded with the effect of the spatial variation in our sample, further complicating possible inferences.

Lek switching and evolution of leks

Intra-seasonal lek-switching by males has been reported in several avian lekking species, but the observed (or inferred) prevalence of this behaviour has tended to be low (reviewed in Lanctot et al. 1997). Recent studies have shown that lek-switching is rare but fairly regular among males of the Greater Sage-grouse *Centrocercus urophasianus* (Gibson et al. 2014; Fremgen et al. 2017). Conversely, lek switching was frequently observed in two other lekking members of the Scolopacidae family, the Buff-breasted sandpiper *Calidris subruficollis* and the Ruff *Philomachus pugnax*, both long-distance migrants. Buff-breasted sandpiper males readily switch between lek attendance and solitary display, with 20% of males displaying at multiple leks (Lanctot et al. 1997). Ruffs also readily change leks within the breeding season, although this behaviour was mainly restricted to satellite males, which form a distinct, genetically determined morph in this species (Lank & Smith 1987, Widemo 1998). Our results showing that many Great Snipe males change leks frequently are consistent with the possibility that, among lekking bird species, long-distance migrants are particularly prone to lek-switching due to low dispersal costs.

When it comes to the evolution of lekking systems, intra-seasonal lek-switching seems a largely overlooked feature of avian lekking systems. Only the game-theoretic model of lekking (Höglund & Alatalo 1995), which has apparently not been further developed in the last 30 years, makes clear predictions regarding lek-switching. According to this model, if males can be divided into high-ranking attractive birds ("hotshots") and low-ranking individuals who surround them at leks and try to parasitise on their attractiveness (Höglund & Robertson 1990), then the latter group of males is expected to switch leks frequently (Höglund & Alatalo 1995: 190). This is consistent with the pattern observed in our data, where about half of the males changed leks quite frequently, while others changed infrequently, including 25% of birds that never changed leks. In the absence of data on the lek behaviour of our males, we are left to speculate whether this heterogeneity in male lek-switching behaviour may be related to their quality and mating prospects.

We note that 25% of males not changing leks in our study is broadly comparable to the proportion of dominant males obtaining matings (15%) found by Hoglund & Robertson (1990), while 51% of males changing leks only once or never is comparable to the proportion of males obtaining matings in other studies (Höglund & Lundberg 1987; Fiske et al. 1994). Small sample sizes preclude more detailed analyses of inter-individual heterogeneity in the probability of lek change, but we conclude that the overall picture suggests that there are two types of males in our sample, consistent with the hotshot model.

Our data shows that in a lekking system with characteristics consistent with the hotshot model, intra-seasonal dispersal may be a common strategy adopted by the majority of males. This is probably facilitated by low dispersal costs and informed dispersal of birds through the utilisation of previous knowledge of lek location or the ability to quickly locate unknown leks by use of acoustic cues. In any case, freely dispersing males that sample many leks are a relatively novel feature of the lekking ecology of a bird described as "the most convincingly 'classic' of lekking animals" (Sæther et al., 2005). We believe that applying elements of patch selection theory using personal and public information (Doligez et al. 2003, Danchin et al. 2004, Schmidt et al. 2010) to lekking systems with regular inter-lek switching would be a fruitful area for further research.

Conservation implications

The majority of Great Snipe males in our study population make use of multiple leks within a single breeding season, with some birds spending a comparable number of nights displaying at two or three sites. Regardless of the causes, alternating use of different leks, usually separated by no more than 50 km, is thus a typical behaviour for many males of the species. The utilisation of space by lekking males is best described therefore in terms of a network of nearby leks rather than a single lek, suggesting that the spatial requirements of the species are in fact much greater than that suggested by single-site studies. Thus, successful conservation of local snipe populations with different individual mating strategies may require protection of clusters of nearby leks, equivalent to separate habitat patches in a meta-population design. This suggests that the protection of whole river valleys (or extensive sections of valleys) should be a conservation target for the species. Conversely, protecting only the 'best' (largest, most stable) leks may not be sufficient if adjacent, smaller leks are destroyed by habitat alteration or loss. This makes species potentially more vulnerable to habitat loss than other species that frequent similar habitats but do not use regular intra-season dispersal as part of their breeding strategy.

Our results also have implications for the design of species surveys that use counts of lekking males, summed across sites, as a proxy for local population size (Kålås 2000, Korniluk et al. 2015). The results of such surveys are prone to upward bias if different leks are not visited simultaneously (e.g., when a single observer or team of observers visits multiple leks on successive nights). With non-synchronised counts, dispersing males are likely to be counted twice at different leks, leading to inflated estimates of local population size. In our study population, non-synchronised surveys are expected to provide reliable results only during the first few days of May, when male movement between leks is absent or rare. Yet, for most of the breeding season, Great Snipe lek surveys should be highly synchronized across multiple display sites to obtain unbiased population data, in line with conclusions for other lekking species showing significant inter-lek movements (Blomberg et al. 2013, Fremgen et al. 2017). We also suggest that records of single displaying males found outside established leks should not be included in monitoring schemes, as they are likely to represent individuals dispersing from leks already surveyed.

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Figures and tables

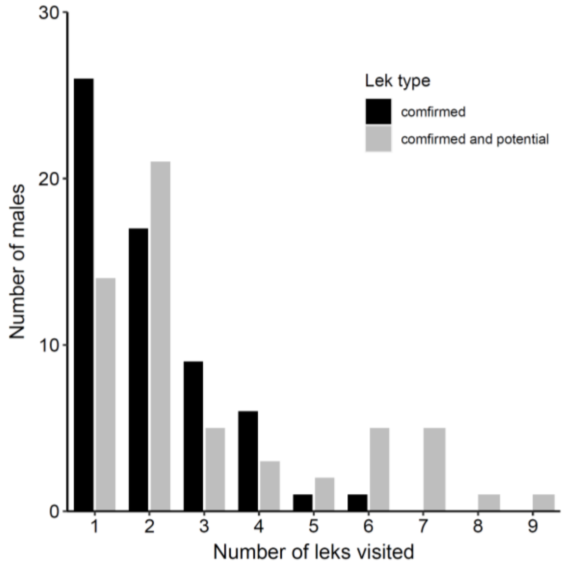

Fig. 1 Number of leks visited by the Great Snipe males (N=57) within lekking season (1 May – 15 June) taking into account confirmed and potential leks (A) and only confirmed leks (B).

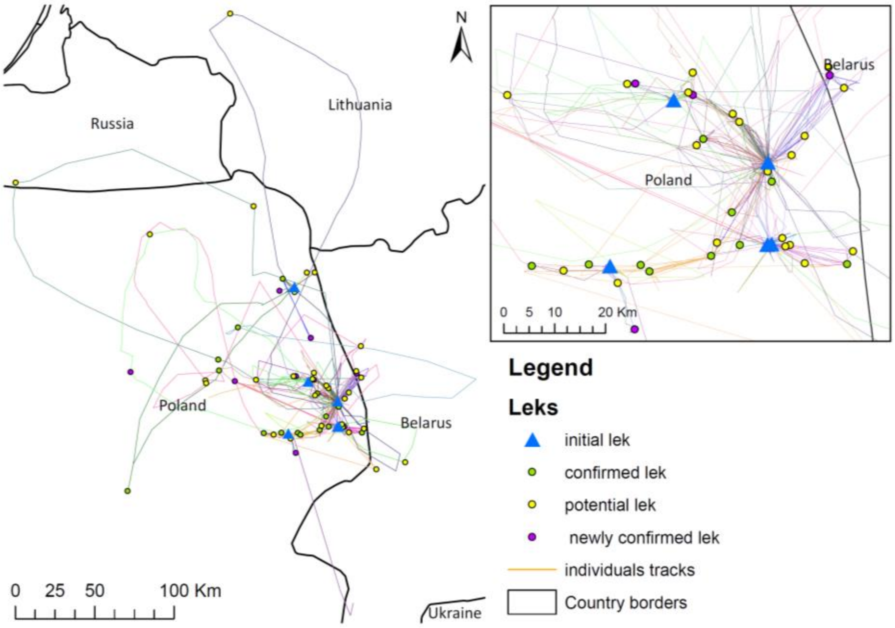

Fig. 2 Great Snipe male inter-lek movements within the lekking season (1 May – 15 June) in the years 2013-2015 and 2017-2018 based on GPS-UHF loggers positions (N=57). Dots and triangle indicates a classified lek type: *initial leks* – leks where males were equipped with GPS loggers, *confirmed leks* – stable leks known form particular or a previous year, *potential leks* – cluster of male GPS positions (~50 m radius) that were at a distance greater than 1 km from the confirmed leks and males were found there on at least two different nights, *newly confirmed leks* – potential leks where at least 2 displaying

males were found within a lekking season. Coloured lines represent different individuals and merges successive GPS fixes indicating male movement paths.

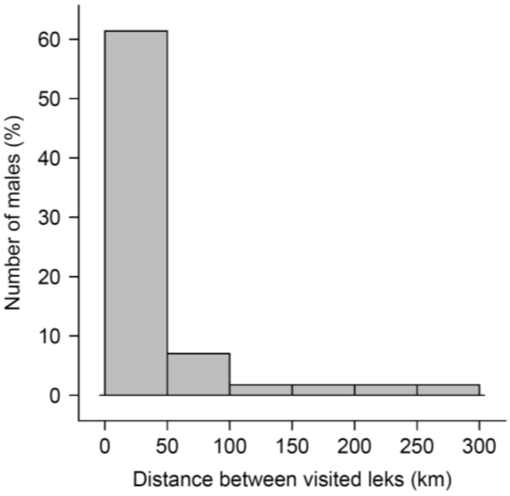

Fig. 3 The distribution of the maximum distances between initial leks (a lek were a male was trapped) and the furthermost lek visited by the Great Snipe male within a lekking season (N=43).

