Can hedgerow management mitigate the impacts of predation on songbird nest survival?

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Abstract

Nest predators can have significant impacts on songbird reproductive success. These impacts may be amplified by habitat simplification and here we test whether sympathetic management of farmland hedgerows can reduce nest depredation, especially by corvids. We test whether songbirds select nest sites according to structural features of hedgerows (including nest visibility and accessibility), and whether these features influence nest predation risk. Songbirds selected nesting sites affording higher vegetation cover above the nest, increased visibility on the nest-side of the hedgerow and reduced visibility on the far side of the hedge. Nest survival was unrelated to corvid abundance and only weakly related (at the egg stage) to corvid nest proximity. Nest survival at the chick stage was higher where vegetation structure restricted access to corvid-sized predators (averaging 0.78 vs. 0.53), and at nests close to potential vantage points. Overall nest survival was sensitive to hedgerow structure (accessibility) particularly at low exposure to corvid predation, while the overall impact of corvid exposure was dependent on the relationship involving proximity to vantage points. Nest survival over the chick stage was much higher (0.67) in stock-proof, trimmed and mechanically cut hedgerows, (which tended to provide lower side visibility and accessibility) than in recently laid, remnant or leggy hedgerows (0.18). Long-term reductions in the management of British hedgerows may therefore be exposing nesting songbirds to increased predation risk. We recommend regular rotational cutting of hedgerows to maintain a dense woody structure and thereby reduce songbird nest predation.

Keywords: nest predation, corvids, farmland birds, predator-habitat interactions, farmland conservation

1. **Introduction**

Nest predation is the main cause of nestling mortality in birds (Ricklefs, 1969), with losses to predators approaching 69% in some altricial species (Remes and Martin, 2002), sometimes leading to population sinks (Rogers et al., 1997). Species suffering high levels of nest predation have evolved behavioural and life-history strategies to minimise predation risk (Dunn et al., 2010; Eggers et al., 2005a; Martin, 1995) such as shorter nestling periods and multiple broods each year (Martin, 1995). Parents tend to reduce investment in a nest when predation risk is high, through reduced egg size (Fontaine and Martin, 2006), clutch size (Julliard et al., 1997) and clutch mass (Fontaine and Martin, 2006). High levels of activity around the nest may attract predators and parents often reduce activity when the risk of nest predation is high (Conway and Martin, 2000; Dunn et al., 2010; Eggers et al., 2005b).

Behavioural adjustment by adult birds to reduce nest predation risk (Dunn et al., 2010; Eggers et al., 2005b) is dependent not only on predator activity, but also on the cover around the nest and the availability of food for chicks (Eggers et al., 2008). In areas where food abundance is low, high corvid abundance is associated with reduced nestling growth in a farmland songbird (Dunn et al., 2010). Ecological factors affecting the likelihood of nest predation include nest density (Cresswell, 1997; Schmidt and Whelan, 1998), predator abundance and nest type (i.e. cavity vs. open-cup, Fontaine et al. 2007). Nests that are more visible are more likely to be depredated at the egg stage (Martin et al., 2000; Matessi and Bogliani, 1999). Predation rates tend to increase with reduced vegetation cover, vegetation height, and nest height (e.g. Cresswell 1997), all features that are likely to interact to influence nest detectability and accessibility (Cresswell, 1997), although there is no evidence for nest size affecting predation risk (Weidinger, 2004). Factors affecting nest predation risk may differ between predators: corvids are more likely to depredate poorly concealed nests, whereas well concealed nests are more likely to suffer depredation by rodents (Weidinger, 2002). There may be a trade-off for nest survival between nest concealment and the ability of parent birds to detect an approaching predator (Cresswell, 1997; Gotmark and Post, 1996; Weidinger, 2002).

Corvids are important nest predators, especially in farmland environments (Andren, 1992; Luginbuhl et al., 2001), and their populations in the UK have increased steadily since the 1960s, coincidental with the declines in many farmland songbirds (Gregory and Marchant, 1995). Whilst no clear link has been found between declining abundance of farmland songbirds and increasing abundance of corvids (Gooch et al., 1991; Madden et al., 2015; Newson et al., 2010; Thomson et al., 1998), local examples have shown predation impacts through farming management. Organic farms harbour more corvids, but fewer songbirds (Gabriel et al., 2010) and gamebird management (corvid control and sympathetic habitat management) is associated with higher nest survival and higher breeding densities of songbirds (Stoate and Szczur 2001, White et al. 2008, White et al. 2014). An extensive analysis of song thrush and blackbird nest record cards found fine-scale spatial associations between corvid densities and nest survival rates (Paradis et al., 2000). That corvids are responsible for high numbers of nest losses is indisputable (Andren, 1992; Bradbury et al., 2000; Luginbuhl et al., 2001), and the linear nature of hedgerows in farmland landscapes may increase the risk of nest depredation (Chamberlain et al., 1995). Legal control of corvids is advocated and practiced for game management, and specifically for songbird conservation, but the control of one native species to benefit another is expensive and not universally accepted as a management practice. Thus, reducing corvid nest predation through habitat management would be desirable if possible, and, alongside measures to increase food availability during summer and winter, providing productive nesting habitat might help reverse population declines amongst some farmland bird species (Fuller et al., 1995). To our knowledge, no previous study has investigated impacts of hedgerow structure or management on nest predation risk in songbirds. The aims of the current study were (1) to identify the structural features of farmland hedgerows that influence nest site selection by songbirds, (2) to assess the relative importance of hedgerow structure and corvid abundance / proximity in determining nest predation risk, and (3) to identify aspects of hedgerow management that reduce nest predation risk.

2. Methods

2.1 Study sites

The fates of 399 songbird nests were monitored during April-July 2003 and 2004 across 11 farmland sites in total across two regions in eastern England (five in Cambridgeshire, Bedfordshire and Hertfordshire, and six in Leicestershire and Rutland). Not all sites were monitored in both years: 10 sites (5 in each region) were monitored in 2003 and seven sites (3 and 4 respectively) in 2004. The main species monitored were Blackbird *Turdus merula* (n=140), Chaffinch *Fringilla coelebs* (83), Dunnock *Prunella modularis* (17), Linnet *Carduelis cannabina* (103), Yellowhammer *Emberiza citrinella* (28) and Song Thrush *Turdus philomelos* (8).

2.2 Nest finding and monitoring

Hedgerows were selected to cover the full range of hedgerow characteristics and management types present across study sites. Studied hedgerows ranged from intensively managed (usually less than 1 m high, with thin woody vegetation with gaps), through managed (usually greater then 1 m high and cut or trimmed within the last 3 – 4 years) to unmanaged (usually >3 m high, not regularly cut or trimmed, often with trees and tall shrubs). Hedgerows next to busy roads, gardens, woods or woodland strips, or those planted within the last 5 years, were not selected for study.

