Informed renesting decisions: the effect of nest predation risk

Veli-Matti Pakanen · Nelli Rönkä · Robert L. Thomson · Kari Koivula

Abstract Animals should cue on information that predicts reproductive success. After failure of an initial reproductive attempt, decisions on whether or not to initiate a second reproductive attempt may be affected by individual experience and social information. If the prospects of breeding success are poor, long-lived animals in particular should not invest in current reproductive success (CRS) in case it generates costs to future reproductive success (FRS). In birds, predation risk experienced during breeding may provide a cue for renesting success. Species having a high FRS potential should be flexible and take predation risk into account in their renesting decisions. We tested this prediction using breeding data of a long-lived wader, the southern dunlin Calidris alpina schinzii. As predicted, dunlin cued on predation risk information acquired from direct experience of nest failure due to predation and ambient nest predation risk. While the overall renesting rate was low (34.5%), the early season renesting rate was high but declined with season, indicating probable temporal changes in the costs and benefits of renesting. We develop a conceptual cost-benefit model to describe the effects of the phase and the length of breeding season on predation risk responses in renesting. We suggest that species investing in FRS should not continue breeding in short breeding seasons in response to predation risk but without time constraints, their response should be similar to species investing in CRS, e.g. within-season dispersal and increased nest concealment.

Keywords Cost of reproduction · Information use · Nest survival · Replacement clutch · Migratory shorebird

Introduction

Breeding attempts initiated immediately following failure of a first attempt are a common feature of the life history of birds. This behaviour, termed renesting, aims to increase the current reproductive success (CRS) of individuals. However, life history theory predicts a trade-off between CRS and future (residual) reproductive success (FRS). Investing in renesting to boost CRS may lead to increased physiological stress and suppress or delay activities crucial to survival, and therefore result in reduced FRS (Nager et al. 2001; Stearns 1992; Schmidt and Whelan 2010). The extent of this life history trade-off and consequently the probability of investing in a second breeding attempt may depend on the life history characteristics of the species (r and k strategists), the environment (e.g. length of the breeding season) and individual quality (Hipfner et al. 1999; Roper et al. 2010; Schmidt and Whelan 2010; Becker and Zhang 2011). The trade-off exerts strong selection pressures for second breeding to be attempted only when prospects for success are high and costs to FRS are low (Schmidt and Whelan 2010).

Predation risk impacts the success of any reproduction event. Nest predation is the main cause of breeding
failure for most bird species (Martin 1995). Breeding habitat selection decisions that minimize predation risk therefore form a critical part of any reproduction event. Birds show remarkably fine-tuned adjustments in breeding habitat or nest site selection decisions and dispersal strategies relative to predation risk (Amat and Masero 2004; Fontaine and Martin 2006a, b; Lima 2009; Morosinotto et al. 2010; Pakanen et al. 2011a). Recent evidence strongly suggests that individuals acquire information from the environment to make these initial reproductive decisions (Schmidt et al. 2010, Hanssen and Erikstad 2013; Kearns and Rodewald 2013). However, many individuals will lose their nests and face the decision of whether to renest. The potential influence of nest predation risk on these renesting decisions remain largely unexplored (Martin and Briskie 2009; Roper et al. 2010; Schmidt and Whelan 2010).

Animals should cue on information that predicts reproductive success. A nest predation event likely suggests a higher probability that a future reproductive event may also be at risk of nest predation because predators are likely to return to previous sites of predation (Martin et al. 2000). Therefore birds may use observed predation risk as a cue for low projected renesting success and make optimal decisions based on its effect on the life history trade off (Schmidt and Whelan 2010). There is evidence that predation risk affects within-season dispersal of individuals between successive clutches (Chalfoun and Martin 2010a). Due to different selection pressures, decisions may differ between life histories investing in either CRS or FRS (Martin and Briskie 2009). Species investing in CRS (r strategists) may show positive relationships between predation risk and nesting attempts because these short-lived species are unlikely to nest in the future (Martin and Briskie 2009). The opposite relationship would be expected for species investing in FRS which have more to lose while attempting to invest in the current reproduction.