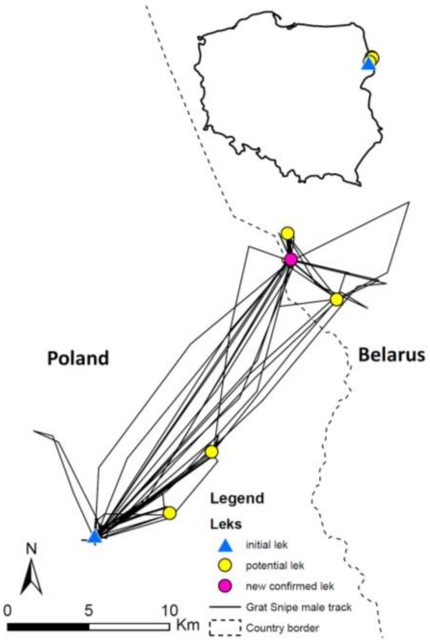

Fig. 4. Great Snipe male GPS track (black line) from 4 May to 15 June 2017 presenting 43 transitions between leks within the lekking season. Dots and triangles indicate a classified lek type: *initial* – leks where males were equipped with GPS loggers, *potential leks* – cluster of male GPS positions (~50 m radius) that were at a distance greater than 1 km from the confirmed leks and males were found there on at least two different nights, *newly confirmed leks* – potential leks where at least 2 displaying males were found within a lekking season.

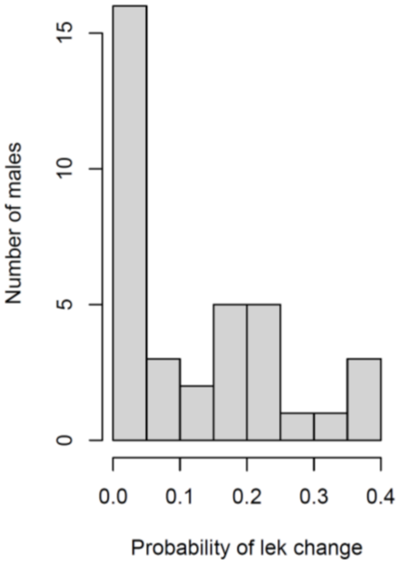

Fig. 5. Between-individual variation in daily probability of lek switching by male Great Snipes. Data for 36 males from years 2015, 2017 and 2018.

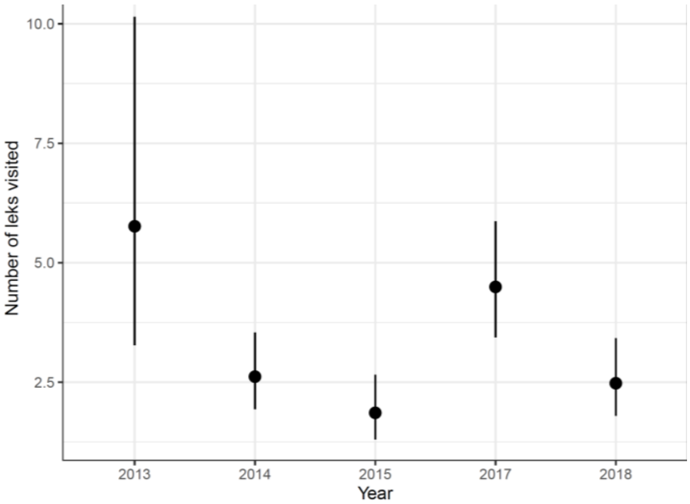

Fig. 6. Number of leks visited by Great Snipe males within the lekking season across five study years. . Dots indicate mean values as estimated from Poisson GLM model with number of tracking days (to correct for variable exposure time) as an offset variable; whiskers show 95% confidence intervals.

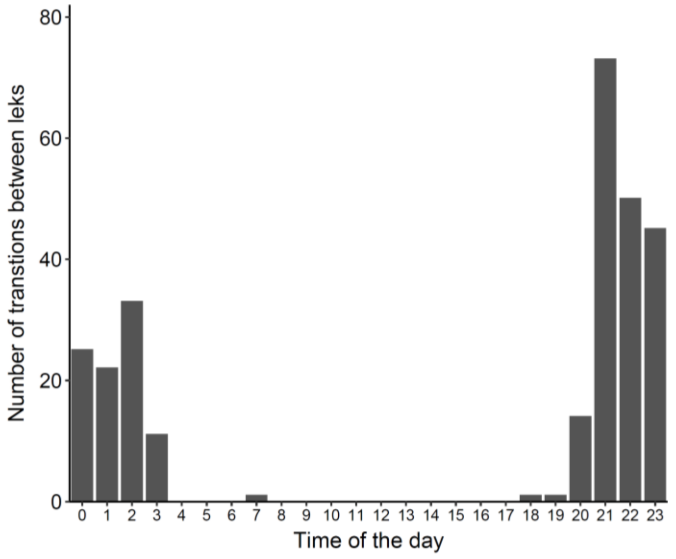

Fig. 7 Diurnal variation in times (UTC+2 - local time) of inter-lek switches of Great Snipe males (N=36) registered in the years 2015, 2017, and 2018.

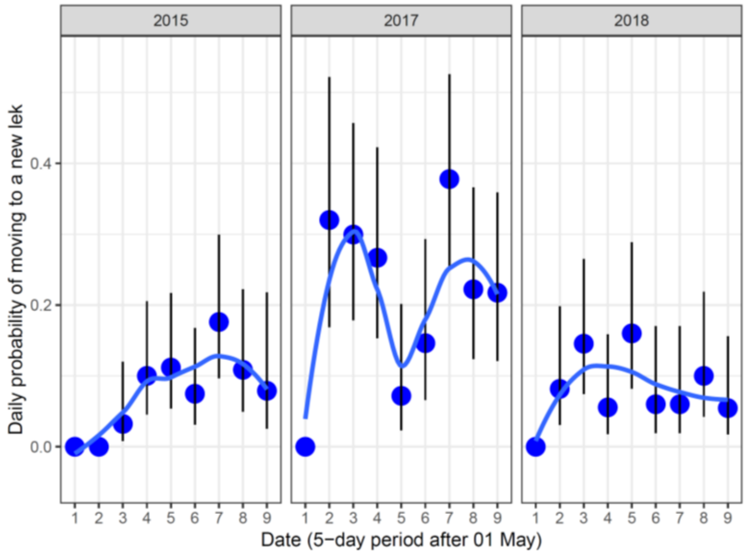

Fig. 8. Seasonal and between-year variation in daily probability of lek switching by male Great Snipes in three study years as estimated by MSMR model (see Methods). Seasonal variation was assessed using consecutive 5-day periods, starting from 01 May. For illustrative purposes, estimates from the saturated model (M5, see Table 1) are provided alongside with their 95%CIs and trend lines (blue) fitted with loess smoother. The top-ranked model assumed period-specific variation for the first two study years (as shown here) but constant lek switching probabilities across the season in the last study year. Data for 36 males from years 2015, 2017 and 2018

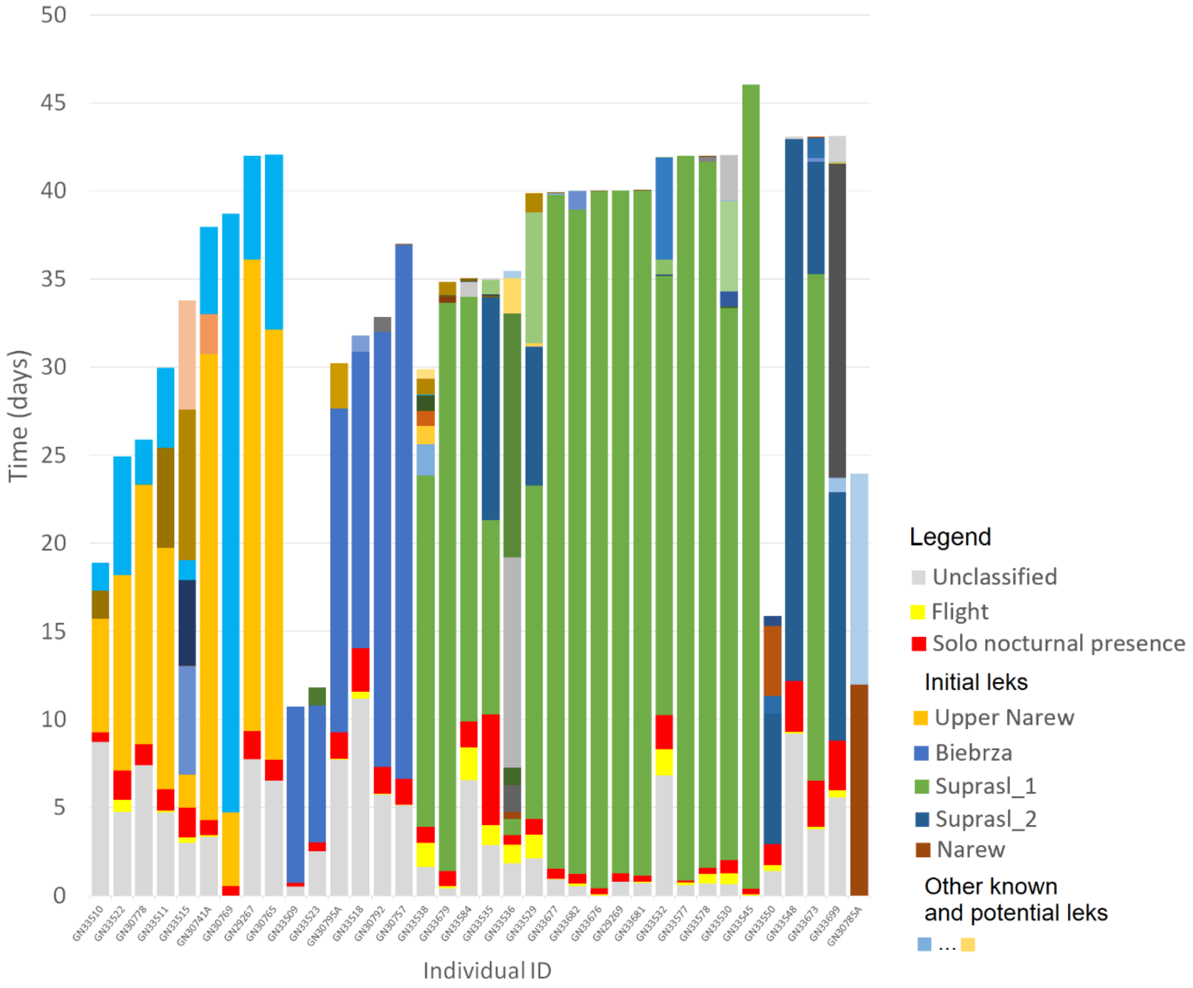

Fig. 1S. Proportion of time Great Snipe males spent in the following categories represented by different colours (based on data obtained in 2015, 2017, 2018; N=36): Initial leks – time spent within a radius of 500 m from the leks where the male was trapped, confirmed and potential leks – time spent within a radius of 500 m from confirmed or potential leks, flight – time when a male was flying with a speed >3m/s, solo nocturnal presence - a nocturnal position that was not assigned to the above categories, unclassified – the remaining time not assigned to any of the above categories.