Each hedgerow was cold-searched for nests at approximately weekly intervals between early April and late July. For each nest, the species was noted and the nest was inspected every 5–7 days until either the young fledged or the nest failed. Nest contents and adult activity were recorded during each visit. Nest success was inferred by an empty undamaged nest where the young were old enough to have fledged since the previous visit. Nest failure was either known (nest contained cold eggs, egg fragments or dead chicks) or was inferred from empty (often damaged) nests on a date prior to a plausible fledging date. For analytical purposes the date of failure was assumed to be the mid point between the last two visits. If there was evidence a nest had been pulled down from below, we assumed predation by a mammal, although we acknowledge that predator identification based on field signs is not always reliable (Pietz and Granfors, 2000). As we were specifically interested in corvid predation, nests for which mammalian predation was presumed were excluded from analyses (n=11, 2.8 %), as were any nests for which the outcome was uncertain (n=18, 4.5 %). A small number of failures caused by starvation, abandonment, human interference, or egg infertility (eggs not hatched or chicks found dead in the nest) were also excluded (n=24, 6.0 %). Analyses were restricted to nests located within the woody vegetation of the hedge;

nests located on the ground or within field boundary vegetation were excluded. First egg date (FED; a day-specific integer where 1st January = 1) was deduced from incomplete clutches, hatch dates and estimated chick ages (e.g. Green, 2004). If FED could not be determined to within 3 days then the nest was excluded from analyses.

2.3 Nest site characteristics

Data describing nest site characteristics were collected for 338 nests within ten days of the nesting attempt ending and are defined in Table 1a (brief descriptions only are given here). We recorded nest height above the ground, along with the shortest horizontal depth and vertical depth between the nest and the hedgerow edge. We measured nest dimensions to allow the calculation of nest volume, and identified primary and surrounding plant species supporting the nest. Hedgerow height and width at the nest were measured to calculate cross-sectional area at the nest site.

Nest concealment was assessed in three different ways: light penetration at the nest (measured with a light meter), horizontal visibility (counts of white circles on a black card positioned next to the nest) and vertical vegetation cover (assessed from a digital image; see Table 1a for details). Nest accessibility (a binary variable) was assessed by attempting to manoeuvre two different sized balls from the hedgerow edge to the nest without breaking any woody vegetation (Table 1a). The smaller ball had a circumference (30.5 cm) that was similar to the maximum body girth of a magpie *Pica pica* (measured as 28 cm), and was intended to highlight potential accessibility to a corvid. Accessibility with the larger ball (69cm) was intended to indicate easy access to a foraging corvid.

Locations of carrion crow *Corvus corone* and magpie nests were recorded, and the distance to the nearest corvid nest (corvid distance) subsequently calculated for each songbird nest. We also recorded distance to the nearest wood or woodland strip (wood distance), and distance to the nearest tree, pylon, telegraph pole or other vantage point at least 5 m in height (vantage distance) as corvids are visually-oriented predators known to utilise vantage points when searching for prey (Macdonald and Bolton, 2008).

2.4 Corvid abundance

The relative abundance of corvids (magpie, carrion crow, jackdaw *Corvus monedula* and jay *Garrulus glandarius*) was assessed using a transect method (Stoate and Szczur, 2001) on between 2 and 13 occasions (mean ± SE: 5.08 ± 1.00 visits) at each site during April-June of each year. Transects were spaced approximately 600 – 700 m apart and followed field boundaries; mean transect length was 5.75 ± 1.15 km (± 1 SE).

Each transect was walked at a steady pace, and all corvids were recorded. The total number of corvids per km within 100m of the observer, averaged over all transects, was taken as an index of corvid abundance for each site in each year.

2.5 Hedgerow characteristics and nest site selection

Data describing hedgerow characteristics were collected for 391 nests and described the section of hedgerow 30m either side of each nest. Firstly, the hedgerow aspect was recorded, and hedgerow management and cutting style were categorised (as in Table 1b). The percentage of gaps within the same stretch of hedgerow was estimated, along with the number of trees. The occurrence and timing of a hedgerow cut during the previous 5 years was determined during farmer interviews. The width of vegetated margins on both sides of the hedgerow was measured.

In order to identify structural features of hedgerows that were selected or avoided by nesting songbirds, we repeated the nest site measurements for primary supporting and surrounding vegetation, horizontal visibility and vertical cover at six locations spread at 10m intervals either side of the nest (if an interval fell within a hedgerow gap, then a point 5 m either side of the gap was measured instead). The measurements were collected at the same height in the hedgerow as the nest. These data were collected for 333 nests.

2.6 Statistical analysis

2.6.1 Nest site selection

To determine the features of hedgerows selected by nesting birds, the key features of nest sites thought to indicate aspects of nest visibility and accessibility (vegetation cover, horizontal visibility from each side of the nest, primary species and surrounding species; Table 1) were compared with the six adjacent non-nest locations using conditional logistic regression stratified by nest identifier to allow for the non-independence of nest and non-nest locations (Anteau et al., 2012).

2.6.2 Likelihood of nest predation

We used generalised linear mixed models (GLMMs) with binomial error structures and logit link functions to determine whether nest site characteristics influenced the likelihood of nest predation at the egg (n=202 nests) and chick (n=190) stages. GLMMs were fitted using the 'glmer' function within the *lme4* package (Bates and Maechler, 2009) in R v 2.10.1 for Mac (R Core Development Team, 2009). A hedgerow identifier nested within farm was included as a random effect to control for the non-independence of nests within the same hedgerow, or on the same farm, as well as to control for spatial autocorrelation. The response variable was the daily whole nest failure rate (DFR) in which nest outcome at the relevant nest stage (0 = successful, 1 = depredated) was the binomial numerator and the number of exposure days during the relevant nest stage declared as the binomial denominator (Aebischer, 1999; Hazler, 2004). Our aim was to identify predictors of nest survival associated with hedgerow structure and corvid abundance / distance, and any interactions between the two. All GLMMs initially included a set of fixed variables (irrespective of their statistical significance) for factors that might have affected nest survival but were unrelated to hedgerow structure or predator abundance (we call these 'base models'). These included mean-centred FED (for egg stage survival) or hatch date (for chick stage survival) as linear and quadratic terms to allow for non-linear temporal variation in predation risk across the breeding season. They also included species, nest contents (clutch or brood size for egg and chick stage models respectively) and year. We tested each 'base variable' within the base model, and excluded those with $p>0.10$ to avoid overfitting, resulting in a 'final base model' which remained fixed for the rest of the model selection.

