Assessing the impact of mowing on Common Redshanks *Tringa totanus* breeding on saltmarshes: lessons for conservation management

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Summary

Informed application of habitat management measures is crucial, especially in saltmarshes that function as last refuges for breeding waders in Europe. Despite a reduction in agricultural use of saltmarshes since the establishment of the Wadden Sea National Parks at the end of the 1980s, there remains controversy regarding management measures such as the timing of mowing. We modelled the proportion of nests and chicks that would be jeopardised by mowing at different dates, using long-term breeding data of the Common Redshank *Tringa totanus* – an endangered and widespread indicator species of saltmarshes – from four study sites in the German Wadden Sea. At two study sites in the western Jadebusen, the proportion of broods that were at risk of being killed when mowing began on 1 July ranged between 78% in early, to 96% in late, breeding years, averaging 87%. Although Common Redshanks in the eastern Jadebusen started breeding one week earlier, the model still predicted a loss of 73% of chicks; while 97% of broods were at risk on the island of Wangerooge. Postponement of mowing to 1 August reduced these proportions to 21%, 11% and 32%, respectively. This study is the first to model the positive effects of delayed mowing of saltmarshes on ground-nesting birds. By implementing adjusted mowing dates in addition to previously suggested reductions in artificial drainage, direct and indirect adverse effects caused by mowing and drainage, such as an increased predation risk, are likely to be reduced, such that a 'favourable conservation status' according to the EC Habitats Directive may be achieved.

Introduction

During recent decades, the populations of most meadow birds – i.e. waders that breed to a large extent on wet grasslands and saltmarshes, such as Northern Lapwing *Vanellus vanellus*, Black-tailed Godwit *Limosa limosa*, Eurasian Curlew *Numenius arquata* and Common Redshank *Tringa totanus* – have declined rapidly throughout Central and North-west Europe (Burfield and van Bommel 2004, JMBB 2013, Malpas *et al.* 2013, EBCC 2015). Meadow birds are therefore among the most endangered groups of bird species today and the focus of bird protection across Europe (e.g. Burfield and van Bommel 2004, Südbeck *et al.* 2007, Malpas *et al.* 2013). Specific habitat management plans and government agri-environment schemes have, however, not yet managed to stop the decline (Wilson *et al.* 2007, Breeuwer *et al.* 2009, van Turnhout *et al.* 2010).

Meadow bird population declines are driven by low reproductive rates, while there is no evidence for increasing mortality rates in adult birds (e.g. Hötker *et al.* 2007, Roodbergen *et al.* 2012). These low reproductive rates are primarily a result of the loss of breeding and foraging areas through habitat loss and degradation; especially landscape fragmentation, drainage and intensification

of agriculture during the second half of the 20th century. In addition, and also as a consequence of habitat deterioration, predation intensity has increased, which has caused a further decline of breeding success (Langgemach and Bellebaum 2005, Teunissen *et al.* 2005, Koffijberg *et al.* 2006, Laidlaw *et al.* 2015).

Nowadays, coastal saltmarshes are among the most important breeding sites for waders in North-west Europe (e.g. Koffijberg *et al.* 2009) and could function as last refuges. The saltmarshes of the Wadden Sea hold the largest proportion of breeding waders in Germany. For example, almost 65% of the 14,500 pairs of Common Redshank (hereafter: Redshank) breed in saltmarshes along the Wadden Sea coast, predominantly on mainland saltmarshes (Hötker *et al.* 2007). While populations of Redshanks declined dramatically across Central and North-west Europe in the second half of the 20th century (Burfield and van Bommel 2004, JMBB 2013, Malpas *et al.* 2013, EBCC 2015), Redshank populations in the Wadden Sea saltmarshes remained stable and even increased slightly in some areas at the end of this period. Studies in the German Lower Saxony Wadden Sea, however, indicate that current reproduction in mainland saltmarshes is insufficient to maintain the breeding population (Thyen *et al.* 2008), which explains why the Redshank has recently changed in status from stable to declining (Koffijberg *et al.* 2009).

