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Effect of farmland type and vegetation height on habitat use and breeding success of northern lapwings in south-east Norway

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Master of Science in Ecology

Preface

This master thesis concludes my master's degree in Ecology at the Norwegian University of

Life Sciences. This thesis would not have been possible without crucial support from many

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Abstract

Habitat use is a key element to understanding how endangered species should be protected from further decline. The northern lapwing (*Vanellus vanellus*) is a red-listed farmland species threatened by multiple factors such as agricultural intensification, predation and environmental factors. Habitat use and hatching success was monitored frequently during the breeding season in 2019 in 28 localities in south-east Norway with known occurrence of lapwings. Lapwings preferred short vegetation and avoided tall vegetation, particularly as the breeding season progresses. They preferred short-height habitat types such as tilled fields, vegetation islands, roads and piles, and avoided tall-height habitat types such as autumn sown fields.

Out of 65 nests discovered in total, 50 % resulted in successful hatching whereas 30 % nests failed to produce chicks. Hatching success depended on habitat type selected for nest placement, but not vegetation height. Furthermore, results indicated that lapwings were more selective about their habitat after their chicks had hatched compared to the habitat chosen for nest placement.

Findings of this study suggest that the farmland landscape can be altered in order to increase hatching success. I recommend the following measured to prevent further population decline of lapwings in the study area: 1) switching from autumn sown cereals to spring sown cereals; 2) mark nests and avoid them during farmland activities; and 3) create set-asides and vegetation islands than may function as refuge from tall vegetation late in the breeding season.

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1 Introduction

Agricultural practices have undergone dramatic changes in the past century, becoming more intensive. Agricultural intensification is an important driver of the decline of soil, plant, insect and bird biodiversity in farmland habitats across Europe (Donald et al., 2001; Flohre et al., 2011; Hannappel & Fischer, 2019; Tsiafouli et al., 2015). One of the affected farmland bird species is the Palearctic wader, the northern lapwing (*Vanellus vanellus*), hereafter referred to as lapwing. The population trend is currently decreasing both in Norway and in Europe (BirdLife International, 2017; Heggøy & Øien, 2014), and the causes for this decline is usually attributed to agricultural practices, predation and environmental factors. Understanding the factors affecting local population dynamics of lapwings is crucial in order to implement effective measures against further population decline.

1.1 Background

Farmland may provide a diverse mosaic of habitat types. It can roughly be divided into two groups: 1) cropped habitats, in which the land is annually replanted with crops such as i.e. cereal, vegetables, berries and fruits, and 2) non-cropped habitats where the land is not annually replanted, i.e. pastures, hay meadows and fallows. Surrounding field margins (i.e. ditches and hedgerows), ponds, streams, woods and infrastructure add to the overall habitat diversity in the farmland landscape. In addition to this spatial variability between different farmland fields, there is also temporal variability within each field. Within a year, vegetation height and humidity conditions changes, and a cropped field may be harvested multiple times during the growing season. Fields can even vary between years due to for instance crop rotation or when a crop field is turned into a fallow field. This matrix of habitat types within a farmland landscape may support a high diversity of species, including arable plants, birds, insects and other invertebrates (e.g. Holland et al., 2006).

Agricultural intensification involves maximizing primary production for human consumption (Krebs et al., 1999). In Norway, agricultural practices have gone through a profound intensification during the past century. The number of farms have declined by 75 % during 1950-2005 while the farmland area have remained constant, meaning that each farm has

quadrupled in size on average (Ladstein & Skoglund, 2008). In the same time period, cereal and meat production have tripled, and productivity per working hour have increased eightfold (Ladstein & Skoglund, 2008).

This green revolution is a result of new knowledge, new technology and governmental subsidies. Farmers started to exchange their horses for tractors in the 1950s (Bjerkely, 2018; Fjellstad & Dramstad, 1999). In south-east Norway, the government stimulated farmers to specialize themselves in cereal production. For instance, Norwegian authorities subsidized drainage piping and filling of ravines in order for cereal fields to become bigger and flatter (Bjerkely, 2018). Species-rich meadows and pastures were to a large extent converted into species-poor cereal monocultures (Fjellstad & Dramstad, 1999). Together, all these measures affected farmland biodiversity. Noteworthy, it is the interaction of the multiple effects of agricultural practices rather than the effects of single components that makes agricultural intensification the main cause of farmland biodiversity decline in Europe (Benton et al., 2003; Newton, 2004).

Population changes in lapwings have followed the development in agricultural practices. From the beginning of the 20th century and onwards, the Norwegian lapwing population expanded northwards and inwards, and is now found across the whole country (Gjershaug et al., 1994; Heggøy & Øien, 2014). The population likely peaked in the 1970s with an estimated 60,000 breeding pairs (Kålås & Byrkjedal, 1981). Since then, the population has decreased drastically. In only a couple of decades the population has declined by more than 75 % (Heggøy & Øien, 2014).

1.2 Threats to the Northern Lapwing

The lapwing is currently categorized as Near Threatened on the Global Red List (IUCN, 2020), Vulnerable on the European Red List (BirdLife International, 2015) and Endangered on the Norwegian Red List (Henriksen & Hilmo, 2015). Population decline is mainly attributed to low recruitment rate rather than poor adult survival (see e.g. Newton, 2004; Roodbergen et al., 2012). I highlight agricultural practices, predation and environmental conditions as the most important factors affecting population dynamics of lapwings today.