We then followed a two-stage approach which aimed to identify predictors of nest survival while balancing the likelihood of type I and type II errors (Pearce-Higgins et al., 2009). First, each of the 15 hedgerow characteristics and corvid variables listed in Table 1a (logarithm or arcsine transformed as necessary) was added to the final base model one at a time. For those variables that were potentially influential on nest survival ($p<0.1$; Table 2) we checked for multicollinearity by examining correlations between variable pairs (detailed in Appendix 1). This was done separately for nest site character and hedgerow management variables. As potentially influential variables exhibited little inter-correlation (all r values<0.5; Appendix 1), all were retained in a second stage of multivariate testing. This second stage involved the addition of all potentially influential hedgerow/corvid variables to the final base model, followed by sequential backwards deletion in which the least significant term (assessed using p value) was removed until all remaining hedgerow/corvid terms were either formally significant ($p<0.05$) or potentially influential ($p<0.1$). We report the latter to avoid type 2 errors but interpret such relationships more cautiously. We finally tested two-way interactions between our best measures of corvid exposure (corvid abundance and corvid distance) and our measure of nest visibility most relevant to corvids flying overhead or walking along the top of a hedgerow (vegetation cover), to assess whether more visible nests were more likely to be depredated in areas of higher corvid exposure. Whilst stepwise model construction has been criticised in the literature (Whittingham et al., 2006), it has since been shown that stepwise approaches perform just as well as other methods (Murtaugh, 2009). Information theoretic methods were not employed as these require estimation processes that approximate the likelihood rather than the model (Bolker et al., 2009).

To estimate the scale of effect at the whole nest level, we combined corvid and nest access variables from our final models to predict overall nest survival rates for accessible and inaccessible nests (small ball access) and high and low potential corvid exposure (corvid distance and vantage distance). We predicted at both levels for binary data, and at levels of the 10th and 90th percentiles from the raw data to provide whole egg-stage, whole chick-stage and whole nest-stage survival proportions.

2.6.3. Management associations with nest predation

The GLMMs for egg (n=209) and chick stage (n=195) nest survival were extended to test for any influence of our 8 hedgerow management variables (Table 1b). Model selection proceeded as described above (2.5.2) with each management term initially added in turn to the base model, followed by backwards deletion on the significant one-at-a-time predictors. Because several of the management variables were categorical and were likely to have co-varied, no interactions were considered.

3 **Results**

3.1 Nest site selection

Nest locations were characterised by higher vegetation cover compared to non-nest sites, along with higher visibility from the side of the hedgerow closest to the nest and lower visibility from far side of hedgerow (Table 3, Figure 1). Bramble was most likely to be selected as the primary support for nests (rose the least), while ivy was the preferred surrounding species (locations with rose or no surrounding species being avoided; Table 3).

3.2 Effects of hedgerow structure and predators on nest failure rates

Mean DFR at the egg stage was 0.032, equivalent to 0.35 failure over a 13-day incubation period. For nests reaching the chick stage, mean DFR was 0.035 equivalent to 0.38 failure over a 13-day chick-rearing period.

Egg stage DFRs declined significantly with increasing clutch size, and exhibited a weak negative relationship with distance to the nearest corvid nest (Appendix 2; Table 4).

After allowing for a marked seasonal decline in chick stage failure rates, DFRs were higher for nests that were accessible with a small ball (Figure 2a; DFRs of 0.047 and 0.019 for accessible and inaccessible nests respectively, equivalent to failure rates of 0.467 and 0.219 over a 13-day chick-rearing period), and for nests located further away from vantage points (Figure 2b; Table 4).

The effect size of nest accessibility in terms of overall nest survival (averaged between high and low corvid exposure) was 0.143, compared to a mean effect size of 0.031 for corvid exposure (averaged between accessible and inaccessible nests; Table 5). The sensitivity of overall nest survival to nest accessibility was particularly high when corvid exposure was low (0.360 vs. 0.569, Table 5). When we excluded from these calculations the (counterintuitive) positive relationship between chick stage nest failure and vantage point distance, overall nest survival was similarly sensitive to corvid exposure (mean effect 0.178) and nest accessibility (0.141; Table 5).

3.3 Effects of hedgerow management on nest failure rates

There was a statistically weak effect of time since last cut on egg stage DFR (Table 6) with nests in recently cut hedgerows experiencing higher failure rates (nest failure over the 13-day chick period was 0.693 in hedgerows cut during the preceding year compared to 0.237 in hedgerows cut 4 years previously; Appendix 3). Chick stage

DFRs differed between hedgerow management (Table 6). In leggy, remnant and recently laid hedgerows, the DFR averaged 0.125, equivalent to a nest failure rate of 0.824 over the 13-day chick-rearing period. Conversely, in mechanically cut, trimmed but dense, and stock-proof hedgerows, DFR averaged 0.030, equivalent to 0.327 nest failure across the chick-rearing period (Figure 3). Hedgerow management categories associated with this higher predation risk (leggy, remnant, recently laid) were characterised by relatively high horizontal visibility and high small ball accessibility (Table 7).

4 Discussion

To our knowledge, this is the first study to consider the potential for hedgerow management to ameliorate the impacts of avian nest predators on farmland songbirds. In farmland environments, 50% of hedgerows have been removed since 1945 and the diversity and quality of remaining hedgerows has declined (Robinson and Sutherland, 2002). This deterioration of linear hedgerow nesting habitat may have allowed songbird nests to become more susceptible to nest predation in agricultural landscapes (Evans, 2004; Hinsley and Bellamy, 2000; Whittingham and Evans, 2004). We found songbirds to select nest sites based on vegetation characteristics likely to provide concealment and limit access to predators. We found evidence for both vegetation and corvid variables influencing nest survival, suggesting that improving hedgerow structure can mitigate corvid predation. Critically, we found that hedgerow management can influence nest survival, with much lower nest failure rates in hedgerows that were managed to create a dense structure (e.g. stock-proof or mechanically cut) compared to unmanaged (e.g. leggy and remnant) hedgerows.

4.1 Nest site selection

Songbirds selected nest sites with high vegetation cover above the nest, which is likely to afford a degree of protection from corvids flying overhead or foraging along the top of hedgerows (Cresswell, 1997), as corvids tend to depredate more visible nests (Matessi and Bogliani, 1999; Weidinger, 2002). Denser vegetation cover may also confer protection from adverse weather. Songbirds also selected nest sites that conferred relatively high visibility on the nest side of the hedge, and relatively low visibility on the far side (Götmark et al., 1995). When faced with an approaching predator, incubating or brooding parent birds tend to flush sooner when visibility from the nest is higher (Burhans and Thompson, 2001), which may reduce the risk of attracting attention to the nest, or disclosing the exact location of the nest by flushing late. Bramble was selected as the primary nest support, possibly because its dense and thorny character may restrict nest detection and access by predators. Ivy was selected for vegetation surrounding the nest, probably as this evergreen species provides increased cover above the nest especially early in the breeding season when well-hidden nest sites are less abundant (e.g. White et al. 2008). Rose species were avoided for both primary and surrounding vegetation, possibly because of their late leafing and relatively sparse leaf cover.