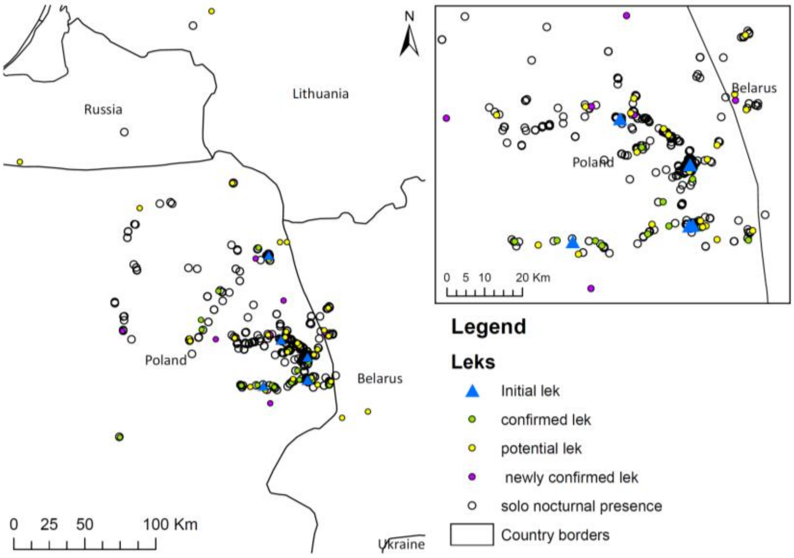

Fig. 2S. Sites where Great Snipe males tracked within the years 2015, 2017 & 2018 (N=36) stayed at night solo (black dots) outside the classified leks (coloured dots and blue triangle).

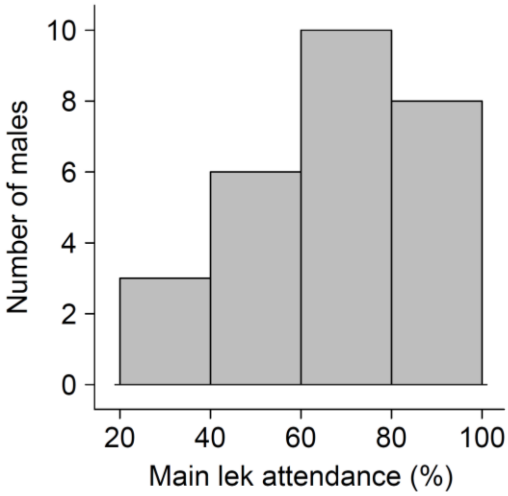

Fig. 3S. The percentage of time spent at the main lek (a lek where males spent the most of the time within a lekking season) by Great Snipe males that move among leks intraseasonally (N=27)

Table 1. Model selection results for the effects of a year and 5-day period within the year on the inter-lek daily transition rates (ψ) estimated using multistate mark-recapture models. Structure of ψ estimates was given separately for each of the three study years, separated by slashes. Numbers denote estimates which are different for particular years; e.g. "period1/period2/const" means that ψ estimates in the first and second study year were assumed period-specific and different for each of the two years, while for the third study year they were assumed constant. AICc, Akaike's information criterion corrected for small sample sizes; Delta AICc, difference between AICc of the top model and the focal model; AICc weight, Akaike's model weight; K, number of parameters in the model. All models included estimates for S and p parameters (not shown; see Methods).

Model	ψ (yr2015/yr2017/yr2018)	AICc	Delta AICc	AICc weight	K	Deviance
M1	period1/period2/const	1273.761	0	0.62568	21	1147.447
M2	const1/const2/const1	1276.534	2.7734	0.15636	4	1184.957
M3	period/const1/const2	1276.752	2.9909	0.14024	13	1166.906
M4	const1/const2/const3	1278.545	4.7843	0.05721	5	1184.951
M5	period1/period2/period3	1280.597	6.8358	0.02051	29	1137.595
M6	const/const/const	1316.942	43.1811	0	3	1227.378

Table 1S. Summaries of inter-lek Great Snipe male movement between leks within a season. Each record indicates a different individual, except for the following self-explanatory column names: *initial lek* – a lek where a male was equipped with a GPS logger, *leks switches* – the total number of transitions between leks, *max lek distance* – a maximum distance calculated based on distances between the lek where a male was trapped (initial lek) and the male's furthermost position assigned to a confirmed or potential lek, *max confirmed lek distance* - a maximum distance calculated based on distances between the lek where a male was trapped (initial lek) and the male's furthermost position assigned to a confirmed lek, *maximum foray* – the distance between the initial lek and the furthermost male's position registered within a season (including those not assigned to leks), *main lek* – summarised time a male spent in a 500 m radius of the lek where it spent the most of its time, *other leks* - summarised time a male spent in confirmed and potential leks. *flight* – summarised time when the GPS speed was >3m/s and was outside confirmed or potential leks, solo nocturnal presence – summarised time of nocturnal positions that were not assigned to the above categories.

Tracking period		Tracking duration [days]	Sample size [GPS fixce]	Lek switches	Leks visited	Comf. leks visited	Max lek distance	Max comfired lek distance	Max foray	Duration in behavioural categories [days]				
from	to									Main lek	Other leks	Flight	Solo nocturnal presence	Not classified
2013-05-29	2013-06-15	16.9	397	2	2	2	0.52	0.52	0.87	-	-	-	-	-
2013-05-29	2013-06-15	16.8	321	0	1	1	-	-	0.60	-	-	-	-	-
2013-05-15	2013-05-28	12.9	323	10	3	2	48.72	0.43	50.29	-	-	-	-	-
2013-05-22	2013-06-03	12.8	301	17	6	3	16.75	15.78	16.75	-	-	-	-	-
2014-05-19	2014-06-12	24.9	74	4	2	1	12.14	0.59	12.14	-	-	-	-	`
2014-05-19	2014-06-13	25.6	247	0	1	1	-	-	2.25	-	-	-	-	-
2014-05-19	2014-06-15	27.9	198	0	1	1	-	-	1.27	-	-	-	-	-
2014-05-19	2014-06-06	18.7	69	0	1	1	-	-	4.10	-	-	-	-	-
2014-05-19	2014-06-03	15.8	96	2	2	2	9.60	9.60	9.60	-	-	-	-	-
2014-05-19	2014-06-13	25.9	334	4	2	2	8.78	8.78	8.78	-	-	-	-	-
2014-05-19	2014-06-15	27.6	183	5	3	3	34.79	34.79	34.79	-	-	-	-	-
2014-05-25	2014-06-15	21.0	493	4	2	1	2.74	1.10	2.74	-	-	-	-	-
2014-05-03	2014-05-19	15.8	723	1	2	1	9.99	0.82	9.99	-	-	-	-	-
2014-05-04	2014-06-15	42.9	601	4	2	2	2.20	2.20	2.20	-	-	-	-	-
2014-05-10	2014-06-02	22.8	406	13	5	5	72.52	72.52	72.52	-	-	-	-	-
2014-05-03	2014-06-15	42.8	965	11	7	3	48.07	48.07	48.07	-	-	-	-	-
2014-05-11	2014-06-15	34.7	322	1	2	1	10.21	0.28	12.63	-	-	-	-	-
2014-05-12	2014-06-15	33.8	162	2	3	2	13.71	13.71	13.71	-	-	-	-	-
2014-05-13	2014-06-03	21.7	182	3	3	2	15.32	15.32	121.36	-	-	-	-	-
2014-05-13	2014-06-15	33.4	80	0	1	1	-	-	19.60	-	-	-	-	-
2014-05-13	2014-06-04	22.7	120	4	3	2	13.54	13.54	13.54	-	-	-	-	-
2015-05-09	2015-06-15	37.0	1505	2	2	1	3.56	0.50	3.56	30.27	0.13	0.02	1.48	5.13
2015-05-09	2015-06-11	32.8	1407	3	2	1	3.60	0.50	6.71	24.71	0.85	0.04	1.52	5.72
2015-05-01	2015-05-30	30.2	1267	12	2	2	9.00	9.00	9.00	18.38	2.58	0.09	1.48	7.70
2015-05-10	2015-05-20	10.7	533	0	1	1	-	-	1.35	10.00	0.00	0.00	0.21	0.51
2015-05-09	2015-06-10	31.8	1189	2	2	2	166.15	166.15	166.15	16.82	0.91	0.42	2.49	11.15
2015-05-28	2015-06-09	11.8	75	2	2	1	15.87	0.50	15.87	7.78	1.01	0.00	0.50	2.52
2015-05-04	2015-06-15	42.0	1380	0	1	1	-	-	1.99	32.67	0.00	0.00	1.58	7.75
2015-05-09	2015-06-15	37.9	1354	6	2	1	3.94	0.89	6.73	31.40	2.26	0.10	0.86	3.32
2015-05-04	2015-06-15	42.1	1115	0	1	1	-	-	1.73	34.35	0.00	0.00	1.18	6.53
2015-05-04	2015-06-12	38.7	219	0	1	1	-	-	1.21	38.14	0.00	0.00	0.55	0.00
2015-05-04	2015-05-30	25.9	901	2	2	2	15.74	15.74	16.60	17.26	0.04	0.00	1.20	7.39
2015-05-21	2015-06-09	18.9	292	1	2	2	15.56	15.56	15.56	8.03	1.60	0.00	0.55	8.72
2015-05-08	2015-06-07	30.0	1370	8	2	2	15.75	15.75	15.75	18.26	5.68	0.11	1.20	4.72
2015-05-08	2015-06-11	33.8	1540	27	6	3	26.87	24.75	33.30	8.56	20.22	0.32	1.69	2.99
2015-05-21	2015-06-15	24.9	150	0	1	1	-	-	11.76	17.85	0.00	0.67	1.67	4.76
2015-05-01	2015-05-12	12.0	476	0	1	1	-	-	0.72	11.97	0.00	0.00	0.02	0.00
2017-05-04	2017-06-13	39.9	2000	22	9	3	52.72	22.82	76.40	18.90	16.62	1.36	0.90	2.10
2017-05-04	2017-06-15	42.0	2152	43	6	2	22.54	21.30	28.56	31.31	8.69	0.62	0.76	0.64
2017-05-03	2017-06-14	41.9	2033	11	7	4	84.28	77.37	160.91	24.93	6.74	1.49	1.93	6.82
2017-05-11	2017-06-15	35.0	1324	8	7	4	31.97	22.80	55.74	12.64	12.13	1.16	6.25	2.85
2017-05-11	2017-06-15	35.0	1374	21	7	6	40.75	40.75	81.37	13.84	17.76	1.05	0.55	1.84
2017-05-11	2017-06-10	29.9	1033	13	8	4	245.08	79.59	245.08	19.94	6.03	1.37	0.90	1.64
2017-05-04	2017-06-15	42.0	2096	0	1	1	-	-	18.18	41.14	0.00	0.17	0.09	0.59
2017-05-04	2017-06-15	42.0	2098	15	4	4	11.96	11.96	29.63	40.10	0.34	0.55	0.34	0.67
2017-05-11	2017-06-15	35.0	1911	16	5	3	253.40	3.64	253.40	24.12	1.03	1.86	1.46	6.57
2018-05-03	2018-06-15	43.1	1672	2	2	1	3.09	0.41	3.09	30.78	0.15	0.10	2.85	9.21
2018-05-03	2018-05-19	15.9	485	4	4	3	55.77	55.77	105.88	7.41	5.56	0.33	1.19	1.39
2018-05-03	2018-06-15	43.1	1718	12	6	4	23.37	22.58	25.56	28.78	7.80	0.16	2.59	3.76
2018-05-03	2018-06-15	43.1	1657	15	6	3	136.26	112.18	136.26	17.84	16.48	0.42	2.79	5.56
2018-05-06	2018-06-15	40.0	1651	0	1	1	-	-	1.55	38.77	0.00	0.00	0.46	0.80
2018-05-01	2018-06-15	46.0	1956	0	1	1	-	-	0.73	45.66	0.00	0.08	0.29	0.00
2018-05-06	2018-06-15	40.0	1649	2	2	2	2.45	0.47	2.97	39.60	0.01	0.08	0.33	0.00
2018-05-06	2018-06-15	39.9	938	4	4	3	3.65	3.65	3.65	38.23	0.17	0.02	0.59	0.93
2018-05-06	2018-06-10	34.9	1412	16	7	4	20.33	20.33	20.97	32.24	1.21	0.14	0.84	0.42
2018-05-06	2018-06-15	40.0	1650	2	2	2	2.63	0.92	21.76	38.91	0.01	0.06	0.32	0.72
2018-05-06	2018-06-15	40.0	956	4	2	2	13.70	13.70	23.63	37.71	1.06	0.13	0.56	0.55

