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Original article

Does intraspecific competition facilitate age separation in timing of southward migration in waders?

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ABSTRACT

In many Palaearctic wader species there is a clear separation in the timing of adult and juvenile southward migration. This phenomenon is traditionally explained by the selection on adults to depart early from breeding grounds and necessity of juveniles to prepare longer for migration. In this study we hypothesize that late departure from natal grounds may also be adaptive for juveniles, as it allows them to avoid intensified interference competition at stopover sites with adult, usually more dominant conspecifics. To test this hypothesis we analysed long-term data on stopover behaviour of juvenile wood sandpipers (*Tringa glareola*) staying at a central Polish stopover site under varying levels of competition from adult birds. The results clearly indicated that juveniles were highly disadvantaged by the simultaneous presence of adults at the same staging site, as under intense competition from older conspecifics they refuelled more slowly and attained lower fat reserves. It was also found that juveniles which were forced to compete with adults left the site quickly and possibly searched for more favourable staging places. All these imply that delayed departure from natal grounds may be adaptive for juvenile waders, allowing them to mismatch the timing of their first migration with the peak of adult passage and, thus, reduce the negative consequences of intraspecific competition during migration.

1. Introduction

Many wader species show distinct separation in the timing of southward migration between adults and juveniles (Figuerola and Bartolero, 1996; Blomqvist et al., 2002; Hedenström, 2004). This phenomenon is commonly attributed to the fact that juveniles require much more time to prepare for the autumn migration than adults. Also in some species, only one sex tends to remain with the young until they are fully grown, allowing the other sex to leave the breeding grounds early in the season. Such patterns were recorded, for example, in the curlew sandpiper (*Calidris ferruginea*) and ruff (*Philomachus pugnax*), where only females look after the young (Holmes and Pitelka, 1964; Van Rhijn, 1985), or in the long-toed stint (*Calidris subminuta*), where the whole responsibility for raising chicks falls to males (Myers et al., 1982; Snow and Perrins, 1998). In consequence, the general sequence of post-breeding migration starts with failed breeders, which are followed by the successful breeders of non-parenting sex, later by the successful breeders of parenting sex, and finally by juveniles (Newton, 2008).

However, some other selection forces have been also proposed to facilitate age separation in the timing of autumn migration in waders. Firstly, adults of most wader species undergo a complete moult during post-breeding period (Prater et al., 1977). Since moulting is considered an energetically expensive process, there could be a certain trade-off between accumulating fat loads necessary for migration and their utilization for feather replacement, especially when food resources are limited (Merilä, 1997). Replacement of flight-feathers also impairs flight ability, which imposes additional energetic costs during migration (Swaddle and Witter, 1997), as well as it increases vulnerability to predators along the flyway (Lind, 2001). For this reasons, in many wader species, adults delay initiation of moulting until they reach wintering grounds, where they can allocate most their energetic resources to this process. Consequently, it may be highly adaptive for adults to leave breeding grounds before food supply collapses and minimize the timing of migration in order to replace the worn breeding plumage as soon as possible. By contrast, selective pressure of moulting may be negligible for juveniles, as they usually moult only partially and do not replace flight-feathers (Prater et al., 1977).

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Finally, separation between adults and juveniles at the later stages of migration may be enhanced by the lower efficiency of migration in the first-year individuals. Inexperienced juvenile birds of many wader species have been demonstrated to forage less effectively during stopovers on their first southward migration (Goss-Custard and Durell, 1987a; Dierschke et al., 1997; Iwajomo et al., 2013). In consequence, they require relatively more time to accumulate fat reserves sufficient for further migration, and thus they make longer and more frequent stopovers (Helseth et al., 2005). Furthermore, if juveniles do not have opportunity to learn migratory behaviour from more experienced conspecifics, they are likely to choose staging sites of poorer quality and use less direct migration routes than adults (Alerstam, 1990). As a result, in many avian species, migration of juveniles proceed at a slower rate than in adults (Ellegren, 1990; Hake et al., 2003), which produces even more pronounced separation in the timing of arrival at wintering grounds between both age classes.

In this study, we propose an additional selective pressure which may facilitate separation in the timing of adult and juvenile southward migration in waders. We hypothesize that late departure from natal grounds may be also adaptive for juveniles, allowing them to avoid intensified interference competition with adult conspecifics during migration. It has been demonstrated for several species of waders that adults are dominant over juveniles (Groves, 1978; Burton and Evans, 2001) and have capabilities of relegating them to less attractive foraging patches (Goss-Custard et al., 1982; Warnock and Takekawa, 1995; Fernández and Lank, 2006). The aim of this study was to test whether migrating juveniles are disadvantaged by the competition from adults in the wood sandpiper (*Tringa glareola*), a wader species that shows a partial age separation in the timing of southward migration. For this purpose we analysed long-term data on stopover behaviour of juvenile sandpipers staying at a central Polish stopover site under varying levels of competition from adult conspecifics.