4.2 Effects of predator abundance / proximity and hedgerow structure on nesting success

We found a weak negative effect of corvid nest distance on egg-stage nest failure rates, which is likely to be a consequence of increased corvid activity close to corvid nests. Conversely, we found a positive relationship between chick-stage failure rates and distance to vantage point, which is surprising given the expectation that nests closer to vantage points are more likely to be noticed by corvids (Macdonald and Bolton, 2008). However, passerines are known to mediate predation risk through behavioural modifications so may compensate for this increased exposure by reducing nest visitation at times when corvids are present (Dunn et al., 2010; Eggers et al., 2005b). At the chick stage, more accessible nests suffered higher failure rates, suggesting that hedgerow structure can mitigate corvid predation (Evans, 2004). The relatively large difference in nest survival between accessible and inaccessible nests translated into a large effect of nest accessibility on overall nest survival especially when exposure to potential corvid impacts was relatively low (raising average nest survival from 0.360 to 0.569: Table 5). This confirms that hedgerow vegetation structure confers considerable protection to songbird nests against depredation, highlighting a role for hedgerow management in songbird conservation. The overall impact of predator exposure on nest survival depended on the inclusion of the (counterintuitive) positive relationship between chick-stage nest failure and distance to vantage point (Table 5). Including this relationship in predictions rendered overall nest survival relatively insensitive to corvid exposure. However excluding this relationship (which may be artefactual) from predictions, renders nest survival similarly sensitive to corvid exposure and hedgerow vegetation structure (Table 5).

4.3 Management influences on nest success and recommendations

Although the effect of time since last cut on nest survival was statistically weak the effect size was large, with nests more than twice as likely to survive in hedgerows cut 4 years previously than during the past year. Nest survival rates were much higher in stock-proof, trimmed or mechanically cut hedgerows (0.673) than in unmanaged or recently laid hedges (0.176), probably because the more open vegetation structure in unmanaged hedges limited the scope for nest concealment and protection from predators (Cresswell, 1997; Matessi and Bogliani, 1999). Between 1984 and 2007 there was a 24% reduction in the availability of 'managed' hedgerows in Great Britain (Carey et al., 2008; Petit et al., 2003). Although hedgerow removal explains some of this loss up until 1990, since then the loss of managed hedgerows is largely explained by a reduction in hedgerow management activity and a transition to field boundaries dominated by tree-lines and relict hedges especially in arable-dominated landscapes (Carey et al., 2008). The loss of managed hedgerows from such landscapes, coupled with the increase in corvid populations (Gregory and Marchant, 1995), may have increased the vulnerability of hedgerow-nesting songbirds to nest predation (Evans, 2004).

Direct control of corvids can increase nest survival and breeding abundance of some songbird species but is expensive and not universally accepted as a conservation management strategy (White et al., 2014). Our study adds to the increasing literature suggesting that negative impacts of corvids can be mitigated by improving habitat quality (Dunn et al., 2010; Eggers et al., 2008; Evans, 2004). Associations with hedgerow management were particularly clear-cut in determining chick survival with stock-proof and trimmed hedgerows providing the highest nestling survival rates (Fig. 3). In England, a new agri-environment scheme (Countryside Stewardship; Natural England, 2015) started in 2016 and promotes environmental management of hedgerows by specifying minimum dimensions (2 m tall and 1.5 m wide) and cutting regimes (outside the breeding season, no more than one year in three and leaving at least one-half of hedgerows untrimmed each year). These cutting regimes can improve moth and parasitoid diversity (Facey et al., 2014), and increase resources such as flowers and berries (Staley et al., 2012), and our data suggest these guidelines should also benefit nesting birds. Our data emphasise the importance of regular hedgerow trimming to promote a dense woody structure and prevent succession to tree lines, and the avoidance of overly frequent cutting (our data suggest a cut every 3-4 years might be optimal to promote songbird nest survival; Appendix 3). Rotational hedge cutting regimes within a farm (i.e. cutting 1/4 - 1/3 of hedgerows each year) is one way to provide heterogeneity and ensure a continuous supply of other resources such flowers and berries to meet other wildlife conservation objectives as well as improve passerine nest survival.

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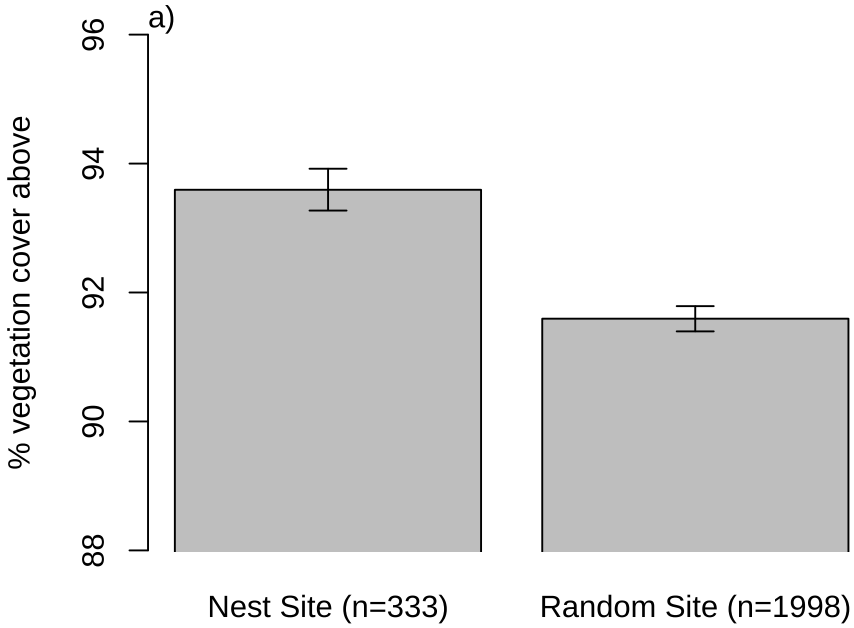
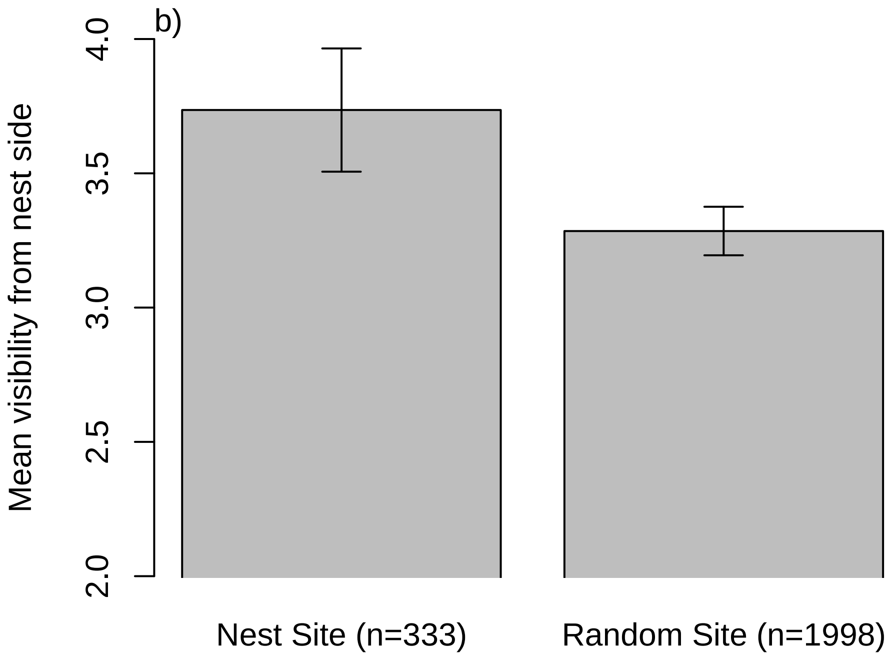
Figure 1.

