Landscape effects on nest site selection and nest success of Lapwing *Vanellus vanellus* in lowland wet grasslands

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Capsule: Northern Lapwing *Vanellus vanellus* avoid nesting close to small woodland patches but nest predation rates do not vary with distance to woodland patches, either because risky areas are avoided or perceived nest predation risk doesn't reflect actual risk.

Aims: To explore the effects of woodland patches in wet grassland landscapes on nest distribution and success of Lapwings.

Methods: We quantified the effect of woodland patches on the distribution and outcome of Lapwing nests across four wet grassland sites by mapping nest distribution and monitoring nest outcomes.

Results: Lapwing nested significantly further from woods than expected by chance. Neither nest predation rates nor the probability of predation occurring at night (thus primarily mammalian predators) or day (primarily avian predators) varied in relation to distance from woodland patches.

Conclusions: High levels of nest and chick predation in wet grassland landscapes limit the capacity for breeding wader populations to be self-sustaining. Consequently, identifying manageable landscape features that influence predation rates is an important focus of conservation research. Lapwing avoid breeding close to woodland but, as nest predation rates don't vary with distance from woodland patches, their removal may increase the area of suitable nesting habitat but is unlikely to substantially influence productivity.

Introduction

Global declines in wader populations are a major current conservation concern (Stroud. *et al*. 2008). In Europe, long-term population declines are evident in 11 of the 12 wader species monitored within the Pan-European Common Bird Monitoring Scheme (European Bird Census Council 2014) and, in the UK, populations of Lapwing, Common Snipe *Gallinago gallinago*, Common Redshank *Tringa totanus*, and Eurasian Curlew *Numenius arquata* have all declined to such an extent that they are now either red- or amber-listed (Hayhow *et al.* 2015). These declines have largely been driven by land drainage and intensification of agricultural management removing the resources required for nesting and chick-rearing (Wilson *et al.* 2005, Eglington *et al.* 2008, Amar *et al.* 2011).

Habitat fragmentation is resulting in once-widespread species being increasingly confined to remaining pockets of suitable habitat, and such fragmentation generally leads to reduced nest survival due to predation (Stephens *et al*. 2004). This, combined with increases in generalist predator **number**s, can result in unsustainably high levels of wader clutch loss (Macdonald & Bolton 2008), making predation a significant limiting factor for these species. In these circumstances, increasing the availability of suitable habitat is typically insufficient to arrest population declines without also identifying means of reducing levels of nest predation (Smart *et al*. 2013).

The effectiveness of direct predator control at reducing levels of wader nest predation varies depending on the local predator community and context (Bolton *et al*. 2007), is time consuming and therefore costly and any benefits are lost when control ceases. If predation rates vary in relation to manageable landscape characteristics, these could potentially offer longer-term, more sustainable means of improving productivity and aiding recovery of wader populations.

Landscape structure could influence wader nest success by altering predator distribution, abundance or activity, and thus the risk of nests being located by predators (e.g. (Whittingham & Evans 2004), Eggers *et al.* 2006, Laidlaw *et al.* 2015). However, such effects may be masked if areas in which predation risk is high are avoided as breeding locations (Martin 2011, Lima 2009, Zanette *et al.* 2011, Lima 2009). Avoidance behaviour could thus reduce the impact of habitat-specific nest predation risk. For example, nesting close to habitat edges may increase exposure of nests to predators from the surrounding landscape. Elevated levels of predation of artificial nests have been recorded near to habitat edges in forest fragments (Hartley & Hunter 1998), in open prairie habitats (Burger *et al.* 1994) and, for artificial and real nests, in marshlands (Batáry & Báldi 2004). However, other studies have reported little or no evidence for variation in nest predation rates with distance from habitat edges ((Stroud *et al*. 1990), (Nour *et al.* 1993), (Lahti 2001)), which could reflect either no effects of habitat edges on predator activity or effective avoidance of risky areas by species vulnerable to nest predators. Increases in nesting density with distance from woodland edges have been shown in grassland passerines (Renfrew 2005) and, in the UK uplands, breeding wader abundance increases with distance from plantation edges, Wilson *et al.* 2014), suggesting either avoidance of woodlands by these species or lower survival of individuals breeding close to woodlands. The landscapes in which waders breed can differ greatly in the amount, type and distribution of woodland. Small patches of woodland are common in lowland wet grassland landscapes, but the influence of these woodland patches on the nesting distribution and nest success of the important wader populations that breed in these areas is not well understood.