Factors influencing flight initiation distance in a cryptic bird species – the Great Snipe Gallinago media

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Abstract

Predator-prey interactions are one of the most powerful evolutionary forces shaping the diversity of the animal kingdom. Numerous anti-predator adaptations have evolved, including spatial and temporal predator avoidance, weaponry, morphological defences or camouflage. A well-known and widely used anti-predator behavioural response is the escape, which in the case of a cryptic prey relies largely on the interaction between an individual coloration and its environment, modified by threat perception dependent on const and benefits balance of the flight decision. Flight initiation distance (FID), which is the distance between predator and prey at which the prey flees, is a widely used metric that allows scientists to study those circumstances represented by measured variables. However, most research focuses on one or a few factors, leaving the effect of a wide range of variables on the prey's FID largely unexplored. Using a multivariate analysis, based on a four-year study at five different sites, we assessed the FID of the foraging male Great Snipe Gallinago media, a cryptic wader species. We found that Great Snipe FID was negatively related to vegetation density and height, suggesting that dense and tall sward provides better camouflage for foraging males. Our model also showed that the flight decision of the male Great Snipe varied with day and cloud cover, with the lowest FID at midday and a significant increase in FID when cloud cover was greater than 40%. As the Great Snipe is darker dorsally, we link these relationships to reduced detectability in strong sunlight caused by countershading. We also found that the better the foraging opportunity (expressed in earthworm abundance), the greater the FID, contrary to Ydenberg and Dill's (1986) economic models which suggest that the prey with foraging opportunity should have a greater cost of flight than a prey without, and thus a shorter FID. We also found that FID increases significantly late in the lekking season, which given males' demanding energy needs for display purposes, may be related to males' greater investment in predator avoidance at a time when mating opportunity is low. We also found that the larger the group of prey and intruders, the greater the distance at which males escaped. Finally, we found that despite taking into account many factors that were significantly related to a prey's escape decision, FID differed between study sites, suggesting that a direct comparison of this fearfulness measure should be carried out with great caution.

Keywords

camouflage, crypsis, predation, risk-assessment, escape decision, FID, lek, countershading, foraging, earthworms, mating opportunity

Introduction

Predator-prey interactions are among the major selective forces behind evolutionary change (Caro 2005). A large part of phylogenetical variation in morphological traits and behaviours of prey species may be interpreted in terms of the evolution of numerous anti-predator adaptations. These include weapons, morphological defences such as shells, and the ability to shed tails or camouflage (Caro 2005, Cooper & Blumstein 2015). Aside from these adaptations, to reduce the likelihood of predation, a prey must make a behavioural decision under specific circumstances when a predator-prey encounter takes place (Lima & Dill 1990). Since a decision which reduces predation risk also affects other important aspects of an animal’s life, such as foraging or reproduction (Lima & Dill 1990), a prey often faces opposing selective forces associated with a particular action (Ydenberg & Dill 1986, Broom & Ruxton 2005, Cooper & Frederick 2007). One well-known and widely used anti-predator behavioural responses is the escape. The economic models proposed by Ydenberg and Dill (1986) assume that prey will begin fleeing when the cost of not escaping is equal to the cost of fleeing. Furthermore, optimal escape models predict that the prey should maximise its fitness by adjusting its flight decision to the costs and benefits of alternative strategies (Cooper & Frederick 2007). A well-known metric of an animal's threat perception that allows the investigation of factors influencing the escape decision is the flight initiation distance (FID), the distance at which prey begins to flee from an approaching threat (Gulik 1986, Ydenberg & Dill 1986, Cooper &

Frederick 2007, Møller 2014). The decision to flee is known to be influenced by numerous factors directly related to predator presence and behaviour, including predator number and abundance, speed and direction of approach (Blázquez *et al.* 1997, Cooper 1997, Geist *et al.* 2005, Guinness *et al.* 2019), or a hiding opportunity such as the distance to a refuge location (Kramer & Bonenfant 1997, Stankowich & Blumstein 2005, Cooper & Samia 2018). Reviews of FID variation between bird species have also shown that FID is a species-specific trait (Blumstein *et al.* 2003), and that birds with larger bodies, omnivorous or carnivorous diets, and with a later age of first reproduction tend to have longer FIDs (Blumstein 2006, Weston *et al.* 2012). Individuals are also aware of the direct costs of fleeing, for example the loss of a feeding opportunity (Stankowich & Blumstein 2005, Møller 2015, Møller *et al.* 2015) or when the decision to flee is linked to social aspects of life (Stankowich & Blumstein 2005). For example, lower flight initiation distance was found in Broad-headed skinks *Eumeces laticeps* when they were likely to miss out on mating opportunities (Cooper 1999). Finally, flight initiation distance may differ between intra- and infra-specific morphological differences of individuals (Blumstein 2006, Ozel & Stynoski 2011, Møller *et al.* 2019). A widespread anti-predator morphological adaptation in the animal kingdom is camouflage, which allows individuals to avoid detection, thus saving time and energy rather than escaping from an approaching predator (Ydenberg & Dill 1986, Ruxton *et al.* 2004). Empirical studies have confirmed that more cryptic animals - both within and between species - have shorter flight initiation distances (Ozel & Stynoski 2011, Møller *et al.* 2019).

While many studies have used flight initiation distance as a proxy for fearfulness in a variety of circumstances, they often examined a single or a few factors influencing the decision to flee. There are however less studies considering a wider range of factors that simultaneously influence a prey's decision to flee in the natural environment. A multivariate inference could possibly better explain the fleeing decisions of a prey and show less biased than studies examining single factors in isolation. As such, studies analysing multiple factors behind the variation in FID may be more productive, particularly given that the costs and benefits of fleeing can change temporally and spatially (Ydenberg & Dill 1986, Lima & Dill 1990, Lima & Bednekoff 1999, Kotler *et al.* 2004), as well as being dependent on weather conditions and food resources (Stankowich & Blumstein 2005, Møller 2015). Finally, in the case of a cryptic prey, the level of camouflage also plays a role. (Cooper & Sherbrooke 2010, Møller *et al.* 2019).

In this study, we investigated how fine-scale habitat characteristics, food abundance, weather conditions, time of day and the time of season, as well as intruder and a prey group size, influence the flight initiation distance of a cryptic bird species treated as potential prey. In addition, we tested whether the distance between the prey and a site of important social interaction (a lekking site) is associated with flight decisions. We also tested whether variations in FID can be explained by variations between study sites. Our study subjects were males of the Great Snipe *Gallinago media*, a medium-sized cryptic wader known for its nocturnal lekking behaviour (Lemnell 1978) and strong habitat specialisation at fine and landscape scale (Løfaldli et al. 1992, Kålås *et al.* 1997, Korniluk *et al.* 2021). The species is also known as an extreme food specialist ,feeding primarily on earthworms *Lumbricidae*, which constitute up to 90% of its prey [Løfaldli *et al.* 1991]). During the breeding season, lekking male Great Snipes are engaged in energy-demanding nocturnal displays, with estimated energetic costs exceeding 5 times the basal metabolic rate (BMR; Höglund *et al.* 1992). As females prefer to mate with males with the highest display rate (Höglund & Lundberg 1987, Höglund & Robertson 1990a), male display behaviour is underlined by a strong sexual selection (Höglund *et al.* 1992). Furthermore, males that may lose about 5% of their body mass during a single night, are also under a high pressure to replenish the lost energy while foraging during the subsequent day. The ability for efficient rebuilding of energy reserves enables them to display vigorously throughout the following night, influencing future mating opportunities and fitness.

However, males may be physiologically constrained in their attempts to rapidly replenish lost energy reserves, given the maximum known refuelling rates for birds. For example, migratory waders of comparable size to the Great Snipe are expected to refuel at a rate of no more than 4.2% of lean body mass per day (Lindström 2003). Consequently, at least some males may not be able to fully recover and may progressively lose weight during the breeding season (Höglund *et al.* 1992, Witkowska *et al.* 2022). In this context, the decision to interrupt foraging is likely to be quite costly for male Great Snipes that forage during the day and are faced with a predator encounter. This makes them an interesting model for studying the factors that influence prey's decision to flee.

