

Variable flight initiation distance in incubating Eurasian curlew

Adriaan de Jong · Carin Magnhagen · Carl-Gustaf Thulin

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Abstract Flight initiation distances (FIDs) of nesting birds approached by a predator likely reflect evolutionary stable strategies in which birds make trade-offs between adult survival and reproductive success. Here, we test if FID (a) had an impact on hatching success, (b) was adjusted to current conditions, and (c) was consistent for individual nests. All experiments were performed with a human approaching incubating Eurasian curlews *Numenius arquata*, a ground-nesting wader species under high egg predation pressure. Our results show that hatching success was higher in nests where the incubating parent left at intermediate FIDs compared to short and long ones, and that FID decreased with date and time of the evening. Further, FIDs from repeated approaches were not consistent within nests. We suggest that incubating Eurasian curlews follow a “surprise” strategy, where an element of randomness is superimposed on a context-adjusted norm to prevent predators from predicting their FID behaviour.

Keywords Hatching success · Predation · Risk assessment · Parental investment · Nest defence

Introduction

When a mobile animal detects an approaching predator, it has to decide whether to stay or to flee (Stankowich and Blumstein 2005; Cooper 2008). The decision-making

process includes a trade-off between the risk of getting harmed or killed and the costs of fleeing (Ydenberg and Dill 1986; Lima and Dill 1990). The outcome of this decision is commonly measured by the flight initiation distance (FID), the distance at which the perceived risk outweighs the benefits of staying (Cooper and Frederick 2007).

Wild animals normally presume humans to be potential predators (Lima and Dill 1990; Frid and Dill 2002; Beale and Monaghan 2004), and human “predators” have been frequently used in FID studies (e.g. Kramer and Bonenfant 1997; Blumstein et al. 2005; Cooper and Whiting 2007). Results of such studies have been used, for example, in the design of buffer zones around wildlife refuges (Blumstein et al. 2003).

For incubating birds, the FID decision also includes elements of parental care, and FID behaviour is likely to affect reproductive success and, thus, fitness (Clark and Ydenberg 1990a; Lima 2009). Now, the costs and benefits for both parent and offspring have to be weighed in, and under natural selection, populations are expected to develop a FID behavioural norm that optimises overall reproductive success in a complex cost–benefit analysis (Clark and Ydenberg 1990b). General adjustments to the variables in the cost–benefit analysis, such as age, sex, remaining proportion of the incubation period and potentially harmful ambient temperatures, will be included in the behavioural norm (e.g. Biermann and Robertson 1981; Camfield and Martin 2009).

At individual level, the incubating bird is likely to diverge from this norm in response to habitat characteristics, weather, life-history prerequisites, physiological condition, experience and personality (Dingemanse et al. 2009; Møller and Garamszegi 2012). Adjustment of FID has been shown for mode of approach (Eason et al. 2006), direction of approach (Kramer and Bonenfant 1997) and human disturbance level (Webb and Blumstein 2005). In the agricultural landscape, where our study was conducted, many predators (e.g. red

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A. de Jong (✉) · C. Magnhagen · C.-G. Thulin
Department of Wildlife, Fish, and Environmental Studies, Swedish
University of Agricultural Sciences, 901 83 Umeå, Sweden
e-mail: adriaan.de.jong@slu.se

C.-G. Thulin
Department of Animal Nutrition and Management, Swedish
University of Agricultural Sciences, 750 07 Uppsala, Sweden

foxes *Vulpes vulpes* and goshawks *Accipiter gentilis*) operate from the surrounding forest, while human disturbance is primarily connected with roads and buildings. Consequently, landscape characteristics around individual nests will possibly correlate with FID behaviour.

Because location and inhabitants are fixed, a certain level of consistency in FID behaviour within nests could be expected, and fixed personality types of the parent birds would further reduce variation in FID behaviour (Dingemanse and Réale 2005). Repeated FID measurements on nests will reflect FID consistency but demand that potential effects of habituation are controlled for (Nisbet 2000; Madsen and Boertmann 2008).

In this study of FID behaviour and ecology, we used data from nests of farmland-breeding Eurasian curlew *Numenius arquata* to test the H_0 's of the following hypotheses:

- H₁. Hatching success varies with FID behaviour.
- H₂. FID is adjusted for date, time of the day, distance to the nearest road and distance to the nearest forest edge.
- H₃. When provocations are repeated, variance in FID within nests is significantly smaller than the overall variance in FID.