1.2.1 Agricultural practices

The most important factor contributing to population decline in European lapwing populations is agricultural intensification as a whole, which is a factor causing or is likely causing rapid declines, defined as 20-30 % decline over 10 years (European Commission, 2009). Agricultural intensification is believed to be the main cause for population decline in Norwegian lapwing populations as well, due to its degrading effect on breeding sites (Heggøy & Øien, 2014).

Nest loss due to mechanical operations is an immediate threat. The onset of mechanical activities in relation to the lapwing breeding cycle is an important aspect in explaining the inter-year variability in lapwing nests destroyed by farming activities (Baines, 1990). The onset of mechanical activities depends especially on climatic conditions. Recently, both the onset of sowing by farmers and egg laying by lapwings has advanced as a response to climate change. However, egg laying has advanced faster than the sowing date, resulting in an increasing phenological mismatch (Santangeli et al., 2018), with higher nest loss being a probable outcome.

Northern lapwings may partially compensate for clutch loss through replacement clutches. However, the likelihood of laying a replacement clutch decreases as the breeding season progresses. It is not uncommon to harvest crops more than once in a single growth season, leading to a narrower window between sowing and harvesting, and possible interference between harvesting and the incubation period. Furthermore, female body condition is lower when replacement clutches are laid (Lislevand & Byrkjedal, 2004), suggesting that replacement clutches are less successful. This could in turn contribute to population decline.

Homogenization of farmland fields and land drainage could be linked to fewer foraging opportunities (Newton, 2004). For example, agricultural intensification promotes a less diverse soil food web consisting of smaller-bodied organisms (Tsiafouli et al., 2015). Poorer foraging conditions affect parental quality, which is linked to chick survival (Blomqvist et al., 1997). Scarcity of food may also affect the body condition of chickens (see Kentie et al., 2013), making them more vulnerable to disturbance, and in worst case lead to starvation.

1.2.2 Predation

Predation is of medium importance in explaining population decline in Europe, meaning that they cause or likely cause 10-20 % decline over 10 years (European Commission, 2009). Both ground predators and avian predators threaten the breeding success of reproducing lapwings, mainly through removing eggs and young fledglings. For example, field experiments with fence enclosures revealed that chicks were prone to predation from nocturnal ground predators, and that chick survival is significantly lower outside such protective fences (Rickenbach et al., 2011). Hooded crow (*Corvus cornix*) and red fox (*Vulpes vulpes*) are common predators of lapwings in Norway (e.g. Heien et al., 2018).

Anthropogenic change in habitat condition could make lapwings more vulnerable to predator attacks. For example, tall sward height in spring sown fields has been related to population decline in lapwings (Bell & Calladine, 2017). One possible reason is reduced detection of both avian predators and ground predators.

There is likely a site-specific variation in the relative importance of agricultural practices and predation in explaining local population decline in lapwing populations. Even though agricultural intensification is regarded as the main threat to lapwing populations, some studies conclude that predation is the main factor affecting breeding success in lapwings to a point below a sustainable population size (Baines, 1990; Schekkerman et al., 2009). Furthermore, the relative importance of egg predation seem to depend upon the density of lapwings in an area (Baines, 1990), which is linked to the efficiency of anti-predator defence. Anti-predator defence is more efficient when a larger group of lapwings is present. Predation can therefore locally be the most important factor affecting population decline in Lapwing where there are many predators in relation to lapwings.

1.2.3 Environmental conditions

It is generally challenging to assess the importance of environmental conditions as a threat to lapwings. Lapwings have long life cycles and overlapping generations, whereas the time frame of most studies are short. However, there is sufficient evidence to conclude that environmental conditions affect population dynamics of lapwings. For instance, favourable

climatic conditions during ca. 1870-1940 partly facilitated the expansion of lapwings in Norway through fewer cold winters and hence, higher winter survival (Harris, 1964; Heggøy & Øien, 2014). Furthermore, dry winters in parts of south-west Europe has likely caused food scarcity and increased competition for resources (European Commission, 2009). More recently, the amount of precipitation has been documented as a main factor affecting population size of lapwings (Laursen et al., 2018). Increased precipitation could be linked to more optimal foraging conditions. However, intense rainfall can significantly reduce chick body condition (Eglington et al., 2010). Because the occurrence of extreme rainfall events is projected to increase in the future (Rajczak & Schär, 2017), the breeding success of lapwings is at risk.

1.2.4 Other threats

Harvesting (hunting and egg collection) were as of 2009 practiced in 8 European countries, mostly in France, Italy, Greece and probably Spain (European Commission, 2009). Lapwings may overwinter in several of these countries (Shrubb, 2010). Harvesting is not a significant contributor to the sharp population decline experienced in Europe during the 1980s (Souchay & Schaub, 2016), but the impact of hunting may become more serious as the populations continue to decline. In Norway, where the species is present only during the breeding season, there could be carry-over effects from harvesting at wintering sites which is difficult to account for when studying population declines.