Presumably, the cryptic morphology of the Great Snipe may reduce its detectability by potential predators, allowing for the postponement of the flight decision and thus saving time and energy for efficient rebuilding of energy reserves (Ydenberg & Dill 1986, Møller *et al.* 2019). Given the selection pressures outlined above, we expect Great Snipe males to select daytime locations that provide both good foraging opportunities and camouflage to remain cryptic. According to general economic escape models (Ydenberg and Dill 1986, Cooper & Frederick 2007), in this study we also assume that the Great Snipe decides to flee when the risk of predation is equal to the cost of flight, and that the level of crypsis associated with background matching can modify an individual's fearfulness and thus the decision to flee. Based on the above assumption we formulate and then test six hypotheses related to Great Snipe flight initiation distance (Table 1). Given that Great Snipe males prefer to forage close to the lek (Korniluk *et al.* 2021), which may be related to energy management in a manner similar to the central-place foraging theory (Orians & Pearson 1979) we also test how distance to the lek interacts with FID. Finally, by examining the relationship between FID and study site, we will check whether some other factors that we have not considered and that are related to the identity of the study site could additionally account for variations in male Great Snipe FID. More specifically, in this paper, we tested whether the FID of male Great Snipes encountered by human observers during daytime foraging in the breeding season was related to the factors listed below.

(1) Group size. We expect that males foraging with conspecifics should have a greater FID, in line with early-warning hypothesis (Stankowich & Blumstein 2005; see also Barnard 1980, Mayer *et al.* 2019, Morelli *et al.* 2019).

(2) Background matching. FID is generally lower for prey that has a better background match (Cooper & Sherbrooke 2010, Ozel & Stynoski 2011, Møller *et al.* 2019). Great Snipe males prefer to forage in places with intermediate sward height and density (Løfaldli et al. 1992, Korniluk et al. 2021) and a substantial amount of bare ground (Korniluk *et al.* 2021). Given that cryptic animals should select microhabitats that provide them with a high level of camouflage (Ruxton *et al.* 2004, Cooper & Sherbrooke 2012), we expect to find the lowest FID in vegetation of intermediate height and density and a negative relationship between FID and bare ground proportion. However, if the choice of foraging site is shaped by the trade-off between high crypsis and best foraging opportunities, a different set of habitat characteristics could be found to provide one or the other.

(3) Feeding opportunity. The Ydenberg and Dill 1986 model predicts that prey with feeding opportunity should have a greater cost of fleeing than a prey without such an opportunity, and thus shorter FID. Given that the Great Snipe has high energy demands associated with lekking behaviour (Höglund *et al.* 1992), and that replenished energy resources may contribute to higher mating success (discussed in the Introduction), shorter Great Snipe FID is expected at sites with more earthworms, a major Great Snipe food resource (Løfaldli *et al.* 1991). However Møller (2015) found that the fleeing decision of a foraging prey may be caused by a multitude of factors (e.g. food mobility, adult annual survival rates and preys' visual acuity) and claims that it should depend on whether food can be easily recovered. In the case of the Great Snipe, a rapid return to the same foraging site is unlikely because Great Snipe males avoid flying during the day (Korniluk & Chylarecki 2023 in press) and we have never observed an individual returning to a site from which it has been flushed. It should therefore be very costly for Great Snipe males to flee from sites with an abundance of earthworms and thereby pass up a feeding opportunity, and we therefore expect to find a negative relationship between food abundance and Great Snipe male FID.

(4) Camouflage provided by countershading. The plumage of the Great Snipe is darker dorsally, which is known as countershading, a colour gradient in animals in which body parts exposed to the sky are darker and those in the shade are lighter (Thayer 1896). One of the proposed functions of countershading is to reduce detectability by predators and is therefore considered as a form of protective colouration (reviewed in Ruxton *et al.* 2004 and Rowland 2009). According to Penacchio *et al.* 2015a, in the case of our study design, where we flush a snipe from the ground, the camouflage benefit resulting from countershading may occur by way of two mechanisms. First, shadows cast by sunlight on the body, which might otherwise be destructive for matching with the background (also called self-shadow concealment). The second is called obliterative shading, where countershading hides three-dimensional objects that would otherwise be visible by shading on a uniformly coloured body (Thayer 1896). However, the provision of background matching and thus camouflage by countershading is critically influenced by animal shape and posture, as well as by light intensity and angle, which vary according to the time of day and the weather conditions (Penacchio *et al.* 2015b, 2018, Cuthill *et al.* 2016). Ambient light intensity and angle should therefore somehow influence the level of prey crypsis and hence the decision to flee (Ruxton *et. al* 2004, Stankowich &

Blumstein 2005). As light conditions change during the day and greater cloud cover is associated with lower light intensity, these variables can be considered as proxies for light intensity interacting with the level of camouflage caused by countershading (Cuthill *et al.* 2016, Penacchio *et al.* 2018). However, it is difficult to predict which light conditions caused by solar radiation (time of day) and cloud cover are associated with the highest level of Great Snipe camouflage caused by countershading. On the other hand, low light conditions may be associated with the lower visual ability of predators to detect prey (Ruxton et al. 2014). In poorer light conditions (morning and evening, greater cloud cover), Great Snipe males could potentially allow a closer approach before fleeing than in higher ambient light intensity, and thus we may find a shorter Great Snipe male FID in the morning and evening, greatest at midday, and a negative relationship between cloud cover and Great Snipe FID.

(5) Mating opportunity. The costs and benefits of fleeing may change temporally (Ydenberg & Dill 1986, Lima & Dill 1990, Lima & Bednekoff 1999). The differences in escape behaviour between breeding and non-breeding seasons have been studied in different bird species and showed mixed results in terms of flight initiation distance (Glover *et al.* 2011, Morelli *et al.* 2019, Novčić & Parača 2022). We expect that in the case of the Great Snipe, male risk taking should be related to mating opportunities at the lek, which change with the progression of the breeding season. In general, fewer females are observed at the very beginning of the season, with a spike in the middle and substantial decrease in the last part of the season, when most females are already fertilised and incubating (Höglund & Robertson 1990b, Fiske & Kålås 1995, Kålås *et al.* 1995).The date can therefore be considered as a proxy for mating opportunity. An experimental study on Broad-headed skinks *Eumeces laticeps* shows that increasing risk (shorter FID) was accepted when reproductive benefits were greater (Cooper 1999). We therefore expect a U-shaped curvilinear relationship between FID and date in the male Great Snipe.

(6) Intruder number. The number of intruders should increase the perception of risk, as a greater number of predators may disperse prey attention and thus increase the level of fearfulness (Ruxton *et al.* 2004). Furthermore, in the case of a human predator moving across meadows or fens (the case of our study), a larger group produces a higher level of noise, which may contribute to faster detection of predators. We therefore expect that the number of

intruders will increase the risk perception of Great Snipe males and therefore expect that more observers will correlate with a greater FID.

(7) Distance to lek. Given that Great Snipe males prefer to feed closer to the lek (Korniluk et al. 2021), we decided to add this external factor to the set of variables. However, the function of distance to the lek is difficult to explain in terms of risk assessment of the Great Snipe. However, given that males have a strong need for energy replenishment due to the energy demanding nocturnal lekking behaviour (Höglund *et al.* 1992), and that the energy required to return from foraging sites to the lek increases with increasing distance from the lek, we expect shorter FID with increasing distance to the lek. This is because males foraging at a greater distance from the lek require more energy to fly to such sites than males foraging closer, and flushing is associated with an energetic cost both in terms of movement and loss of time that could be spent foraging (Møller 2015).

(8) Study site. Although our study is based on several factors that may influence Great Snipe flight decisions, there are still some crucial factors that influence the species' risk-taking decisions that can vary from study site to study site. The most important of these is exposure to predators (Lima & Dill 1990, Lima & Bednekoff 1999, Broom & Ruxton 2005). In general, higher predator densities were associated with higher levels of fear and vigilance and thus greater flight initiation distance (Blázquez *et al.* 1997).

Methods

Study area

This four-year study was conducted at three sites in north-eastern Poland (Odrynki [2013 & 2014] - 52°55'N, 23°39'E, Lipsk [2020] - 53°42'N 23°20'E, Gugny [2021] 53°18'N, 22°38'E) and two sites in central-eastern Poland (Perespa [2020] - 50°33'N, 23°43'E, Blota Serebryskie [2021] 51°7'N, 23°40'E). The study sites were located in floodplain meadows of the Upper Narew River valley (Odrynki - see Korniluk et al. 2021 for details), alkaline fens of the Upper (Lipsk) and Lower (Gugny) Biebrza River basins, the Sieniocha River valley (Perespa), and calcareous fens on chalk bedrock (Błota Serebryskie) - descriptions of these habitats are given in Wołejko et al. 2019.At all of these sites, a stable great snipe lek (active every year for at least 3 years) with approximately 10-20 males was located. Fieldwork was conducted in the vicinity of leks during the main part of the lekking season (2 May - 21 June). We only sampled during the day (two hours after sunrise and two hours before sunset) to avoid sampling near and during male display activity. During the day, Great Snipe males spend most of their time foraging (Höglund et al. 1992, Løfaldli et al. 1992), so we assumed that most, if not all, of the sites were used by birds for foraging.

Data collection and FID

An expected Great Snipe male location was approached every one to three days with a lack of rainy and strongly wind (<5 m/s) conditions, based on the radio location of 23 males equipped with VHF transmitters (Odrynki site, for details see Korniluk et al. 2021) and GPS diurnal positions of 31 GPS-logged males (the remaining 4 sites, 5 g GPS-GSM tag, manufactured by INTERREX-TRACKING, deployed with elastic leg-loop harnesses). Untagged individuals (or those with unknown or uncertain logger ID) flushed along the walk towards the expected male location were also included in the study. We assumed that most of the untagged birds were males, as at this time many females were sitting on the nest, where they spent ~90% of their time incubating (Løfaldli 1985), and thus the possible effect of a few sample females seems negligible. We tracked each tagged individual only once a day to avoid sampling non-foraging areas after disturbance. This time lag also reduced autocorrelation caused by non-independence of observations of the same individual (Muff et al. 2020, Korniluk et al. 2021). Great Snipes were approached by 2 observers (with some exceptions - see results) at normal walking speed until flight was detected. Observers wore natural-coloured clothing to avoid the effect of different intruder detectability. For all flushed individuals, we measured the flight initiation distance (FID) by recording the number of calibrated 1m steps, which roughly corresponds to the number of metres (Møller *et al.* 2008). FID was the distance between the nearest observer and the exact location from which a Great Snipe was flushed. The starting distance was not recorded as the snipe search was carried out during a continuous exploration of the study sites. We also recorded a number of flushed individuals and included them in the analysis, additionally noting that a prey's group size may influence anti-predator behaviour and escape responses (Stankowich & Blumstein 2005).

