

Vegetation height and egg coloration differentially affect predation rate and overheating risk: an experimental test mimicking a ground-nesting bird

H. Gillis, B. Gauffre, R. Huot, and V. Bretagnolle

Abstract: Avian eggs need to be laid in protected environments to develop and survive. Nest predation is known as the main cause of breeding failure for many birds, but nest microclimate conditions are also important for embryo development. These two selective pressures are particularly marked in ground-nesting birds. Vegetation height has been shown to be a critical factor for nest-site selection in ground-nesting birds because it can counteract predation and overheating simultaneously. It is therefore difficult to disentangle the respective influences of these risks on selection of a particular nest vegetation height. To develop a conceptual framework for understanding and predicting the relative effects of vegetation on predation and nest microclimate during a breeding season, we used vegetation height to manipulate differentially these two risks. We therefore exposed artificial nests to a wide range of vegetation heights, replicated the experimental tests during spring, and manipulated egg color to estimate predation risk. We confirmed that tall vegetation is relevant to protect unattended eggs against both risks. Whereas predation risk is stable for a given vegetation height, overheating risk presents inter- and intra-seasonal variations. Therefore, over a breeding season, for a given vegetation height, the respective strengths of the two risks are unbalanced and depends on egg coloration. The breeding strategy of ground-nesting birds thus should have been shaped by both selective pressures, but the ultimate choice may depend on the species-specific laying dates and alternative behavioral strategies for protecting the clutch. This study provides new perspectives to investigate avian parental behaviour.

Key words: nest concealment, vegetation height, egg overheating, egg predation, Montagu's Harrier, *Circus pygargus*.

Résumé : Les œufs d'oiseaux nécessitent un environnement protégé pour leur développement et leur survie. Chez la plupart des oiseaux, la principale cause d'échec d'un nid est la prédation, mais les conditions microclimatiques au nid sont également cruciales pour le développement de l'embryon. Ces deux pressions sélectives sont particulièrement marquées chez les oiseaux nichant au sol. Étant donné qu'elle peut contrer simultanément les risques de prédation et d'insolation, la hauteur de végétation s'est révélée être un facteur critique pour le choix du site de nidification chez les oiseaux nichant au sol. Il est, pour cette raison, difficile de distinguer les influences respectives de ces deux risques sur la sélection d'une certaine hauteur de végétation au nid. Afin d'établir un schéma conceptuel permettant de comprendre et prédire les effets respectifs des deux pressions au cours d'une saison de reproduction, nous avons utilisé la hauteur de végétation pour manipuler différemment ces deux risques. Nous avons donc exposé des faux nids à une large gamme de hauteurs de végétation, reproduit les tests durant le printemps et manipulé la couleur des œufs pour évaluer le risque de prédation. Nous avons confirmé qu'une végétation haute est efficace pour protéger les œufs contre les deux risques. Le risque de prédation est stable pour une hauteur de végétation donnée tandis que le risque d'insolation présente des variations inter- et intra-annuelles. Au cours d'une saison de reproduction, pour une hauteur de végétation donnée, les forces respectives des deux risques sont donc contrastées et dépendent de la couleur des œufs. La stratégie de reproduction des oiseaux nichant au sol a donc certainement été façonnée par ces deux pressions de sélection et le choix ultime d'une hauteur pourrait dépendre de la date de ponte spécifique ainsi que d'autres stratégies de protection de la couvée. L'étude ouvre de nouvelles perspectives pour l'étude du comportement parental chez les oiseaux.

Mots-clés : camouflage du nid, hauteur de végétation, insolation des œufs, prédation des œufs, Busard cendré, *Circus pygargus*.

Introduction

Terrestrial vertebrates have developed two main strategies to ensure embryo development: embryos of viviparous species develop inside the body of the mother, guaranteeing protection from hostile environments, whereas in oviparous species, females lay eggs. In that latter case, whereas females

avoid the costs of embryonic development inside their body, in return eggs must be laid in environments safe with regard to their development. Two main environmental constraints have been identified for eggs: abiotic (mainly related to physical factors such as temperature, salinity, and humidity) and biotic selective pressures (predation, parasitism) (Holway 1991; Martin 2001). Although predation is considered the

Received 10 October 2011. Accepted 24 February 2012. Published at www.nrcresearchpress.com/cjz on 11 May 2012.

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most important cause of breeding failure in birds (Ricklefs 1969), birds are endothermic organisms and therefore their eggs also require an appropriate physical environment that ensures optimal temperature conditions (Walsberg 1985; Webb 1987; Ghalambor and Martin 2002; Lusk et al. 2003). Egg hypothermia may lead to developmental abnormalities of the embryo, whereas hyperthermia may be responsible for embryo malformations or even death (Bakken et al. 1978; Conway and Martin 2000).