We investigated the effects of nest predation risk on renesting decisions using a long-term breeding dataset of southern dunlin (Calidris alpina schinzii). Our study population breeds on coastal meadows of the boreal zone in Finland (Pakanen et al. 2011b). Reported renesting rates after breeding failure vary from 3 to 81 % for different subspecies of dunlin (Soikkeli 1967; Naves et al. 2008; Jamieson 2011; Gates et al. 2013). Dunlin are long-distance migrants making them time limited during the breeding season. They are long lived [e.g. 75–80 % yearly survival (Pakanen 2011)] and can be considered bet-hedgers relying on a long life span to ensure breeding success at least in some years (Piersma and Baker 2000). Such a life history strategy should select for ceasing breeding after nest failure, if within-season prospects of future success are not good (Schmidt and Whelan 2010).

Nest predation in dunlin varies considerably between years and sites and accounts for roughly 74 % of all nest failures (Pakanen 2011). The main nest predators include marsh harrier (Circus aeruginosus), hooded crow (Corvus corone), American mink (Mustela vison) and raccoon dog (Nyctereutes procyonoides; own observations). These predators are territorial or have restricted home ranges and likely cause relatively predictable levels of nest loss if they are locally present during the breeding season. Breeding habitat consists of short vegetated meadows, where predators and alarming birds are detectable from a long distance. The breeding site boundaries are distinctive, bordered by unsuitable habitat such as reed bed or forest. Dunlin and other meadow birds spend their entire breeding season at the meadow, they display, mate, breed, brood and forage in the same area and should therefore be able to gather detailed information on predators locally. Other causes of nest loss include flooding or trampling by cattle (Pakanen et al. 2011b). In contrast to predation, these processes are likely unpredictable to breeding dunlin. For example, flooding occurs when strong low pressure fronts and wind push water to the end of the Bothnian Bay raising water levels up to +100 cm. These erratic weather occurrences cause small-scale catastrophes for meadow-breeding birds, but should have lower significance in terms of threats to future reproduction, and adaptive responses to them are not expected (Burger 1982).

Temporal and spatial variability in nest predation and the contrast between the predictability of different nest loss causes allows us to test the predictions that (1) the propensity for renesting is negatively correlated with site-specific predation pressure (measured by site-specific daily nest predation), and that (2) dunlin are less likely to renest after their nest is depredated compared to being destroyed by non-predation causes of failure. We also examine the adaptive value of cueing on nest predation risk by examining if renesting success is associated with the suspected cues.

Materials and methods

Our data were collected on grazed coastal meadows of the Baltic Sea near Oulu (64°50′N, 25°00′E), Finland during 2002–2011. Our study meadows hold nearly all breeding dunlin within the northern Bothnian Bay (Pakanen 2011). Territory and bird monitoring was started in late April when the dunlin arrive at the breeding sites. This is ca. 2 weeks before the initiation of laying. We searched for dunlin and their nests intensively until mid-July and monitored nest fates every 1–7 days until hatching. Territories were searched by making observations of individuals at the meadow. Nests were mostly found by observations of flushing individuals or by following individuals returning to their nest. Nest coordinates were taken with the Global Positioning System for most of the nests starting from
2003. For nests found during incubation, laying dates and estimated hatching dates were calculated by egg flotation (Liebezeit et al. 2007). Incubating and brooding adults were caught and marked with individually identifiable combinations of a metal and three ultraviolet-resistant colour rings (Hughes). Laying season length was calculated from the initiation dates of the first and last nests.

Nests failed due to predation, flooding, trampling by cattle or abandonment. Nests were considered depredated if the eggs disappeared before the estimated hatching day and there were no signs of other causes of failure such as flooding or trampling (Rönkä et al. 2006). Nest failure was considered to have occurred on the mid-point date between nest visits unless more accurate information (e.g. flooding day) was available. After nest failure, replacement nests were searched for intensively (see above).

