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ORIGINAL ARTICLE

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Interactive effects of time and vegetation on reproduction of redshanks (*Tringa totanus*) breeding in Wadden Sea salt marshes

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Abstract As shown for various species, nesting waders are non-randomly distributed on wetlands and preferentially select riparian nest-sites adjacent to limnic or marine waterbodies. Studying the redshank *Tringa totanus*, we tested the hypotheses that, in a coastal wader species which conceals its clutch in vegetation, predation and hatching success are affected by vegetation zonation, and that breeding in lower salt marsh areas has negative consequences for reproduction. We further predicted effects of timing of breeding and breeding experience/age of adults potentially reflected by egg biometrics both on nest-site selection and reproduction. Effects of vegetation, space, time and individual quality on hatching success of redshanks were studied in the German part of the Wadden Sea. Dominant plant species, vertical vegetation structure and nest concealment varied significantly between nests. Variation in nest concealment was relatively low: about 90% of clutches were classified as being well concealed. This variation was explainable by vegetation structure but not by vegetation composition at the nest-site, distance to shoreline, and time of clutch initiation. Vertical vegetation structure varied by dominant plant species but not by distance to shoreline and time of clutch initiation. Hatching success of clutches was low (10.6%) due to high predation (daily predation rate: 7.4%). Hatching success and duration of clutch survival were negatively and predation positively related to the date of clutch initiation. Furthermore, negative relationships were found between egg size and predation and duration of survival, respectively. We assume that concealed nests, early breeding and breeding experience diminish predation in salt marsh breeding redshanks. Thus, redshank reproduction appears to be affected by interactive effects of timing of breeding and vegetation facilitating early breeding. In contrast to open-nesting species, breeding in riparian habitats next to waterbodies may be disadvantageous for species breeding concealed in vegetation if these are covered by less structured vegetation.

Keywords Egg biometrics · Hatching success · Nest concealment · Nest predation · Trade-off

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Introduction

The choice of an appropriate nesting habitat including a well suited nest-site is one of the most important life-history decisions of birds. Habitat and, as a subset of that, nest-site selection is a behavioural response to various proximate cues aimed at meeting the life-history needs of individuals (ultimate factors of habitat selection), e.g. to maximise reproductive success. In general, nesting habitat and nest-site selection are characterised by several trade-offs to guarantee a habitat with sufficient food supply and a nest-site safe against predation and adverse weather. Different habitats are sequentially filled, with high quality habitats (i.e. those which guarantee highest reproduction) occupied first and with higher densities than poorer ones (Hildén 1965; Cody 1985; Bernstein et al. 1991; Newton 1998). Besides intraspecific competition, selection of nesting habitats can be frequently explained by further inter- and intraspecific interactions within a community such as associative breeding and temporal and spatial predator avoidance (Lack 1968; Newton 1998).

Nesting habitat selection of many wader species may also be characterised by another trade-off between selecting a habitat near supra- or eulittoral foraging territories and selecting a nest-site which is safe from flooding. Many wader species display a heterogeneous distribution on breeding habitats caused by competition for preferred nesting sites adjacent to limnic or marine waterbodies (e.g. Grover and Knopf 1982; Ens et al. 1992; Thyen 1997; Milsom et al. 2000). Access to feeding sites and inaccessibility of nest-sites for ground predators are assumed to be important proximate cues promoting this distribution. For example, in Eurasian oystercatchers *Haematopus ostralegus*, nesting next to tidal flats can have positive consequences for reproduction due to improved access to foraging territories for chicks as well as brooding adults (Ens et al. 1992). Nevertheless, it is questionable if breeding next to waterbodies in limnic and marine habitats is generally advantageous for breeding success of waders. At least at relatively undisturbed sites, nesting habitat is characterised by zonated or patchy vegetation of different composition and structure according to elevation and succession (Ellenberg 1996). Since predation is a main factor restricting breeding success of birds and since many bird species have to rely on concealing their clutch in vegetation to protect it passively from predation (Ricklefs 1969; Nilsson 1984; Bennett and Owens 2002), hatching and breeding success of less aggressive species susceptible to predation should vary with succession. In the case of zonated European salt marshes, potentially less productive and less structured early succession stages of lower salt marshes (e.g. *Puccinellia*-communities) are located nearer to tidal flats than those of upper salt marshes (e.g. *Festuca*-, *Elymus*-communities) (Ellenberg 1996). Thus, hatching success of species dependent on concealing their clutch in vegetation should increase temporally with succession and spatially with zonation and distance to shoreline.

Derived from these considerations, the hypothesis was tested that salt marsh succession affects nest predation and hatching success of species concealing their nest in vegetation. The study was conducted on redshanks *Tringa totanus* breeding in the Wadden Sea. Similar to oystercatchers, salt marsh breeding birds of this species feed mainly on tidal flats. In contrast, chicks appear to remain within salt marsh foraging territories until fledging (Großkopf 1959; Glutz von Blotzheim et al. 1977; Thompson et al. 1990). Compared to that of many other coastal birds, redshank anti-predator response is relatively ineffective, resulting in a higher dependence on cover and camouflage of clutches in appropriate vegetation (Glutz von Blotzheim et al. 1977). Therefore, during nest-site selection in salt marshes, redshanks are possibly forced to trade-off between selecting less concealed nest-sites near potential foraging territories and selecting well concealed sites relatively far from these territories (see above). Habitat selection of redshank is relatively well known, whereas the reproductive consequences of this selection are poorly studied. Several studies have shown higher abundance of pairs in *Elymus*- and other upper salt marsh plant communities compared to those of lower salt marshes (Norris et al. 1997; Thyen 2000; Esselink 2000). Thyen (1997, 2000) found that redshank hatching success varied among salt marsh habitats according to vegetational, physiognomic and topographic parameters. However, the means by which these habitat parameters affected hatching success could not be exactly defined. Hence, in the present more detailed study, effects of nest-site characteristics on redshank reproduction were examined by testing the following assumptions. We assumed that hatching success was higher in relatively well structured vegetation of advanced succession stages compared to vegetation of early succession. It was consequently predicted that hatching success increases spatially by distance of nests to shoreline in accordance with the chronosequence of vegetation reflecting succession. To discriminate between effects of vegetation and spatial habitat parameters and those originating from individual quality, the effects of timing of nest initiation and of egg biometrics potentially reflecting body mass and/or age of adults (Großkopf 1958; Thompson and Hale 1991) were additionally studied. We predicted that high quality nest-sites (i.e., potentially those of advanced succession stages, see above) not only provide higher hatching success but were occupied earlier and by potentially more experienced birds (as indicated by egg biometrics) than low quality sites.