a)


a)
% vegetation cover above
96
94
92
90
88
Nest Site (n=333)
Random Site (n=1998)

b)


b)
Mean visibility from nest side
4.0
3.5
3.0
2.5
2.0
Nest Site (n=333)
Random Site (n=1998)

c)

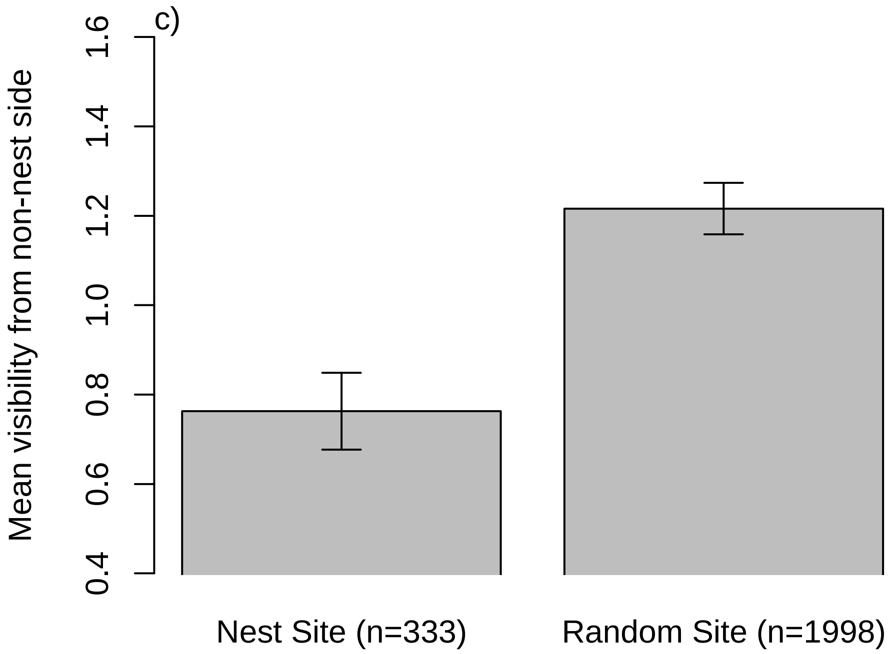
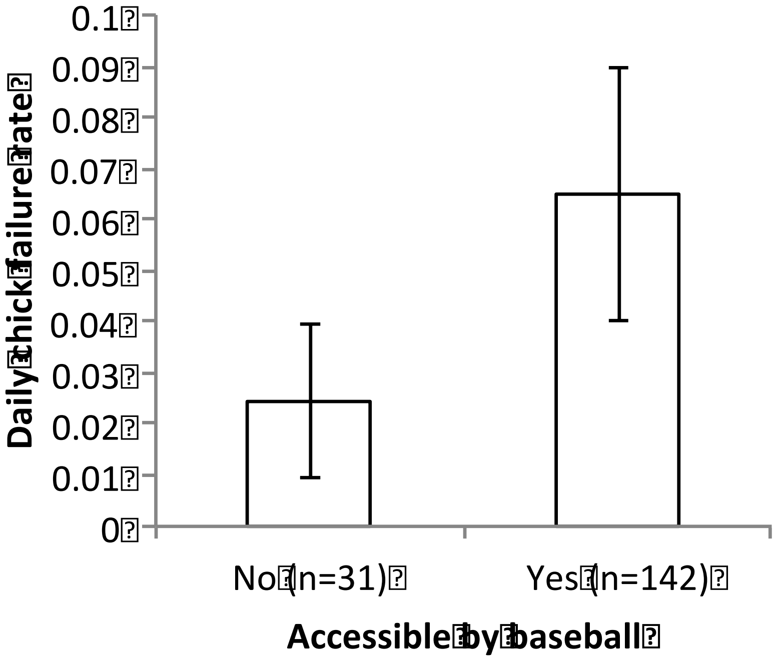

c)
Mean visibility from non-nest side
0.4
0.6
0.8
1.0
1.2
1.4
1.6
Nest Site (n=333)
Random Site (n=1998)

Figure 2

a)


Daily chick failure rate
0.1
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
No (n=31)
Yes (n=142)
Accessible by baseball

b)

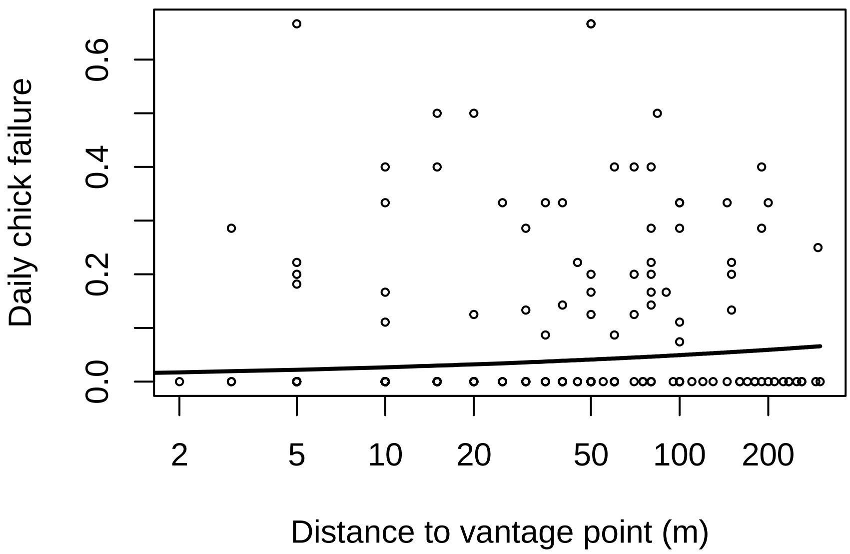

Daily chick failure
0.0
0.2
0.4
0.6
2
5
10
20
50
100
200
Distance to vantage point (m)

Figure 3.