The state of preservation of the 'Atlantic salt meadow' habitat type (Annex I code 1330, *Glauco-Puccinellietalia maritimae*; EC 1992) is classified as 'unfavourable to inadequate' (BfN [Federal Agency for Nature Conservation of Germany] 2013), even though agricultural use of saltmarshes has been reduced since the establishment of the Wadden Sea National Parks at the end of the 1980s (Esselink *et al.* 2009). This unfavourable conservation status is also reflected by the Red List of threatened breeding birds of Germany (Südbeck *et al.* 2007), as well as the 'sustainable development indicator' for 'species diversity and landscape quality' (Wahl *et al.* 2011). The subset of the latter developed for 'coastal and marine habitats' declined almost continuously from c.80% in 2001 to merely 56% in 2009, where 100% represents the target value for 2015 (Wahl *et al.* 2011). Besides large-scale coastal construction works, long-term and intensified agricultural use caused this unfavourable preservation status, and remains a hazard (Esselink *et al.* 2009).

Mowing of saltmarshes is one of the current management schemes in foreland areas on the mainland coast of Lower Saxony (Esselink *et al.* 2009). Although foreland saltmarshes are usually mown only once a year, there is an ongoing discussion regarding the timing of mowing that would best reconcile the management aims of the National Park to achieve 'favourable breeding conditions' (CWSS 2010) and the purposes of the Fauna Flora Habitat Directive (EC 1992). For ground-nesting birds, mowing acts as a fatal mechanical disturbance. It can cause both direct loss of eggs and chicks, as well as indirect effects, for example, reductions of food availability (e.g. Rickert *et al.* 2012, Klink *et al.* 2013) or increased vulnerability of chicks to predators (e.g. Schekkerman *et al.* 2008, 2009). Such non-lethal effects are known to impact on behaviour, condition and reproduction (Cresswell 2011). To our knowledge, no attempts have yet been made to quantify the effects of mowing on reproduction of waders breeding on saltmarshes. Based on previous studies (Thyen *et al.* 2008, Exo 2010), however, we predict that a substantial proportion of Redshank broods are at risk of being crushed by mowing, and that a postponement of the mowing dates can reduce this proportion significantly. We therefore assess whether, and to what extent, timing of mowing has detrimental effects on breeding success, and hence on population dynamics, using the Redshank – a priority species in bird protection and an indicator species of saltmarshes (Koffijberg *et al.* 2006, Krüger and Oltmanns 2008, Wahl *et al.* 2011) – as a model species.

Knowledge of breeding phenology is essential for optimising both the efficiency of saltmarsh management and the design of monitoring programmes. In addition, we therefore ask whether environmental cues could be used as an indicator for the timing of breeding, and thus for adjustment of mowing dates for saltmarshes. We expect that, similar to Black-tailed Godwits (Schröder *et al.* 2012), Redshanks have not advanced the onset of egg-laying to spring warming in recent decades. In contrast to Black-tailed Godwits, however, we expect that the onset of egg-laying cannot be predicted by spring rainfall because (1) invertebrate availability in saltmarshes depends primarily on flooding by tides and not on precipitation, and (2) adult Redshanks prefer to feed on

adjacent mud flats (Thyen *et al.* 2002). Since the overall objective of the study was to provide management recommendations to improve breeding conditions for ground-nesting species on saltmarshes, we discuss the implications of our findings for conservation management of saltmarshes.

Methods

Study sites

With up to 2.4 breeding pairs per hectare (Exo 2010), the Jadebusen (Lower Saxony, Germany) is one of the most important breeding sites for Redshanks within the Wadden Sea area. At the turn of the millennium, about 2,000 pairs bred in its foreland saltmarshes (land between the seawall and the sea; nomenclature of Wadden Sea saltmarshes according to Esselink *et al.* 2009, cf. Dijkema 1987), which represents approximately 15% of the entire Wadden Sea and German populations (Koffijberg *et al.* 2006).

Fieldwork was carried out at four sites: two mainland sites situated in the western Jadebusen (Petersgroden and Idagroden), one mainland site situated in the eastern Jadebusen (Beckmannsfeld) and one site situated on the East Frisian island of Wangerooge (Figure 1, Table 1). The study site on Wangerooge presents a typical example for nesting sites on Wadden Sea islands. Previous studies revealed high breeding densities at all study sites, but variation in breeding success. Primarily due to lower predation, Redshanks breeding in the eastern Jadebusen and on Wangerooge achieve a considerable higher hatching success than birds in the western Jadebusen: Wangerooge 2005 and 2006: 65% and 95% respectively, eastern Jadebusen 2007: 47% and Petersgroden 2007: 9% (Exo 2008, Thyen *et al.* 2008). The total size of the four study sites amounts to 270 ha and all study sites are of habitat type 'Atlantic salt meadow' (*Glauco-Puccinellietalia maritimae*; EC 1992), and feature typical vegetation of low and high marshes (*Puccinellion maritimae* and *Armerion maritimae*, respectively; for details see Thyen and Exo 2005, Büttger *et al.* 2006, Cervencl *et al.* 2011). An evenly distributed dense drainage network has been created at the mainland coast to enable agriculture on newly reclaimed land and to ensure the drainage of the seawalls, whereas a natural system of creeks has developed on back-barrier marshes on Wangerooge.
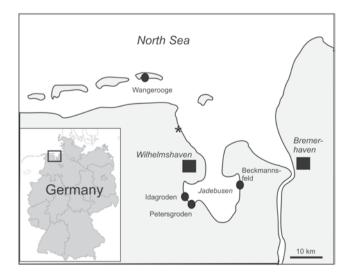