A pair was considered to be the unit making renesting decisions (Wendeln et al. 2000), and different pairs were considered independent statistical units. Possible interdependence within a site was controlled by including site as random factor in the statistical analysis (see below). On occasions, nests were destroyed when only one of the pair had been identified. In such cases, the identified individual was assumed to be breeding with the same partner as in the previous or next year. This is justified by the low divorce frequency of dunlin (Flodin and Blomqvist 2012). If, however, the previous mate was found to have changed its partner or there was other information suggesting otherwise, it was considered a new pair. Renesting outside the study area is likely to be rare because dunlin are highly site faithful (Soikkeli 1967) and because the short breeding season limits the possibility of finding a suitable meadow and territory (or even a new mate). This endangered species is constrained to short vegetated meadows that occur only in actively managed sites, which allowed us to monitor nearly all breeding habitat and movement between sites in the whole Bothnian Bay (Pakanen 2011). Our study area is separated by ca. 400 km from the next breeding population in Pori (ca. five pairs), where breeding dunlin are also followed intensively (Pakanen 2011).

We observed only one between-site movement within a season; this occurred after the death of a mate. No cases of within-season divorces after nest failure were found. This suggests that within-season emigration is rare and that it does not affect our results on predation risk responses. Nevertheless, we measured dispersal distances between first and replacement nests to examine possible differences between causes of failure.

Our dataset included 123 nests with a known cause of failure for which at least one parent was identified. More than half of these nests were depredated \( n = 68 \). The rest were destroyed by flooding \( n = 33 \), trampling \( n = 12 \) or abandonment \( n = 10 \). Nests with unknown parents \( n = 20 \) and those with presumed on-nest adult predation \( n = 5 \) were excluded. Predation of parents during incubation at the nest is clearly visible from detached feathers. In support of this argument, there were no differences between return rates of adults (mortality) that lost their nest to predation compared to non-predation causes [generalized linear mixed effect model (GLMM), \( \beta_{\text{cause of failure}} = 0.33 \) (SE 0.49), \( z = 0.673, p = 0.500 \); individual was included as a random factor].

Renesting propensity is a minimum estimate because some renesting attempts are destroyed before they are found. If the replacement nests are destroyed at different likelihoods for pairs that had initial attempts claimed by predation versus non-predation, then a comparison of renesting propensities may not be valid. We adjusted for this possibility by correcting the average renesting rates by estimating the number of unfound nests prior to their destruction with site-specific daily nest survival rates (DSR) and the Horvitz-Thompson estimator (Dinsmore et al. 2002; Fondell et al. 2006).

Modelling the renesting rate

We used GLMM (binomial probability distribution and logit link) with function glmer in R 2.6.0 (R Development Core Team 2007) to examine renesting decisions (binomial, yes/no). We used a priori models that included hypothetical structures of predation risk proxies; daily site-specific nest predation rate (site = meadow) and cause of nest failure (predation/other); we also included nest failure date and nest type (first/replacement nest). We included interactions in the a priori models because predation risk responses may change during the breeding season or between nest types. We also examined for an interaction between cause of nest failure and predation rate. Pair, site and year were included as random effects in all models. Site-specific nest predation rates were calculated by considering only the surrounding nests, hence excluding the focal nest and its possible replacement. This means that the site-specific predation rate calculations are not linked to the nest fate of the focal nests. This provides us the opportunity to compare predation risk effects from direct experience of predation failure (cause of failure) and that of ambient nest predation risk (site-specific nest predation). Finally, we considered sites with two or fewer nests in addition to the focal nest to provide unreliable data for calculating predation rates. This left 107 nests for modelling the renesting decisions including 60 nests destroyed by predation and 47 nests destroyed by other causes. With these data, the site-specific predation rate was calculated on average from 14.7 nests/site.