2. Methods

Wood sandpipers were captured at Jeziorsko reservoir (51°73′N, 18°63′E), central Poland, during 10 autumn migratory seasons, from 1998 to 2007. The reservoir is one of the most important stopover sites for waders in inland Poland. The favourable feeding conditions are created due to the water management policies, which were developed to ensure considerable seasonal oscillations of water level. In autumn, water level at the reservoir decreases at a constant rate, continuously exposing new areas of mudflats which attract abundant flocks of waders. The maximum concentrations of wood sandpipers at the site approach a thousand of individuals in August (Janiszewski et al., 1998).

Each year, the fieldwork started at the beginning or in the middle of July, dependently on water level, and it lasted until the middle of September, when the migration of wood sandpiper through the reservoir is already finished. In total, we captured 4140 juvenile and 1044 adult sandpipers. All birds were aged on plumage characteristics (Prater et al., 1977), ringed and measured using standard procedures (Svensson, 1992). Each bird was also weighed (±1 g) and had the fat loads assessed within furculum and axilla using a special 5-point scale developed for waders (Meissner, 2000). Fat loads were expressed as a mean score from furculum and axilla, which was subsequently converted into the units of mass following the formula developed by Minias et al. (2010).

In total, 248 juveniles were recaptured during the same migratory season and these data were used to calculate stopover duration and refuelling rates. Stopover duration was expressed as the number of days between the last and the first capture at the site. Refuelling rates were estimated as the difference in the body mass of an individual between the last and the first capture at the site divided by the number of days between encounters. In order to avoid measuring disturbance-related loss of body mass following the capture (Piersma and van Brederode, 1990; Castro et al., 1991), we only considered individuals that were recaptured after two days or later ($n = 209$), as 75.8% of sandpipers recaptured the day after the first capture showed non-positive refuelling rates (on average -0.67 ± 0.43 g/day). Similarly, all birds that showed negative refuelling rates ($n = 34$) were excluded from the remaining dataset, as they were also considered to mostly reflect a capture effect (61.8% were recaptured after 2–3 days after the first capture). In total, refuelling rates obtained for 175 juvenile sandpipers were included in the analyses.

In order to assess the proportion of adults at the site, each migratory season was divided into 5-day periods, starting from 01 July. For each period with at least 10 sandpipers caught, a proportion of adults was calculated from the capture data. Periods with <10 captured birds were disregarded from the analyses. On average, proportion of adults in each 5-day period was estimated basing on age composition of 71.2 ± 7.6 [SE] captured individuals. Proportion of adults was estimated for an average of 6.9 ± 0.8 [SE] 5-day periods per year. For each recaptured juvenile, proportion of adults simultaneously present at the site was calculated for the entire duration of its stopover period. Although age composition of captured birds may not perfectly reflect the age composition of birds at the site due to non-equal catchability of juveniles and adults, any potential bias should be consistent between and within seasons. In consequence, the estimations based on trapping should reliably reflect differences in the proportion of adults staging at the site in different periods.

To assess how the proportion of adults migrating through the reservoir changed over the course of the season we fitted a sigmoid curve. To investigate how competition from adults affected performance of juvenile sandpipers, we analysed how fat loads, refuelling rates and stopover durations of juveniles were affected by the proportion of adult conspecifics present at the site. Basing on the earlier analyses (Minias et al., 2010), we expected a strong relationship between date and the quantity of accumulated fat loads. Thus, juvenile fat loads were analysed with a hierarchical general linear model, where the proportion of adults was nested in the successive 5-day periods of migratory season. Such model allowed us to obtain separate regressions between fat loads of juveniles and the proportion of adults for each 5-day period of the season, so that the relationship was not confounded by date. Juvenile refuelling rates were analysed with a general linear model and stopover duration was analysed with a generalized linear model for gamma distribution, which is the expected probability distribution of inter-event intervals (Addison et al., 2007), such as the time intervals between the first and the last capture at the site. In both models we controlled for the effect of date and squared term of date was also included to account for any potential non-linear seasonal effect. In each model, we included the effect of year as a random factor. As birds with larger quantities of accumulated fat stores are known to refuel slower (Minias et al., 2010), we also accounted for the initial body mass of recaptured individuals while analysing refuelling rates. The stepwise procedures of backward removal were used to select for significant independent variables. Significance of particular independent effects in the generalized linear model for gamma distribution was assessed with Wald statistic (W). β coefficients were used to assess the character and strength of significant relationships. All values are presented as means ± SE. All statistical analyses were performed using Statistica 10.0 (Statsoft, Tulsa, OK, USA).