1.3 Habitat selection by the Northern Lapwing

Because population decline is mainly attributed to poor chick survival, understanding which conditions make a habitat type preferable for egg laying and whether such sites are limited is of importance. Generally, it can be said that lapwings depend on a localized mixture of habitats (Newton, 2004). A combination of factors thus likely defines the optimum habitat or composition of habitat types for breeding lapwings.

It has been shown that lapwings show a preference for open arable fields (e.g. Berg et al., 2002; Schmidt et al., 2017). These habitats provide a good view of approaching predators,

which aids the anti-predator strategies of this species. Such sites may be structurally similar to sites in Central-Asia where the European populations of lapwing originates from, which is characterized as nutritious salt meadows with short-grown rushes and sedges (Gjershaug et al., 1994). Also, lapwings may show a preference for proximity to wet areas, shallow pools and sites that are located at low elevations in the field as they likely indicate good conditions for foraging (Kaasiku et al., 2019; Schmidt et al., 2017).

1.4 Research objectives and hypotheses

This study aims to investigate possible factors influencing the population decline of lapwings in Norway. Understanding which mechanisms that primarily affect the observed population decline for this farmland species can help reveal which conservation efforts should be recommended in order to preserve it and the associated farmland biodiversity.

The main objectives of this study are three-folded: 1) Investigate which breeding sites are preferred by Lapwings and whether these sites are limited. Using conditional logistic regression models, I will investigate selection of farmland types and classes of vegetation heights for lapwings in general, during incubation, during foraging, and for lapwings in the company of chicks. 2) Investigate how hatching success varies in relation to different habitat types. 3) Investigate the causes for failed breeding attempts. The results will be used to discuss possible conservation measures for lapwings.

2 Materials and Methods

2.1 Study species

The northern lapwing (*Vanellus vanellus*) is a ground-nesting shorebird which is common in open countryside and particularly in agricultural land (Shrubb, 2010). The Norwegian population is estimated to be about 7 380- 10 000 pairs (Heggøy & Øien, 2014). The lapwing

is a migratory species which is breeding in the study area, but overwinters mainly in coastal Central- and South Europe (i.e. the British Isles, France, Spain, and Portugal). Its spring arrival is typically in late February or early March. Lapwings are territorial and males may engage with several partners in a single breeding season. Records of tetragynous mating system (Hafsmo et al., 2001) and polyterritoriality (Byrkjedal et al., 1997) suggests a high mating flexibility within this species. Eggs are typically laid in early to mid-April and the incubation period lasts for 25-30 days on average, with some individual variation (Gjershaug et al., 1994; Shrubb, 2010). They typically lay a single clutch of 3-4 eggs in nests made of straw, grasses, moss, twigs and so forth, and is placed in shallow depressions on the ground. Their chicks are precocial and become capable of flying within 5 weeks. Migration to more suitable feeding grounds or to overwintering grounds may begin as early as late June, but normally occurs in July and August (Gjershaug et al., 1994).

2.2 Study area

The study area was located in four municipalities in Akershus county (now part of Viken county) in south-eastern Norway, namely Frogn, Ski (now part of Nordre Follo), Vestby and Ås municipalities (Figure 1). The agricultural landscape is characterized by a large proportion of cereal production with some vegetable production, in particular curly kale and faba bean. All sites with known observations of lapwings were evaluated for inclusion in further analyses. Sites were identified based on fieldwork performed by Svein Dale during 1995-2018, and observations of lapwings registered to the bird reporting websites nofoa.no and artsobservasjoner.no. In total, 28 sites were investigated: 4 sites in Frogn, 7 sites in Ski, 14 sites in Vestby and 3 sites in Ås.

The study area lies in the transition between coastal climate and continental climate. During the study period 3 April – 20 June 2019, the weather station at Ås near the Norwegian University of Life Sciences (NMBU) recorded a mean daily temperature of 10.2 °C and a total precipitation of 227.8 mm during the whole study period. April was a dry month with almost no precipitation, whereas rain spells occurred more frequently in May and June. The monthly mean temperature increased steadily with time, but a cold spell occurred in early May where the daily mean temperature dropped to 4.1 °C.

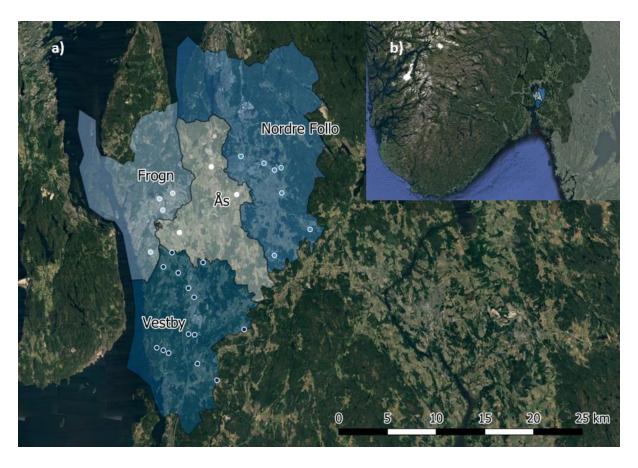


Figure 1: The position of the study sites (a), and the position of the study area in Norway (b). Each dot represents one study site, and each municipality is shaded and named.