Methods

Study area

The studies were conducted on the salt marshes of the Southern Jadebusen (53°26′ N, 8°05′ E), Wadden Sea National Park of Lower Saxony, Germany, in 2000 and 2001. With c. 2 pairs ha^{-1}, the study site has one of the highest redshank breeding densities in Central Europe (Rasmussen et al. 2000; Thyen and Exo 2003). Mustelids, rodents and carrion crows (*Corvus corone corone*) occurred as potential egg predators, herring gulls (*Larus argentatus*) and red foxes (*Vulpes vulpes*) were less abundant (Thyen and Exo 2004).

A total of 15% of the area was covered by a pit from which clay was removed for dike-building. This pit was characterised by muddy sediments. According to biotope maps from 1997, 60% of the study area (60 ha) were characterised by *Puccinellion maritimae* plant communities (“lower salt marsh”) and 25% by *Armerion maritimae* communities (“upper salt marsh”) (classification according to Pott 1992). However, this proportion changed towards a considerably higher share of *Armerion* communities dominated by, for example, *Elymus repens, Festuca rubra* ssp. *litoralis*, and *Elymus athericus* vs. *Puccinellion* communities characterised by species such as *Puccinellia maritima, Triglochin maritimum* and *Plantago maritima* in 2000-2001 (nomenclature according to Wisskirchen and Haeupler 1998). Owing to the lack of updated vegetation maps, current areas of plant communities are not known.

About 30% of the area described above was agriculturally used at a relatively low intensity (cattle grazing and mowing; 50% each). Grazing intensity was one cattle ha^{-1} from May, while mowing was conducted once a year in July.

Recording of nest-site characteristics and hatching success

Searching, marking and inspection of nests were performed according to Exo et al. (1996) and Thyen et al. (1998) from mid-April to the end of June. Inspection intervals were 6 (2000) and 7 (2001) days as a rule but varied between 4 and 7 days mainly due to weather conditions. 90 nests were recorded in total. However, in several cases nests could not be visited regularly due to adverse weather or high tides. Identical samples could therefore not always be taken for all parameter measurements, leading to slightly different sample sizes between parameters.

On finding a nest, nest-sites were mapped using a GPS receiver (Garmin GPS 12). Sites were characterised by composition and vertical structure of vegetation and concealment of nests. Vegetation composition was recorded for about 4 m^2 around the centrally placed clutch applying the Braun-Blanquet (1964) approach (Thyen 1997). Vegetation structure was recorded during the visit following clutch finding. A vegetation stratimeter (Oppermann 1989) was used consisting of an infrared light transmitter panel and a receiver panel arranged in parallel. The stratimeter measured relative transmission of pulsating infrared light through a defined volume of vegetation, i.e. 24 cm (gap between transmitter and receiver panel) × 43 cm × 10 cm (surface of panels). At each nest, ten measurements of 10-cm layers from ground to 100 cm above the nest were performed. Vegetation coverage in different layers above the nest can be derived directly from these measurements. Concealment was determined by measuring light intensity within the nest cup directly above the eggs during the early morning (0600–0900 hours). Measurements were conducted on intact, concealed nests using a luxmeter whose probe was shaded during each measurement. To get a reference value, comparative measurements 1 m above the nests were taken (see below).

Since redshanks are nidifugous birds, only hatching but not breeding success could be determined by regular nest inspections (Exo et al. 1996; Thyen et al. 1998). During each inspection, the status of clutches was recorded. To determine fates of clutches as accurately as possible, estimates of hatching date were calculated from egg biometrics (see below). Egg length, breadth and mass were measured using a calliper (precision ±1 mm) and an electronic balance (precision ±0.1 g). Clutches were classified as being lost or hatched if nests were found empty before or after the estimated hatching date, respectively. In addition, nests of hatched clutches were often still well concealed and small egg shell fragments could be found inside the nest. In a few cases, hatching success could be determined directly by holes and cracks in egg shells indicating imminent hatching or by nestlings found in the nest. In cases of clutch predation, nests were often opened and relatively large egg fragments with remains of yolk could be found in the nest vicinity. We did not determine predator species from the appearance of egg remains due to unreliability of results (Larivière 1999). Clutches were classified as being deserted if eggs were found cold and damp at two successive inspections. Causes of desertion could not be determined. Losses due to flooding and cattle trampling could be easily recognised by definite traces such as mud, hoof tracks and crushed eggs in the nest.