Birds therefore have evolved nesting strategies that respond to these selective pressures periods: to protect eggs from predation, they nest in areas which restrain nest accessibility to predators (Martin and Roper 1988; Martin 1995; Dion et al. 2000), decrease (Tinbergen et al. 1967; Dion et al. 2000) or increase (i.e., colonies) conspecific nest densities, reduce nest detection by using cryptic nests (i.e., nest concealment by vegetation structure; Schieck and Hannon 1993; Dion et al. 2000; Westmoreland and Kiltie 2007), lay mimetic eggs (Solis and de Lope 1995; Avilés et al. 2006; Westmoreland 2008), use active nest defense or mobbing (Cresswell 1997; Arroyo et al. 2001), reduce clutch size (Perrins 1977; Lundberg 1985; Gregoire et al. 2003), or maintain constant presence at nest (Kilner 2006). To avoid extreme temperatures affecting their eggs, birds have also developed various strategies, including selecting nest sites that reduce heat stress (e.g., structural vegetation cover; Colwell 1992; Lusk et al. 2003; Wells and Fuhlendorf 2005), building nests that reduce temperature variations either through particular shapes (Ar and Sidis 2002; Deeming 2002) or nest materials (e.g., Howey et al. 1984; Mayer et al. 2009), and keeping permanent presence at nest (Kilner 2006). Additionally, the white ancestral color of eggs (Kilner 2006) could reduce overheating by reflecting solar radiation (Castilla et al. 2007). However, whereas concealment and parent presence at nest may protect eggs from both predation and overheating, egg coloration interacts with both risks but in opposite ways and thus represents an evolutionary trade-off (Bakken et al. 1978): mimetic-colored eggs reduce predation risk (e.g., Weidinger 2001) but may increase overheating risk in comparison with white eggs for which the reverse consequences are expected.

Compared with the more commonly observed tree-nesting and cavity-nesting birds, ground-nesting species face higher risks of predation (Ricklefs 1969) and overheating (Deeming 2002) because they usually build rudimentary nests at exposed sites that makes unattended eggs more vulnerable (Bakken et al. 1978). Vegetation height has been identified as a critical determinant in the nesting strategy of ground-nesting birds (Helzer and Jelinski 1999), e.g., those breeding in steppe or agricultural landscapes. Because nesting in tall vegetation (thus increasing nest concealment) has the potential to counteract both predation and overheating risks (Colwell 1992; Lusk et al. 2003), it is therefore difficult to disentangle the respective influences of these two risks on microhabitat selection, and ultimately, the evolutionary forces that have shaped particular breeding strategies. As most ground-nesting birds lay mimetic eggs (Magige et al. 2008), one may conclude that predation or camouflage against predators is the most important evolutionary pressure that has shaped the nesting strategy of ground birds (Westmoreland and Kiltie 2007). However, some ground-nesting bird species lay white eggs (e.g., some Anatidae),

suggesting that, in some cases, overheating risk may have been important in shaping breeding strategies.

Many studies have attempted to estimate either predation risk or overheating risk using artificial nests and eggs. In contrast, here we use an experimental design to identify the respective strength of the two selective pressures, predation and overheating, on egg survival over time to propose a conceptual model that embodies the relative importance of these pressures across a breeding season. Therefore, we used vegetation growth during spring as a way to manipulate differentially the two risks. In temperate ecosystems, vegetation height and solar azimuth both gradually increase with season (i.e., spring). Eggs on the ground thus should experience different durations of sun exposure depending on vegetation height relatively to calendar date. By replicating along the breeding season an experiment in which vegetation height was controlled and almost identical in range between replicates, we exposed artificial nests to a constant gradient of predation risk (i.e., varying only with vegetation height) while the overheating risk increased (i.e., with increasing solar azimuths). In addition, we manipulated egg color to estimate predation risk. We used the breeding strategy of the Montagu's Harrier (*Circus pygargus* (L., 1758)) as a conceptual guide for our experimental design. This species lays white eggs mainly in wheat crops (Arroyo et al. 2004) and performs only female brooding. Along a gradient of vegetation height over the course of two complete breeding seasons, predation rate of artificial nests was recorded with white or mimetic dummy eggs while temperature of artificial nests was recorded with data loggers. We first tested that (i) egg predation and overheating risk decrease with vegetation height, and then predicted that (ii) mimetic eggs will be less depredated than white ones, and that (iii) predation risk at a given vegetation height will be constant over a breeding season while overheating risk will increase.

Materials and methods

Experimental design

Experiments were undertaken in an intensively managed farmland landscape located in the region of Deux-Sèvres (46°11'N, 0°28'W), central-western France, during the springs of 2009 and 2010 (for a full description of the study site see Millon and Bretagnolle 2008). In both years, we performed three sessions (for each experiment, i.e., overheating and predation) from the end of April to the end of June to encompass the complete breeding season and a complete range of solar azimuth angles and crop heights. Experimental plots were chosen according to their vegetation height and their crop type (only winter cereals that presented similar crop densities). Vegetation heights were classed in 10 cm inclusive categories and ranged from 30–39 to 120–129 cm. For each session, we tried to maximize the range of vegetation heights at experimental nests, depending on seasonal growth of wheat which affected height availability. Predation and overheating experiments were performed on different dummy nests but in the same plots. A total of 123 and 108 nests were set for the predation and the overheating experiments, respectively (see Appendix A, Tables A1 and A2).

Artificial nests

Artificial nests were standardized: they were made by trampling vegetation and creating a 50 cm diameter “hole” in the crop, were settled at least 20 m away from the border of the field, 2 m from tractor trails to avoid mammalian predators that favor tracks, at least 200 m away from any building (village, farm), and at least 100 m from woods and hedgerows to limit variations in predator community and minimize tree shadow on recorded temperatures.