2.3 Data collection

In the beginning of April, potential sites were surveyed to locate those with lapwings present. During this period, lapwings are actively engaged in flight display and territory establishment. Their conspicuous flight style and alarm calls facilitates detection of individuals and consequently possible breeding sites. All sites with lapwings present were visited every 3-5 days from 23 April and onwards. 10x40 binoculars and a 30x telescope were used to search for birds.

The position of each lapwing upon first sight was recorded on field maps, and the chosen habitat type was recorded. Additionally, the proportions of each habitat type around the lapwings in a 300 m radius were estimated as a measure of habitat availability. The following habitat types were recorded: tilled field, stubble field, fallow field, autumn sown cereal, spring sown cereal, kale, brussels sprout, faba bean (*Vicia faba*), grass, raspberry and other.

Forests and human infrastructure were excluded from the calculations when proportion of habitat types were estimated because lapwings are not expected to use such areas. To avoid pseudoreplication, all individuals within a distance of 100 meters from each other were defined as a group given that they occupied the same habitat type.

Vegetation height for the chosen habitat type and surrounding habitat types was measured with tape measures or otherwise estimated by eye when this was not possible. Vegetation height was categorized as 0 cm (sprouting not detected), 0-5 cm (sprouting detected), 5-10 cm, 10-20 cm, 20-30 cm, 30-40 cm, 40-50 cm and > 50 cm. Vegetation height was not measured for certain habitat types such as uncultivated grass, stubble field, raspberry fields, fallow field and other habitat types where vegetation height was highly variable within the habitat type. Additionally, due to various reasons, vegetation heights were not recorded as consistently very early in the study period. Therefore, there are 94 recorded instances where lapwings selected a habitat with unknown vegetation height.

Behaviour was registered for each individual lapwing or group of lapwings detected. We categorized behaviour into breeding (mating attempt or incubation), foraging, resting/preening, in flight (including flight display), territory defence, anti-predator defence and other.

Hatching success was investigated by following incubating individuals. Incubating individuals were given a unique nest ID, and we made efforts to locate activity near the nest upon every field visit for as long as there was incubation activity. Each nest was given a hatching status at the end of the study period, to assess whether the nest ever produced chicks, whether hatching was likely, whether the breeding attempt failed or whether hatching status was uncertain. This is defined in detail in Table 1.

Table 1: An overview of the total number of registered nests grouped by hatching status. Description of hatching status explain the criteria for a nest to be categorized within the specific category.

Hatching status	Description	Sum
Hatching observed	Chicks were directly observed.	22
Hatching likely	Chicks were not observed, but hatching had likely occurred due to observed stressful behaviour of adult individuals (i.e. alarm calls and anti-predator behaviour) in a period of time when hatching was expected.	11
Uncertain	Incubation was observed, but neither chicks nor stressful behaviour was observed. It is uncertain whether the clutch ever hatched or whether the breeding attempt failed.	11
Failed Land use change Predation	Incubation has been observed, but ceased between field visits. Failed breeding is attributed to land use change when alterations to the nesting habitat were visible between visits, and is attributed to predation when incubation at easily detectable nests ceased for reasons other than land use change.	20 6 14
Total		65

2.5 Statistical analyses

In order to investigate habitat selection by lapwings, we compared observed habitat choice ("case") against random habitat choice ("control"). If habitat choice is random, we expect a proportional relationship between habitat use and habitat availability. Therefore, random habitat choice was simulated based on the habitat availability for a given lapwing individual.

For this purpose, a conditional logistic regression model from the R package "survival" (Therneau, 2015) was fitted. Observation type (case vs. control) was used as the response variable and selected habitat type was used as the explanatory variable. This approach tests whether the observed habitat selection of lapwings differ from random habitat selection. The estimates from the conditional logistic regression are conditional on the matched proportions of habitat types available to each observation of lapwing(s). Because the frequency of

selected habitat types was low for habitat types such as raspberry, fallow field and brussels sprout, these habitat types were redefined as "other habitat" in the analyses.

One could argue that habitat choice of lapwings is influenced by site-specific characteristics. However, random effects cannot easily be added to the conditional logistic regression models in the "survival" package in R. Instead, a conditional logistic regression model was fitted with selected habitat type and site as fixed effects. We compared the models with and without site included as an explanatory variable and selected the model with the smallest Akaike information criterion (AIC) value, which turned out to be the models where site was excluded. Therefore, site was not considered an important factor influencing habitat selection of lapwings.

Conditional logistic regression models were also fitted with observation type (case vs. control) as the response variable and selected vegetation height as the explanatory variable. 40-50 cm and >50 cm vegetation height categories were merged into a >40 cm vegetation height category because few lapwings selected these vegetation height categories.

Conditional logistic regression models investigating habitat and vegetation selection were fitted to four different sub-sets of the total data material. First, they were applied to all lapwings that selected a habitat type or vegetation height. Incubating individuals were excluded because a nest is stationary, and hence there is not really a choice of habitat type or vegetation height once the nest is placed. Second, I fitted the models to foraging lapwings. Third, the models were fitted to lapwings at the first observation of incubation (nest site selection). Last, models were fitted to adult lapwings seen with chicks.