Data analysis and statistics

Three variables characterising nest-sites were derived from the measurements described above. "Dominant plant species" is defined as the species with highest "cover-abundance index" (Braun-Blanquet 1964) in the vegetation record of a nest-site. In 93% of records, cover-abundance index of dominant species indicated a horizontal coverage of between 25% and 100% (Mühlenberg 1989). To reduce the number of variables describing vertical coverage of nest-site vegetation and, thus, to simplify analyses, a "vertical coverage index" was derived from the vegetation stratimeter measurements. Vertical coverage index is defined as the mean coverage of the three variables revealed as contributing significantly to the discrimination of nest-sites, i.e. coverage of the layers 20–30 cm, 30–40 cm and 40–50 cm above the nest (see Results). Furthermore, a "nest concealment index" was calculated from luxmeter measurements. It is defined as light intensity within nest in terms of the percentage of surrounding daylight measured 1 m above the nest.

To study spatial aspects of nest-site selection, effects of distance to shoreline on hatching success were examined. Distance to shoreline was determined by calculating the nearest distance of the nest to the shoreline using a geographical information system (ArcView 3.2a).

Besides vegetation and spatial parameters of nest-sites, some supplementary parameters on timing of breeding and egg biometrics were analysed. Since clutches were mostly found after completion, hatching dates were estimated by egg biometrics according to the method given by Green (1984) (446,508 × mass in g × length^{-1} in mm × breadth^{-2} in mm –197). From observed clutches surviving the incubation period, precision of this method was about ±2 days. Date of clutch initiation was calculated by the minimum estimated hatching date of eggs × clutch^{-1} –24 days (which is the average duration of incubation according to Glutz von Blotzheim et al. 1977). To guarantee comparability between the two study years, "relative date of clutch initiation" was calculated by relating dates of clutch initiation to the first laid clutch of a season whose date of initiation was set to 0. "Duration of clutch survival" was calculated by subtracting the date of clutch initiation from the date of clutch loss or hatching. As far as the date of clutch loss or hatching was not definitely known, the date was determined by the method given by Mayfield (1961). Duration of clutch survival is defined as the percentage of the total incubation time of 24 days.

Besides the parameters directly measured (see above), egg volume was calculated by 0.51 × length × breadth^2 (Hoyt 1979). All analyses including egg biometrics are based on means per clutch.

Daily survival probability (DSP), daily predation rate (DPR) and hatching success were calculated according to Mayfield (1961). Standard error of DSP was calculated according to Johnson (1979). Pairwise comparisons of DSP were made using the method given by Hensler and Nichols (1981). It was assumed that the incubation period of redshanks lasts 24 days and that all eggs of a clutch experienced the same fate. Except for a very few cases, the latter assumption was verified during fieldwork. No reliable discrimination between first and replacement clutches could be made. Thus, hatching success is related to clutches rather than to breeding pairs.

Statistics were performed according to Jongmann et al. (1995), Backhaus et al. (1996) and Sachs (1997) applying SPSS for Windows 10.0 statistical package. In some analyses, metrically scaled variables needed to be grouped. Vertical coverage index and nest concealment index were classified by cluster analyses (Ward method, squared Euclidean distance) and subsequently tested by discriminant analyses. Distance of nest to shoreline, date of clutch initiation, and egg biometrics were classified in three groups which were distinguished by 33 and 67% percentiles. To analyse effects of vegetational and spatial nest-site characteristics on hatching and predation of clutches, multiple logistic regression models were applied. All multivariate analyses were applied by entering predictor variables simultaneously. In case of parametric tests, nest concealment index and duration of clutch survival were arcsine square root transformed and log-transformed, respectively, to generate homogeneity of variances and normal distribution. All other variables included in parametric tests met the test assumptions without transformation. All tests were two-tailed.

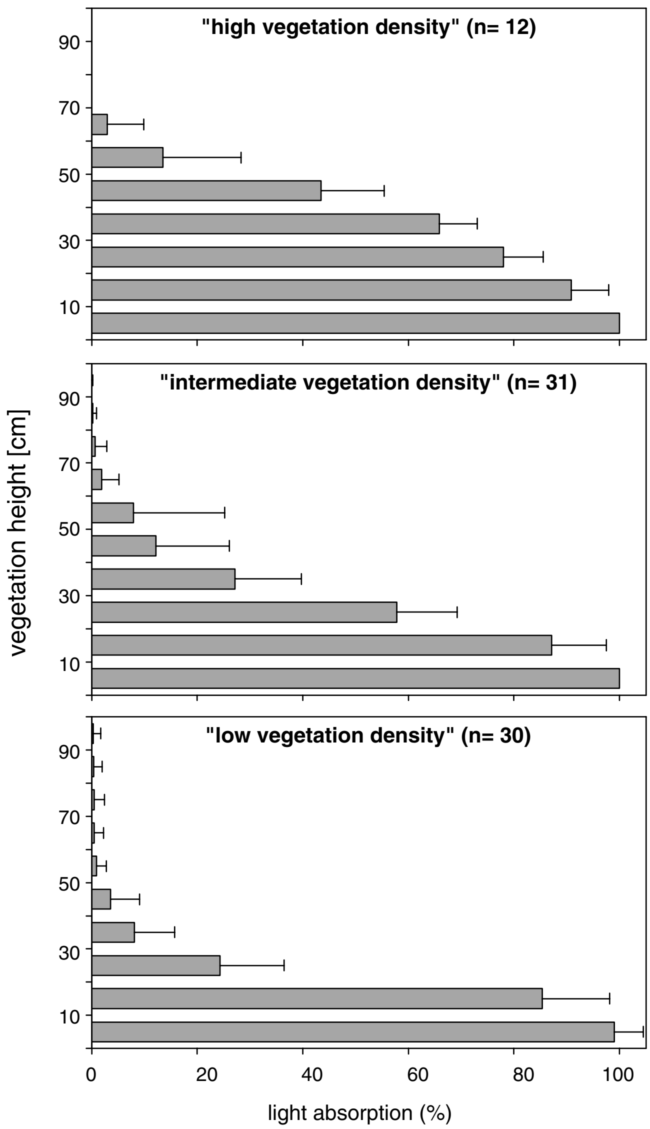

Fig. 1 Vertical vegetation structure at three groups of redshank *Tringa totanus* nest-sites differentiated by a cluster analysis. For each vegetation layer above the nest, mean relative light absorption ± SD is presented indicating the vegetation coverage of the respective layer. n = number of nests