If waders in lowland wet grassland avoid nesting close to woodlands, as seen in the uplands, this could render large areas of potentially suitable lowland habitat unusable, thus limiting the capacity for species recovery. Similarly, if woodland patches are used by nest predators, nest predation may vary with proximity to woodland. Previous studies of breeding waders on grasslands have shown that mammalian predators, particularly red foxes, *Vulpes vulpes*, are responsible for the great majority of wader nest losses (Macdonald & Bolton 2008), and that lapwing nests that are closer to patches of tall (primarily grass) vegetation have lower predation rates (Laidlaw *et al.* 2015). As these patches of tall vegetation support small mammal populations that are otherwise rare in wet grasslands (Laidlaw *et al.* 2013), the greater success of wader nests close to tall vegetation may result from foxes concentrating on small mammal prey in these areas. If woodland patches provide similar small mammal prey resources, nest predation by mammalian predators may be lower close to woodland. Alternatively, if woodland patches provide perching locations from which avian predators can hunt, nest predation by avian predators may be greater for nests close to woodland patches. While the identity of nest predators is rarely known, most mammalian nest predation occurs at night while avian predators operate primarily during daylight, thus nocturnal and diurnal nest predation are generally good proxies for mammalian and avian predators, respectively (Eglington *et al*. 2009)**.** To assess the influence of woodland patches in lowland wet grassland landscapes on breeding wader distribution and success, we therefore quantify variation in nest location, nest predation and timing of predation (night or day) of Lapwing nests in relation to proximity to woodland patches, on four sites in eastern England.

Materials and Methods

Four wet grasslands sites on the Alde-Ore estuary in Suffolk, UK were studied between 31st March and 30th June 2014 (mean ± SD ha: 117.4 ± 67.5). These sites were at least 3 km apart and contained grasslands with a mix of sward heights and wet features in the form of shallow floods and footdrains. At all four sites, fields are managed by cutting or grazing with sheep or cattle, and the sites are surrounded by a mix of arable farmland and dry grassland, with a vegetated sea wall separating them from intertidal habitats along one boundary. Small patches of woodland are present on all sites (mean number per site = 5 ± 2 SD; mean woodland patch size = 1.3 ha ± 1.1 SD) (Figure 1).

Lapwing nests were located during twice weekly visits to each site by observing incubating adults. Eggs were weighed and measured, to calculate predicted hatching dates (Smart 2005), a temperature logger was inserted beneath the nest lining, and the position of the nest was recorded using a Garmin Etrex 30 handheld GPS.

Temperature loggers recorded temperature every eight minutes, and were retrieved once the nest was empty. The resulting temperature traces were used to determine the date and time of hatching or failure. Hatched nests were identified as being empty within two days of predicted hatch date and in which tiny eggshell fragments were found within the undisturbed nest lining. Predated nests typically had remains of predated eggs or a disturbed nest lining, and were empty prior to predicted hatch dates. Trampled nests (containing broken eggshell and contents) and abandoned nests (containing cold, intact eggs) were also recorded.

The positions of all woodland patches, ditches, field margin vegetation (hedges or tall vegetation fringe) and within-field tall (>50 cm) vegetation and wet features were mapped using a combination of GPS and ground-truthed aerial imagery, and imported into ArcGIS along with the positions of all nests. Wet features are known to attract nesting Lapwing (Eglington et al. 2010) and thus their influence on nest location had to be taken into account when assessing effects of woodland patches on nest distribution and success. The effects of ditches, field margin and within-field tall vegetation were included in initial analyses but, as they had no significant effects on nest site selection or predation, these were excluded from further consideration in this study.

The effects of woodland patches on (1) nest site selection, (2) daily nest predation rate and (3) time of nest predation were assessed using generalised linear models with a logit link function and binomial error distribution. Daily predation rate was calculated using the extension to Mayfield estimate methods described by (Aebischer 1999) (Table 1). Nest locations were compared to randomly located points generated using the Create Random Points function in ArcGIS. The number of random points generated for each site reflected the number of nests at that site (rounded up to the nearest five), and random points were excluded from areas of unsuitable nesting habitat (standing water and vegetation height greater than 15 cm) (Winspear & Davies 2005). The timing of nest predation was classified as day or night, as defined by the hours of civil twilight.

Results

Across all sites, a total of 77 nests were monitored (12, 28, 13 and 24 per site) of which 32% hatched, 53% were predated, 9% failed due to trampling and 5% failed due to flooding or abandonment.