I investigated whether habitat preference for the total number of lapwings changed over time, using logistic regression models. Selection of a certain habitat type (true or false) was the response variable. The proportion of the respective habitat type and day after 1 April were the explanatory variables. Backward eliminations of the full models were performed using the R package "stats". The most parsimonious models (i.e. models where AIC-values were the lowest) were retained. Prior to the tests I excluded incubating individuals, and observations where a given habitat type was absent or completely dominating. The level of significance was corrected using the Bonferroni method (n = 8 tests). Similar approaches were applied in order to explore whether preference for vegetation heights changed over time. Here too, the level of significance was corrected using the Bonferroni method (n = 7 tests).

The relationship between colony size and hatching success was investigated using Spearman rank correlation tests. Colony size was calculated as the mean number of observed lapwings on a given locality over time. This estimate is based on observations recorded after escalation of field visits (23 April), in order to exclude early field visits where migrating birds are expected to occur. Spearman rank correlations were estimated both with and without weighing for the number of nests in a locality, using the package "wCorr" (Emad & Bailey, 2017) and "stats", respectively.

Two-sided Fisher exact tests were applied to investigate the relationship between hatching success and chosen habitat type or vegetation height interval upon nest placement.

For all analyses, the level of significance was set to p-value <0.05. All analyses were performed in R version 3.6.1 (R Core Team, 2019).

3 Results

3.1 Habitat availability

Throughout the study period, cereal fields accounted for the largest proportion of available habitat types (Figure 2). However, the habitat availability varied over time. Generally, autumn sown cereal, grass and kale and seemed to be more or less uniformly available during the study period. Stubble field and tilled field were widely available in the beginning of the study period, declined sharply towards the end of April and remained low for the rest of the study period. The availability of spring sown cereal and faba bean were sparse in the beginning of the study period but increased sharply towards the end of April and remained stable throughout the rest of the study period.

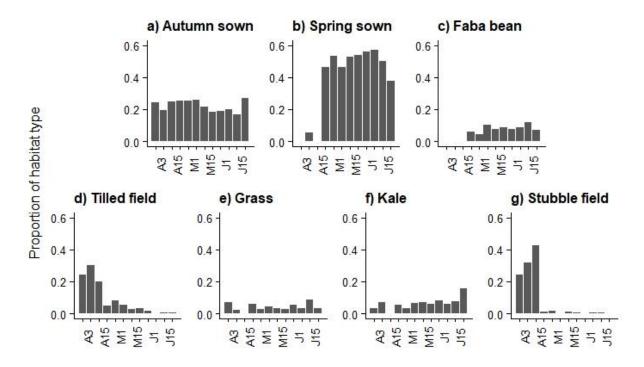


Figure 2: Proportion of available habitat over time for the following habitat types: autumn sown cereal (a), spring sown cereal (b), faba bean (c), tilled field (d), grass (e), kale (f) and stubble field (g). Time scale is broken into weeks. Time labels are shown as abbreviations where the letter represents the month (A: April, M: May, J: June), and where the number represents the date, e.g. A3 equals 3 April.

Additionally, there was a visible shift in available vegetation heights as time progressed. (Figure 3). In the beginning of the study period there was a higher abundance of short vegetation, whereas the availability of vegetation heights shifted towards taller vegetation as the breeding period progressed. In the final week of the study period, more than 70 % of the available vegetation heights were more than 40 cm tall.

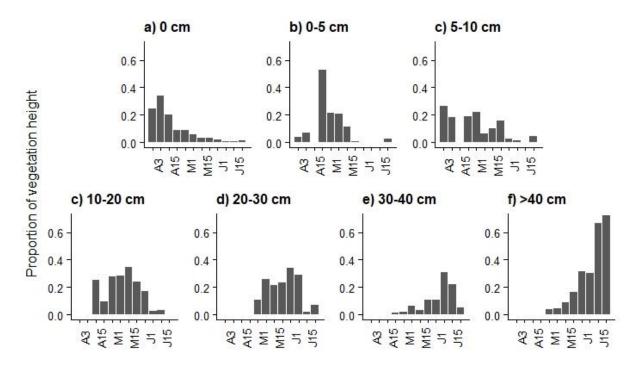


Figure 3: Proportion of available vegetation height over time, for vegetation heights of 0 cm (a), 0-5 cm (b), 5-10 cm (c), 10-20 cm (d), 20-30 cm (e), 30-40 cm (f) and more than 40 cm (g). Time scale is broken into weeks. Time labels are shown as abbreviations where the letter represents the month (A: April, M: May, J: June), and where the number represents the date, e.g. A3 equals 3 April.

Overall, lapwings selected cereal most often (about 60 % of all recorded cases), whereas habitat types such as faba bean, tilled field, grass, kale, and stubble field were selected less than 10 % of the time (Table S1). Lapwings selected other habitat types 10.3 % of the time, where fallow field, brussels sprout and raspberry accounted for roughly 60 % of these instances (Table S1).

3.2 Habitat selection

Habitat selection varied across different subsets of lapwings. According to the conditional logistic regression models, lapwings overall showed a significant preference for grass, faba bean, tilled field and other habitat, and showed a significant avoidance of autumn sown field (Figure 4a). "Other habitat" included less common habitat types such as onion fields and oilseed radish (*Raphanus sativus* var. *oleiformis*), and atypical habitat types such as roads,

and piles of stone, -sand or -earth. Lapwings were indifferent to spring sown fields across all subsets, showing no preference nor avoidance for this habitat type (Figure 4).