Seasonal declines in renesting propensity may be partly caused by differences in individual quality and/or age, so that early breeding individuals have more time and/or are
more able to make replacement nests (Hïpfner et al. 1999). The effect pair age on renesting was explored using a smaller dataset (89 nests with known parents’ ages; first-time or experienced breeders). Pair age was scored by male age, except in cases when only the female of the pair was identified. Both sexes incubate and brood chicks, but females may leave brooding for the male soon after the hatching. In addition to pair age, a priori models included nest age at failure, date of nest failure and the predation risk proxies. Interactions between the age variables and other variables were included because predation risk responses may differ with age of the pair or that of the nest. We restricted interactions to one per model due to restrictions from the sample size.

Akaike’s information criterion corrected for small sample size (AICc) was used to assess the relative fit of the models. Model comparison was done on the basis of their AICc values (ΔAICc), where a difference of >2 was considered to infer a real difference in model support (Burnham and Anderson 2002). We also calculated evidence ratios that quantify the relative support for explanatory variables by comparing Akaike weights (w) of constrained and reduced models (wC/wR) (Burnham and Anderson 2002). If an addition of a variable resulted in ΔAICc ≤2 from the top supported model, this variable was considered to be an uninformative parameter (Arnold 2010). We further consider model selection uncertainty when multiple models received support (models within 4 ΔAICc units) not by model averaging regression coefficients but rather by calculating weighted estimates for the model predictions, the renesting rates (Burnham and Anderson 2002). We assessed model performance by examining the success of the models in predicting each data point using the area under the receiver-operating characteristic curve [area under the receiver-operating characteristic curve (Zweig and Campbell 1993)].

Nest survival

We examined if cueing on site-specific nest predation risk prior to making renesting decisions would be adaptive by examining variables that encompass local nest predation risk. First, we compared daily predation rates of replacement nests for initial nests lost to predation against nests lost to non-predation causes. Second, we examined if site-specific predation rates explained the predation rate of replacement nests. In the latter analysis, the replacement nests themselves were not included in the estimates of site-specific predation rates. Nests failing from other causes were considered to have survived until the estimated day of failure. DSR were calculated and modelled with MARK using the AIC in model comparison (White and Burnham 1999; Dinsmore et al. 2002).

Results

Annual laying periods lasted 34 days on average and there was considerable between-year variation in both start and cessation dates (Table 1). Average dates of failure were the same for depredated nests and nests destroyed for other causes (Table 1). In addition, the average dates of failure for initial nests that were replaced were similar for predation and non-predation causes (Table 1). We found 34 replacement nests (28% of all lost nests, n = 123) of which 32 were after failure of the first nest and only two were replacements of replacements (Table 1). When correcting for the estimated number of replacement nests that were destroyed before being found, the corrected renesting rate is 36.9% for all nests and 46.7% for first nests (Table 1). Renesting intervals were on average 4.7 days long (Table 1).

Dispersal distances between successive nests varied from 23 to 915 m and renesting always occurred at the same site. Distances did not differ following nests lost to predation and non-predation causes (163.5 m, SD 182.21, n = 12; 164.6 m, SD 216.18, n = 16, respectively). Most replacement nests (82%) were positioned closer to or at the shoreline indicating preference for the shoreline in renesting.

Modelling the renesting rate

Renesting frequency decreased with season (Fig. 1). Date of nest failure was included in all top models and received the strongest support (∆AIC = 35.92, Appendix 1, models A1 and A19). In addition, the variables encompassing nest predation risk improved the model fit when included with the date of failure (Appendix 1, Table A). Both the cause of nest failure (∆AIC = 8.87, evidence ratio = 84, Appendix 1, models A1 and A9) and site-specific nest predation rate (∆AIC = 4.06, evidence ratio = 7.6, Appendix 1, models A1 and A6) received support. Renesting after predation was about half as likely as after failures caused by other factors (Table 1). This pattern was especially clear during the period when initiation of replacements peaked (25 May) being 3.12 less likely after predation (Fig. 1). The probability of renesting was also shaped by site-specific predation rates so that renesting rates were lowest in the meadows with highest predation rates.