Nests were found, on average, 8.7 days (± 8.2 SD) from the start of incubation, and were located between 71 and 1815 m from woodland patches (mean 717 m ± 327 SD), with 88% being located over 500 m from the nearest woodland. The maximum distance of potential nesting habitat to woodland patches was 2065 m. Nests were distributed closer to wet features and further from woods than randomly located points (full model: χ^2_5=34.7, p<0.001, Table 2.1, Figure 2.1). This model successfully classified 63.5% of nests and 74% of random points.

For the 65 nests for which outcome (hatched or not) was known (Figure 2.2) and exposure days could be calculated (12 of the 77 nests were excluded from this analysis due to being found at or after hatching or data loggers failed, and hence outcome dates were lost), the Mayfield estimate of mean daily predation rate was 0.05 (± 0.008 SE). There was no significant variation in daily predation rate of these nests between sites or in relation to either distance to the nearest woodland patch or wet feature (Table 2.2).

Predation events occurred throughout the breeding season and, of the 39 predated nests for which time of predation was available, 68% were predated at night (Figure 2.3 and Figure 3). However, there was no significant difference in the relative frequency of nocturnal and diurnal predation events among sites or in relation to either distance to the nearest woodland patch or the nearest wet feature (Table 2.3).

Discussion

In wet grassland landscapes in which small woodland patches are common, Lapwing nests were located significantly further from woods than expected by chance, however the rate and timing of predation did not vary in relation to these landscape features. In this study the presence of woodland patches did not therefore appear to strongly influence the probability of Lapwing nests being predated in these landscapes.

Avoidance of woodland patches was quite strong (only 12% of nests were within 500 m of woods despite ~30% of the suitable nesting habitat being within 500 m of woods at these sites (mean site area = 42.2 ha ± 32.4 SD). The spatial scale of this avoidance of woodlands is similar to that previously found in a range of wader species breeding at higher elevations (Stroud *et al*. 1990, Wilson *et al.* 2014). Lapwing nests were significantly more likely to be located closer to in-field wet features (as has also been shown elsewhere; Eglington *et al.* 2010), and so it is not clear whether the removal of woodland patches alone would necessarily increase the area for nesting Lapwing at these sites, unless in-field wet features were already present or were subsequently developed within the areas previously close to woodland.

Increased levels of predation of Lapwing nests close (< 50 m) to trees and other avian perches have been reported (Berg *et al*. 1992) but in our study all nests were located more than 70 m from woodland patches, and thus particularly risky locations may well have been avoided by these birds prior to our study. Waders have also previously been shown to avoid nesting close to tall structures which can potentially be used as perches by avian predators (Wallander *et al.* 2006). Other than woodlands there were very few structures, apart from gateposts which were less than 2 m high, across the sites so tall structures were unlikely to have been important in this study.

A wide range of potential predator species were observed across the sites, including Red foxes *Vulpes vulpes*, Eurasian badgers *Meles meles*, Eurasian otters *Lutra lutra,* Carrion crows *Corvus corone*, Herring gulls, *Larus argentatus*, Greater black -backed gulls *L. fuscus*, Lesser black -backed gulls *L. marinus*, Grey herons *Ardea cinerea* and Marsh harriers *Circus aeruginosus*. The majority (68%) of nest predation events occurred during the hours of darkness, suggesting that mammalian predators were responsible for most of the nest losses, and Red foxes have been shown to be the main nest predator of waders on grasslands across Western Europe (Macdonald & Bolton 2008). However, diurnal predation events were also recorded in this study, and thus avian predators may also be involved. This range of both diurnal and nocturnal potential predator species, and the likely differences in how they interact with woodland patches, may contribute to the absence of an overall effect of woodlands on the timing of nest predation.

The absence of any change in nest predation rates with distance from woodland patches suggests that the lack of nests close to woods is more likely to result from lapwing actively avoiding these areas than from nests close to woods being predated prior to being detected. Avoidance of areas close to woods could reflect a greater perceived predation risk in these areas, perhaps because trees prevent clear lines of sight from nest locations and thus increase the perceived vulnerability to predators of incubating adults.