Figure 1. Location of the four study sites in the Lower Saxony Wadden Sea National Park, Germany. * – location of the weather station Wangerland-Hooksiel (circles = study sites, squares = major cities).

Table 1. Characteristics of the four study sites in the Lower Saxony Wadden Sea, Germany (cf. Figure 1). Given are the coordinates, the study periods, the size of the study areas, the density of breeding Common Redshank pairs per hectare [bp/ha], the number of clutches investigated (total, minimum and maximum number per year) and the percentages of the study sites used for agriculture.

study site	location	study period [years]	size [ha]	density [bp/ha]	total number of clutches (min - max)	agricultural use
West Jadebusen						
Petersgroden	53°26'N 08°05'E	2000 - 2008	60	1.6 - 2.4	318 (22 - 55)	ca. 15% mown; in some years ca. 15% is used for extensive cattle grazing
Idagroden	53°28'N 08°03'E	2007, 2008	70	1.4 - 2.0	73 (36 - 37)	no land use for approx. a decade
East Jadebusen						
Beckmannsfeld	53°31'N 08°19'E	2007, 2008	80	1.4 - 2.0	72 (28 - 44)	ca. 10% mown
Wangerooge	53°47'N 07°54'E	2003, 2005, 2006	60	2003: 1.2	36 (10 - 15)	no land use for > 3 decades

Saltmarshes on Wangerooge and at Idagroden have not been used for agriculture for more than three decades and one decade, respectively (Table 1), and only minor parts of the study sites at Petersgroden and Beckmannsfeld are mown. In cases where mowing of saltmarshes is authorised within the National Park, it is allowed only once a year, usually after 1 July. When weather conditions are appropriate, farmers start mowing as early as possible; sometimes even earlier than 1 July (e.g. at Beckmannsfeld on 26 June in 2008). In general, saltmarshes are cut within just 2–3 days.

As breeding success of Redshanks has not been monitored in the framework of the Trilateral Monitoring and Assessment Program (TMAP) to date, an evaluation of the target for 'natural breeding success' is not yet possible (Koffijberg *et al.* 2009, Thorup and Koffijberg 2016). To assess the natural breeding phenology and success of Redshanks breeding on saltmarshes, we therefore concentrated primarily on pairs breeding in fallow saltmarshes. In agricultural areas, we marked Redshank nests and convinced farmers to exclude nesting sites from mowing or to postpone mowing, such that we were able to model potential losses by mowing based on phenological data from undisturbed Redshank nests.

Monitoring of nest sites and breeding phenology

Data on breeding biology were collected according to standard methods assessed for the Joint Monitoring of Breeding Birds (JMBB) in the Wadden Sea (Thyen *et al.* 1998, Koffijberg *et al.* 2011). From mid-April to late June/early July, each study site was visited at weekly intervals. Redshank nests were located by pacing up and down the saltmarsh sites and thereby usually flushing the incubating birds. Nests were marked inconspicuously with a short bamboo cane placed approx. 3 m away from the nest site. Nests were revisited almost weekly. In total, data of 499 clutches were analysed, 391 clutches from the western Jadebusen, 72 clutches from the eastern Jadebusen, and 36 clutches from Wangerooge (Table 1).