Variables used to explain FID

We measured fine-scale habitat variables that are biologically meaningful for foraging Great Snipes (according to [Løfaldli *et al.* 1991, Korniluk *et al.* 2021]) at each precise site from which individuals were flushed (for a detailed description of the sampling protocol, see Korniluk et al. 2021). For this study, we selected 8 fine-scale habitat variables and additionally we measured 2 weather variables in the field, which we believe may play a role in risk-taking behaviour and thus influence the escape decision of individuals (Table 1). As the intruder group may influence the risk assessment of the prey (Geist et al. 2005), we include the number of observers as a fixed factor in the analysis (variable obsN, Table 1). To minimise observer bias, we calibrated the assessment of habitat variables with the observers who carried out the fieldwork prior to each field season. We also included as fixed factors the study site and the year in which the fieldwork was carried out. The habitat variables used in the model to explain individual FID were as follows. Vertical vegetation cover (VegCovV), which is the percentage of vegetation covering a blank piece of paper (10 x 10 cm) placed at the exact location from which the snipe was flushed, as assessed by the observer looking vertically from above; mean horizontal vegetation cover (VegCovH), calculated as the mean of four distances (towards N, E, S, W) from which the observer could not see a snipe decoy (placed at the location from which the birds were flushed); the denser the vegetation, the shorter the distance. The height of the shrub and tussock was measured with a ruler (+/- 5 cm). The estimated proportion of bare ground (BareGr) within the 50x50 cm plot (flushing site in the middle). To assess earthworm abundance, soil samples (15x15x10 cm depth, cut with a steel frame) were collected from the flushing site. Total earthworms wet biomass weight was assessed in the lab using an electronic analytical scale (±0,001 g). Weather variables were assessed by the observers during the field work and included: the percentage of cloud cover (Cloud) assessed to 10% accuracy and ambient temperature measured with a thermometer (Temp). In addition, date (1 was the first day of May) and flushing time (converted to decimal format) were recorded, as these may influence an individual's risk-taking decisions (Date and Time variables, Table 1).

Statistical analyses

We used generalised linear models (GLMs) with Poisson error distribution to find the relationship between male Great Snipe FID and candidate predictors that may influence the fleeing decision of individuals (Table 1). We used an information theoretic approach (Burnham & Anderson 2002) to assess and compare all possible combinations of explanatory covariates using Akaike's information criterion (AIC). All continuous variables were checked for correlation (removed if Pearson's correlation was >0.7) and possible non-linear effect on Great

Snipe FID by comparing linear and quadratic terms in univariate GLMs for each covariate. We used the R environment (R Core Team 2019) to fit GLMs, and the MuMin package (Bartoń 2019) to perform model selection and find significant variables affecting Great Snipe FID. Given the interpretability issues linked to model averaging (Cade 2015), and that our goal in variable selection was to find a significant effect, we abandoned it. Furthermore, the top model selected has relatively good support (compared to the top models with delta score <2 - considered the most informative according to Burnham & Anderson (2002), see Results section and Table 2). In addition, the models were nested within delta 2 (Table 2), so in accordance with the 'nesting rule' (Arnold 2010, Richards et al. 2011, Harrison et al. 2018), we decided to accept the top-ranked model as the sole basis for our inference. For the most informative model, we used the effects package (Fox 2003) to estimate and visualise fixed effects and their 95% confidence intervals. Given that in this study we aim to explain how habitat characteristics that surround a single individual influence its sensation of being cryptic (demonstrated in FID variation), a group effect may bias the results. Therefore we first checked whether there was an effect of prey number on FID using a GLM with Poisson error distribution, with FID as a response and number of individuals as an explanatory factor variable, and decided not to include in the main model the cases where more than one individual was flushed.

Results

Sampling effort and prey group effect on FID

During this 4-year study, we collected data from 517 escape events involving male Great Snipes (Odrynki 2013 & 2014 = 69, 83 respectively, Lipsk = 80, Perespa = 101, Gugny = 69, Błota Serebryskie = 115). These include instances of a known individual based on VHF tracking (n=116), GPS-GSM tracking (n=98) and untagged or uncertain ID individuals (n=303) found on the way to the expected male location. Approaches were mostly made by two people (n=486), occasionally by one (n=16) or three observers (n=15). We never managed to see an individual before it was flushed and never saw any movement that might indicate pre-flight movement. Sampling was distributed up to about 2 km from the leks (mean = 391 m, SD=341.72 m). Flight initiation distance varied between 1 and 60 m (mean = 11.3 m, SD = 8.21 m). One individual was flushed in 79% of flight events (n=411), two males were found in 13% of cases (n=70), while three (n=23), four (n=7) and seven (n=6) birds were found in the remaining 14% of flight events. We found significantly shorter FID ($p<0.001$, Fig. 1) regarding instances where one individual was flushed (mean=10.4 m, sd=7.37 m) compared to two (mean=12.9, sd=9.06), three (mean=15.3, sd=9.25), four (mean=15.6, sd=11.56) and seven (mean=33.7, sd=11.59) individuals. We therefore decide not to include in further analysis cases where more than one individual was flushed (n=106).

Variables explaining FID

The top-ranked model included two variables describing sward structure, earthworm abundance, date and time of day, distance to lek and cloud cover as predictors explaining FID of Great Snipe males (Table 2). In addition, the model showed that FID was dependent on the study site and the number of approaching observers. We didn't find any evidence to support the assertions that vertical vegetation cover, bare ground percentage, tussock height and temperature influence the flight initiation distance of Great Snipes. The top model was about two times more informative than the second of the candidate models within Delta 2 (evidence ratio = 1.83; Table 2).

Flight initiation distance of the Great Snipe was strongly positively related to horizontal vegetation cover, with an FID of around 6-7 m when vegetation cover was very dense and allowed us to see the decoy bird from a distance of less than 5 m (Fig. 2A). FID continued to increase sharply to values of around 12 m with decreasing vegetation density (expressed as increasing horizontal cover), until the growth stopped at a distance of around 25 m. The model showed a weak negative relationship between Great Snipe FID and vegetation height, with FID decreasing from over 9 m to around 7 m as vegetation height increased from 0 to 100 cm (Fig. 2B).

There was a clear positive relationship between FID and earthworm abundance, with FID increasing approximately fivefold as earthworm biomass increased from 0 to 400 g/m^2. Flight initiation distance (FID) of the Great Snipe showed a quadratic relationship to date with a lowest value (around 9 m) between 10 and 30 May and sliding/progressively higher values before this period. From the beginning of June, the model suggests an increase in FID to around 11 m.

We found a clear U-shaped relationship between FID and time of day when birds were approached, with the lowest FID (around 9 m) at midday and the highest above 12 and 11 m in the early morning and evening respectively (Fig. 5A). The modelled FID displayed a positive relationship with cloud cover, with a rather weak effect in the range between 0 and 40% of cloud cover, and a strong effect in the remaining range of cloud cover (40-100%) with a steep increase in FID from about 8 m to 13 m (Fig. 5B).

Our model showed a decrease in Great Snipe FID (from about 9 to 6 m) with increasing lek distance across the range from a few to 2000 m (Fig. 6). The study site was a significant factor influencing the variation in Great Snipe FID. The lowest FID was predicted at Błota Serebryskie and Perespa (~7 m), intermediate at Gugny and Lipsk (~9 m), while the highest at the Odrinki site varied in two study years by around 10 m. The 95% CIs of the predicted FID within each study site fluctuated about +/- 1-1.5 m from the mean (Fig. 6).

The model also showed that the number of observers had a significant effect on the Great Snipe FID, with the predicted FID for one man (sliding over 5m) being approximately 3m and 2m shorter than the FID for two and three men approaching respectively. However, the confidence intervals suggest that a significant difference was only confirmed between one and two observers (Fig. 8).

Discussion

Great Snipes foraging in groups were more likely to flee from a greater distance than when foraging alone. Flushing events with two or more individuals had a significantly longer FID than those where one individual was flushed. However, the differences in FID within the group of two, three and four individuals were not significant. The largest FID (mean 33.7 m) was found in a group of seven individuals and was approximately two times higher than in the group of three and four individuals and approximately three times higher than in the cases where one and two individuals were found. The meta-analysis of the risk assessment of prey in a group shows mixed results. Some species tolerate a closer approach when in larger groups (e.g. due to the probability of predation in a large flock), but the terrestrial animals (with many examples in birds e.g. Barnard 1980, Mayer *et al.* 2019, Morelli *et al.* 2019) had greater flight initiation distances in larger groups, consistent with the early warning hypothesis (Stankowich & Blumstein 2005). However, these relationships were associated with gregarious animals where individuals were aware of being in a group. Given that Great Snipes forage in dispersed groups, it is very unlikely that group awareness is always (if ever) present, and thus that social affiliation as such influences the flight decision of individuals. We suggest that a greater flight initiation distance of Great Snipes found in groups occurs because a group consists of individuals that vary in their risk assessment (caused by factors described in this paper and other factors e.g. individual personality). Hence we suggest that flushing a male triggers or accelerates the flight decision of conspecifics. The larger the group, the greater the variation in risk assessment and hence the greater the FID. In order to understand this relationship, it is important to note that we observed two general flight responses of Great Snipes foraging in groups: A) all conspecifics flee immediately after the first individual is flushed (the majority of cases), or B) conspecifics wait for a short time (at the same time, the distance between the observer and a flushing site of the first individual is reduced) and then flee. Such behaviour can be explained according to the predictions of general economic escape models (Cooper & Frederick 2007, 2010). The flushing of the first snipe in the group increases the level of fear of the other individuals in the group (because rapid flushing is a real signal of a dangerous presence for conspecifics) and increases the probability of conspecifics being detected, because predators come to a realisation about the cryptic prey's location (a predator - here a mean - sees a fleeing snipe and continues heading straight towards that location). As a result, conspecifics decide to flee immediately (response A - distance becomes less than the economically predicted FID) or their level of anxiety increases but the distance between conspecifics and the observer is still below the economically predicted FID and so conspecifics flee after a short time until the economically predicted FID is reached (response B).