Methods

Study area and study species

The study was conducted during the breeding seasons of 2009 and 2010 in an open farmland habitat in northern Sweden, from Nordmaling (63.6°N, 19.4°E), via Umeå (63.8°N, 20.3°E) to Vindeln (64.2°N, 19.7°E). In this region dominated by boreal forest, farmland is mainly found on sediment soils in valleys of rivers and streams. Farming is dominated by dairy production, with ley (sown perennial grasses) and barley *Hordeum vulgare* as the main crops for fodder (Statistics Sweden 2010).

The Eurasian curlew is a large ground-nesting Scolopacidae wader of open habitats throughout temperate and northern boreal regions of Europe and Asia. Median clutch size is four eggs, and the 4-week incubation effort is shared by the adults (Glutz von Blotzheim et al. 1977; Cramp 1983). In contrast to ducks and geese, Eurasian curlews do not cover their nest when left unattended (Kresinger and Albrecht 2008). For a human observer, both adult Eurasian curlews and their eggs are well camouflaged, but a review of 21 European studies revealed an average nest predation rate of 71 % (MacDonald and Bolton 2008).

Data collection

Eurasian curlew nests (23 in 2009 and 14 in 2010) were located by visually detecting adult birds sitting on or leaving

their nest. Of the 37 nests, 36 were on ley and one in a recent birch plantation on former grassland. Hatching success was 59 % ($n=22$), while nest failures were caused by predation in 14 cases and by ploughing in one.

FID measurements were obtained by allowing an assistant to approach the nest in a steady walking pace along a straight line (approach distances ranged from 50 to 334 m). At the moment the incubating bird left the nest, the position of the assistant was marked, and the distance between this position and the nest was measured. We maximised the distance between the nest and the starting point of each approach within the limits set by terrain conditions, accessibility and the need to vary the approach direction between provocations (below). To look for repeatability of FID behaviour within nests, we made up to three provocations per nest with a minimum interval of 3 days. Only nests with eggs were included; thus, we excluded nests in which newly hatched chicks were brooded by a parent. In total, we made 76 successful FID measurements on 37 nests, of which 26 nests rendered two observations and 13 nests three observations.

All provocations were made during the evening (2045–2350 hours CET) to mimic the behaviour of mammalian predators (e.g. red fox and European badger *Meles meles*) (MacDonald and Bolton 2008) and to reduce the risk of interference by human activities (e.g. farming and recreation). Note that in May and June, when the experiments were conducted, evenings and much of the nights are not dark in the study area.

For nests with multiple FID measurements, the median time between consecutive provocations was 7 days. In addition, no nest was approached by the same assistant more than once; each approach was made from a different direction, and different cars were used on each occasion (unless the car could be effectively hidden from the incubating bird). Finally, nests found in 2010 within 1 km from a 2009 nesting site were not included in the study. Given the site fidelity of breeding Eurasian curlews (Berg 1994; Busche 2011), this made it unlikely that the same pair was exposed to our experiment 2 years in a row. By this combination of precautions, we argue that the risk for an effect of habituation was very low (c.f. St Clair et al. 2010).

Hatching success was inferred from characteristic shell remains of hatched eggs, newly hatched chicks in or near the nest, or adults with chick-guarding behaviour. Adult Eurasian curlews soon abandon predated nests, which are mostly just empty, although some contain eggshell fragments left by avian predators. When predated, the nest cup is usually disrupted by the predator.

Vegetation height (single tall straws excluded) was measured to the nearest centimetre with a ruler at five positions: next to the right side of the nest and at a 50-cm distance in four directions (3, 6, 9 and 12 o'clock relative the line of approach). These five measurements for each nest were averaged to produce the vegetation height variable.

Nearest distances from each nest to public roads, forest edges, houses and solitary trees were taken from the digital map database of the county boards of Sweden (<http://gis.lst.se/lanskartor/>) with additional information from aerial images (www.hitte.se) and field observations.