A previous study of breeding lapwing on lowland wet grasslands has shown lower nest predation rates close (within ~100-200 m) to areas of tall vegetation such as field verges (Laidlaw *et al.* 2015), potentially reflecting predators concentrating on small mammal prey in these areas (Laidlaw *et al.* 2013). The lack of association between proximity to woodland patches and nest predation rates or timing of predation suggests that woodland patches may either (a) not provide the same conditions for small mammals as grassy field verges, (b) attract avian predators and thus offset any benefit of reduced mammalian predator impact or, alternatively, (c) the avoidance of woodland patches by nesting lapwing may constrain the capacity to identify their influence on nest predation rates. Our analyses of distance to woodland used the straight-line distance which presumes that predator movement around the sites is not constrained by any landscape features. While ditches could potentially constrain the movement of mammalian predators between fields, previous studies have found no evidence of foxes concentrating their activity along these features (Eglington *et al.* 2009), and, in these study areas, the distance of many of the woodland patches from the study fields (Figure 1) meant that direct and indirect (avoiding ditches) distances were very similar.

We have shown that the presence of woodland patches in lowland wet grassland landscapes may influence the distribution of breeding Lapwing and could result in large areas of potentially suitable habitat being unused for nesting. Consequently, in these landscapes, restoration of wet grassland habitats might be best located away (i.e. > 500 m) from woodland and woodland creation away (i.e. > 500 m) from fields suitable for breeding waders, and incorporating these criteria into agri-environment options designed to support breeding waders may help to avoid habitat creation in areas where parts of the landscape may be effectively unavailable to nesting lapwing. However, our findings also suggest that such habitat modifications may be unlikely to reduce nest predation rates, and thus the presence of woodland patches is not sufficient to inform or target predator control strategies, and other management practices that increase productivity, such as predator control or landscape manipulation to provide ample alternative food resources for predators, will still be needed to reverse wader population declines.

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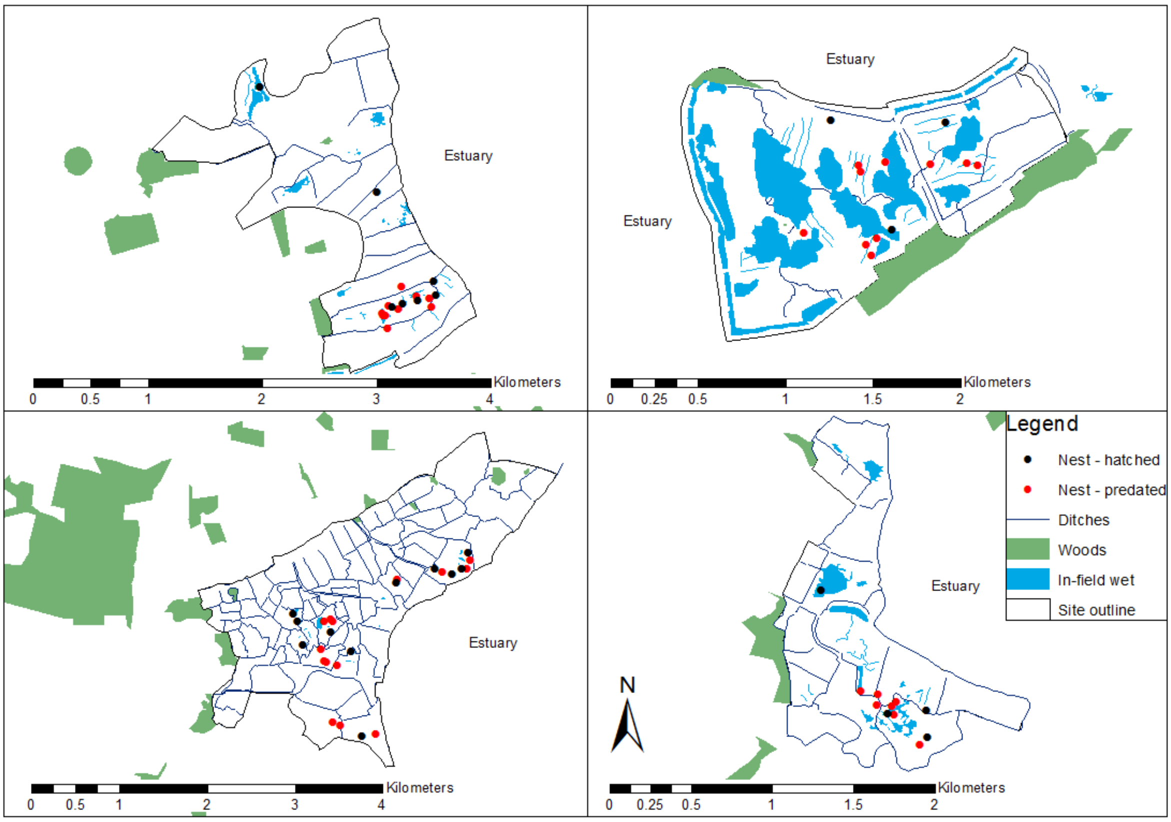
Table 1. Descriptions of response and explanatory variables used in models of landscape effects on Lapwing nest site selection and nest outcome. Full model structures are shown for each analysis.