Predation experiment

In each artificial nest, we placed one white plaster egg (plaster eggs were obtained by using an infertile Montagu's Harrier egg to shape the mold). Eggs were marked with a small symbol (applied with pencil) facing towards the soil to detect whether the dummy egg was manipulated by a predator. Eggs were exposed for 7 days and checked 24 h after installation and subsequently every 48 h. Regular nest visits were performed to avoid several predation events on the same nest. Installation and visits were performed at dusk to avoid visual detection by bird predators and boots were worn to prevent spread of human odors for mammalian predators. Nests were considered depredated if the egg had disappeared, showed predation marks made by teeth, beaks or claws, or had been manipulated (as assessed by the mark on the egg), and the trial was stopped for this particular nest. If “depredated” eggs were still in the nest, we tried to identify the predator type (bird versus mammal) using predation marks left on the plaster egg.

In 2009, a single nest with a white egg was placed in each selected plot ($n = 51$). In 2010, to assess differences in egg detectability and predation in relation to egg coloration, we also placed 29 artificial nests with one mimetic plaster egg (painted in khaki green to mimic wheat color) among the 72 experimental plots chosen for white dummy eggs. The color of mimetic eggs was chosen in relation to eggs of the Little Bustard (*Tetrax tetrax* (L., 1758)), a ground-nesting species also breeding on the study area (but in different crops: alfalfa and grasslands) that lay eggs of approximately the same size as our plaster eggs. These additional nests were set at least 50 m away from the “white egg” nests and were only placed in low vegetation categories (from 30–40 to 60–70 cm) to maximize predation risk (see Appendix A, Table A1). To check differences in egg perception by predators, we quantify ultraviolet (UV) reflectance chroma percentage (i.e., measure of the “purity” or “saturation” of the color; Endler 1990) of both egg colors (three eggs replicates per color) with a handheld reflectance spectrophotometer operating at wavelengths of 300–700 nm (USB2000; Ocean Optics, Inc., Dunedin, Florida, USA).

Overheating test

To obtain a proxy of microclimate conditions (i.e., temperatures) in different vegetation heights, we used disc-shaped temperature data loggers (DS1921G Thermochron® iButton; Maxim, Sunnyvale, California, USA) programmed to record temperature every 3 min with 0.5 °C precision. For each session, loggers were mounted on a nail and stuck in the ground of an empty artificial nest (same plots but different nests than the ones used in the predation experiment to avoid loggers being stolen by egg predators, especially corvids) for 4 days.

Loggers were not in direct contact with soil but on a small layer of trampled wheat. Tests were only performed when weather was sunny (and weather forecast were such for the next 4 days), i.e., when overheating risk is maximal (Appendix A, Table A2). To evaluate the effect of extreme microclimate conditions, we only used data of the warmest 24 h among the four recording days. We choose to determine a temperature and exposure duration value to estimate a threshold for which nest microclimate conditions became unfavorable for nesting and thus when overheating risk could be considered. Therefore, we considered that a logger recording temperatures ≥ 41 °C for ≥ 15 min (five successive records) would reach this threshold. These values (i.e., temperature and duration) were not arbitrarily chosen because in most species, egg exposition to 41 °C for a few minutes is lethal (off-bout durations in several species: Conway and Martin 2000; lethal egg temperature: Webb 1987; Magige et al. 2008). Additionally, to improve robustness of the analysis and to reduce potential bias owing to interspecific variations in lethal egg temperature and (or) exposure duration, we also tested other threshold temperatures and durations. Hence, we explored exposure time (daily cumulative number of records) at temperature thresholds from 30 to 55 °C on the session involving the widest range of vegetation height categories (second session in 2010).

For each session, we replaced julian date by solar radiation because we assumed that the latter would better explain differences in overheating probability and unveil potential intra-seasonal variations. We recovered a solar radiation index to account for the increase in solar azimuth with season and therefore radiation. The global solar radiation at ground level ($\text{kW}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$) of Poitiers (i.e., the closest location available, ca. 50 km away from study plots) was thus calculated with the software CalSol (INES, Le Bourget du Lac, France) for the warmest day of each session.

Statistical analyses

Statistical analyses were performed with R version 2.12.1 (R Development Core Team 2010). We used generalized linear models (GLM) to analyze the effect of vegetation height on white-egg predation and overheating probabilities. A generalized linear mixed model (GLMM) was used to test the effect of egg color on predation probability. We indeed accounted for the fact that the two nests (with different egg colors) were in the same field. Therefore, field identity was treated as a random effect in the latter case. We tested a priori hypotheses and therefore ran complete models without performing model selection.

In the first analysis, “white-egg predation”, the dependent variable was coded as a binomial variable (predation was considered after 7 days exposure). Independent variables considered in the model (with logit-link function) were vegetation height (cm) and session date (julian days, i.e., 1 = 1st January) as continuous variables, and year as a two-level factor (2009 or 2010). In the second analysis, differences in predation rate according to egg color was investigated by including only plots with both egg colors in the model ($n = 29$). Apart from egg coloration (a two-level factor: white or green), fixed effects included in the model were those found to have significant effects in the first analysis (i.e., “white-egg predation” analysis).