Results

Vegetational nest-site characteristics

Forty-six percent of all 90 redshank nest-sites studied were dominated by *Elymus repens*, 31% by *Festuca rubra* and 14% by *Puccinellia maritima*. The vegetation of the remaining nest-sites (9%) was dominated by *Plantago maritima*, *Triglochin maritimum*, *Aster tripolium* or *Elymus athericus*. All measured nest-sites ($n = 73$) could be classified by a cluster analysis in three groups of significantly different vertical vegetation structure (discriminant analysis: function 1: $\chi^2 = 176.67$, $df = 20$, $p < 0.001$; function 2: $\chi^2 = 37.34$, $df = 9$, $p < 0.001$) (Fig. 1). Similarly, 95% of 69 measured nests could be grouped in well and less concealed ones (discriminant function: $\chi^2 = 76.37$, $df = 1$, $p < 0.001$) (Fig. 2).

Nest-sites dominated by different grass species could be separated by physical parameters (Fig. 3). As revealed by a discriminant analysis (function 1: $\chi^2 = 57.45$, $df = 20$, $p < 0.001$; function 2: $\chi^2 = 14.73$, $df = 9$, $p = 0.099$), vegetation coverage of the three layers between 20 and 50 cm height above the nest contribute significantly ($p < 0.001$ each) to discrimination of nest-sites characterised by different grass species. In the respective layers, vegetation coverage was denser at *E. repens*-sites (60.2 ± 15.7% to 22.4 ± 20.0%) than at sites dominated by *F. rubra* (29.4 ± 21.1% to 4.6 ± 10.0%) or *P. maritima* (37.9 ± 19.3% to 6.2 ± 7.1%). In contrast, nest concealment index made no significant contribution to discrimination of nest-site groups defined by dominant plant species ($F = 0.22$, $df_1 = 2$, $df_2 = 67$, $p = 0.802$). However, there was a significant positive relationship between vertical coverage indices of nest-sites and nest concealment (linear regression: $y = 6.13 + 0.10x$, $R^2 = 0.07$, $p = 0.032$, $n = 69$).

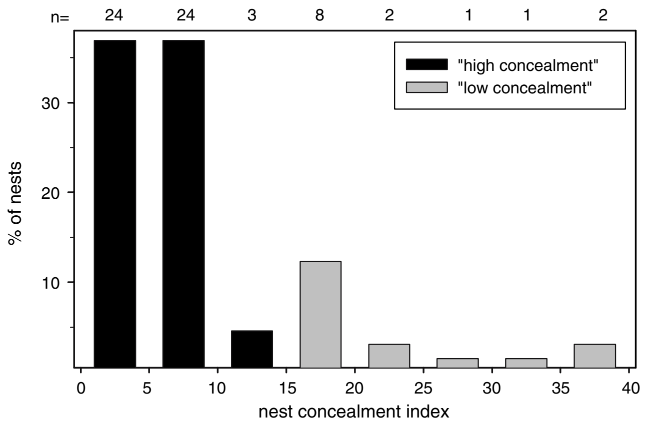

Fig. 2 Frequencies of redshank nests of different concealment and discrimination of the nests as revealed by a cluster analysis. Nests not classified (5 of 69) by the analysis are not considered

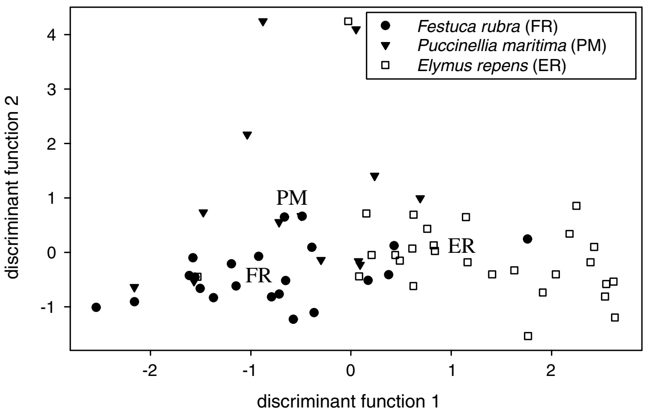

Fig. 3 Results of a discriminant analysis separating redshank nest-sites dominated by different salt marsh grasses by variables of vertical vegetation structure (nine variables of vertical vegetation coverage of 10-cm layers between 10 cm and 100 cm vegetation height, cf. Fig. 1) and nest concealment. Abbreviations indicate group centroids

Spatial variability of nest-site characteristics

Distance of nests to shoreline did not vary between nest-sites characterised by different dominant plant species (Kruskal-Wallis-test: $\chi^2=4.87$, $df=2$, $p=0.088$, $n=77$). Distance to shoreline was not correlated with either nest concealment index (rank correlation analysis: $r_S=0.09$, $p=0.458$, $n=69$), vertical coverage index ($r_S=0.22$, $p=0.071$, $n=73$) or relative date of clutch initiation ($r_S=0.08$, $p=0.516$, $n=85$).