Interactions between date of failure and proxies of predation risk (Appendix 1, models A3 and A4 vs. A1) and the interaction between the predation risk proxies (Appendix 1, model A2 vs. A1) did not increase the explanatory power of the models. The same applies for the nest-type effect (first vs. renest) which was supported when modelled alone (∆AIC = 9.56, Appendix 1, models A18 and A23) but did not receive support when included in the model with date of failure (Appendix 1, models A1 and A5).
Despite the fact that experienced pairs started laying earlier than first-time breeders (ANOVA, age; $df = 1$, $F = 10.06$, $p = 0.002$), pair age did not explain variation in renesting when included in the best model (Appendix 1, models B1 and B2) or when modelled alone (Appendix 1, models B21 and B22). Nest age at failure received support ($\Delta AIC = 6.36$, Appendix 1, models B18 and B21) but there was no support when it was included in the best model (Appendix 1, models B1 and B3).

Mean daily nest survival (all causes of failure included) for replacement nests was 0.94 (SE = 0.014, $n = 27$), which predicts 20% success for a 26-day nest period. Overall replacement nest survival was not associated with the cause of first nest failure (Appendix 2, models A2 and A3), suggesting that replacement nests were detected with similar efficiency between the depredated and non-depredated classes. Cause of failure was not strongly associated with failure from predation or other causes of failure (Appendix 2, models B2 vs. B3 and C1 vs. C2). However, the model averaged estimates of replacement nest survival from predation indicated slightly (but not significantly) lower values after the first nest was depredated (0.961, SE 0.022) than if it was destroyed by other causes (0.976, SE 0.011). The reverse pattern applied for survival from other causes.

### Table 1
Details of laying dates, renesting interval, failure dates and renesting rates for a southern dunlin *Calidris alpina schinzii* population breeding at Bothnian Bay, Finland

<table>
<thead>
<tr>
<th></th>
<th>Mean</th>
<th>Median</th>
<th>Range and/or SD</th>
<th>$n$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Laying dates and renesting interval</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Start of laying</td>
<td>May 3rd</td>
<td>May 3rd</td>
<td>27 April–9 May</td>
<td>10 Years</td>
</tr>
<tr>
<td>Cessation of laying</td>
<td>June 6th</td>
<td>June 5th</td>
<td>31 May–14 June</td>
<td>10 Years</td>
</tr>
<tr>
<td>Length of laying period</td>
<td>34.0 days</td>
<td>33 days</td>
<td>28.0–42.0 days, SD 5.0</td>
<td>10 Years</td>
</tr>
<tr>
<td>Renesting interval</td>
<td>4.7 days</td>
<td>5 days</td>
<td>1.0–7.5, SD 1.7</td>
<td>28 Nests</td>
</tr>
<tr>
<td><strong>Date of failure</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>First nest (predation)</td>
<td>May 30th</td>
<td>May 31st</td>
<td>15 May–28 June</td>
<td>52</td>
</tr>
<tr>
<td>First nest (non-predation)</td>
<td>June 2nd</td>
<td>May 27th</td>
<td>17 May–30 June</td>
<td>40</td>
</tr>
<tr>
<td>Replacements (predation)</td>
<td>June 14th</td>
<td>June 15th</td>
<td>28 May–1 July</td>
<td>16</td>
</tr>
<tr>
<td>Replacements (non-predation)</td>
<td>June 23rd</td>
<td>June 25th</td>
<td>2 June–11 July</td>
<td>15</td>
</tr>
<tr>
<td>Replaced nests (from predation)$^a$</td>
<td>May 24th</td>
<td>May 25th</td>
<td>15 May–9 June</td>
<td>13</td>
</tr>
<tr>
<td>Replaced nests (from non-predation)$^a$</td>
<td>May 26th</td>
<td>May 26th</td>
<td>18 May–3 June</td>
<td>21</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Lost</th>
<th>Replaced</th>
<th>Renesting rate (%)</th>
<th>Corrected rate (%)$^b$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>First nests</strong></td>
<td>92</td>
<td>32</td>
<td>34.5</td>
</tr>
<tr>
<td>Predation</td>
<td>52</td>
<td>13</td>
<td>25.0</td>
</tr>
<tr>
<td>Non-predation</td>
<td>40</td>
<td>19</td>
<td>47.5</td>
</tr>
<tr>
<td>Replacements</td>
<td>31</td>
<td>2</td>
<td>6.3</td>
</tr>
<tr>
<td>Predation</td>
<td>16</td>
<td>0</td>
<td>0.0</td>
</tr>
<tr>
<td>Non-predation</td>
<td>15</td>
<td>2</td>
<td>13.3</td>
</tr>
</tbody>
</table>