Phenological data for all clutches were standardised by calculating the laying date of the first egg. If a clutch was found within the egg-laying phase, the corresponding number of laying intervals was subtracted from the date the clutch was found, assuming a five-day-period for the time between laying the first and the fourth egg. If a complete clutch was found, the expected hatching date was calculated for each egg according to Green (1984) by means of biometric measurements (Thyen and Exo 2005), after which the onset of egg-laying was estimated by subtracting 24 and 5 days for the

incubation and laying period, respectively (i.e. 29 days; Stiefel and Scheufler 1984), from the expected hatching date of the first egg. Laying dates were used for comparisons of risk by agricultural activities between areas as well as years. To estimate how long Redshank chicks are potentially at risk from agricultural activities, it was assumed that chicks spend 21 days in the vicinity of their nest, as telemetry studies have shown that Redshank chicks stay within an area of about 0.4 ha around their hatching place during the first three weeks of life before they leave the breeding sites (Thyen *et al.* 2008). We therefore define 21-day-old chicks as 'fledged' and determined 'fledging dates' by adding 21 days to hatching dates. All dates were expressed as Julian dates (with 1 January as day 1).

Statistical analyses

To test for differences in the start of egg-laying between years or study sites, an analysis of variance (ANOVA) and Mann-Whitney U-tests were carried out. A Spearman's rho correlation analysis was performed to check for a change in egg-laying over years for data from Petersgroden. These analyses were run in IBM SPSS Statistics 20.

To describe the seasonal distribution of clutches per site and year (number of clutches as dependent variable; cf. Table 3 and Figure 2), we used a generalized linear mixed model (GLMM). This model was fitted in R 3.0.3 (R Development Core Team 2014) using the function 'glmer' from the package 'lme4' with a Poisson error distribution and the log link function. Laying date of the first egg was used as explanatory variable. Because we expected the number of clutches to increase strongly at the beginning of the breeding season before decreasing more slowly after a peak, due to the initiation of replacement clutches, we modelled a polynomial relationship between the number of clutches and Julian date. Since we were interested in the variance explained by each polynomial degree, we used orthogonal polynomials. Starting with the fourth degree, we compared all models with lower-order polynomials of Julian date using the Bayesian information criterion (BIC). The BIC values increased during a step-by-step exclusion of the highest-order polynomial from GLMM. As a result, the polynomial of fourth degree (and all lower-order polynomials) of Julian date remained in the final model. Year was included as an explanatory variable in the full model to correct for changes over time, but because its effect was not significant, it was dropped. We used the logarithm of the size of the study sites as an offset to model the density of clutches per hectare. To account for different sample sizes (number of years) and variation in the number of clutches between the four study sites, we integrated study site and year as crossed random factors. The final model was used to predict hatching and fledging dates by shifting the model curve calculated for egg-laying dates by adding 29 days (for hatching dates) and 21 days (for fledging dates). Based on the predicted function of fledging dates, we used a sigmoid function to estimate the percentages of fledglings predicted to have left the breeding grounds on a specific date. The same GLMM was then computed for each study site and year separately to illustrate the variation between sites and years. According to the reduced datasets (subsets for sites and years), year and/or site were implemented as random factor(s). For the years 2000–2002 and 2004, only data from Petersgroden were available. Therefore, a GLM was calculated for these four years.

Environmental predictors of Redshank breeding

Three parameters were tested as proxies to characterise annual Redshank phenology: (1) temperature-sum data – the sum of all daily average temperatures for days with daily averages ≥ 5°C from 1 February to 30 April, (2) accumulated precipitation from 1 February to 30 April and (3) the number of spring tides and the date of the last spring tide from 1 February to 30 April with critical sea levels above which the study sites would be flooded. For that purpose, we used data collected by the German Meteorological Service (DWD) at Wangerland-Hooksiel from 2000 to 2008 (for location see Figure 1) and sea level data from Wilhelmshaven 'Alter Vorhafen' provided by the Federal Institute for Hydrology of Germany (BfG). The critical sea levels per site were defined

based on digital elevation maps of the breeding sites (M. Karle pers. comm.). The critical sea level for the Jadebusen sites was accordingly determined to be 2.4 m, and that for Wangerooge to be 2.1 m. A linear mixed model (LMM) was used to test the predictive power of the environmental variables on the timing of Redshank breeding. To exclude a possible bias caused by the timing of laying of replacement clutches, we used the mean laying dates for the first 10 clutches of each year as a dependent variable and the weather and tide variables as fixed effects. Year was included as categorical random effect. The analysis was performed using the function 'lmer' from the R-package 'lme4' and the BIC was used for model selection.