Foraging lapwings showed a significant selection for faba bean and other habitat, and also a tendency to select stubble fields (Figure 4b). Autumn sown fields were on the other hand avoided. Lapwings were not very selective about habitat types for nest placement, apart from showing a significant preference for faba bean (Figure 4c). Finally, lapwing showed a significant preference for other habitat types when in company with chicks (Figure 4d). In the majority of these cases, lapwings were seen on roads or piles of earth.

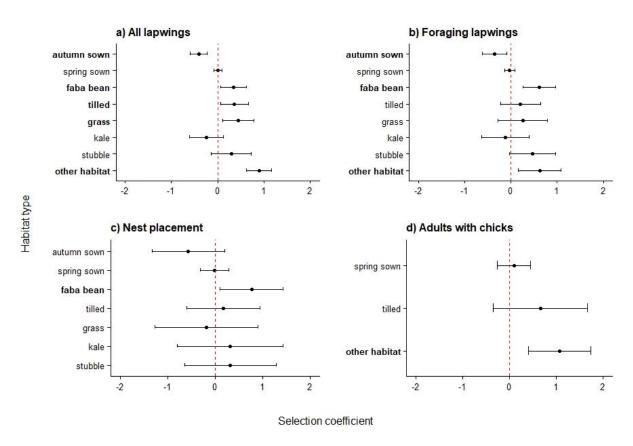


Figure 4: Coefficients from the conditional logistic regression models assessing the likelihood to select various habitat types for lapwings in total (a), foraging lapwings (b), nest replacement (c) or lapwings with chicks (d). Mean coefficient estimates are shown as dots, and error bars delineate the 95 % confidence interval. Positive selection coefficients imply preference whereas negative selection coefficients imply avoidance. Significant preference or avoidance is marked in bold on the vertical axis.

In general, lapwings avoided tall vegetation (Figure 5). Lapwings in total and foraging lapwings significantly avoided patches with >40 cm vegetation height (Figure 5a-b).

Lapwings with chicks showed a significant preference for short vegetation and a significant avoidance of tall vegetation (Figure 5d). Due to low sample size in this subset, vegetation height categories were merged together.

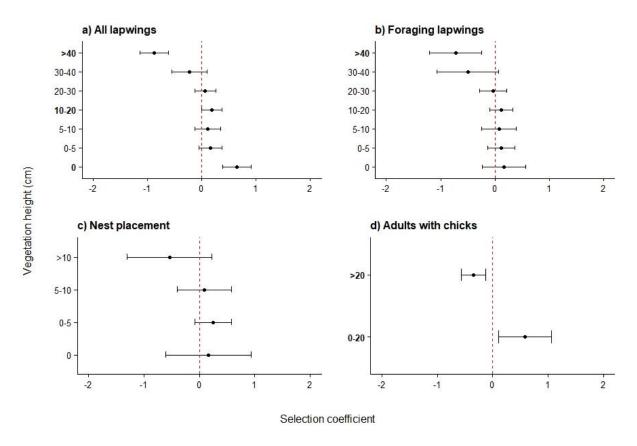


Figure 5: Coefficients from the conditional logistic regression models assessing the likelihood to select various vegetation heights for lapwings in total (a), foraging lapwings (b), nest replacement (c) or lapwings with chicks (d). Mean coefficient estimates are shown as dots, and error bars delineate the 95 % confidence interval. Positive selection coefficients imply preference whereas negative selection coefficients imply avoidance. Significant preference or avoidance is marked in bold on the vertical axis.

Finally, nest-placing lapwings tended to avoid tall vegetation as well, although this was not significant (Figure 5c). They did not seem to discriminate between 0 cm, 0-5 cm and 5-10 cm vegetation height upon nest placement (Figure 5c). Out of 50 nests with registered vegetation heights upon first detection of nest, only 5 nests were spotted in patches with >10 cm vegetation height (Table S1, Figure 6). It was not possible to obtain reliable estimates of egg laying dates for most nests. Therefore, the actual distribution of selected vegetation height and availability of vegetation height intervals were likely skewed towards lower vegetation heights than what is portrayed in Figure 6.

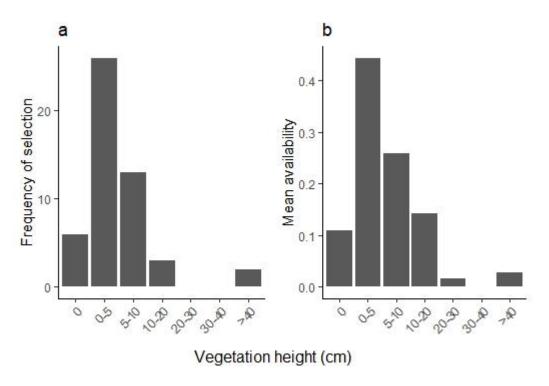


Figure 6: Observed frequency of selected vegetation height upon nest placement (a) and the mean availability of each vegetation height interval upon nest placement (b).