Table 1. Generalized linear model investigating predation rate of white eggs ($n = 123$).

Variable	Estimate	SE	z	p
Intercept (2009) ^a	0.2	0.36	0.56	0.57
Vegetation height	-1.64	0.46	-3.59	<0.001***
Year (2010)	0.07	0.44	0.13	0.90
Session	-0.05	0.21	-0.22	0.82
Vegetation height \times year (2010)	1.24	0.55	2.27	0.02*
Vegetation height \times session	0.36	0.26	1.35	0.18

Note: Estimated coefficients (estimate), standard error around estimation (SE), statistic z , and p values are presented. *, $p < 0.05$; ***, $p < 0.001$.

^a2009 is considered to be the reference year.

Finally, to analyze overheating data, the temperature values were converted into a binomial variable, “overheating”, coded as 1 if the logger recorded temperatures ≥ 41 °C for ≥ 15 min, 0 otherwise. Vegetation height and the index of solar radiation (as continuous variables) and year (as a two-level factor) were the independent variables.

In each analysis, we included all simple effects, as well as second-order interaction terms involving vegetation height, to test our hypotheses.

Results

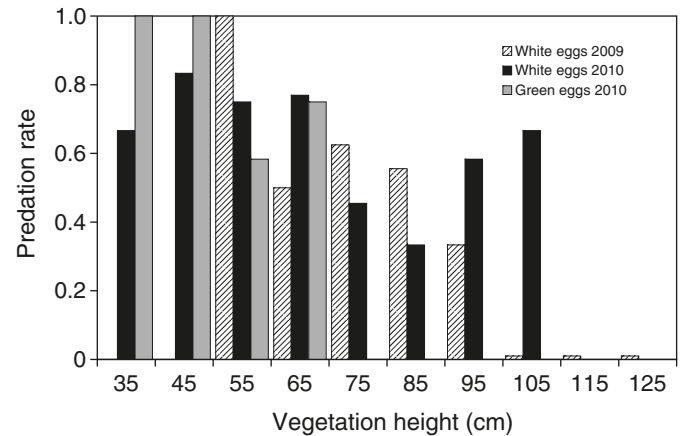
Predation rate

Of the 123 artificial nests with white eggs, 67 were depredated (54.5%): 45.1% ($n = 23$) in 2009 and 61.1% ($n = 44$) in 2010. Among these, 38 nests (56.7%; 16 in 2009 and 22 in 2010) were retrieved empty and causes of predation were therefore not identifiable. In the remaining 29 “depredated” nests, the eggs were still present and the predator could be identified in 21 of 29 nests: 18 (85.7%, 4 in 2009 and 14 in 2010) were depredated by corvids and 3 (14.3%, none in 2009 and 3 in only tall vegetation in 2010) by mammals. Given the high number of unknown predators, depredated nests were pooled for subsequent statistical analyses regardless of the predator.

White-egg predation rate was affected by vegetation height, year, and their interaction (Table 1). Predation decreased significantly with vegetation height in both years, but the slope was weaker in 2010 (Table 1; Fig. 1). This year difference might be due to differences in tested vegetation heights between years. We thus performed a GLM (with identity-link function) to investigate temporal differences in tested heights by examining the effects of year, session, and their interaction. Tested vegetation heights were indeed higher in 2009 (87 ± 19 cm, mean \pm SD) than in 2010 (71 ± 19 cm) ($F_{[1,121]} = 12.9$, $p < 0.001$), and they logically increase with session because of wheat growth (i.e., with season, $F_{[1,121]} = 18.36$, $p < 0.001$; no significant interaction was found).

Egg color also affected the probability of a nest being depredated at low vegetation (30–70 cm). Twenty-two of 29 nests with white eggs (76%) were depredated compared with only 15 of 29 mimetic eggs (46.7%). As the “egg-color” experiment was only performed in 2010, year was not included in the model. Only vegetation height, egg coloration, and their interaction therefore were tested. At low vegetation, green mimetic eggs were less depredated than white ones (Table 2). Predation probability of white eggs remained

Fig. 1. Predation rates as a function of vegetation height. Hatched bars represent predation rates of white eggs in 2009, black bars represent predation rates of white eggs in 2010, and grey bars represent predation rates of green mimetic eggs in 2010. For white eggs in 2009, predation rates were monitored ($n = 11$ nests) in very high vegetation categories (from 105 to 125 cm) but were null. Otherwise, absence of bars means the absence of sampling in corresponding vegetation height.



high, whereas predation probability decreased with vegetation height for mimetic green eggs, as shown by a significant interaction between egg color and vegetation height (Table 2; Figs. 1, 3a–3c). For instance, at a vegetation height of 60–70 cm, predation risk of mimetic eggs was below 20%, whereas it was over 80% for white eggs (Figs. 3a–3c). Spectrophotometry shows that green eggs reflect UV lights less than white ones ($19.5 \pm 0.07\%$ (chroma means \pm SE) for green eggs versus $13.5 \pm 0.12\%$ for white eggs).