Background matching and camouflage

We found that the flight initiation distance of Great Snipes at a foraging site decreased with sward density and height. In line with our assumption that Great Snipes flee later when foraging in a habitat that provides better camouflage, denser and taller vegetation increases the perception of crypticness. The microhabitat preference of foraging Great Snipe for intermediate vegetation heights and densities (Løfaldli *et al.* 1991, Korniluk *et al.* 2021) and a strong preference for bare ground (Korniluk *et al.* 2021) suggests a trade-off between selecting a habitat that provides crypsis and good foraging conditions. This is because less dense vegetation with a high proportion of bare ground (a highly preferred feature of Great Snipe males at the microscale) may play a role in more efficient probing, and thus locating and securing food more efficiently (Korniluk *et al.* 2021). On the other hand, shorter and less dense vegetation allows the Great Snipe to detect predators earlier, so the greater FID we found in these conditions may support the model prediction of Broom & Ruxton 2005 that cryptic prey will flee immediately upon detecting the predator. However, as we were never able to see a foraging Great Snipe, we can expect that if birds detect us in the early stages of approach, they will stay still to reduce detectability (Ioannou & Krause 2009, Samia *et al.* 2016), monitor our approach (habitat preference for less dense vegetation may play a role here), and decide to escape when the risk of predation is equal to the cost of escape. Our results thus find stronger support for the economic model of escape decision (Ydenberg and Dill 1986) and general economic escape models (Cooper & Frederick 2007, 2010), which predict shorter FID with increasing crypsis level. We didn't find any support that tussock height and vertical vegetation cover impact on Great Snipe escape decisions (these variables were not present in the top models and had no significant effect in the first models where they were present). From these two variables, it was highly expected that individual vertical vegetation cover would play a role in providing camouflage (Korniluk *et al.* 2021). However, it may also play an important role in avoiding avian predators (Korniluk *et al.* 2021) rather than ground predators, which we investigated in this study. Our model predicts that the flight decision of the male Great Snipe varies throughout the day, with the lowest FID at midday and higher FID in the morning and evening. We also found a strong positive relationship between FID and cloud cover when the cloud covered more than 40% of the sky. Both results suggest that poorer light conditions (but possibly a lower sun elevation angle in the case of the time of day) are associated with greater Great Snipe FID. The increased camouflage level of a cryptic prey (here manifested in a lower FID) with increasing light could be provided by countershading, although it is strongly dependent on illumination (Cuthill *et al.* 2016). It was also found that cloud cover and solar radiation levels play a role in the camouflage provided by countershading (Penacchio *et al.* 2015a, 2018). The fact that we observe the effect of cloud cover below 40 on FID may be due to the fact that in more than half of the cases the Great Snipe actually experienced full sunshine, and thus in most of these cases camouflage was provided by countershading. A strong positive relationship between cloud cover and Great Snipe FID may also be related to photoperiodism to some extent (PARKER *et al.* 1952) that regulates many aspects of a bird's behavioural and physiological responses (MENAKER & UNDERWOOD 1976). Male Great Snipes that display nocturnally (but move to leks often at dusk) may perceive the time of the day based on the light intensity. Thus, when ambient light intensity is low due to cloud cover, the mechanism described above may operate - males are more alert because night and lekking time are approaching. This interpretation is also supported by field observations. During extreme midday darkness caused by storm clouds, we observed males fleeing to the lek and beginning to display as at dusk (M. Korniluk unpublished). The amount of ambient light may therefore be a proximate cause of the time perception of male Great Snipes. The lowest FID at midday may also be partly related to avian predator avoidance, as this group (raptors) is most active at this time of day and Great Snipes strongly avoid flying during the day (Korniluk & Chylarecki 2023).

Feeding opportunity

We found that the escape decision of male Great Snipes was dependent on foraging opportunity: the more earthworms were found at a foraging site, the greater the flight initiation distance. This result is contrary to what we would expect according to the model predictions of Ydenberg and Dill 1986 and our expectation that, given the high energy demands of lekking behaviour and the constraint of returning quickly to the foraging site, the cost of fleeing from a food-rich site is very high for male Great Snipes. A possible explanation for this positive relationship is that males that have good foraging opportunities should also have higher energy reserves (they forage for some time in an earthworm rich site) and thus the cost of fleeing and losing a high quality foraging site is lower for them than for males that forage in low earthworm rich sites. In other words, the probability that a Great Snipe will accumulate sufficient energy reserves for an energetically demanding nocturnal lekking activity (Höglund *et al.* 1992) is higher on the high earthworm abundance sites, and thus such individuals may invest in reducing their predation risk, which would be manifested in higher FID. Our interpretation is supported by an experimental study in which Turnstones Arenaria interprets that were supplemented with mealworms had greater FID, which was explained by the fact that birds in better condition could afford to respond by flying away earlier (Beale & Monaghan 2004). Furthermore, if we assume that males that forage in areas of high food abundance have a higher fat load, then their ability to escape from predators will be lower (Lima 1986) and therefore FID should be higher (Ydenberg and Dill 1986), which is supported by our results. We therefore suggest that this cost-benefit balance depends on the energetic resources of the male (fat load) and that earthworm abundance is probably a proxy for this trait.

Mating opportunity

We found a slight curvilinear negative relationship between Great Snipe flight initiation distance and date in the period from the start of the breeding season (2 May) to around 20 May. However, the confidence intervals within this period indicate that this trend was not significant. A weak but significant positive effect of date on Great Snipe FID was found from around 20 May until the end of the study period (late June). This change can be explained by the opposite distribution of mating opportunities for males throughout the breeding season due to a change in the number of females present at the lek (Höglund & Robertson 1990b, Fiske & Kålås 1995). This is consistent with our expectation that male risk taking can be related to mating opportunity. Males may therefore invest more in avoiding predation later in the breeding season (demonstrated by way of a greater FID) because the chance for female courtship is low at that time, as was found in Broad-headed skinks that had greater FID when reproductive benefits were low (Cooper 1999).

Intruder number

We found significantly lower FID in instances where a single male approached the Great Snipe compared to instances where two and three observers did so. The number of intruders may therefore increase the risk perception of the Great Snipe, which is consistent with our expectation. For example, Crimson Rosellas Platycerus flushed at greater distances when approached by two people compared to one, while this effect was not significant for Pied Currawongs Strepera graculina (Geist et al. 2005). However, the study of seven wading bird species on the coast of Australia shows no significant differences in FID when approached by one or two dogs (Guinness *et al.* 2019).The risk assessment of the prey in relation to an intruder group may therefore be a species-specific trait.

Distance to lek

The greater the distance from the lek, the shorter the FID of Great Snipe males, in line with our expectations. This relationship can be explained by the extreme energy requirements of males due to the energy-demanding lekking behaviour (Höglund *et al.* 1992). Moving to a foraging site further away from the lek requires more energy than moving to a site closer to the lek. Males foraging closer to the lek should therefore have greater energy reserves, and thus this relationship may have a similar cost-benefit trade-off to the central-place foraging theory (Orians & Pearson 1979). We therefore suggest that, similar to the relationship between Great Snipe FID and foraging opportunity (the more earthworms found, the higher the FID), FID here may also depend on male energy resources.

Study site effect

Despite taking into account a large set of microhabitat variables that may play a role in camouflage provision of cryptic prey, light intensity related to better background matching caused by countershading, time of the season related to mating opportunity, feeding opportunity and finally a prey and intruder group, in explaining the escape decision of Great Snipe males, we still found that FID differs between study sites. The fact that no differences were found at the Odrynki study site between two years reinforces our assumption that some other significant factors influencing FID are hidden away within the idiosyncrasy of the study area. A strong factor that may influence the risk assessment of the Great Snipe that we didn't take into account is the presence of predators in a particular study site that may strongly influence the fearfulness of the prey and thus its FID (Blázquez *et al.* 1997, Ruxton *et al.* 2004). FID can also increase with the speed of a human’s approach (Cooper 1997, Stankowich & Blumstein 2005). We have tried to keep this constant, but we can also expect that a different walking behaviour of the observers could also be associated with the perceived risk of the prey and thus have an effect on FID. In the case of our study sites, it is very likely that observers' walking behaviour varied between study sites because the research was conducted in different habitats (floodplains and mires) that vary greatly in vegetation structure and swampiness, which affects observers' walking behaviour and noise production.

Our results clearly show that studying animal behaviour, which has often been used as an index of disturbance effects and a measure of animals’ risk assessment is very challenging. Many factors should be taken into account simultaneously in relation to the ecology of the species.

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Figures and tables

Table 1. Factors tested in this study to explain FID of male Great Snipes encountered by human observers during daytime foraging in the breeding season and predictor variables with their ecological meaningfulness.

Factor influencing FID	Reference	Predictor variables and their ecological meaningful
Group-size. We expect that males foraging with conspecifics should have a greater FID according to the early warning hypothesis.	Stankowich & Blumstein 2005, Mayer *et al.* 2019, Morelli *et al.* 2019	**IndNumb** – number of individuals when flushed
Background matching. Higher level of camouflage is related to background matching and associated with FID. We expect that selected by the Great Snipe males intermediate sward structure and substantial amount of bare ground play a role in providing males with a high level of background matching and thus camouflage.	Ydenberg & Dill 19to e86, Cooper & Frederick 2007, Cooper & Sherbrooke 2010, Korniluk *et al.* 2021, Melo *et al.* 2021	**VegCovH** – horizontal vegetation cover, **VegCovV** – vertical vegetation cover, tussock height (**Tussock**) and **VegHeight** – vegetation height are describing a vegetation structure, bareground share (**BareGr**) provides a dark background. Those variables are associated with Great Snipe background matching.
Feeding opportunity. A prey that has a feeding opportunity and high energy demands should have a greater cost of fleeing than a prey without, and thus shorter FID. We expect a negative relationship of Great Snipe male FID and earthworm abundance.	Ydenberg & Dill 1986, Höglund *et al.* 1992	**Eworm** - Earthworm abundance at foraging sites (main Great snipe food *Lofaldi et al. 1992*) is a proxy of a feeding opportunity.
Camouflage provided by countershading. The Great Snipe is darker dorsally. Male background matching can be thus enhanced by the countershading that is strongly illumination dependent and thus light intensity should interact with FID. We expect to find some relationship between ambient light intensity and FID, however hard it is to be predicted.	Ruxton *et. al* 2004, Cuthill *et al.* 2016, Penacchio *et al.* 2018	**Cloud** – cloud cover and daytime (**Time**) can be considered as a proxy of light intensity that has a critical meaning in providing a visual camouflage by countershading. background matching
Mating opportunity. Given that the risk assessment changes in lifecycle and can be related to mating opportunity, we expect	Ydenberg & Dill 1986, Lima & Dill 1990, Cooper 1999, Lima & Bednekoff 1999	**Date** – a breeding season progression. Female presence at the leks during the breading season has close to normal

a U shaped relationship between Great Snipe males' FID and date.		distribution (Höglund & Robertson 1990, Fiske & Kålås 1995) and should be related to males mating opportunity. Date is thus a proxy of Great Snipe males' mating opportunity.
Intruder number. If intruder number increased the perception of risk, then we would expect that more intruders would result in greater FIDs.	(Blumstein 2003, Ruxton *et al.* 2004)	**ObsNum** – Number of observers approaching the Great Snipe.