Logistic regression models revealed that the most important factor affecting the probability of selecting a certain habitat type was the proportion of the given habitat type. The probability of selecting a habitat type increased with the proportion of the given habitat type (Table 2). Interestingly, some habitat preferences changed over time (Table 2). Results indicated that the probability of selecting autumn sown cereal declined significantly over time, whereas the probability of selecting tilled field, grass and other habitats significantly increased over time. For the remaining habitat types, there were no statistically significant effect of time on the probability of selecting a habitat type.

Only one interaction term was significant. The effect of day on probability of selecting grass depended on the proportion of grass, or vice versa. When grass proportion was low, the probability of selecting grass increased with time. When grass proportion was high, the probability of selecting grass decreased with time.

Table 2: Results from logistic regression models regarding preference for habitat types. The response variable is the probability of selecting a specific habitat type. The explanatory variables in the full models was days after 1 April, proportion of the specific habitat type available in a 300 m radius around the lapwings, and the interaction term between the two. Backward elimination of full models was performed, and the most parsimonious model is presented in the table. Bonferroni-corrected p-values are reported. Significant explanatory variables are marked in bold.

Habitat type	Explanatory variable	Estimate	Standard error	p-value
Spring sown cereal (n = 403)	Proportion	4,98	0,50	<0.001
Autumn sown cereal	Day	-0,03	0,01	<0.01
(n = 308)	Proportion	6,51	0,92	<0.001
Faba bean (n = 82)	Day	-0,05	0,02	0.10
	Proportion	7,13	1,77	<0.001
Tilled field (n = 90)	Day	0,05	0,02	<0.01
	Proportion	7,27	1,50	<0.001
Grass (n = 144)	Day	0,04	0,01	<0.05
	Proportion	9,06	3,20	<0.05
	Day*Proportion	-0,20	0,07	<0.05
Kale* (n = 112)	Proportion	6,73	1,44	<0.001
Stubble field (n = 53)	Day	0,04	0,02	0.64
	Proportion	10,70	3,07	<0.01
Other habitat	Day	0,05	0,02	<0.05
(n = 153)	Proportion	11,11	3,25	<0.01
	Day*Proportion	-0,14	0,06	0.09

^{*):} Including the interaction term in the full model resulted in multicollinearity issues. Therefore, the full model consisted only of additive effects.

Lapwings selected 10-20 cm vegetation height most often (more than 20 % of all recorded cases), and selected generally vegetation heights of less than 30 cm most often (Table S1). Logistic regression models revealed that preferences for certain vegetation heights changed over time whereas all models were positively influenced by the proportion of the given vegetation height (Table 3). The probability of selecting short height classes (0 cm and 0-5 cm) increased over time, whereas the probability of selecting tall height classes (> 40 cm) decreased over time (Table 3).

Table 3: Results from logistic regression models regarding preference for vegetation heights. The response variable is the probability of selecting a specific vegetation height interval. The explanatory variables in the full models was days after 1 April, proportion of the vegetation height available in a 300 m radius around the lapwings, and the interaction term between the two. Backward elimination of full models was performed, and the most parsimonious model is presented in the table. Bonferroni-corrected p-values are reported. Significant explanatory variables are marked in bold.

Vegetation height				
category	Explanatory variable	Estimate	Standard error	p-value
0 cm (n = 116)	Day	0.11	0.02	<0.001
	Proportion	12.78	2.76	<0.001
	Day*Proportion	-0.16	0.06	0.07
0-5 cm (n = 166)	Day	0.05	0.02	<0.01
	Proportion	9.08	1.36	<0.001
5-10 cm (n = 144)	Proportion	7.79	1.27	<0.001
10-20 cm (n = 197)	Day	0.04	0.02	0.08
	Proportion	7.51	1.08	<0.001
20-30 cm (n = 201)	Day	0.04	0.02	0.08
	Proportion	8.99	1.30	<0.001
30-40 cm (n = 101)	Day	0.03	0.02	1
	Proportion	8.38	1.72	<0.001
>40 cm (n = 180)	Day	-0.07	0.02	<0.05
	Proportion	4.35	1.07	<0.001

3.2 Hatching success

In total, 65 individual nests were detected across all study sites (Table 1). Half of the nests produced chicks or likely produced chicks. 20 nests failed during the breeding season, and the majority of the nests failed due to predation (Table 1). Furthermore, hatching success varied on a local scale, here exemplified through the different municipalities (Figure 7). Within each municipality, proportion of successful nests can be calculated as the number of nests with observed or likely hatching, divided by the total number of nests in the municipality. The success rate lied somewhere between 0.6-0.93 in Frogn, 0.67-0.8 in Ski, 0.5-0.58 in Vestby and 0.18-0.45 in Ås. Estimated success rate varies according to whether nests with uncertain hatching status is considered failed or hatched.

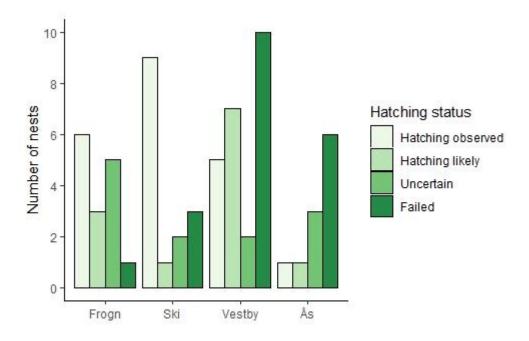


Figure 7: Total number of nests, grouped by hatching status, in each municipality included in the study. A detailed description of the different hatching statuses is given in Table 1.