Overheating risk

As expected, there were differences in temperatures between low and tall vegetation (Fig. 2a). Temperatures higher than 50 °C were recorded in 30–40 cm vegetation, whereas at 100–110 cm vegetation, the maximal recorded temperature was only 35 °C (Fig. 2a). Overheating risk (i.e., unfavorable nest microclimate conditions) appeared much stronger in 2010 than in 2009, as revealed statistically by the difference in intercept in the year effect (Table 3). But for both years, the risk obviously increased with solar radiation (Table 3). However, in 2009, vegetation height did not affect recorded temperatures, whereas in 2010, overheating risk decreased significantly with vegetation height (Table 3). Here again, we suspect differences in tested vegetation heights between

Table 2. Generalized linear mixed model investigating the effect of egg color on predation rate in low vegetation categories ($n = 58$).

Variable	Estimate	SE	z	p
Intercept (white) ^a	5.89	2.09	2.81	0.005**
Vegetation height	0.02	2.23	0.01	0.99
Color (green)	-5.13	2.12	-2.42	0.01*
Vegetation height \times color (green)	-5.30	2.562	-2.10	0.03*

Note: Estimated coefficients (estimate), standard error around estimation (SE), statistic z , and p values are presented. The plot identity was treated as a random effect. *, $p < 0.05$; **, $p < 0.01$.

^aWhite is considered to be the reference color.

years to be the main reason for the difference in overheating risk between years (see section “predation rate” in the Results).

We used the data from the second session of 2010 to illustrate graphically exposure time above a given threshold temperature (from 30 to 55 °C) for any given vegetation height in the range 35–105 cm (Fig. 2*b*). As expected, exposure time decreases with vegetation heights but does so more rapidly as the temperature threshold increases (Fig. 2*b*). At 41 °C (i.e., the lethal egg temperature), exposure time was low except for very low vegetation height (below 60 cm).

Contrasting predation and overheating risks across spring

Using model predictions obtained from the two experiments, we explored graphically predation and overheating model outputs (GLMs and GLMM) according to vegetation height, egg color, and season as a way to build a conceptual representation of the relative importance of predation and overheating pressures over a breeding season (Figs. 3*a*–3*c*). Data from the year 2010 was used to model both risks. Under temperate latitudes, Figs. 3*a*–3*c* suggests that early in the breeding season (i.e., at low solar radiation), predation risks for both white and mimetic eggs could be more important than overheating risk (Fig. 3*a*). With the advance of spring, overheating risk increases with solar radiation, and at some undetermined stage in the season, overheating may exceed predation risk (Figs. 3*b*, 3*c*). Late in the season therefore, only very tall vegetation may reduce overheating risk (Fig. 3*c*).

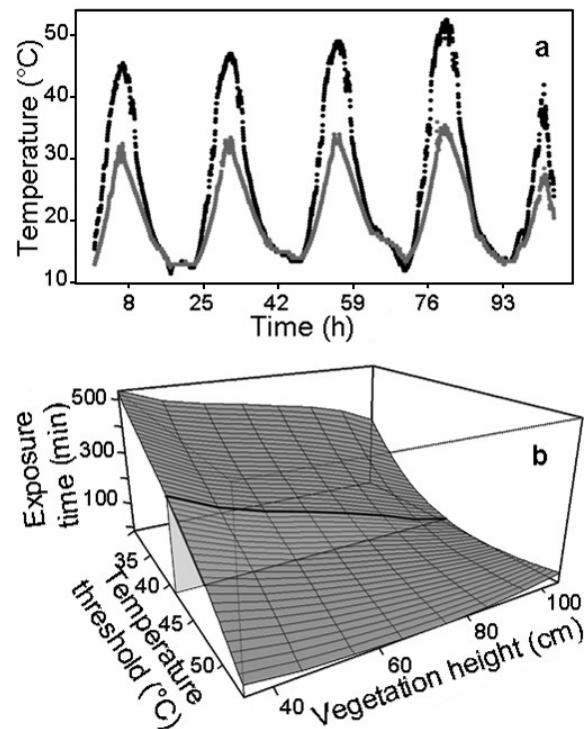
Discussion

In this study, we demonstrated that for ground nests, predation and overheating risks decrease with vegetation height at the nest. We also validated that egg coloration influences predation rate. Predation risk is constant over a breeding season, whereas overheating risk presents inter- and intra-seasonal variations. Thus, we highlighted the unbalanced aspect of the relative importance of the two selective pressures over a breeding season at least in the temperate environment.

Possible experimental bias

The use of artificial nests and dummy eggs to measure predation rates has long been disputed (Major and Kendal 1996; Moore and Robinson 2004), because of both positive (adults could defend nests: Davison and Bollinger 2000) and negative (adults could unveil nest location through their activity: Zuria et al. 2007; Moore and Robinson 2004) biases.

Fig. 2. Temperature raw data of the intermediate session in 2010 (21–25 May). (a) Recorded temperatures of two data loggers placed in low vegetation (30–40 cm; black circles) and in tall vegetation (100–110 cm; grey circles). (b) Daily exposure time (cumulative number of records) as a function of different threshold temperatures (30–55 °C) and vegetation height. For information, the grey vertical plane in *b* represents the critical temperature (41 °C) of most real eggs.