Model assumptions were assessed graphically (Korner-Nievergelt *et al.* 2015). The amount of over-dispersion in GLMMs was analysed by adding an observation-level random effect to check whether the BIC increased (Korner-Nievergelt *et al.* 2015). In GLMs, over-dispersion was measured by comparing the residual deviance with the residual degrees of freedom. As recommended by Bolker *et al.* (2008), we applied Bayesian statistics to calculate uncertainty estimates of the GLMM and GLM predictions. This was done for all models by using 95% credible intervals (CrI) obtained from 100,000 simulations performed with the function 'sim' of the R-package 'arm' (version 1.7-07). Likelihood ratio tests were performed to check the significant influence of explanatory environmental variables in the LMM.

Results

Breeding phenology

In the western Jadebusen, the majority of Redshanks started egg-laying around mid-May (median [for all clutches including replacements]: 16 May, earliest date: 14 April 2006, latest date: 20 June 2003; $n = 391$; Figure 2a, Figure S1 in the online supplementary material). The onset of laying differed significantly between years (ANOVA, $F_{8,317} = 3.296$, $P < 0.001$; Figure S2), with the earliest laying date being observed in 2000 (median: 7 May) and the latest in 2006 (median: 17 May).

In 2007 and 2008, Redshanks started egg-laying significantly earlier in the eastern than in the western Jadebusen (6 vs. 14 May, $n = 72$ and $n = 125$, respectively, Mann-Whitney U-test, $Z = -4.870$, $P < 0.001$). However, there was no difference in the onset of laying between the western
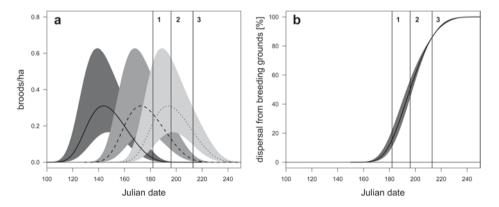

Figure 2. (a) Seasonal distribution of Common Redshanks clutch initiation dates (solid curve), estimated hatching dates (dashed curve) and estimated fledging dates (dotted curve) in the Lower Saxony Wadden Sea, Germany, 2000–2008 ($n = 499$). (b) Dispersal of Common Redshank fledglings from the breeding grounds (derived from the full model considering all years and sites). Fledglings leaving the breeding territory at a given date are presented as cumulative percentages. Vertical solid lines mark dates possible for the start of saltmarsh mowing (1 = 1 July, 2 = 15 July, 3 = 1 August). Model lines are given with 95% credible intervals in grey.

Jadebusen and Wangerooge (western Jadebusen: 17 May, Wangerooge: 20 May, $n = 110$ resp. 36; $Z = -0.677$, $P = 0.499$, years: 2003, 2005, 2006). Assuming a breeding period of 29 days, median hatching dates in the western Jadebusen ranged from 5 June in 2000 to 15 June in 2006. In the eastern Jadebusen, chicks hatched on average on 4 June in the years 2007 and 2008.

At Petersgroden, where we had information on laying dates for nine years, we did not observe a trend in the onset of laying over time ($R_s = 0.117$, $n = 9$, $P = 0.765$ [mean egg-laying date for the first 10 clutches each year]). The linear mixed model showed a significant relationship between the temperature sum and the number of tides with water levels above 2.4 m (Jadebusen) and 2.1 m (Wangerooge) and the timing of the 10 earliest clutches of each year (Table 2). Higher temperature sums led to earlier breeding, as did lower numbers of tides above the critical water level. Precipitation and the date of the last tide above the critical water level did not show a significant relationship with laying date.

Table 2. Estimates of environmental predictors for the 10 earliest clutches of each year based on a linear mixed model. Year was included as random intercept; as the critical sea level we assumed 2.4 and 2.1 m for Jadebusen and Wangerooge, respectively.

Explanatory variable	Estimate	Std. Error	t-value	Credible intervals (2.5%)	Credible intervals (97.5%)
Intercept	124.98	9.62	12.991	108.03	142.02
Temperature sum (rescaled)	-15.45	9.46	-1.634	-32.24	1.19
Number of tides above critical sea level	0.94	0.20	4.723	0.59	1.29

Predicting mowing influence

The number of Redshank clutches varied with all polynomials of Julian date (negatively with 2nd and 4th degree polynomials, positively with the 3rd degree polynomial), but not with a linear Julian date term (Table 3). In data subsets (study sites and years, respectively), the 2nd and 4th degree polynomials degree were always significant different from zero, while linear and cubic relationships were significant only in some.

Table 3. Regression coefficients for the number of clutches in different data sets (study sites and years) derived from GLMMs. Coefficients that are significantly different from zero are presented in bold. Uncertainty of coefficients is given as 95% credible intervals in parentheses. Stars (*) mark data sets analysed with a GLM.