Effects on hatching success and duration of clutch survival

In 2000 and 2001, hatching success of redshank was low due to high clutch predation. No interannual difference in DSP was found (Table 1; Hensler and Nichols test: $Z=0.12$, $p=0{,}904$). Besides predation, desertion of clutches (5.5% of all clutches found), trampling by cattle (3.3%) and flooding (2.2%) were further causes of clutch losses. DSP and hatching success was relatively high at nest-sites dominated by *Festuca* and *Elymus* and at sites relatively far from the shoreline. Variations in daily predation rate were reverse. No variations in DSP by vertical coverage index and nest concealment index were found.

A multiple logit regression analysis revealed no effect of "dominant plant species at nest site", "vertical coverage index", "nest concealment index" and "distance to shoreline" on survival or predation of clutches ($p>0.150$ each). Similarly, neither duration of survival of all clutches nor that of depredated clutches was affected by vegetation and spatial variables according to an ANCOVA ($p>0.150$ each).

Variability and effects of timing of breeding

Relative date of clutch initiation did not vary significantly by dominant plant species at nest-sites (Kruskal-Wallis-test: $\chi^2=2.34$, $df=2$, $p=0.310$, $n=77$). However, clutches found at *Elymus*- and *Festuca*-sites tended to be produced earlier than those at *Puccinellia*-sites (Fig. 4). In addition, no relationships between relative date of clutch initiation and vertical coverage index (linear regression: $p=0.693$, $n=73$) and nest concealment index ($p=0.224$, $n=69$) respectively were found.

Daily survival probability of clutches laid early in the breeding season was considerably higher than that of those laid later whereas DPR varied oppositely (Fig. 5). As revealed by logit regression analyses, hatching of clutches ($n=69$) was negatively ($B\pm SE=-0.13\pm0.05$, $R^2=0.23$, $p=0.008$) and clutch predation positively ($B\pm SE=0.65\pm0.03$, $R^2=0.13$, $p=0.012$) affected by date of clutch initiation (Fig. 6). Additionally, clutches laid relatively early within the season survived for a longer period than those laid relatively late even if they were depredated later in the season (linear regression: all clutches: $y=70.02-1.02x$, $R^2=0.18$, $p<0.001$, $n=80$; depredated clutches: $y=53.8-0.64x$, $R^2=0.12$, $p=0.008$, $n=59$).

Variability and effects of egg biometrics

Egg biometrics varied between nest-sites characterised by different dominant plant species and with initiation date but not with distance to shoreline, vertical coverage index and nest concealment index (Table 2). Eggs found at *F. rubra* sites were heavier than those at *P. maritima* sites (21.6 ± 1.3 g vs 20.5 ± 1.5 g; Scheffé test: $p=0.048$; *E. repens*: 21.0 ± 1.5 g). Average egg volume × clutch^{-1} was negatively related to date of clutch initiation (linear regression: $y=22.5-0.03x$, $R^2=0{,}06$, $p=0.029$, $n=85$).

Clutches with relatively high average egg volumes had a higher DSP and a lower DPR than those with

Table 1 Survival and hatching success of redshank *Tringa totanus* clutches in 2000 and 2001 discriminated by different variables

Group	n_{total}	n_{failed}	$n_{predated}$	ED	DSP ± SE	DPR	HS (%)
Total	83	71	59	796	0.911 ± 0.010	0.074	10.6
Dominant plant species at nest-site							
A *P. maritima*	13	12	10	93	0.871 ± 0.035	0.108	3.6
B *F. rubra*	25	22	17	258	0.915 ± 0.017 ^{d}	0.066	11.8
C *E. repens*	37	29	25	413	0.930 ± 0.013 ^{d}	0.061	17.4
D Other species	8	8	7	32	0.750 ± 0.077 ^{b,c}	0.219	0.1
Vertical coverage index							
A High	10	8	7	116	0.931 ± 0.024	0.060	18.0
B Intermediate	29	25	20	258	0.903 ± 0.018	0.078	8.7
C Low	29	26	22	253	0.900 ± 0.019	0.087	7.4
Nest concealment index							
A High	49	41	34	445	0.908 ± 0.014	0.076	9.8
B Low	12	12	11	83	0.855 ± 0.039	0.133	2.4
Distance to shoreline							
A Near	24	24	21	169	0.858 ± 0.027 ^{b,c}	0.124	2.5
B Intermediate	34	27	22	376	0.928 ± 0.013 ^{a}	0.059	16.7
C Far	25	20	16	251	0.920 ± 0.017 ^{a}	0.064	13.6

Data from both breeding seasons were pooled for analyses
n Number of nests, *ED* exposure days, *DSP* daily survival probability of nests, *DPR* daily predation rate of nests, *HS* hatching success (each according to Mayfield 1961), *SE* standard error (according to Johnson 1979). See text for classification of grouping variables (cf. Figs. 1 and 2). Superscript characters indicate significant differences ($p \leq 0.05$) in DSP among groups as calculated according to Hensler and Nichols (1981)