Statistical analysis

The data set included the variables FID (continuous, in metre), *date* (continuous, May 1=1), *time* (continuous, hours measured to the minute, 2100=0), *vegetation height* (continuous, in centimetre), *nearest road* (continuous, in metre), *nearest forest edge* (continuous, in metre), *nearest house* (continuous, in metre), *nearest tree* (continuous, in metre) and *hatching success* (binary, success = 1, failed = 0). We pooled the data for 2009 and 2010 because values of FID and the potentially explanatory variables did not differ significantly between years (Wilcoxon rank sum tests, all P values >0.05).

In the initial data exploration, we used the Shapiro–Wilk tests and quantile-quantile plots to check for normal distribution of individual variables, and the Kendall tests and pairwise plots to explore correlations between variables. Based on the results of the Shapiro–Wilk tests over a range of variable transformation options, we square-root-transformed the FID variable ($\sqrt{\text{FID}}$) and natural log-transformed the nearest road and nearest forest edge variables. Due to significant correlation with the date variable (Kendall tau=0.45), we excluded the vegetation height variable from further analyses. We also excluded the nearest house and nearest tree variables, because the former was correlated with the nearest road variable (Kendall tau=0.28) and the latter with the nearest forest edge variable (Kendall tau=0.41). All the excluded variables had lower explanatory potential than their correlated counterparts. In the correlation matrix of the remaining potentially explanatory variables, all two-sided Kendall tau values were <0.25 (P values >0.05). In addition, plots of $\sqrt{\text{FID}}$ by date and time did not indicate curvilinear relationships between these pairs of variables.

The square root transformation of the FID values did improve the distribution but did not lead to a clearly normally distributed data set (Shapiro–Wilk $W_{75}=0.94$, $P<0.001$, all values; $W_{36}=0.94$, $P=0.033$, first provocations). Consequently, we used nonparametric statistical methods whenever possible but accepted parametric methods when no appropriate nonparametric alternatives were available.

FID and hatching success

First, we used the Wilcoxon rank sum test with continuity correction to test for differences in FID between failed ($n=15$) and successfully ($n=22$) hatched nests. Secondly, we divided the observed FIDs into three approximately equally

large-sized classes and used equal proportion tests (Newcombe 1998) for differences in hatching success between these classes. Additionally, we analysed the relationship between hatching success and date with a logistic model (binomial GLM). In these analyses, we only used data from the first provocations ($n=37$) in order to avoid potentially confounding effects of repeated measurements, FID-related bias of nest survival and habituation.

FID adjustment

In the absence of a nonparametric counterpart, we used multiple linear regression models to study the effect of the variables date, time, $\ln(\text{nearest road})$ and $\ln(\text{nearest forest edge})$ on response variable $\sqrt{\text{FID}}$ for first provocations. For evaluation, we performed nonparametric Kendall correlation tests between $\sqrt{\text{FID}}$ and each of the potentially explanatory variables.

FID consistency

For nests with data from two provocations ($n=26$), we applied a Kendall correlation test on FID values of the first and second provocation. For nests with three provocations ($n=13$), we accounted for repeated measurements in the analysis of variance by using a general linear model of FID by nest with nest as a random factor (Minitab 16.1.0).

Unless mentioned elsewhere, we used R x64 version 2.14.1 (R Development Core team 2011-12-22), with the packages Kendall version 2.2 (McLeod 2011) and lattice version 0.19-30 (Sarkar 2008) for statistical analyses and plotting.