Table 2. Ranking of models explaining Great Snipe males' flight initiation distance. Shown are the 4 best models within 2 Delta AICc units to give a better idea of the relative strength of the most informative model from the best model selected. Variables: VegCovH, Time, CloudCov, VegCovV, BareGr, Date, entered with a squared term. AICc Akaike´s information criterion corrected for small sample size; Delta AICc difference in AICc between the focal model and the best model in the set; w Akaike weight of the focal model; R^2 likelihood-ratio based on pseudo-R-squared indicating a goodness-of-fit.

Model Rank	Candidate model	AICc	Delta AICc	w	R^2
1	VegCovH + VegHeight + Eworms + Time + CloudCov + Dete + ObsNu + LekDist + StudyS	2979.9	0.00	0.403	0.669
2	VegCovH + VegHeight + Eworms + Time + CloudCov + Dete + ObsNu + LekDist + StudyS + VegCovV	2980.6	0.77	0.274	0.672
3	VegCovH + VegHeight + Eworms + Time + CloudCov + Dete + ObsNu + LekDist + StudyS + Temp	2981.7	1.81	0.163	0.669
4	VegCovH + VegHeight + Eworms + Time + CloudCov + Dete + ObsNu + LekDist + StudyS + BareGr	2981.7	1.85	0.160	0.671

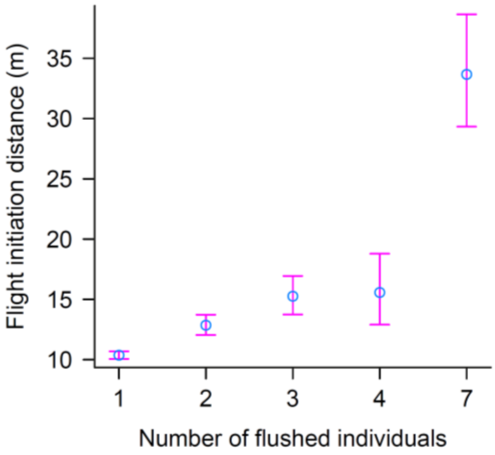

Fig. 1 The predicted flight initiation distance of the Great Snipe (n=517) at the foraging sites in relation to the number of flushed individuals.

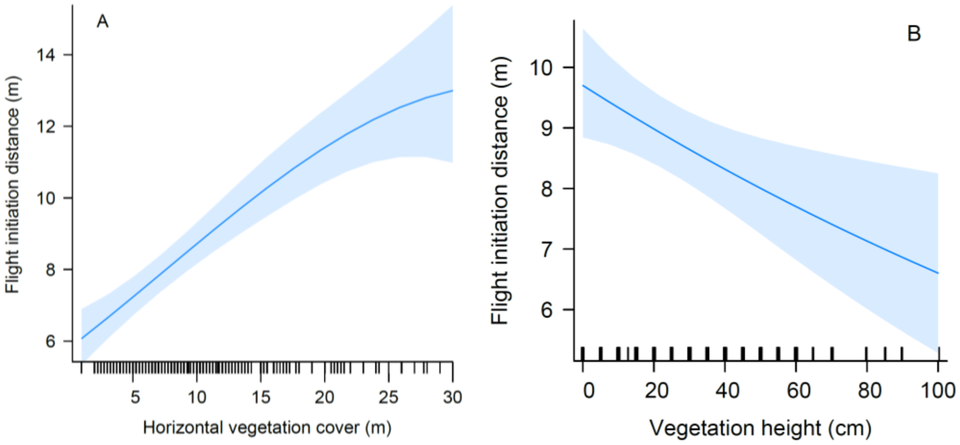

Fig. 2. The predicted flight initiation distance of the Great Snipe at the foraging sites (n=401) in relation to horizontal vegetation cover (A), vegetation height (B)

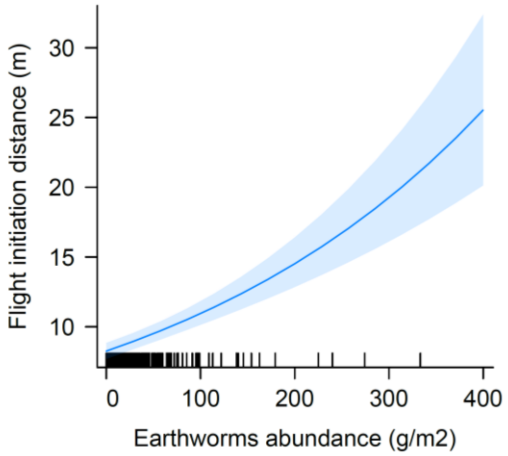

Fig. 3. The predicted flight initiation distance of the Great Snipe at the foraging sites (n=401) in relation to earthworm abundance.

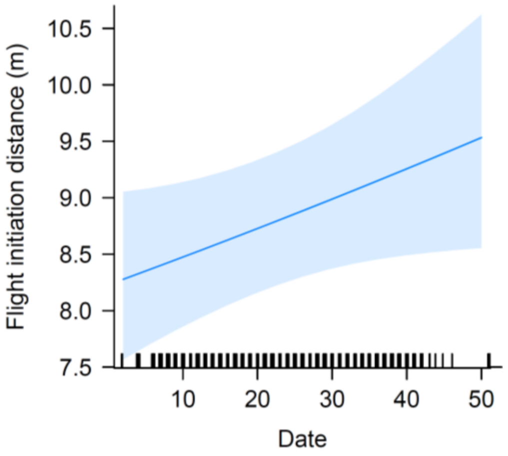

Fig. 4 The predicted flight initiation distance of the Great Snipe at the foraging sites (n=401) in relation to date.

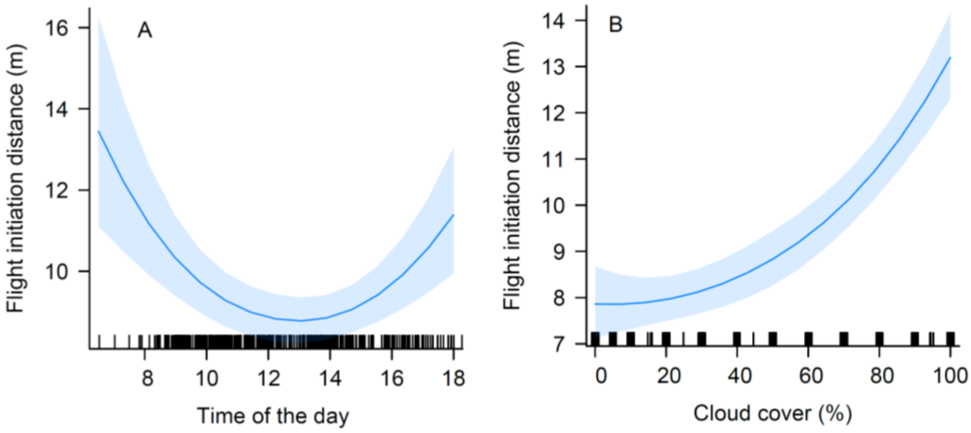

Fig. 5. The predicted flight initiation distance of the Great Snipe at the foraging sites (n=401) in relation to time of day (A) and cloud cover (B).

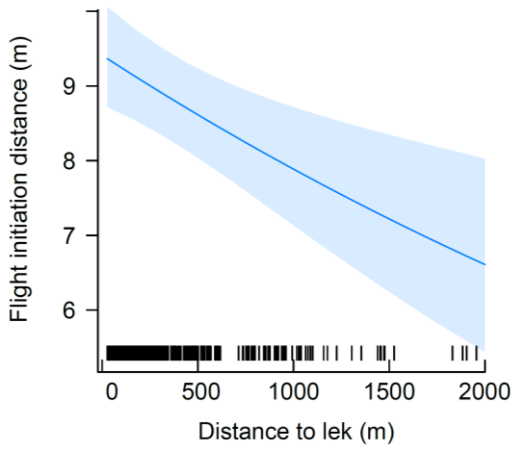

Fig. 6. The predicted flight initiation distance of the Great Snipe at the foraging sites (n=401) in relation to distance to the lek.

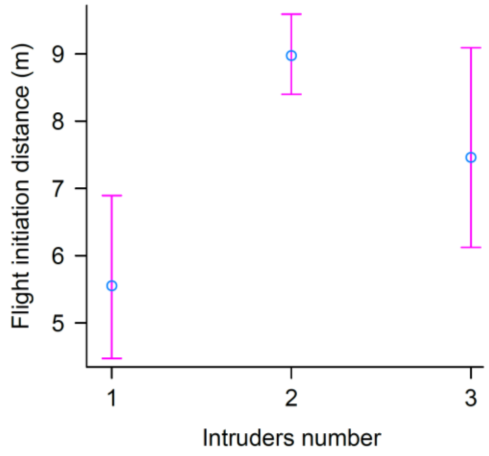

Fig. 7 The predicted flight initiation distance of the Great Snipe (n=401) at the foraging sites in relation to intruder number (number of observers approaching a prey).

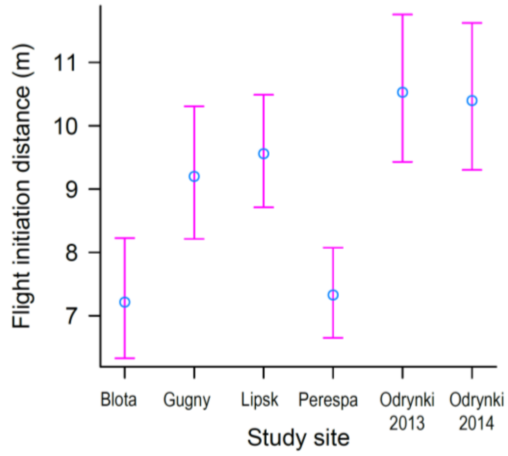

Fig. x The predicted flight initiation distance of the Great Snipe (n=401) at the foraging sites in relation to the number of flushed individuals.