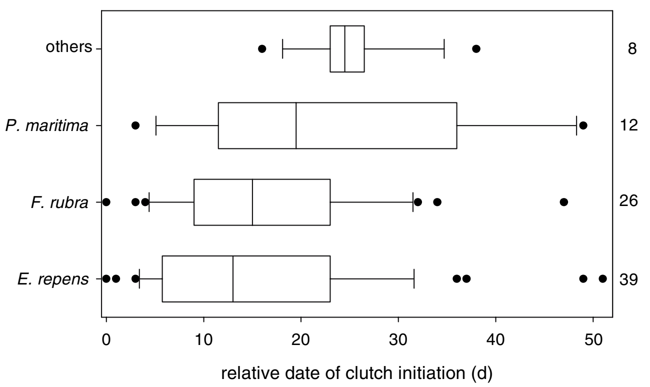

Fig. 4 Relative dates of clutch initiation at nest-sites characterised by different dominant plant species. See text for species comprised by "others". Whiskers indicate 10 and 90% percentiles, left and right boundaries of boxes mark 25 and 75% percentiles, lines within boxes represent medians, numbers right from the graph: *n* per group

relatively light eggs (Fig. 5). Significant positive relationships between egg biometrics and duration of survival of depredated clutches were found (linear regression: average egg mass * clutch^{-1}: $y = -53.1 + 4.45x$, $R^2 = 0.07$, $p = 0.05$, $n = 59$; average egg volume × clutch^{-1} : $y = -91.8 + 6.03x$, $R^2 = 0.13$, $p = 0.005$, $n = 59$). Predated clutches with relatively heavy and large eggs survived for a longer period than those with smaller eggs. No comparable results were found for duration of survival of all clutches.

Discussion

The results suggest that the consequences of nest-site selection for reproduction of redshank depend slightly on vegetation succession: hatching success appears to increase with chronosequence and distance to shoreline. However, this variation cannot directly be explained by composition and structure of vegetation. The results suggest that hatching success depends on timing of breeding and individual quality of breeders. Succession, composition and structure of salt marsh vegetation may nevertheless be of substantial importance for redshank reproduction by providing specific requirements on nest-sites (e.g. structure as proximate cue for concealment) and by interacting with timing of breeding.

Causal and functional aspects of nest-site selection

Although nest-site selection of redshank was not studied but rather consequences of this selection, the present results permit some interesting insights into its causation. One of the most fundamental findings is that nest concealment varied only slightly between nests (approx. 89% of nests were classified as being "well concealed") and that variation in concealment was not explicable by distance of nests to shoreline, time of clutch initiation or vegetation composition. Instead, concealment was explainable by vegetation structure which in turn did not depend on distance to shoreline and time within breeding season. These facts suggest firstly not that concealment itself is a proximate cue promoting nest-site selection but more likely vegetation structure of the potential nest-site. Furthermore, neither phenology nor zonation nor space per se are obviously responsible for selection of nest-sites in salt marsh-nesting redshank. The factors causing this selection are possibly random, adaptive or "extrinsically induced". On the one hand, they could be related to a sufficient supply of suitable territories with respective nest-sites and/or a relatively

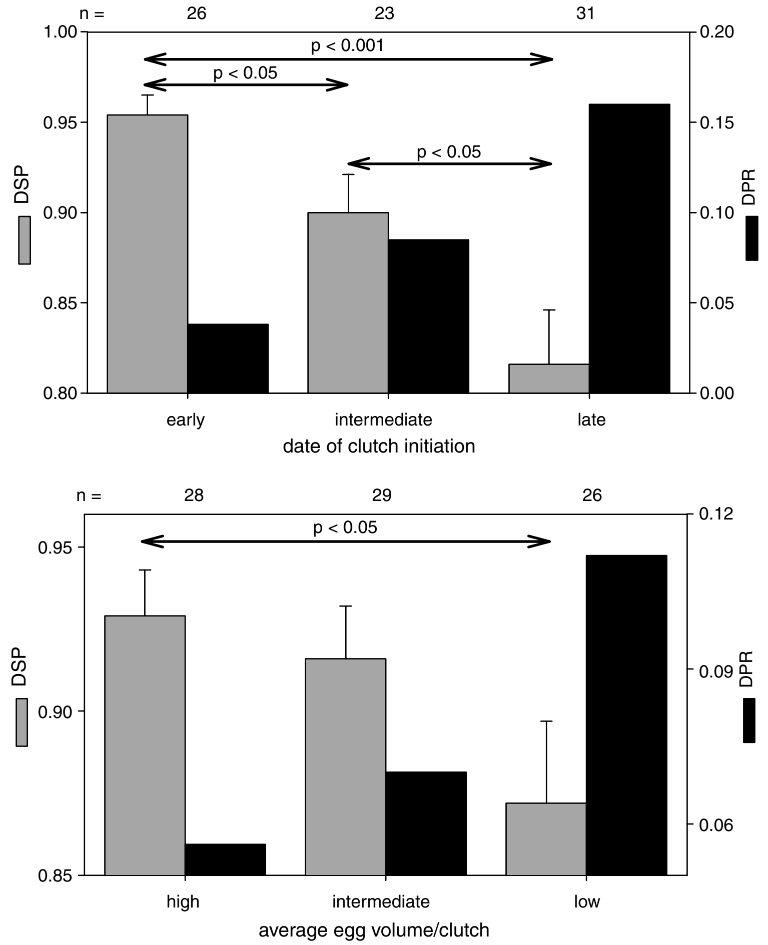

Fig. 5 Daily survival probability (*DSP*) ±SE and daily predation rate (DPR) of groups of redshank nests distinguished by date of clutch initiation (*upper graph*) and average egg volume × clutch $^{-1}$. *n* Number of observed clutches per group. *Arrows* indicate significant differences among groups as calculated according to Hensler and Nichols (1981)

narrow intrinsically fixed requirement of redshank on concealment of potential nest-sites. The high predation pressure found in the study area is, on the other hand, a third possible explanation for the findings mentioned above. Even if constraints on foraging ecology of incubating and chick rearing adults cannot be excluded,