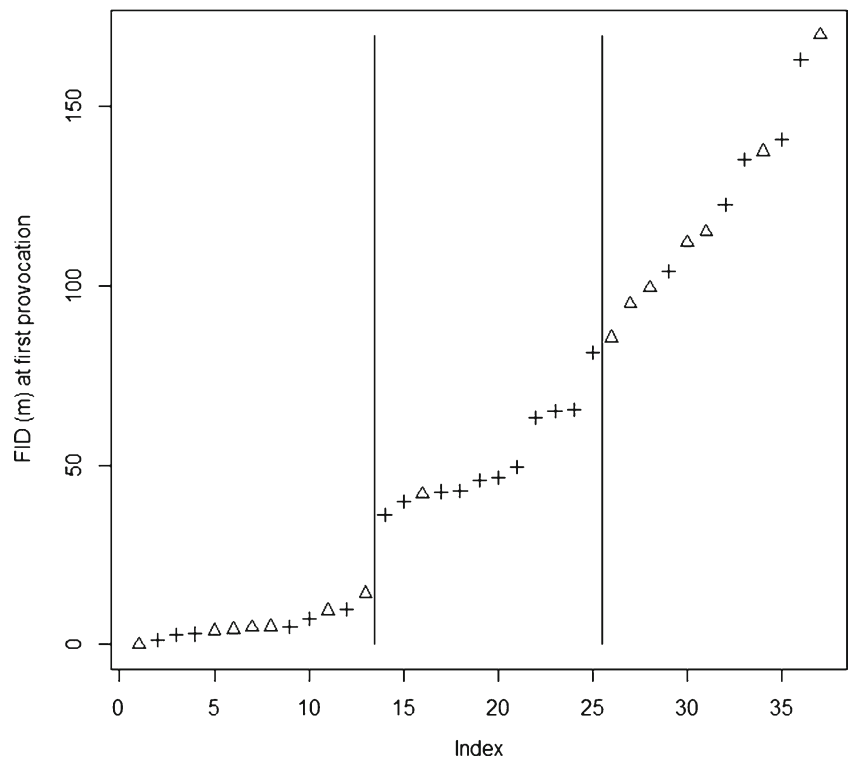
Results

FID and hatching success

FID measurements did not differ between nests with successful and failed hatchings ($W_{15,22}=160$, $P=0.89$). Thus, we found no support for larger FIDs being generally associated with better or poorer hatching success. However, nests in the middle third of the FID range were significantly more successful than nests with shorter and longer FIDs ($\chi_1=6.84$, $P=0.009$, Fig. 1). When only survival to the next nest visit was considered (median time lapse = 8 days), this pattern was even more pronounced (no losses for intermediate FIDs and 29 % loss among short and long FIDs). These results show that the H_0 of H_1 could be rejected at 99 % confidence level.

Furthermore, the logistic regression model showed that the hatching success increased with date ($z_{35}=2.1$, $P_{(>|z|)}=0.04$), from around 25 % for nests first provoked on May 10 to over 90 % on June 5 (Fig. 2).

Fig. 1 Ordered FID values at first provocation. Successfully hatched nest, *plus sign*; failed nest, *triangle*. Vertical lines mark the borders between the three FID classes: short ($n=13$), medium ($n=12$) and long ($n=12$). Median FID values were 5 m for class short, 46 m for class medium and 119 m for class long