$^a$ Nests that were replaced after failure, include both first nests and replacements

$^b$ Corrected rate was calculated by estimating number of unfound nests prior to their destruction

![Fig. 1](image-url) Predicted renesting propensities (lines) for pairs that lost their nest to predation or to non-predation causes in relation to date of failure of their first nest. Estimates are weighted averages (including models with $\Delta$Akaike’s information criterion $\leq 4$) calculated under mean predation rates. Individual nest observations are shown by dots ($n = 107$).
of failure: depredated (0.977, SE 0.014) and other causes (0.969, SE 0.012). Similarly, there was some support for site-specific predation rates affecting replacement nest survival (negatively) from all causes (Appendix 2, models A1 vs. A2) and from predation (Appendix 2, Tables B1 vs. B3). However, these effects remained weak and the confidence intervals of the regression coefficients exceeded zero.

Discussion

We found that renesting decisions of dunlin were explained both by the timing of nest failure and nest predation risk. Dunlin seemed to adjust renesting decisions in relation to cues of predation risk that were available from direct experience of nest predation and from ambient nest predation risk in the environment (site-specific predation rates). Renesting decisions were best explained by personal nest predation experiences of breeding pairs. This result is intuitive because a direct encounter with a predator destroying a pair’s nest likely gives an acute perception of risk and should provide predictability to the risk of a future nesting attempt in that season (Chalfoun and Martin 2010b). This result was expected, especially because dunlin is a long-lived species. Our study therefore provides relatively rare evidence of how predation events may impact renesting, which is an important reproductive decision that contributes to individual fitness.

A distinct advantage of our dunlin study system is that the individuals show high site fidelity. In addition, our study population incorporates the entire local dunlin population that is isolated by 400 km from other breeding sites. This means that it is highly unlikely that dispersal away from sites within the season could explain the lowered renesting probability after the nest predation we document. Furthermore, we found between-season dispersal distances to be short, to occur within a meadow, not to differ by cause of failure, and that they were directed towards the shoreline. Therefore, these short within-season movements were likely undertaken in order to provide better feeding conditions for late-hatching young rather than in response to predation. Our results therefore point to the impact of nest predation as a predictor of renesting decisions.

Patch-specific predation rate also explained renesting probabilities in our dunlin population. Information on local nest predation risk is likely to be accumulated by a pair’s own observations of predators, alarm calls from both conspecifics and heterospecifics and perhaps observing destroyed nests within the meadow. It may also include information from observations of behaviour of other individuals indicating their success [public information (Danchin et al. 2004; Seppänen et al. 2007)]. This could be gained from observations of brooding individuals or from the proportion of incubating individuals. In general, the response to site-specific predation rate seemed robust. However, because there is a possible correlation with past and future predation rates and because we could not correct for the fates of nests not found, site-specific nest predation is likely to be a mixture of both an actual response in renesting and increased nest predation before the replacement nests were found. We cannot separate the effects. Our field work efficiency was nevertheless high and most replacement nests were found in early incubation, which suggests that our results are reliable.