Data sets	Intercept	Julian date	Julian date^2	Julian date^3	Julian date^4
Study sites					
West Jadebusen	**-3.2 (-3.5, -2.8)**	**17.7 (4.9, 30.3)**	**-84.2 (-94.0, -74.4)**	**14.9 (12.7, 17.1)**	**-14.8 (-16.9, -12.6)**
East Jadebusen	**-3.4 (-3.7, -3.1)**	**-13.7 (-18.3, -9.2)**	**-31.6 (-37.4, -25.6)**	0.6 (-2.1, 3.2)	**-5.0 (-7.3, -2.7)**
Wangerooge	**-5.8 (-6.7, -4.9)**	**37.0 (10.1, 64.0)**	**-64.8 (-79.3, -50.4)**	**11.9 (6.5, 17.3)**	**-9.6 (-14.8, -4.5)**
Years					
2000*	**-2.6 (-2.8, -2.4)**	**3.7 (1.2, 6.1)**	**-22.2 (-25.2, -19.1)**	**7.7 (6.2, 9.3)**	**-4.4 (-6.0, -2.7)**
2001*	**-4.8 (-5.6, -3.9)**	**-9.4 (-16.9, -1.9)**	**-44.8 (-57.0, -32.4)**	-1.9 (-6.2, 2.4)	**-10.1 (-15.2, -4.9)**
2002*	**-4.3 (-5.1, 3.6)**	**-9.4 (-17.0, -1.9)**	**-39.1 (-50.1, -28.0)**	1.7 (-2.5, 5.9)	**-7.7 (-12.2, -3.2)**
2003	**-4.0 (-4.8, -3.2)**	11.0 (-1.6, 23.6)	**-37.3 (-43.7, -30.9)**	**8.1 (4.8, 11.3)**	**-4.0 (-6.9, -1.0)**
2004*	**-3.1 (-3.4, -2.7)**	**4.6 (1.1, 8.0)**	**-22.7 (-27.2, -18.3)**	**2.8 (0.6, 5.0)**	**-3.3 (-5.5, -1.0)**
2005	**-5.0 (-7.0, -2.9)**	**36.4 (13.7, 59.1)**	**-48.4 (-63.8, -33.0)**	**11.7 (7.5, 15.9)**	**-6.9 (-10.1, -3.6)**
2006	**-4.0 (-6.4, -1.6)**	12.8 (-0.3, 26.0)	**-35.9 (-53.3, -18.3)**	1.3 (-0.5, 3.1)	**-6.0 (-7.8, -4.2)**
2007	**-3.2 (-3.4, -3.0)**	1.0 (-8.2, 10.1)	**-34.5 (-38.5, -30.5)**	**6.0 (4.1, 7.9)**	**-5.7 (-7.7, -3.7)**
2008	**-3.2 (-3.6, -3.1)**	10.1 (-8.2, 28.4)	**-41.5 (-46.7, -36.4)**	**5.4 (3.4, 7.4)**	**-6.5 (-8.4, -4.5)**
All sites & years	**-3.6 (-4.5, -2.7)**	4.5 (-23.5, 32.9)	**-100.2 (-114.9, -85.4)**	**13.5 (11.4, 15.6)**	**-15.6 (-17.8, -13.5)**

About 32% of Redshank clutches were still incubated on 1 July, when mowing would start (Figure 2a). Given that Redshank chicks usually stay in the vicinity of their nest for about three weeks after hatching (Thyen *et al.* 2008), 85% (all sites and years) of broods were at risk of being killed by mowing when mowing would start on 1 July (Figure 2b, Table 4). This percentage varied

Table 4. Expected brood loss (in percentages) by mowing at three dates. Given are estimates from GLMMs and GLMs (data set marked with *) for the different data sets (study sites and years) with 95% credible intervals (lower and upper CrI). The expected losses predicted from the full model (considering all sites and years) are presented in bold.