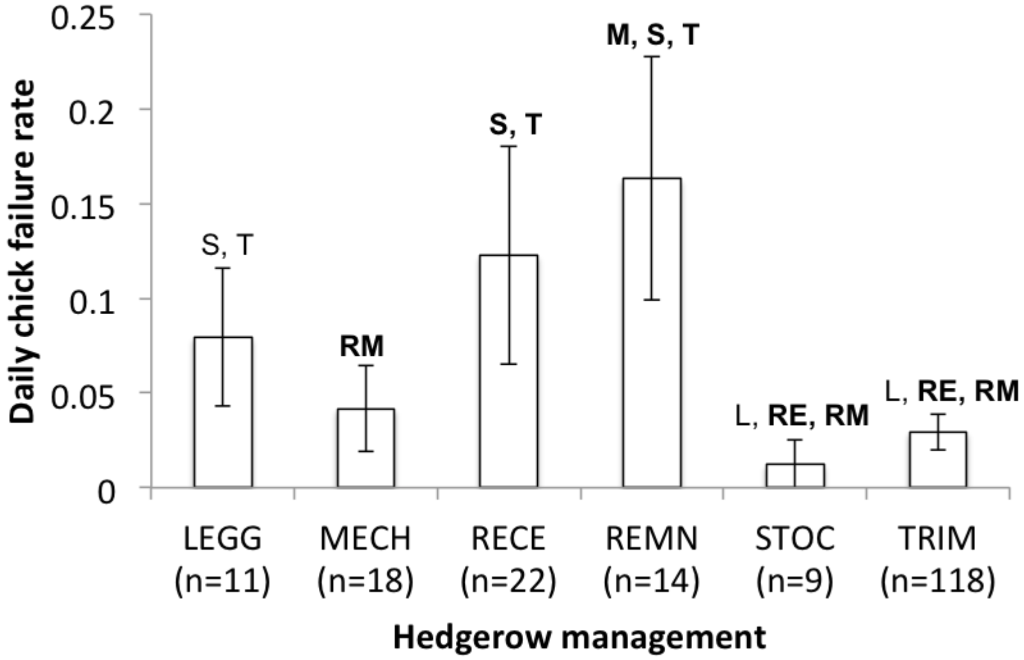

0.25
0.2
0.15
0.1
0.05
0
Daily chick failure rate
S, T
RM
S, T
M, S, T
L, RE, RM
L, RE, RM
LEGG (n=11)
MECH (n=18)
RECE (n=22)
REMN (n=14)
STOC (n=9)
TRIM (n=118)
Hedgerow management

Figure and Table Legends

Figure 1. Differences between nest sites and non-nest sites in 1) vegetation cover above the nest, 2) visibility of the nest from the closest side of the hedgerow and 3) visibility from the far side of the hedgerow. Bars show raw means ± 1 SE.

Figure 2. Effect of a) nest accessibility (measured with a small ball) and b) distance from the nearest vantage point, on chick stage failure rate. For a) Bars show predicted mean ± 1 SE failure rates assuming mean hatch date. For b), points show raw data and the line is predicted from the final model for accessible nests assuming mean hatch date.

Figure 3. Effect of hedgerow management on chick stage nest survival. Bars show predicted means ± 1 SE assuming mean hatch date and mean brood size, and numbers indicate sample sizes. Categories of hedgerow management are: LEGG: Overgrown and leggy; MECH: mechanically cut; RECE: recently laid; REMN: remnant; STOC: unclipped and stock-proof; and TRIM: trimmed and dense. Letters above bars show where significant differences lie (L = LEGG; M = MECH; Re = RECE, RM = REMN, S = STOC; T = TRIM); letters in bold denote differences significant at $p<0.05$, letters not in bold denoted marginally significant ($P<0.1$) differences.

Table 1. Descriptions of variables considered in analyses of a) nest and corvid characteristics and b) management characteristics considered in nest survival models.

Table 2. Results of univariate tests for the initial base models to assess associations with whole nest failure rates, followed by screening of explanatory variables against the final base model for a) Hedgerow characteristics and b) Hedgerow management analyses at the egg and chick stage separately. Terms with the variable name in bold were included in interactions to examine the potential for interactions between nest visibility and predator metrics. Terms where the statistics are highlighted in bold are those that were highlighted as potentially important at $p<0.1$ by univariate testing and were thus included in subsequent multivariate analyses.

Table 3. Results from a conditional logistic regression determining which features differed between nest sites and random sites within the same hedgerow. χ^2 values are from comparison of the final model with and without the term.

Table 4. Factors affecting the probability of nest predation at the egg and chick stages. a) lists variables retained in multivariate GLMMs (at P<0.01) while b) lists variables that were tested but failed to achieve this level of statistical significance. See section 2.5 for further details of model selection.

Table 5. Predicted daily nest survival rates (DSR) and whole nest survival rates at the egg and chick stages separately, and combined, assuming 13-day incubation and chick-rearing periods. Predictions are for combinations of high and low vegetation access (Small ball accessibility: Y = high access; N = low access) and high and low corvid exposure (corvid distance and distance to vantage point: near = high corvid; far = low corvid), predicted from the final models (Table 4). Continuous variables are predicted at levels of the 10^{th} and 90^{th} percentiles from the raw data. To test the sensitivity of our nest survival predictions to the potentially counterintuitive effect of vantage distance, we re-ran our predictions from the models excluding this variable (figures in brackets).

Table 6. Hedgerow management terms affecting the probability of nest predation at the egg and chick stages. a) lists variables retained in multivariate GLMMs (at P<0.01) while b) lists variables that were tested but failed to achieve this level of statistical significance. See section 2.5 for further details of model selection.

Table 7. Summary statistics (Mean ± SE) and GLMMs comparing vegetation structure between a) nest sites and b) random locations within the same hedgerow in high (Leggy, recently laid and remnant) and low (mechanically cut, stock-proof and trimmed; see Figure 2) predation risk hedgerow managements. For a) GLMMs contain hedgerow within farm as random terms, and for b) GLMMS contain an additional nested random term of nest ID (to control for multiple random points per stretch of hedgerow). Small ball accessibility was not measured at random locations.

Table 1

a)

Variable	Description	Median (Range) or levels (for factors)
Nest height	Height of the rim of the nest cup above ground level (m)	1.350 (0.300 – 2.300)
Horizontal depth	Shortest horizontal distance of the edge of the nest cup to the nearest hedgerow edge (m). A hedgerow edge is defined as the beginning of dense thick twigs, as determined by using the weight of a cricket ball to move any light vegetation out of the way and determine where the hedgerow ends. Thus, widely spaced, thin twigs do not constitute the edge, whereas dense thick twigs do.	0.550 (0.050 – 1.800)
Vertical depth	Shortest vertical distance of the nest rim to the top of the hedgerow (m)	1.194 (0.200 – 3.650)
Nest volume	Maximum vertical x horizontal dimensions (cm^3)	1040.0 (117.8 – 5542.0)
Primary species[a]	Primary supporting woody plant species	Blackthorn, Bramble, Hawthorn, Rose and Other
Surrounding species[a]	Surrounding vegetation not supporting the nest but offering protection	Bramble, Ivy, Rose, None and Other
Cross-sectional area	Hedgerow height at the nest x hedgerow width at the nest (each ± 5 cm; area in m^2). Height and width were measured so as to include woody hedgerow vegetation and recent growth, but exclude trees	5.57 (1.23 – 22.5)
Light penetration	Assessed using two light meters (Wavetek Metreman LM631; range 0.01 – 20,000	0.011 (0.001 – 0.226)