Other biases have been identified, e.g., differences in local predator species preying upon artificial versus natural nests (Martin 1987; Mezquida and Marone 2003), differences in nest and egg realism, egg type (plaster, plasticine, real quail eggs), and egg size (Bayne et al. 1997; Davison and Bollinger 2000; Dion et al. 2000). There is no consensus on how to conduct this type of experiment. However, as our aim was not to mimic real predation rates but only to detect the influence of nest characteristics (i.e., in absence of parents: Gregoire et al. 2003), we chose to use artificial nests and eggs to measure predation rates relative to nest concealment levels regardless of adult behavior (see also Howey et al. 1984; Davison and Bollinger 2000; Dion et al. 2000).

Similarly, temperatures measured by nest data loggers do not correspond to core egg temperatures (Webb 1987). Real

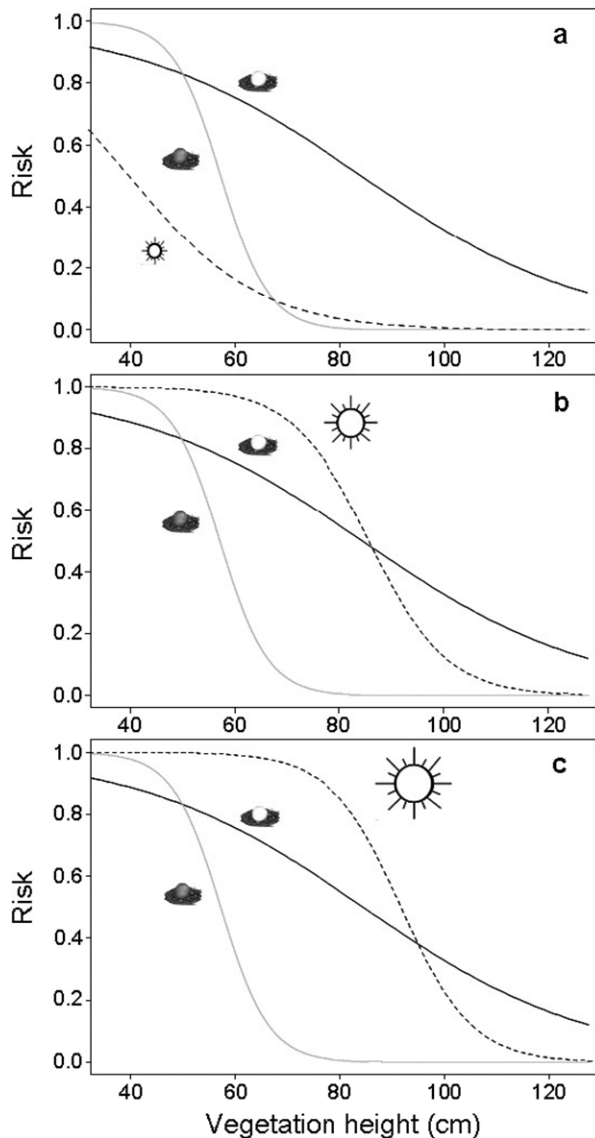
Table 3. Generalized linear mixed model investigating overheating risk ($n = 108$).

Variable	Estimate	SE	z	p
Intercept (2009) ^a	-2.87	0.78	-3.67	<0.001***
Vegetation height	0.35	0.75	0.47	0.64
Solar radiation	1.94	0.52	3.68	<0.001***
Year (2010)	3.02	0.90	3.34	<0.001***
Vegetation height \times year (2010)	-2.89	1.07	-2.69	0.008**
Vegetation height \times solar radiation	-0.53	0.46	-1.14	0.25

Note: Estimated coefficients (estimate), standard error around estimation (SE), statistic z , and p values are presented. **, $p < 0.01$; ***, $p < 0.001$.

^a2009 is considered to be the reference year.

Fig. 3. Conceptual representation of the relative importance of predation and overheating pressures over a breeding season using models' predictions for 2010. (a) First, (b) second, and (c) third sessions (gradient of solar radiation). Black and grey solid lines represent predation risk for white eggs and mimetic eggs, respectively. Broken lines represent overheating risk. The modelled predation rate for mimetic eggs was extrapolated to all the range of vegetation. Risk represents predation rate or overheating risk predictions from the best fitted models.



temperature experienced by the embryo may differ because neither heat transfer characteristics of the egg nor egg coloration and adult incubation behavior were taken into account in our experiment. However, nest microclimate measured here must influence egg temperature. We modeled overheating risk using a temperature threshold of 41 °C (15 min duration), as this temperature is usually lethal for bird embryos (Webb 1987). However, using different temperature thresholds have led to similar results (Fig. 2b): exposure time decreased monotonically with increasing temperature threshold and increasing vegetation height further reduced exposure time. Additionally, we did not measure differences in overheating between white and mimetic (green or dark) eggs. However, there is some evidence that pigmented eggs get warmer than nonpigmented ones (Montevicchi 1976; Underwood and Sealy 2002; Magige et al. 2008; but see Westmoreland et al. 2007).