If predation risk proxies are reliable as assumed, one could predict an association between proxies and consequent renesting success. This was not observed from the present data although the coefficients for interactions between the site-specific predation rate and renesting success were negative suggesting some correlation between past and future predation within a season. That the tendency remained non-significant could well be because of weak tests of the small data and because replacements were not a random sample with respect to predation risk variation. The latter is because the birds breeding in high-risk conditions avoided renesting. The results leave the question about adaptive potential open for future studies.

We do not know of prior studies addressing renesting decisions in relation to predation risk. Similar trends in renesting rates can be calculated from savannah sparrow (Passerculus sandwichensis) data in Perlut and Strong (2011) where the renesting rate after nest failure due to predation was 10.2% vs. 18.6% after non-predation causes of failure. The difference is not significant ($\chi^2 = 1.47$, df = 1, $p = 0.2$). It is likely that the life history (position in the $r/k$ continuum) and environmental differences (e.g., breeding season length) that cause variation in fitness benefits gained from renesting (trade-off between CRS and FRS) also define the ability and need to respond to nest predation risk (Roper et al. 2010). In contrast to waders, short-lived passerines have lower FRS and invest more in CRS. They commonly renest after predation and may even reduce their effort in current nests in order to be able to invest more in subsequent nesting attempts (Martin 1995). In such species, within-season dispersal and changes in nest site camouflage or other characteristics may be efficient responses to nest predation risk (Chalfoun and Martin 2010a).

The renesting rate of dunlin declined strongly during the season. Such a decline is expected if the length of the season is linked to both the benefits (to CRS) and the associated costs (to FRS; Fig. 2). Seasonal declines in renesting are common in birds and become stronger among species breeding in more northern latitudes (Arnold et al. 2010; Jamieson 2011). While such a temporal pattern can also be created by between-individual quality differences (Hipfner et al. 1999), our results on quality measured by
Fig. 2 A conceptual model showing the relationships between the costs (grey upward-pointing line) and the benefits (black downward-pointing line) of renesting as a function of the breeding season, and how they determine the length of the potential breeding season (a period during which benefits outweigh costs; line arrow). Renesting is most likely when the difference between the costs and benefits is greatest (i.e. start of the season, 0 % has passed) and ceases when the costs are higher than the benefits (solid black line arrow). Perceived nest predation risk may change (grey arrows) the levels of predicted costs (grey dash; increased risk of predation to incubating adult) and benefits (black dash; poor nest success), and hence reduce the length of potential breeding season (dashed black arrow) and the renesting rate.

Pair age were inconclusive. Nevertheless, the life history of migratory waders likely promotes actual calendar effects on fitness (Yasué and Dearden 2008). For example, the low renesting success relative to the general nest success in our study population (20 % vs. all nests 42 %), and the declining juvenile survival with hatching date (Pakanen 2011) suggest that investing in renesting late in the season has low fitness benefits. In line with this, the return rate of chicks from replacement nests is only a fraction of that for chicks from first nests [2.7 and 17.2 %, respectively (Pakanen et al., unpublished data)]. This could be related to temporal variation in food abundance and predator activity on both breeding and non-breeding sites (Meltofte et al. 1997; Lank et al. 2003; Baker et al. 2004). Furthermore, the difference in renesting intervals between populations with short seasons [season length 28–34, interval 4–5 days (this study; Naves et al. 2008)] and populations with longer seasons [season length 40–100, interval 9–10 days (Amat et al. 1999; Yasué and Dearden 2008; Jamieson 2011)] illustrates the need for fast decisions.

Renesting may incur survival costs and reduce FRS in long-lived migratory waders (Piersma and Baker 2000; Schmidt and Whelan 2010). Delayed autumn migration may be the key cost to survival for waders, whose natural history is characterized by an early departure from breeding sites after nesting (Myers 1981; Meltofte et al. 2007). In most species, one sex, usually females, leave weeks before their chicks fledge. This strategy allows individuals to spend their annual cycle in high-quality environments, increasing survival (Piersma and Baker 2000). Selection pressures such as temporal variation in food abundance at staging sites (Baker et al. 2004; Meltofte et al. 2007) or predation danger peaks during migration (Lank et al. 2003; Hope et al. 2011) may determine the best time windows for successful migration for adults, and thus affect the length of the breeding season (Jamieson 2011). These constraints through CRS and FRS are relaxed in non-migratory wader species breeding in the tropics, e.g. Malaysian plovers (Charadrius peronii), that have long breeding seasons in favourable conditions. Consequently, they can breed multiple times and probably without substantial costs to FRS (Yasué and Dearden 2008).

