Osnabrücker Naturwissenschaftliche Mitteilungen
Band 32, S. 239 – 241, 2006

The importance of early breeding in Black-tailed Godwits *(Limosa limosa)*

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Zusammenfassung: Anthropogene Veränderungen unserer Landschaft verstärken die negativen Auswirkungen eines späten Brutbeginns von Uferschnepfen. Dies trifft insbesondere in den intensiv bewirtschafteten Grünlandgebieten der Niederlande zu, welche zugleich das Hauptbrutgebiet der Westeuropäischen Uferschnepfenpopulation darstellen. Die immer früheren Mahdtermine führen dazu, dass späte Brutvögel nahezu keinen Bruterfolg mehr erzielen können. Die „fitness landscape" von Uferschnepfen hat sich folglich in den letzten Jahrzehnten stark verändert. Hier untersuchen wir die individuelle Variation von Legedatum und Bruterfolg in einer Population, die nicht von einem frühen Mahdtermin beeinflusst wird. Wir können zeigen, dass auch ohne menschliche Eingriffe in einem extensiver bewirtschafteten Grünlandgebiet das Legedatum eines der wichtigsten Faktoren ist, die bei Uferschnepfen den Bruterfolg beeinflussen.

Summary: Human impacts on the landscape have increased the penalties for Black-tailed Godwits laying their eggs too late, especially in the very intensive agricultural landscapes of The Netherlands. Thus, godwits have experienced a dramatic change of their fitness landscape, because the advance in mowing date made late clutches worthless destroying either eggs or chicks. To determine the driving forces of the recent population decline we study the individual variation in timing of breeding with respect to reproductive success in a population unaffected by mowing. Our results show that even in a low intensity agricultural area it is very important for godwits to breed early in the season.

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1 Introduction

The environment of meadowbirds in The Netherlands was subject to extreme changes during the last century (Beintema et al. 1995). Detrimental conditions – in particular the advanced mowing date – are thought to have lead to the elimination of most offspring of birds that initiate breeding late in the season (for an overview see: Kruk et al. 1996). The temporal nature of this anthropogenic effect has obviously a different impact on late and early breeders. The negligible reproductive success of late breeders has been mentioned as a possible reason for the heavy decrease in many meadowbird populations (Kruk et al. 1997). To determine the driving forces of the population decline it can be revealing to look at the individual variation in timing of breeding with respect to reproductive success. Hence, in this project we ask: what determines why some godwits are early breeders and others not? And how does the timing of egg laying influence reproductive success in populations that do not suffer from advanced mowing dates?

The majority of the European population of Black-tailed Godwits breed in The Netherlands (Beintema & Müskens 1987; Piersma 1986); here they are still one of the more abundant breeding birds in what is left of the low intensity agricultural areas. Due to their relatively late breeding season Black-tailed Godwits are particularly vulnerable to early mowing dates (Kruk et al. 1997). Despite much concern and debates, the decrease in numbers is going on unabated since the 1970's (Beintema et al. 1995; Teunissen, 2005). We assume that the natural variation in individual timing of breeding correlates with individual quality and reproductive success, and thus can be related to the mechanisms causing the population decline. Therefore we test whether body condition and timing of egg laying are correlated with components of reproductive success in a population of the Black-tailed Godwit that is unaffected by mowing.

2 Methods

Our study area, the Workumerwaard in Friesland is a low intensity agricultural pasture complex of about 300 ha; mowing is delayed every year after 15th of June, thus not threatening godwit nests or chicks. In 2004, 77 nests where found. Eggs were measured, the average egg volume per nest was calculated (Romanoff & Romanoff 1949) and lay day was estimated (van Paassen et al. 1984). Early and late nests were defined by whether the birds initiated their nest before or after the mean lay day. Daily nest survival probabilities were calculated following Johnson (1979). 66 adult Godwits have been caught and individually colorringed, weighed and measured. Sex of adults was determined biometrically (individuals with bill length>99mm were classified as female), female condition was calculated as residuals from a linear regression of mass and tarsus-toe (p<0.001). 107 chicks from 31 nests were caught, ringed and measured. We used the daily nest survival probability, average egg volume and average chick mass as estimates for reproductive success. Statistica® 7.0 was used for statistical analysis.

3 Results and Discussion

The mean lay day was the 24th of April. 40 nests were initiated before this day and 37 after. Daily nest survival probability was significantly different for early (0.996) and for late (0.989) nests (Fig. 1a). Average egg volume per nest declined with lay day (Fig. 1b). Average chick mass per nest was significantly lower in late chicks (Fig. 2a). Females which initiated nests early were in a significantly better body condition than those that layed late (Fig. 2b).