Analysis	Response		Explanatory variables (fixed factors)
1: Is nest site selection affected by proximity to woods and wet features?			
	Nest or random location		Distance to woods, distance to wet features, (site)
2: Is nest predation rate affected by proximity to woods and wet features?			
	Daily predation rate		Distance to woods, distance to wet features, (site)
3: Is the timing of nest predation affected by proximity to woods and wet features?			
	Day or night		Distance to woods, distance to wet features, (site)
Response variable descriptions			
Analysis	Variable	Distribution	Description
1	Nest or random	Binomial	All nests (n=77) and random points (n=85)
2	Daily predation rate	Binomial	Predated (n=39) and other outcome (n=26) accounting for exposure days
3	Day or night	Binomial	Period of failure of predated nests (night n=26, day n=13; period defined by hours of civil twilight)
Explanatory variable descriptions			
Analysis	Variable	Factor levels	Description
1,2,3	Site	Four sites	Four wet grassland sites in Eastern England
1,2,3	Distance to wet features	Continuous	Shortest linear distance to nearest within-field flood or footdrain(m)
1,2,3	Distance to woods	Continuous	Shortest linear distance to nearest wood(m)

Table 2. Results of generalised linear maximal models exploring the influence of woods and in-field wet features on nest site location, daily nest predation rate and timing of nest predation (day or night). Significant effects are highlighted in bold.

Analysis	Variable				
1: Does nest site selection vary with distance to woods and wet features?					
		Wald	expB	df	p
	Constant	0.087	0.849	1	0.77
	Site	2.097	-	3	0.55
	Distance to wet features	**15.679**	**0.994**	**1**	**<0.001**
	Distance to woods	**5.375**	**1.002**	**1**	**0.02**
2: Does nest predation rate vary with distance to woods and wet features?					
		χ^2		df	p
	Constant	22.46		1	<0.001
	Site	0.81		3	0.85
	Distance to wet features	0.57		1	0.45
	Distance to woods	0.49		1	0.48
3: Does the timing of nest predation vary with distance to woods and wet features?					
		Wald	expB	df	p
	Constant	0.398	0.319	1	0.53
	Site	1.016	-	3	0.8
	Distance to wet features	2.262	1.014	1	0.13
	Distance to woods	0.087	0.999	1	0.77

303



304 **Figure 1.** Locations of hatched and predated Lapwing nests and key landscape components at the

305 four study sites on the Suffolk coast, eastern England.