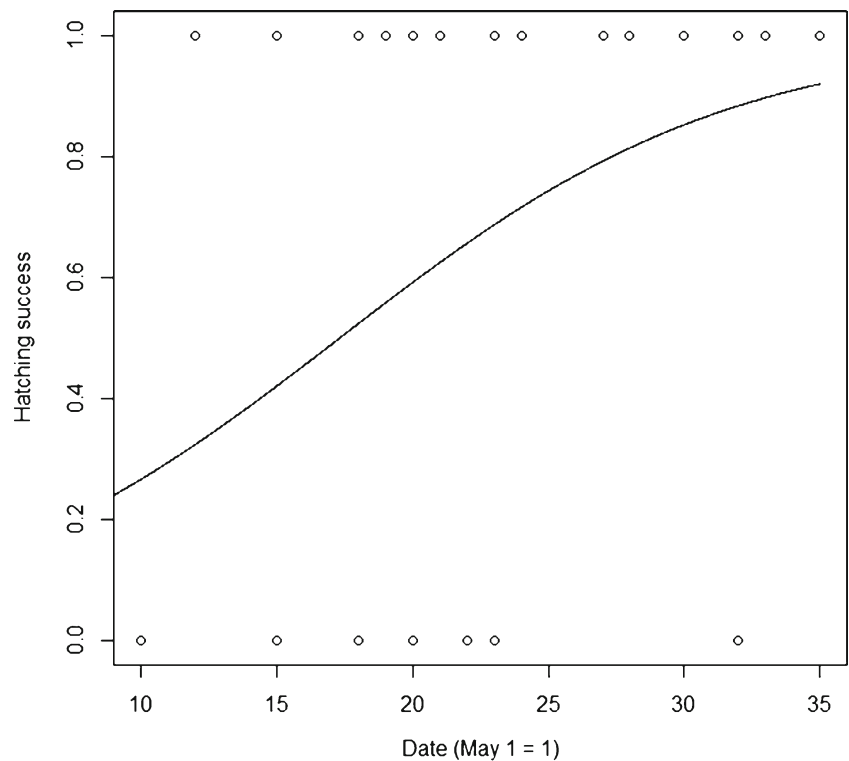


FID adjustment

The multiple regression model of $\sqrt{\text{FID}}$ with variables date, time, $\ln(\text{nearest road})$ and $\ln(\text{nearest forest edge})$ fitted the data ($F_{4, 32}=3.2, P=0.027, \text{adj. } R^2=0.19$), but the probability ($>|t|$) values of the $\ln(\text{nearest road})$ and $\ln(\text{nearest forest$

edge) variables indicated that the model would improve if these variables were omitted. With these two variables omitted, the model fitted the data better ($F_{2, 34}=6.3, P=0.005, \text{adj. } R^2=0.23$), and all coefficient estimates had probability ($>|t|$) values <0.03 . Coefficient estimates were 1.4 (SE 0.6) and 2.4 (SE 0.8) for date and time, respectively,

Fig. 2 Graphical representation of a binomial (logistic) model of hatching success by date. The incidence curve depicts expected hatching success over date (May 1=1). Only the FID at first provocation subset ($n=37$) was included in the model



corresponding with estimated effect sizes of 2.0 m per week and 5.7 m per evening hour. Visual inspection of correlation and residual plots revealed that this regression model met the requirements of linearity and of homoscedasticity and normality of errors. The preference for the simpler regression model was in harmony with the pairwise nonparametric Kendall correlations (Table 1); date and time were correlated with $\sqrt{\text{FID}}$, but the other variables were not. The analysis of FID adjustment showed that the H_0 of H_2 could be rejected at 95 % confidence level and at 99 % confidence level when the set of explanatory variables was reduced to contain only date and time.

FID consistency

The analysis of FID consistency showed that FIDs of first and second provocations were not correlated (Kendall tau = -0.037, two-sided $P=0.81$, 26 pairs, Fig. 3). For nests with three provocations, the variation in the FIDs within nests (Fig. 4) obscured any potential differences in FID among nests ($F_{1,2}=0.75$, $P=0.69$). Consequently, the H_0 of H_3 could not be rejected.

Discussion

FID and hatching success

Higher hatching success at intermediate FIDs is concordant with an evolutionary stable strategy, where two or more counteracting interests are balanced in a compromise: here, the survival of the incubating parent versus the survival of eggs. Montgomerie and Weatherhead (1988) defined nest defence as “behaviour that decreases the probability that a predator will harm the contents of the nest (eggs or chicks) while simultaneously increasing the probability of injury or death to the parent”. Although this definition clarifies the cost–benefit aspect (e.g. fleeing vs. guarding), it does not automatically translate into long FIDs being good only for the incubating parent and short ones only for the eggs. For example, hiding on the nest to avoid detection by the predator could well be beneficial for the incubating parent, and

leaving early could be advantageous for the eggs, if the eggs are better camouflaged than the adult or the smell of the adult guides predators to the nest (c.f. Reneerkens et al. 2005).

FID adjustment

According to the multiple regression model, FID was reduced by 2.0 m per week and 5.7 m per evening hour (at population level), while an effect of the distances to the nearest road or the nearest forest edge could not be shown. When compared to the observed variation in FID (range = 0–170 m, median = 45.8 m), the effects of date and time are modest. For a potential predator, these effects are probably difficult to comprehend, even though long-lived predators may accumulate experience from a large number of encounters with incubating Eurasian curlews. The lack of significant effects of distance to nearest road and nearest forest edge suggests that incubating adults either are unable or have no reason to adjust their FID behaviour to these factors.

The reduction of FID by date fits the parental investment theory, because the chances for successful hatching (and thus the “value” of the eggs) increase over the incubation period (Fig. 2), while the parent’s chances to produce a new clutch during the current breeding season gradually decrease (c.f. Biermann and Robertson 1981; Montgomerie and Weatherhead 1988). Thus, investments in the current offspring should increase with time, as seen here, although the date variable is only a population level proxy for incubation time. We were unable to determine the onset of the incubation period of individual nests, because the location of Eurasian curlew nests during egg laying is prohibitively difficult. With true measurements of the timing of provocations over the incubation period, a more pronounced effect of date could be expected.