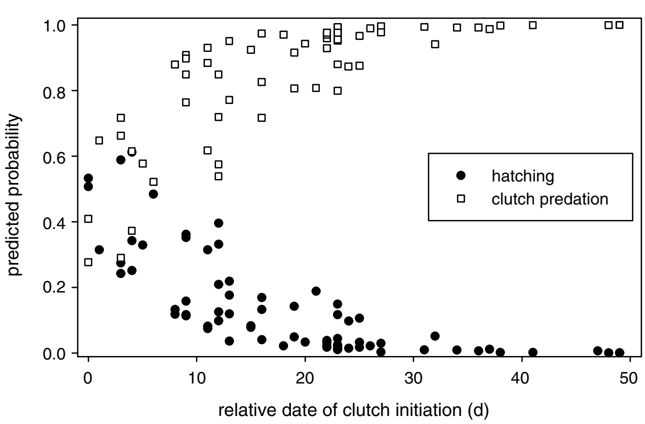

Fig. 6 Relationships between date of clutch initiation and hatching probability and nest predation probability, respectively, as predicted by logit regression analyses. Clutch losses different from predation were excluded from the analysis examining predation

breeding far from the shoreline in well structured vegetation may be a kind of "predator avoidance strategy" forced on the birds as a result of high predation pressure. As many other bird species, redshanks can learn from reproductive failure and react by shifting nest-site location in the following season (Thompson and Hale 1989). Furthermore, there are several examples for birds breeding non-randomly distributed (Burger 1985; Tryjanowski et al. 2002) or in more concealed locations (Newton 1998) in response to predator occurrence. However, experience-based learning forced by high predation-pressure in former seasons is hardly a plausible explanation for the nest-site selection found in the study area: egg mass and volume, assumed to reflect age and/or breeding experience of adults (Thompson and Hale 1991), did not vary between sites of different vegetation structure and concealment. Thus, experienced birds probably did not select more concealed nest sites than less experienced ones. Additionally, it may be difficult for birds to perceive and assess predator occurrence prior to nest-site selection and breeding (Sutherland 1996). This should be particularly true if predation pressure is highest later in the breeding season as it appeared to be in the present study (see below). These considerations as well as the relatively high red-

Table 2 Results of two ANCOVAs examining variations in egg biometrics by vegetational, spatial and temporal nest-site characteristics

	df	Average egg mass per clutch		Average egg volume per clutch	
		F	*p*	*F*	*p*
Dominant plant species at nest-site	2	3.04	0.035	2.15	0.102
Vertical coverage index	1	1.02	0.317	0.56	0.455
Nest concealment index	1	1.42	0.237	0.81	0.371
Distance to shoreline	1	1.71	0.195	1.77	0.188
Relative date of clutch initiation	1	2.65	0.108	4.12	0.046

$n = 69$ nests found in 2000 and 2001. Variables on vertical coverage, nest concealment, distance to shoreline and date of clutch initiation were included in analyses as covariates. Effects of interactions among independent variables were not considered

shank breeding pair abundance found in the study area (Rasmussen et al. 2000; Thyen and Exo 2003) are arguments against an effect of predation pressure on nest-site selection and, thus, the nest-site characteristics found.

Salt marsh-nesting Eurasian oystercatchers prefer breeding near tidal flats with positive consequences for breeding success due to optimal access to intertidal foraging territories (Ens et al. 1992). In redshank, neither a comparable "spatial affinity" to tidal flats nor positive consequences of breeding next to tidal flats for reproduction could be proved. At least in terms of hatching success, which may not be representative for breeding success, for redshank it appears to be more likely disadvantageous to breed in areas near tidal flats if these are covered by *Puccinellia*-communities (see below). Since there was a strong influence of predators on hatching success, the questions arise if selecting nest-sites in obviously attractive salt marshes under high predation pressure is a kind of "ecological trap" or if there are mechanisms besides nest-site selection guaranteeing sufficient hatching and breeding success.

Effects of nest-site characteristics on predation and hatching success

Since predation is a major cause of breeding failure in birds, many species should camouflage or conceal their nest from predators to increase fitness (Ricklefs 1969; Nilsson 1984; Collias and Collias 1984; Bennett and Owens 2002). However, many studies have failed to prove any effect of nest concealment on predation and offspring survival. Most authors attribute this phenomenon to a negative relationship between intensity and efficiency of anti-predator behaviour of parents and nest concealment ("optimality theory of nest defence"). The real effect of nest concealment may be masked by an adjusted adult behaviour varying interspecifically as well as intraspecifically (Götmark et al. 1995; Cresswell 1997; Weidinger 2002; Burhans et al. 2002). In other studies, an absence of an effect of nest concealment on offspring survival was attributed to the occurrence of incidental rather than actively searching predators (Vickery et al. 1992; Schmidt et al. 2001). Thus, besides habitat and nest-site characteristics, studies on nest predation should ideally include further parameters, e.g. parental behaviour and predator-prey interactions (Schmidt 1999).

For hatching success of salt marsh-breeding redshank, it should be advantageous to breed relatively remote from the shoreline at well structured and well concealed sites in upper (*Elymus, Festuca*), rather than in lower, salt marsh vegetation (*Puccinellia*) to reduce predation. However, similar to the studies cited above, neither a spatial variation in nest concealment nor relationships between hatching success and predation and concealment were found. Rather, hatching success and predation were strongly related to timing of breeding. The absence of significant effects of nest concealment on predation could partly be explicable by the activity of olfactorially searching or incidental species such as mustelids (*Mustela* spp.) and rodents (*Microtus*/*Apodemus* spp., *Rattus norvegicus*). However, there should be further mechanisms explaining these findings.