Obviously, as mentioned earlier, parental incubation behaviour (i.e., off- and on-bout durations and frequencies) play an important role in nest protection against both risks (Conway and Martin 2000). However, in this study we focused on the efficiency of concealment offered by vegetation to protect nest from predation and overheating regardless of parental behaviour. We believed that parental incubation behaviour could be influenced by the degree of nest concealment, a hypothesis already suggested by Conway and Martin (2000).

Therefore, we are confident that our experimental design provided a conceptual representation of the relative importance of predation and overheating pressures over a breeding season and along a vegetation height gradient for a ground-nesting bird in a temperate environment.

Predation risk

Our study indicates that predation rate did not vary along a breeding season (no intraseasonal variations) but did so between years. The former result is consistent with previous studies (Bayne et al. 1997; Burhans and Thompson 1998), suggesting that the predator community does not change over a breeding season (Bayne et al. 1997). However, between-year variations suggest that some differences in predator community or behavior could have occurred between our 2 years of experimentation. Actually, this year effect could result from differences in tested vegetation heights between years, but also from three particular cases of mammalian predation in tall vegetation in 2010. However, the strong negative relationship between observed predation rate and vegetation height suggests that the predator community involved is mainly composed of avian predators because vege-

tation height should have less or no effect on nest detectability by mammals. These results are consistent with the predator marks on the eggs. Moreover, our experimental results agree with previous studies that suggested concealment is relevant where avian predators are dominant (Sugden and Beyersbergen 1986, 1987; Clark and Nudds 1991; Colwell 1992). In particular, Sugden and Beyersbergen (1987) studied predation on duck nests by American Crow (*Corvus brachyrhynchos* Brehm, 1822) according to concealment (vegetation density, height, and type). They found a negative effect of vegetation height on predation rate. However, in their study, different vegetation heights were associated with different vegetation densities and types, a possible bias that we avoided by using a single vegetation type and density.

We also found a significant difference in egg predation based on egg color. White eggs (i.e., the supposed ancestral egg color; Kilner 2006) may be less costly to produce than pigmented ones (Moreno and Osorno 2003). However, most ground nesters choose to pay the energetic cost of egg pigmentation (Kilner 2006) to reduce predation risk (especially by avian predators: Castilla et al. 2007; Westmoreland and Kiltie 2007). Our experiment further revealed an interaction between vegetation height and egg coloration (a result also found by Castilla et al. 2007). At low vegetation height (<50 cm), predation risk is high for both colors, suggesting that neither color nor height are sufficient to avoid nest predation. However, above 60 cm, predation rate of mimetic eggs falls under 0.5; this particular threshold is reached for white eggs at 85 cm. Hence, nest concealment appears to be more efficient in providing protection against predation for mimetic eggs than for white eggs. This matches previous studies that also showed a lower detectability of mimetic eggs by predators (Solis and de Lope 1995; Castilla et al. 2007; Avilés et al. 2006), especially by avian ones (Castilla et al. 2007). Additionally, differences in UV reflectance confirm that white eggs are more detectable by avian predators than green ones (i.e., birds in contrast with mammals have retinal photopigments that allow for ultraviolet vision; see Jacobs 1992). Our results suggest that egg coloration is less efficient than nest concealment to protect unattended eggs from predators (Underwood and Sealy 2002; Kilner 2006), because at very low vegetation (low nest concealment), mimetic and white eggs have very high predation rates (close to 1).

Overheating risk

Our results support the hypothesis that structural cover (in our case, vegetation height) could influence nest microclimate conditions, in particular temperature by shading eggs, and therefore ultimately may affect breeding success (Lusk et al. 2003). When parent brooding behavior is interrupted, eggs are exposed to sunlight: in such situation, vegetation cover could maintain nest temperatures lower than those on bare ground and thus may provide a more stable thermal environment for developing embryos (Lusk et al. 2003). As expected, we found that overheating risk increased with season (i.e., solar radiation) and decreased with vegetation height. However, in 2009, very few nest temperatures ≥ 41 °C were recorded in any session, hence no effect of solar radiation or vegetation height could be statistically detected. This may be as a result of a wet spring (soil moisture might have reduced the nest temperature). Indeed, in spring

2009 (from 27 April to 8 June, i.e., respectively, the earliest start and later end of the overheating experiment in both years), precipitations were more important (110 mm) than in spring 2010 (39 mm). As a consequence and a second reason to find this result, taller vegetation plots were sampled in 2009 than in 2010, where a drier spring led to lower vegetation. Thus, in contrast to predation risk, overheating risk exhibited both inter- and intra-seasonal variations. In 2010, if overheating risk was minimal early in the breeding season, keeping overheating risk low required very tall vegetation at the end of the season. On the other hand, in temperate environments (where this experiment was carried out), breeding very early in the season (i.e., when solar azimuth angle is low) appears to be a good strategy to avoid overheating.

The between-year variation in overheating risk suggests that overheating may highly depend on climate conditions and wheat growth. In dry and warm years, overheating risk may be high because of high temperatures but also because of short vegetation. In the global warming context (higher temperatures and unpredictable precipitations), the importance of overheating risk for vegetation height selection would be enhanced.