Mowing dates	1 July			15 July			1 August		
Data sets	Loss of broods (%)	Lower CrI (%)	Upper CrI (%)	Loss of broods (%)	Lower CrI (%)	Upper CrI (%)	Loss of broods (%)	Lower CrI (%)	Upper CrI (%)
Study sites									
West Jadebusen	86.7	84.8	88.5	54.0	52.7	55.4	20.9	19.5	22.5
East Jadebusen	72.7	71.7	73.6	37.1	36.7	37.5	10.5	9.8	11.4
Wangerooge	96.8	90.4	99.0	73.9	61.3	82.1	32.2	29.7	31.6
Years									
2000*	77.5	77.1	77.9	39.1	38.6	39.7	13.7	12.9	14.8
2001*	85.3	84.4	86.0	49.0	48.9	49.1	13.5	12.7	14.6
2002*	79.8	79.1	80.5	37.8	37.4	38.4	8.3	7.5	9.3
2003	88.1	82.1	92.8	56.1	43.8	68.4	21.7	13.4	32.8
2004*	88.2	87.3	89.0	58.5	58.3	58.6	23.8	23.0	24.7
2005	96.2	84.7	99.1	75.6	53.3	87.8	39.6	24.8	51.1
2006	92.0	74.9	97.4	70.5	52.5	80.2	36.5	30.2	38.5
2007	80.6	78.6	82.3	47.2	46.8	47.5	17.9	15.9	20.1
2008	89.1	82.5	93.5	59.8	56.5	62.6	24.9	19.3	30.3
All sites & years	**84.5**	**77.8**	**89.4**	**49.8**	**43.3**	**55.6**	**16.9**	**16.2**	**17.4**

across study sites (western Jadebusen 87%, eastern Jadebusen 73% and Wangerooge 97%) and ranged from 78% in early breeding years to 96% in late breeding years (Figure S3). Even if mowing were postponed by two weeks (to 15 July), 50% of the chicks would still be jeopardised (Table 4; 54% in the western Jadebusen, 37% in the eastern Jadebusen and 74% on Wangerooge). Postponement of the start of mowing with four weeks (1 August) would reduce the broods at risk to 17% (21% in the western Jadebusen, 11% in the eastern Jadebusen and 32% on Wangerooge).

Discussion

Most Redshanks breeding in the Lower Saxony Wadden Sea area started egg-laying around mid-May in the first decade of the 21st century. This corresponds to observations made in the Dutch Province of Friesland and in East Frisia in Germany in earlier decades (Stiefel and Scheufler 1984, Beintema *et al.* 1995), suggesting that Redshanks have not advanced laying dates, a pattern we confirmed in our Petersgroden data for the years 2000–2008. A pattern of no change in laying date was also observed in Black-tailed Godwits breeding in the Netherlands (Schröder *et al.* 2012). In contrast to grassland breeding Black-tailed Godwits, however, Redshank reproduction advanced with higher pre-breeding temperatures. Inland breeding Black-tailed Godwits instead advanced their laying when precipitation was higher in March, which was suggested to result from precipitation increasing invertebrate availability (Schröder *et al.* 2012). For Redshanks breeding in saltmarshes, we did not expect such an effect: soil moisture, and thus penetrability, is primarily determined by (spring) tides rather than precipitation. Moreover, Redshanks mainly feed on the adjacent mudflats during the pre-breeding season (Thyen *et al.* 2002), which makes tides much more important than precipitation for coastal birds.

Our study shows that the observed initiation of most Redshank broods around mid-May causes these broods to be endangered if mowing starts on 1 July, as is the current rule in saltmarshes along the mainland coast of the Lower Saxony National Park (Kathmann pers. comm.). Approximately one third of pairs still have clutches at the beginning of July (Figure 2a), in late breeding years up to 96% of broods are endangered. Differences between years are caused by (1) variation in the onset of breeding in relation to spring temperature, (2) variation in the number of spring tides during the pre-breeding season, and/or (3) variation in brood loss early in the season, and hence the amount of replacement clutches. Despite these differences, average losses exceeding an order of 50% exclusively by mowing are far too high to maintain the current Redshank population size, as such losses are supplemented by others: total pre-fledging mortality (from egg-laying to fledging) on Wangerooge, for example, was about 50% in the 1950s (Großkopf 1959), without any losses through mowing. To preserve the Redshank population, the annual reproductive success should at least reach a minimum of 0.8 chicks per pair (Exo 2008, 2010).