The reduction of FID over time may be caused by the need to protect the eggs from dangerous cooling when ambient temperatures drop during evening hours (Camfield and Martin 2009). Alternative explanations of the observed time effect are (a) the sexes switched incubation duties during the evening (c.f. Currie et al. 2001), (b) the perception of predation risks changed over time or (c) the physiological condition (e.g. alertness) of the birds changed.

In future studies, the role of additional factors involved in FID adjustment could be tested, e.g. vegetation structure and topography (proxies for visibility), or the occurrence of conspecifics and other birds (c.f. Seppänen et al. 2007).

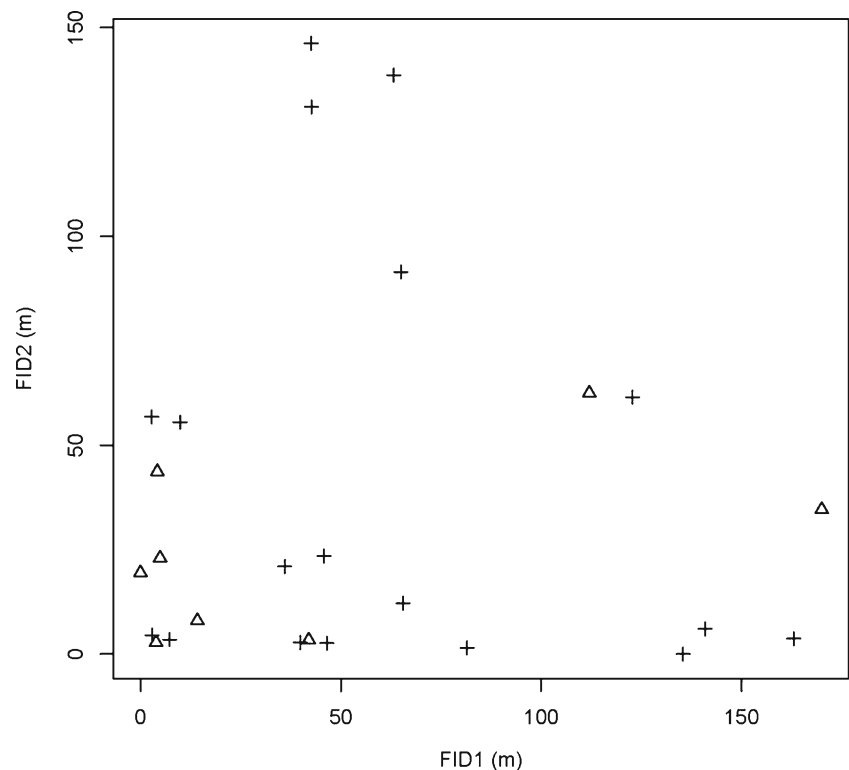
Double role of date

With an impact on both FID and hatching success, date could have a confounding effect on the relationship between

Table 1 Kendall correlations between $\sqrt{\text{FID}}$ and variables date, time, $\ln(\text{nearest road})$ and $\ln(\text{nearest forest edge})$. Only data from first provocations were included

Variables	Kendall tau	2-sided P
$\sqrt{\text{FID}}-\text{Date}$	-0.22	0.066
$\sqrt{\text{FID}}-\text{Time}$	-0.23	0.049
$\sqrt{\text{FID}}-\ln(\text{nearest road})$	0.14	0.232
$\sqrt{\text{FID}}-\ln(\text{nearest forest edge})$	0.03	0.821