	Lux) to assess the amount of light penetration above the nest relative to light levels outside the hedge. Only nests for which simultaneous measures from inside and outside the hedgerow (egg n=158; chick n=147) were included in analyses as the variable used was the ratio of light level above the nest to light level outside the hedgerow	
Horizontal visibility[ab]	Maximum value of a measure from each side of the hedgerow. Assessed using a 14cm x 14cm black card containing a 5 x 5 regular grid of white circles (diameter 12 mm). The card was placed adjacent to each side of the nest (parallel to the hedgerow side) and viewed from three different angles (-45˚, 90˚ and +45˚ to the nest). The number of circles that were at least 75% visible at each angle was summed for each side of the hedgerow, to give a measure (range 1-75) of horizontal visibility on each side of the hedgerow.	4.11 (0-23)
Vegetation cover[a]	% vegetation cover above the nest assessed using a digital photograph taken by placing a Casio EX-Z3 digital camera (set at the widest field of view) on the base of the nest facing vertically upwards. Photoshop software (v 7.0.1) was used to determine the proportion of pixels of sky in the image and thus the % vegetation cover above the nest	96.23 (70.40-99.99)
Small ball accessibility	Accessibility assessed by attempting to manoeuvre a baseball (circumference 30.5 cm) from the edge of the hedgerow to the nest by any route above or level with the nest without breaking any woody vegetation. We assessed whether or not the ball could reach the nest	Yes or No

Large ball accessibility	Accessibility assessed by attempting to manoeuvre a football (circumference 69 cm) from the edge of the hedgerow to the nest by any route above or level with the nest without breaking any woody vegetation. We assessed whether or not the ball could reach the nest	Yes or No
Corvid distance	Distance to nearest corvid nest (m)	270 (40 – 1350)
Wood distance	Distance to nearest wood, copse, spinney or woodland strip (at least 5m wide)	170 (5 – 645)
Vantage distance	Distance to nearest tree, pylon, telegraph pole or any other vantage point >5m in height (m)	40 (3-300)
Corvid abundance	Mean abundance of corvids per km, per site per year.	7.167 (0 – 28.830)

[a] variable included in nest site selection analysis

[b] visibility on each side of hedgerow included in nest site selection analysis as two separate variables but combined (as maximum visibility from either side of the hedgerow) for nest failure analyses

b)

Variable	Description	Median (Range)
Aspect	Aspect of hedgerow	E-W, N-S, NE-SW and SE-NW
Hedgerow management	Category: remnant (REMN), recently laid (RECE), mechanically cut (MECH), trimmed but dense (TRIM), overgrown and leggy (lacking branches and foliage in the bottom 1 m of the hedgerow; LEGG) or uncut and stock-proof (STOC) (from Bickmore, 2002; see Table 7 for further details of structure)	Leggy, Mechanically trimmed Remnant, Recently laid, Trimmed but dense, Stock-proof
Cutting style	Hedgerow shape. Categorised as: 'A' shaped (at least 2 cuts), Chamfered (at least 4 cuts), box (at least 3 cuts), free growth on top (only two sides cut), or free growth all round (uncut)	'A' shaped, Chamfered, Box, Free growth on top, or Free growth all round
% gaps	The % gaps (± 5 %) within the 30m hedgerow section	0 (0 – 30)
Number of trees	Number of trees >10m in height within 30m hedgerow section	0 (0 – 6)
Recent trim	Whether or not a hedgerow had been trimmed in the last 5 years	Trimmed or not
Last cut	Years since last cut	1 (1 – 4)
Margin width	Average width of herbaceous vegetation on both sides of the hedgerow (± 1 m)	2.0 (1.0 – 3.5)

Table 2.

a	**Egg stage**					**Chick stage**				
Base model	Slope	SE	df	χ^2	p	Slope	SE	df	χ^2	p
First egg date/Hatch date	**-0.014**	**0.007**	**1**	**4.529**	**0.038**	**-0.013**	**0.006**	**1**	**5.395**	**0.020**
First egg date^2/Hatch date^2	-0.001	0.001	1	0.509	0.476	-0.001	0.001	1	1.753	0.186
Clutch size/Brood size	**-0.892**	**0.168**	**1**	**28.617**	**<0.001**	0.261	0.172	1	2.459	0.117
Species			5	6.356	0.273			4	1.039	0.904
Year	0.066	0.351	1	0.036	0.850	-0.078	0.337	1	0.053	0.818
Univariate tests										
Nest height	0.034	0.555	1	0.004	0.950	-0.620	0.561	1	1.226	0.268
Horizontal depth	-0.228	0.465	1	0.239	0.625	0.678	0.793	1	0.713	0.399
Vertical depth	-0.209	0.251	1	0.716	0.398	0.046	0.277	1	0.027	0.870
Nest volume	0.092	0.217	1	0.177	0.674	0.063	0.254	1	0.063	0.802
Primary species			**4**	**8.461**	**0.076**			4	2.887	0.577
Surrounding species			4	0.657	0.957			4	1.618	0.806
Cross sectional area	-0.012	0.043	1	0.074	0.786	-0.062	0.274	1	0.051	0.821
Light penetration	4.552	4.318	1	1.024	0.312	-3.760	5.898	1	0.443	0.506
Horizontal visibility	0.162	0.170	1	0.883	0.347	-0.041	0.187	1	0.049	0.825
Vegetation cover	-0.886	1.318	1	0.445	0.505	0.987	1.375	1	0.533	0.466
Small ball accessibility	0.095	0.413	1	0.054	0.817	**0.942**	**0.541**	**1**	**3.627**	**0.057**
Large ball accessibility	-0.062	0.327	1	0.036	0.850	-0.225	0.365	1	0.392	0.531

Corvid distance	**-0.462**	**0.265**	**1**	**2.965**	**0.085**	0.077	0.231	1	0.111	0.739
Vantage distance	-0.002	0.003	1	0.691	0.406	**0.290**	**0.132**	**1**	**4.680**	**0.031**
Corvid abundance	-0.014	0.029	1	0.248	0.619	-0.010	0.268	1	0.002	0.969

b			**Egg stage**					**Chick stage**		
Base model	Slope	SE	df	χ^2	p	Slope	SE	df	χ^2	p
First egg date/Hatch date	-0.013	0.006	1	0.860	0.354	**-0.014**	**0.006**	**1**	**6.395**	**0.011**
First egg date^2/Hatch date^2	-0.001	0.001	1	1.093	0.296	-0.001	0.001	1	0.366	0.545
Clutch size/Brood size	**-0.877**	**0.169**	**1**	**25.176**	**<0.001**	**0.334**	**0.174**	**1**	**3.977**	**0.046**
Year	0.411	0.369	1	1.666	0.197	-0.492	0.319	1	2.330	0.127
Species			5	4.469	0.484			5	3.411	0.637
Univariate tests										
Aspect			3	4.095	0.251			3	0.120	0.989
Hedgerow management			5	3.481	0.626			**5**	**19.132**	**0.002**
Cutting style			4	3.324	0.505			4	7.587	0.108
% gaps	-0.031	0.035	1	0.887	0.346	0.021	0.026	1	0.654	0.419
Number of trees	0.116	0.320	1	0.131	0.718	**-0.643**	**0.363**	**1**	**3.444**	**0.063**
Recent trim	0.881	0.656	1	2.108	0.147	**-1.047**	**0.441**	**1**	**4.990**	**0.025**
Last cut	**-0.400**	**0.228**	**1**	**3.265**	**0.071**	**0.259**	**0.149**	**1**	**2.772**	**0.096**
Margin width	0.081	0.250	1	0.105	0.746	-0.059	0.262	1	0.051	0.821

Table 3.