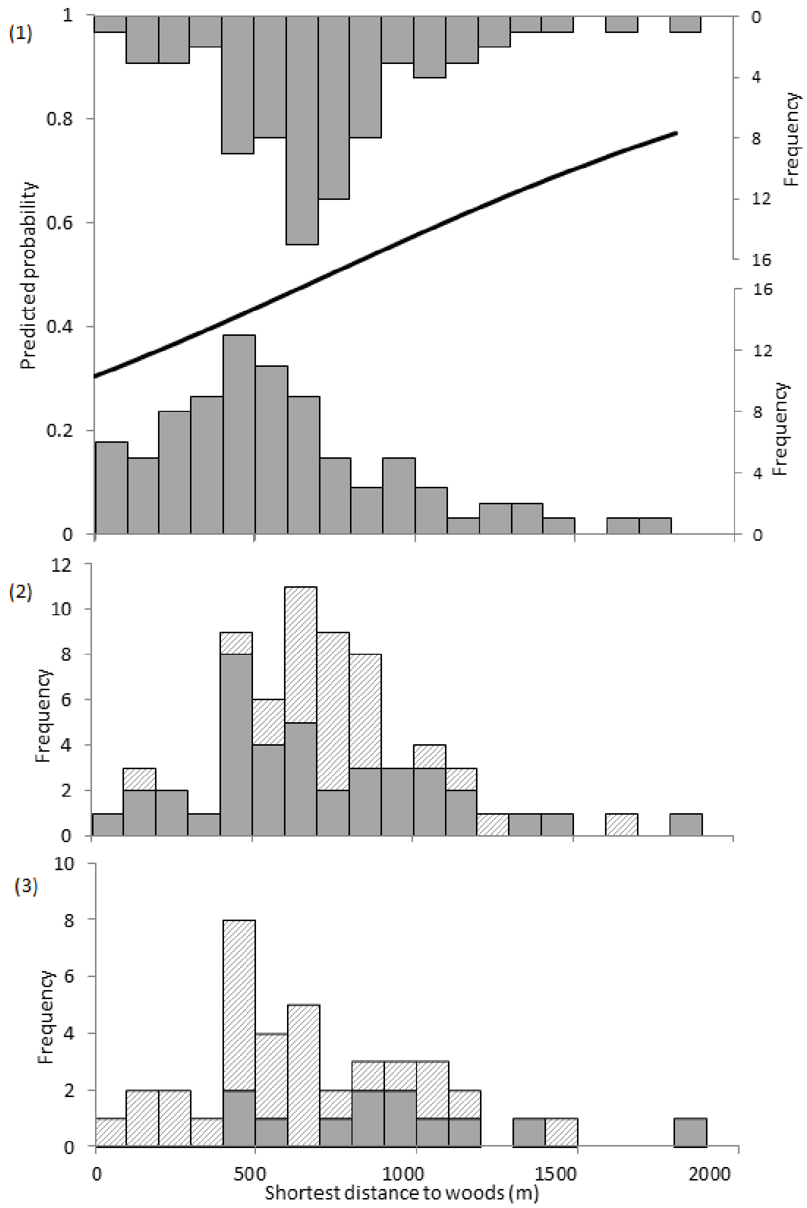


Figure 2. (1)The influence of distance to woodland patches, after controlling for site and distance to wet features, on the location of Lapwing nests (upper bars) compared to random points (lower bars), (2) the number of non-predated (shaded bars) and predated (solid bars) nests, (3) the number of nocturnal (shaded bars) and diurnally (solid bars) predated nests.

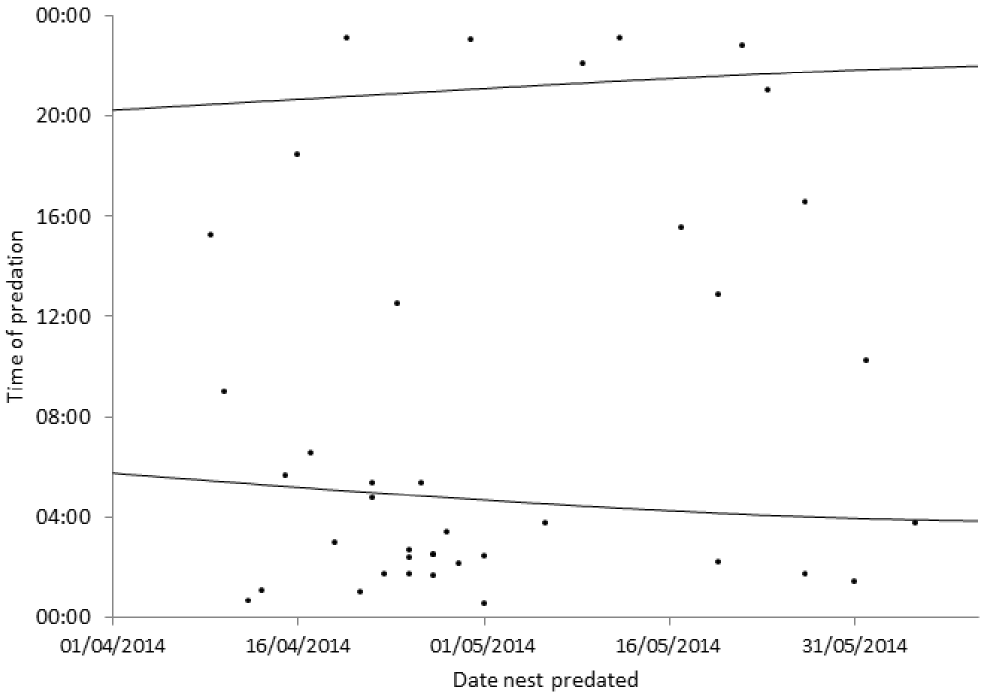


Figure 3. Seasonal and diurnal timing of Lapwing nest predation events. Lines show the timing of dawn and dusk (the beginning and end of civil twilight) throughout the breeding season.