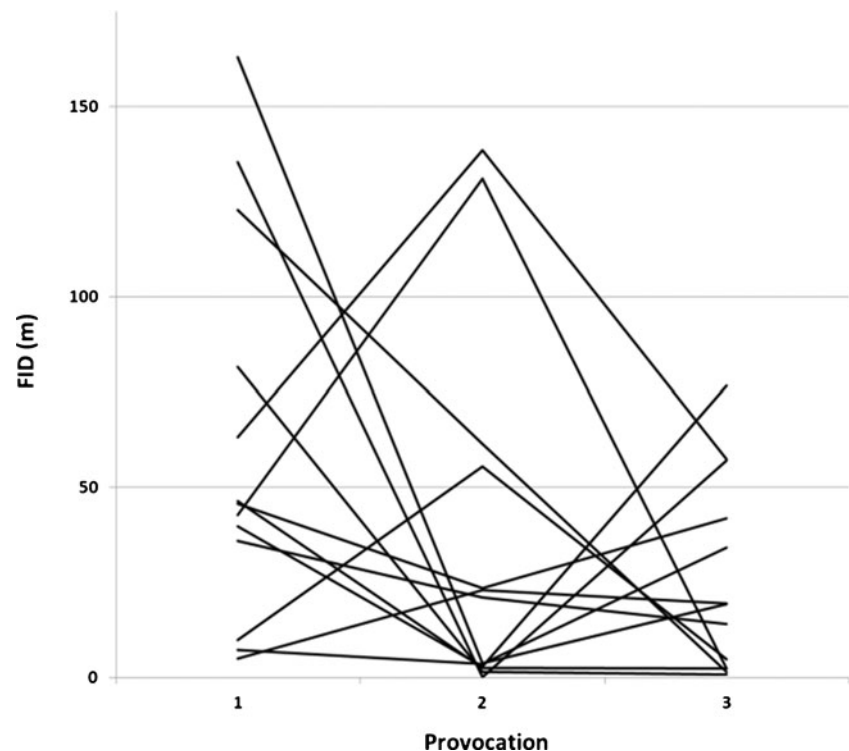
Fig. 3 Scatterplot of FID measurements from first vs. second provocations (26 nests, Kendall tau=-0.037, $P=0.81$). Successfully hatched nest, plus sign ($n=18$); failed nest, triangle ($n=8$)



FID and hatching success. We consider such an effect to be marginal, at worst, for two reasons. First, the effect size of date on FID is small (estimated total reduction of 7 m over the 3.5 week study period) compared with the range of FID values (0–170 m). This means that the distribution of FID values along the y -axis of Fig. 1 would change only

marginally when adjusted for date. Secondly, the modelled relationship between date and hatching success is, albeit non-linear, unidirectional (later measurements always associate with higher hatching probabilities, Fig. 2), while hatching success was better for intermediate FID values than for both high and low ones.

Fig. 4 FID measurements from nests with three provocations ($n=13$). Median values for provocation I 46 m, for provocation II 21 m and for provocation III 19 m. All nests except one hatched successfully



FID consistency

Unfortunately, we were unable to monitor which adult was on the nest at the moment of each provocation. Observational separation between sexes was impossible, mainly due to size overlap, large observation distances and poor light conditions. Instead, we restricted the time frame of our observations (2045–2350 hours) and assumed that this would increase the chances that the same bird was incubating during subsequent nest visits, because sexes are known to take different incubation shifts (Currie et al. 2001). From this, we conclude that the proportion of one individual sampled twice in a row probably was $\geq 50\%$. Thus, for nests sampled twice, FID consistency in individual birds would produce a gathering of data points along the diagonal of Fig. 3 and, for nests sampled three times, an abundance of horizontal line sections in Fig. 4. Neither of these patterns was expressed, nor did the analysis of variance give significant support for the FID consistency hypothesis (H_3).

Thus, we conclude that individual Eurasian curlews vary their FID behaviour between approaches of a human intruder, either under influence of internal and external factors, or as a result of a “surprise” strategy. Assuming that our observations can be transferred to behaviour in response to real predators, this “surprise” strategy could serve to prevent predators from learning to predict the behaviour of incubating adults.

Ecological implication

Haphazard FID behaviour may seem to gainsay the non-linear relationship between FID and hatching success, but it does not. First, our double and triple FID analyses only included nests that survived long enough to be approached multiple times. Nests with intermediate initial FID values were over-represented in the subsequent subsamples. Secondly, punishment for deviations from the behavioural norm is not guaranteed, which means that occasional “mistakes” (short and long FIDs) are acceptable. Instead, the combined guidelines based on our tests of the first and third hypotheses could be phrased: “Vary FID from one confrontation to the next, but avoid short and long FIDs to a great extent”. Applying this guideline, with some adjustments for date and time of the evening, probably helps farmland breeding Eurasian curlews to reduce egg predation and, thus, to improve hatching success.

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Ethical standards The authors declare that this publication complies with the current laws of the country in which the experiment was performed (Sweden).

Conflict of interest The authors declare that they have no conflict of interest.

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