Daily nest survival probability was noticeably higher for early nests than for late ones. Further mean hatchling mass per nest was higher in earlier nests. Females in a good condition laid eggs early and low condition females initiated their nests later in the season. Thus, the individual tim-

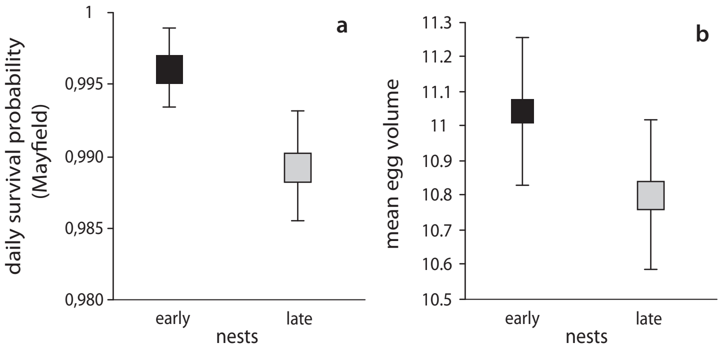

Fig. 1: a: Daily nest survival probability of early (N=40) and late (N=37) nests, z-test: p<0.001, b: The seasonal decline of mean egg volume per nest (N_{early}= 22, N_{late}= 22, t-test: p=0.124, t=1.568). Bars represent 95% confidence intervals.

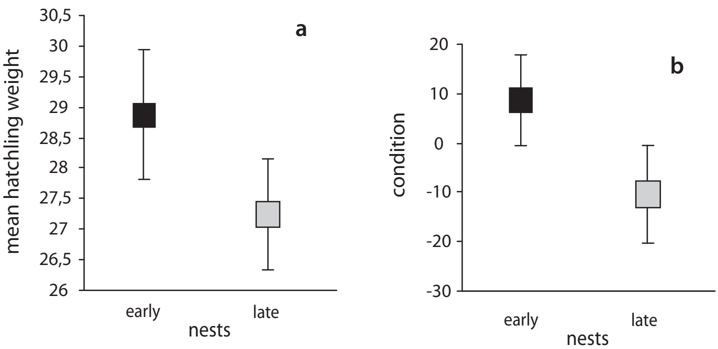

Fig. 2: a: The decline of mean hatchling mass per nest during the season (N_{early}= 13, N_{late}= 18, bars represent 95% confidence intervals, t-test. t=1.568, p=0.019); b: Condition of females with an early and late lay day (N_{early}= 131, N_{late}= 11, bars represent 95% confidence intervals, t-test, t=2.776,, p=0.011).

ing of egg laying seems to be correlated with components of reproductive success. This decline over the season took place in a population unaffected by anthropogenetic influences such as mowing, thus can be considered as natural. However, even late mowing dates can have devastating effects on chick growth, mediated by a lowered density of insects, which are the main prey items for growing godwits. The described pattern has been confirmed in 2005 (own data) and takes place in other populations of Black-tailed Godwits as well (Schroeder et al. 2005). Seasonal declines in reproductive success are well known in many other bird species (Price et al. 1988), and Black-tailed Godwits seem to be no exception.

As not all birds are breeding early, we have to assume constraints on being early. Apparently, only females in a good condition can afford to initiate early nests. Individual body condition on the breeding grounds may also be affected by habitat quality – for instance mediated through food abundance – during non-breeding periods where they spend more than half of a years cycle (Norris et al. 2003; Marra et al. 1998). In the Icelandic population of Black-tailed Godwits (*Limosa limosa islandica*) a link between the quality of wintering habitats and reproductive success was found. Birds feeding on high quality grounds in the winter were the same birds occupying the breeding grounds where high reproduction rates could be attained (Gill et al. 2001). This seasonal carry-over effect could be acting on the nominate race, too, with birds that winter on good quality sites being able to achieve a good condition in time to start breeding early. The conditions in wintering and staging areas of Black-tailed Godwits might affect foraging conditions and thus govern – via body condition – the feasibility to initiate early egg laying. As more and more droughts occur in the sub-Saharan wintering grounds and in southern Spain during the migration period, food abundance in increasingly dry habitats is expected to be rather low. In the context of a strong carry-over effect this could affect body condition on the breeding grounds and could be one of the reasons for the population decline.

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