Direct losses due to mowing were repeatedly described for inland breeding meadow birds (e.g. Kruk *et al.* 1996, 1997, Roodbergen and Klok 2008, Schekkerman *et al.* 2008, 2009). The potential threat by mowing of saltmarshes is even more serious since saltmarshes of the Lower Saxony National Park serve as a last refuge for several endangered bird species (Hötker *et al.* 2007, Exo 2008). In our study sites, direct losses by mowing occurred only exceptionally mainly because we studied Redshanks primarily on saltmarshes without agricultural land use or we could postpone mowing. In 2008, however, we deployed 66 artificial nests (Schlaich unpubl. data) at three sites without conspicuously marking them and without actively attempting to have mowing postponed. On 26 June 2008, 11 out of 20 (55%) artificial nests were destroyed by mowing at Beckmannsfeld, while on 1 July 5 out of 26 nests (19.2%) were destroyed at Petersgroden as well as 6 out of 20 nests (30%) at a further study site in the south-western Jadebusen. Although the sample size of this experimental study is relatively small, these data clearly demonstrate the vulnerability of nests on saltmarshes to mowing. As shown here, the postponement of mowing can significantly increase the probability of fledging of Redshanks. Moreover, abandonment of mowing would be beneficial not only for Redshanks, but also for those species preferring taller vegetation. In Wadden Sea saltmarshes without agricultural land use, for instance, passerines such as the Meadow Pipit *Anthus pratensis*, Yellow Wagtail *Motacilla flava*, Reed Bunting *Emberiza schoeniclus*, and Skylark *Alauda arvensis* manage to breed in high densities (e.g. Wellbrock e*t al.* 2010). All these species have flightless young and are vulnerable to agricultural operations in July.

Direct losses of Redshank broods through mowing can be supplemented by additional indirect negative effects on breeding success, although direct predictions are hard to obtain, as the interactions between agricultural land use, large scale drainage, vegetation structure, predation risk, breeding and foraging conditions, and thus the suitability of saltmarsh areas for breeding birds are extremely complex. Negative effects of mowing are likely to persist in subsequent years. Vegetation heterogeneity, density and height are affected by mowing (Maier *et al.* 2010), altering the nest concealment of Redshanks, which in turn may affect predation risk (Maier 2014, Maier *et al.* prep.) and breeding success (Thyen and Exo 2005, Büttger *et al.* 2006). In addition, mowing is likely to reduce the food supply for chicks, as invertebrate abundance and diversity are often lower on agriculturally used fields than on fallow meadows (e.g. Bakker 1985, Irmler and Heydemann 1986, Irmler *et al.* 2002, Rickert *et al.* 2012, Ford *et al.* 2013, Klink *et al.* 2013). In support of this idea, the body condition of Black-tailed Godwit chicks within agricultural areas is often worse than on unused land, forcing the birds to disperse into more distant fallow sites (Schekkerman *et al.* 2009). Both a poorer body condition and the need to disperse may increase mortality rates. While food availability can be more crucial than food supply for some species (e.g. Butler and Gillings 2004, Vandenberghe *et al.* 2009), in which case the more open mown sites could facilitate foraging, mortality by predation has been shown to be two to three times higher in recently cut or grazed fields compared to uncut ones due to reduced cover in Black-tailed Godwits (Schekkerman *et al.* 2009). Avian predators especially prefer to hunt over recently mown than over unmown areas (Schekkerman *et al.* 2009).

Implications for conservation management

In several meadow birds, nest losses due to agricultural land use could be reduced by less intensive agricultural practices (Hötker *et al.* 2007, Wilson *et al.* 2007, Schekkerman *et al.* 2008, Sharps *et al.* 2015, Sabatier *et al.* 2016). In order to achieve favourable breeding and rearing conditions for the majority of meadow birds, and thus to achieve the quality objective of a 'natural breeding success' (CWSS 2010), an appropriate timing of agricultural use of saltmarshes is essential. In cases where land use should be required for management reasons, it must be handled flexibly and in concert with both local conditions and annual terms. Our experience is that farmers will accept flexible conservation measures aligned to the actual annual conditions much easier than fixed dates. A reasonable timing of mowing should be fairly easy to achieve by close cooperation between the local nature conservation agencies and the National Park authorities.

In addition to reducing agricultural use, reducing artificial drainage of mainland saltmarshes is another high-priority measure (e.g. Esselink *et al.* 2009, Seiberling and Stock 2009). A transformation of the artificial drainage system into a natural free-meandering tidal creek system would favour the spread of site-specific plant and animal communities and thereby improve breeding conditions and food availability for waders. Only if these measures are put into effect, the quality objectives of 'favourable breeding conditions' and 'favourable food availability' as well as the spread of site-specific plant and animal communities can be ensured. Both measures appear indispensable to achieve a 'favourable conservation status' according to the EC Habitats Directive (EC 1992).

Supplementary Material

To view supplementary material for this article, please visit https://doi.org/10.1017/S0959270916000496.

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