As an important limiting factor, breeding season length may affect selection pressures acting on responses to predation risk in renesting behaviour (see also Roper et al. 2010). If the effect of predation risk on the predicted costs and benefits of renesting is constant in time, the period during which the benefits outweigh the costs, i.e. the remaining optimal breeding season (after considering predation risk) increases with length of the breeding season (Fig. 2). Therefore, the decision not to attempt renesting in response to predation risk may be less evident in populations with longer breeding seasons where the costs are outweighed by the benefits for a longer period in the breeding season allowing multiple breeding. In these cases, predation risk may select for other strategies such as dispersal and increasing nest concealment, as shown for species investing in CRS (e.g. Amat et al. 1999). Interestingly, Smith et al. (2010) found that in years of high predator abundance, arctic shorebirds (FRS species) started nesting earlier in the season, at a time when nest predation was lower, which also left more time for renesting.

Due to the reduced time window for viable renesting under predation risk, our conceptual model on the benefits of renesting (Fig. 2) predicts an interaction between breeding season length and predation risk. It predicts that renesting is advantageous early in the season even under predation risk because fitness prospects of renesting (e.g. juvenile survival) are still quite high and costs to survival are low. The effect of predation risk on renesting decisions is strongest when there is still time to renest, but the predicted benefits of renesting are low due to risk of predation. Our data provided only limited support for such an interaction. This may be due to a lack of information on nests destroyed in the earliest season (1–13 May). Furthermore, there is no information on how the perceived predation risk actually affects the predicted costs and benefits. Impacts may differ with season or they may be
so strong that renesting ceases even in the early part of season. This conceptual model requires further empirical testing.

In conclusion, we found that renesting decisions of long-lived migratory dunlin are affected by predation risk measured as a cause of nest failure and site-specific nest predation rate. Our results add to the wide range of avian reproductive strategies that have been found to be influenced by nest predation risk (Martin and Briskie 2009). Further experimental studies (Jakubas and Wojcizulans-Jakubas 2013) where predators are mimicked (dogs etc.) and predation of replacement nests is controlled for are needed to examine life history differences in renesting responses to predation risk, especially in relation to breeding season length. It is evident that studies should consider causes of variation in renesting to better understand the influence of nest predation on avian life histories (see also Roper et al. 2010; Schmidt and Whelan 2010) and on the variation of seasonal productivity of long-lived species (Beintema and Mûskens 1987).

Acknowledgments We are grateful to Aappo Luukkonen and assistants for help in the field and to Jorma Pessa and Sami Timonen for cooperation. This study was funded by the Finnish Cultural Foundation, the Kone Foundation, the Emil Aaltonen Foundation, the Tauno Tönning Foundation, the Finnish Environment Institute and the Academy of Finland (project 128384). We thank Emma Vatka for helping with R and for valuable comments on the manuscript, and Sarah Jamieson, Juan Amat, Indrikis Krams and three anonymous referees for valuable comments on earlier drafts.

References


Chalfoun AD, Martin TE (2010b) Parental investment decisions in response to ambient nest-predation risk versus actual predation on the prior nest. Condor 112:701–710


Meltofte H, Høye TT, Schmidt NM, Forchhammer MC (1997) Differences in food abundance cause inter-annual variation in...
the breeding phenology of High Arctic waders. Polar Biol 30:601–606
Roper JJ, Sullivan KA, Ricklefs RE (2010) Avoid nest predation when predation rates are low, and other lessons: testing the tropical-temperate nesting paradigm. Oikos 119:719–729