Variable	df	χ^2	p
Vegetation cover	1	31.189	<0.001
Horizontal visibility (non-nest side)	1	18.568	<0.001
Horizontal visibility (nest side)	1	17.751	<0.001
Surrounding species	5	20.773	<0.001
Primary species	4	9.845	0.043

Table 4.

a	Egg stage			Direction	Chick stage			Direction
Variable	df	χ^2	p	of effect	df	χ^2	p	of effect
First egg date/Hatch date	1	0.534	0.465	-ve	1	7.737	0.005	-ve
Clutch size/Brood size	1	23.462	<0.001	-ve	-	-	-	N/A
Corvid distance	1	2.965	0.085	-ve	-	-	-	N/A
Vantage distance	-	-	-	N/A	1	4.52	0.034	+ve
Small ball accessibility	-	-	-	N/A	1	3.656	0.056	See Fig 2

b	Egg stage			Chick stage		
Variable	df	χ^2	p	df	χ^2	p
Primary species	4	6.094	0.192	-	-	-
Vegetation cover x Corvid abundance	1	0.461	0.497	1	0.515	0.473
Vegetation cover x Corvid distance	1	0.001	0.972	1	0.334	0.563

Table 5.

	High access, high corvid	Low access, high corvid	High access, low corvid	Low access, low corvid
Predicted egg stage DSR	0.953 (0.953)	0.953 (0.953)	0.981 (0.981)	0.981 (0.981)
Predicted chick stage DSR	0.977 (0.963)	0.991 (0.985)	0.942 (0.963)	0.976 (0.985)
Predicted egg-stage survival	0.533 (0.533)	0.533 (0.533)	0.781 (0.781)	0.781 (0.781)
Predicted chick stage survival	0.743 (0.609)	0.886 (0.824)	0.461 (0.609)	0.728 (0.824)
Predicted overall nest survival	0.396 (0.325)	0.472 (0.439)	0.360 (0.476)	0.569 (0.644)

Table 6.

a	Egg stage			Direction	Chick stage			Direction
Variable	df	χ^2	p	of effect	df	χ^2	p	of effect
First egg date/Hatch date	-	-	-	N/A	1	10.155	0.001	-ve
Clutch size/Brood size	1	37.636	<0.001	-ve	1	1.388	0.239	+ve
Hedgerow management	-	-	-	N/A	5	12.200	0.032	See Fig 3
Last cut	1	3.265	0.071	-ve	-	-	-	N/A

b	Egg stage			Chick stage		
Variable	df	χ^2	p	df	χ^2	p
Recent trim	-	-	-	1	0.744	0.389
Last cut	-	-	-	1	0.148	0.700
Number of trees	-	-	-	1	0.868	0.352

Table 7.

a)

Variable	High predation risk	Low predation risk	χ^2	p
Vegetation cover	93.77 ± 0.62	93.85 ± 0.41	0.15	0.70
Horizontal visibility (nest side)	3.97 ± 0.53	3.72 ± 0.28	1.38	0.24
Horizontal visibility (non nest side)	1.10 ± 0.22	0.68 ± 0.10	0.01	0.95
Horizontal visibility	2.54 ± 0.32	2.20 ± 0.16	0.53	0.47
Small ball accessibility (%)	91.3 ± 0.03	81.5 ± 0.03	3.03	0.08

b)

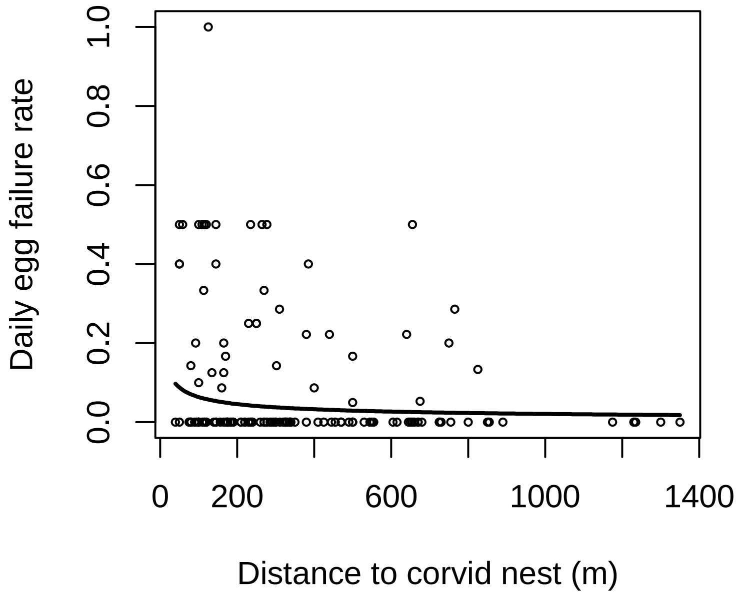
Variable	High predation risk	Low predation risk	χ^2	p
Vegetation cover	90.72 ± 0.42	91.79 ± 0.23	0.01	0.96
Horizontal visibility (nest side)	4.15 ± 0.21	3.08 ± 0.10	3.13	0.08
Horizontal visibility (non nest side)	2.02 ± 0.15	0.98 ± 0.06	18.67	<0.01
Horizontal visibility	3.08 ± 0.16	2.03 ± 0.07	6.63	0.01

Appendix 1. Correlation matrix for all continuous variables highlighted as potentially important by univariate analysis. Figures represent the correlation co-efficient from a Pearson's product moment test. Correlations significant at $p<0.05$ are highlighted in bold.

1)

	Horizontal depth	Vegetation cover	Horizontal visibility	Corvid abundance	Corvid distance
Vegetation cover	-0.04	-	-	-	-
Horizontal visibility	0.05	**-0.35**	-	-	-
Corvid abundance	-0.02	0.01	-0.05	-	-
Corvid distance	-0.07	-0.02	-0.06	**-0.18**	-
Vantage distance	-0.03	-0.02	-0.02	-0.10	0.04

Appendix 2. Effect of distance from the nearest corvid nest on egg stage failure rate. Points show raw data; line is predicted from the final model (Table 4) assuming mean hatch date and brood size.



Appendix 3. Effect of timing of last cut on egg stage nest failure rate. Bars show raw means ± 1 SE; last cut is analysed as a continuous variable but displayed categorically for clarity