Early breeding in birds is commonly assumed to increase post-fledging survival and fitness by increasing experience, social status, body condition, etc., of offspring (Nilsson 1999). Götmark (2002) showed that offspring of great tits *Parus major* benefit from early breeding by avoiding an increased food demand of breeding sparrowhawks *Accipiter nisus*. A similar effect is conceivable in redshank. All species observed as potential egg predators have young at the end of April/beginning of May (Niethammer and Krapp 1978; Glutz von Blotzheim and Bauer 1993; Stubbe and Krapp 1993a; 1993b). Thus, food demand of predators should be high even at the beginning of the redshank breeding season (end of April), but it should increase during development of predator nestlings. Since probability of clutch predation was highest from about 25 days after the start of the season (>0.9, see Fig. 6), early breeders should have a relatively good chance to incubate successfully. Thus, early breeding and temporal avoidance of highest predation pressure may be one aspect of successful incubation of redshank breeding in a predator-rich environment. However, there are further possible explanations for temporal variations in predation and hatching success as suggested by the results that early nests are not only more successful but resist predators for a longer period even if they are predated later in the season. These explanations may include behavioural mechanisms such as active defence, nest guarding and nest attentiveness. The findings of Thyen et al. (2002) being comparable to those of Sasvári and Hegyi (2000) may be evidence of such mechanisms. Redshank clutches were unattended for a considerable share of the time (about 33% of a day). Frequency and duration of off-duty periods varied diurnally and during the season. These findings led to the conclusion that this behaviour might have been a strategy of incubation induced by high predation pressure.

Thus, in salt marshes strongly affected by different predator species, incubating successfully could be based on a complex framework of nest-site supply and various behavioural responses of redshank to environmental conditions. Within this framework, temporal and vegetation parameters may interact since early breeding requires appropriate, i.e. well concealed, nest-sites even early in the season which are apparently provided especially by upper salt marsh vegetation (*Elymus, Festuca*) (cf. Esselink 2000). However, it is unclear whether redshank behaviour is indeed a response to the conditions described. Again, egg biometrics may give some information about this question. Egg mass did vary between nest-sites of different vegetation composition and egg volume was negatively related to time of clutch initiation, similar to the findings of Summers and Underhill (1991). These results may suggest that especially experienced birds of good body condition start breeding early in the season (cf. Großkopf 1958, 1970; Thompson and Hale 1991; Summers and Underhill 1991). This may be a response to former unsuccessful breeding attempts relatively late in the season. In this framework, prospection of one-year-old breeders and floating and queuing could play an important role even in redshank reproduction (cf. Großkopf 1970; Thompson and Hale 1989; Kokko and Sutherland 1998).

Zusammenfassung

Interaktive Effekte von Legezeitpunkt und Vegetation auf die Reproduktion von Rotschenkeln *Tringa totanus* im Wattenmeer

Viele Watvogelarten bevorzugen zur Brut Nistplätze, die in direkter Nachbarschaft zu littoralen oder semiterrestrischen Nahrungshabitaten liegen, woraus eine inhomogene Verteilung der Vögel im Brutgebiet resultiert. Wir untersuchten die Hypothese, dass dieses Habitat- und Nistplatzwahlverhalten für den Schlupferfolg und somit potentiell auch für den Bruterfolg solcher Arten von Nachteil ist, die zur Brut auf versteckte Nistplätze angewiesen sind. An einer häufigen Brutvogelart des Wattenmeeres, dem Rotschenkel *Tringa totanus*, wurde untersucht, ob und wie Schlupferfolg und Gelegeprädation von der Zonierung der Salzrasen-Vegetation beeinflusst wird. Unsere Annahmen waren, dass Rotschenkel in Bereichen des unteren, ufernah und weniger strukturierten Salzrasens mit geringerem Erfolg und höherer Prädation brüten als in oberen und uferfern gelegenen Bereichen. Darüber hinaus nahmen wir an, dass die Qualität der Elterntiere (gemessen an den biometrischen Daten der Eier) sowohl die Nistplatzwahl als auch den Schlupferfolg beeinflusst. Die dominierende Pflanzenart am Neststandort, die vertikale Vegetationsstruktur und der Grad der Verstecktheit des Nestes unterschieden sich signifikant zwischen den einzelnen Nestern. Die Variation der Verstecktheit war allerdings gering, etwa 90% aller Gelege wurden als "gut versteckt" klassifiziert. Diese Variation war nur durch die Vegetationsstruktur erklärbar, aber nicht durch die Pflanzenartenzusammensetzung, die Entfernung des Neststandortes zur Uferlinie und den Zeitpunkt der Eiablage. Die Variation der vertikalen Vegetationsstruktur war ihrerseits nur durch die dominierende Pflanzenart erklärbar. Der Schlupferfolg (10,6% der Gelege) war aufgrund hoher Prädation insgesamt gering. Schlupferfolg und Überlebensdauer der Gelege standen in negativem, die Gelegeprädation in positivem Zusammenhang mit dem Zeitpunkt der Eiablage. Die Ei-Größe stand in negativem Zusammenhang mit der Prädation und der Überlebensdauer des Nestes. Aus diesen Ergebnissen leiten wir ab, dass eine frühe, versteckte Brut sowie Alter oder Erfahrung der Elterntiere die Gelegeprädation mindern. Im Gegensatz zu offenbrütenden Arten dürfte es deshalb für versteckt brütende Arten wie dem Rotschenkel vorteilhaft sein, uferfern zu brüten: Ein früher Legetermin wird offenbar in erster Linie dort ermöglicht, wo die phänologische und sukzessive Entwicklung der Vegetation bereits fortgeschritten ist.

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