Relative roles of predation and overheating risks

We believe our work sheds light on the evolution of behavioral and life-history traits in ground-nesting birds. Overall, in any system, because predation risk often may be constant and overheating risk may change over a breeding season, the relative importance of these two risks are prone to change over a breeding season. These changes may have different consequences on the incubation effort (i.e., off-bout durations), nest defense (i.e., mobbing or lure-predator), and nest-site selection behaviors of birds according to their egg color and breeding timing. By laying mimetic eggs, detection by predators is reduced, but the risk of overheating could be enhanced (at least at temperate latitudes). The majority of ground-nesting birds lays mimetic eggs (Magige et al. 2008), and thus could face higher overheating risk (depending on egg shell pigments: Bakken et al. 1978; egg-shell IR reflectance: Westmoreland and Kiltie 1996) than species that lay white eggs. Our study underlines two possible strategies to counteract this risk: (1) conceal nest in tall vegetation or (2) breed as early as possible in the season to avoid high solar radiation. Most ground-nesting birds actually conceal their nests in dense and (or) high vegetation cover (Colwell 1992) as do the Little Bustards. A third and complementary strategy, unexplored here, could be maintaining constant presence at nest or reducing off-bout durations. Although birds laying white eggs are mainly cavity nesters (Westmoreland and Kiltie 1996; Blanco and Bertellotti 2002), which can be regarded as an extreme case of nest concealment, a few cryptic ground-nesting species also lay white eggs. These species could protect their eggs from predators by maintaining constant presence at the nest (which necessitates biparental brooding), reducing off-bout durations and (or) frequencies, or by concealing eggs in tall vegetation (the situation that we explored in this study). Actually, ground-nesting birds laying white eggs also could protect their eggs against predators by defending the brood. This probably explains why the African Ostrich (*Struthio camelus* L., 1758) lay white eggs on bare ground (Magige et al. 2008).

Montagu's Harriers, by laying white eggs, do not pay the energetic cost of producing colored eggs. The present study, however, suggests that laying white eggs implies the selection of tall vegetation for nesting. This may represent a strong constraint early in the breeding season when females must establish their nests in crops that are around 80 cm high (to limit the main predation risk). Consequently, this pronounced habitat selection reduces suitable habitat availability. Later in the season, they must select habitats at least 95 cm high (to limit both risks but especially overheating); however, because wheat has grown, they may seem less selective according to vegetation height. This selection pattern according to vegetation height actually is observed in this species (V. Bretagnolle, personal communication). Interestingly, this species does not perform biparental brooding to protect their eggs from predators: only the female attends the nest and the male brings her food, which she eats most of the time out of the nest. However, this species further reduces this risk by its ability to defend the brood against predators, even using social defence because the species is colonial (for an experimental demonstration of colonial defence see Arroyo et al. 2001). White eggs may have another advantage: parents may benefit from locating the nest more easily and thus be able to nest in such a uniform farmland landscape (wheat crop; see Underwood and Sealy 2002; Avilés et al. 2006).

Acknowledgements

We thank M. Guérif, J.L. Martin, and A. Millon for helpful suggestions. Many people helped with egg confection and fieldwork, especially V. Lecoustre, R. Guirat, and E. Baron, and are kindly thanked. We also thank J. Hennicke for valuable comments on the manuscript and for improving the English. ANR BIODIVAGRIM and ANR-ERANET ECOCYLCES partly funded this study. H.G. also wishes to thank the ED "Diversité du Vivant" for funding her Ph.D.

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Appendix A

Appendix tables appear on the next page.

Table A1. Plot sample sizes of the predation experiment for each vegetation height category, session, and year.

Year	Session	Date	Vegetation height categories (cm)									Total	
			30-39	40-49	50-59	60-69	70-79	80-89	90-99	100-109	110-119		120-129
2009	1	6-13 May			3	4	3	3	3				16
	2	20-27 May				3	3	3	3	3			15
	3	1-8 June			3	1	2	3	3	3	2	3	20
		Subtotal	0	0	6	8	8	9	9	6	2	3	51
2010	1	3-10 May		5 (5)*	9 (9)*	3	3	4	3				27
	2	21-28 May	3 (3)*	1 (1)*	3 (3)*	5 (4)*	5	4	4	2			27
	3	3-10 June				5 (4)*	3	4	5	1			18
		Subtotal	3	6	12	13	11	12	12	3	0	0	72
	Total	3	6	18	21	19	21	21	9	2	3	123	

*Represents the number of plots where a pair of colored eggs was placed.

Table A2. Plot sample sizes of the overheating experiment for each vegetation height category, session, and year.

Year	Session	Date	Vegetation height categories (cm)									Total	
			30-39	40-49	50-59	60-69	70-79	80-89	90-99	100-109	110-119		120-129
2009	1	5-8 May			3	4	3	3	3				16
	2	19-23 May				3	3	3	2	3			14
	3	1-5 June						3	3	3	2	3	14
		Subtotal	0	0	3	7	6	9	8	6	2	3	44
2010	1	27-30 April	3	3	4	4	3	3					20
	2	21-25 May	3	1	2	5	5	4	4	2			26
	3	4-8 June				5	3	4	5	1			18
		Subtotal	6	4	6	14	11	11	9	3	0	0	64
	Total	6	4	9	21	17	20	17	9	2	3	108	