Breeding lapwing pairs did not benefit from larger numbers. Spearman rank correlation tests revealed that there was no relationship between colony size and hatching index (Figure 8a; $\rho = 0.07$, p = 0.76) or between colony size and proportion of successful nests (Figure 8b; $\rho = 0.07$, p = 0.77). This finding was consistent when weighing for the number of nests in each site as well ($\rho = 0.09$ and $\rho = 0.06$, respectively).

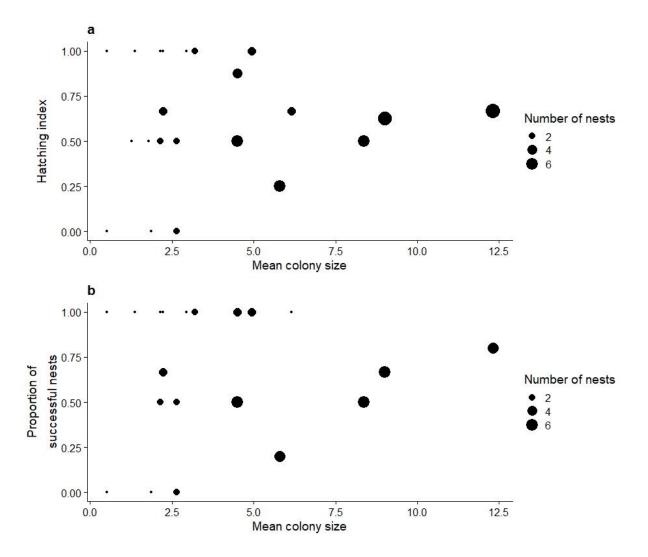


Figure 8: Hatching success in relation to colony size when nests with hatching status "potential" is included (a) or excluded (b). Nests with "observed" or "likely" hatching status were given a score of 1, "failed" 0 and "potential" 0.5. Hatching index was then calculated by summing the scores of each nest and dividing by total number of nests (excluding nests with "uncertain" hatching status). Proportion of successful nests were calculated as the number of nests with observed or likely hatching success divided by total number of nests (excluding nests with "potential" and "uncertain" hatching status). Each point represents a site in the study area, and points are sized according to the number of nests laid in a given site.

Hatching success varied according to the selected habitat type upon egg laying (Table 4). 72 % of nests placed on spring sown fields resulted in observed or likely hatching, whereas hatching success was low on fields with faba bean. The three nests placed on stubble fields were protected by the farmer by putting up sticks close to the nest upon discovery, and therefore deliberately avoided during ploughing.

Sample size was low within several of the different habitat types. Therefore, a two-sided Fisher exact 2x3 test was applied for the three habitat types with the largest amounts of nests ($n \ge 6$ nests); spring sown fields, faba bean and tilled fields. It turned out that hatching success varied depending on the habitat chosen for nest placement (p-value = 0.07).

Table 4: The relationship between hatching success and selected habitat type upon egg laying. Number of nests refers to the number of lapwings that selected the given habitat type upon egg laying.

Chosen habitat type upon egg laying	Number of nests	Percentage successful nests
Autumn sown	4	50 %
Spring sown	18	72 %
Faba bean	8	25 %
Tilled field	6	50 %
Grass	3	0 %
Kale	2	50 %
Stubble field	3	100 %

It did not seem like there was a relationship between vegetation height upon egg laying and the resulting overall hatching success (Table 5). A two-sided Fisher exact test revealed no relationship between hatching success and vegetation height intervals when vegetation height intervals with ≥ 6 nests were included (0 cm, 0-5 cm and 5-10 cm; p-value = 0.90). However, most of the nests were placed in short vegetation, which reflects the distribution of vegetation heights at the time of egg laying (Figure 6). Most nests were laid during April.

Table 5: The relationship between hatching success and estimated vegetation height upon egg laying. Number of nests refers to the number of lapwings that selected the given vegetation height upon egg laying.

Chosen vegetation height upon egg laying	Number of nests	Percentage successful nests
0 cm (no sprouting)	6	50 %
0-5 cm (sprouting)	21	48 %
5-10 cm	9	56 %
10-20 cm	3	100 %
30-40 cm	0	-
> 40 cm	1	0 %

4 Discussion

4.1 Habitat selection

This study documents a dynamic agricultural landscape matrix that alters as time progresses, both in terms of available habitat types and vegetation height classes. In this study, I investigated which breeding sites were preferred by lapwings and whether these sites are limited. My results show that in general, lapwings are very flexible about the habitat types used during the breeding period. They exhibited a strong preference for uncategorised habitat types and a notable avoidance of autumn sown fields. They also showed a significant preference for habitat types such as grass, faba bean and tilled field, all of which had low availability during the study period. They were not selective about spring sown fields, which was the most abundant habitat type.

I argue that lapwings prefer short vegetation. First of all, conditional logistic regression models revealed that lapwings showed a strong significant preference for 0 cm vegetation height, and strong significant avoidance of vegetation height that exceeded 40 cm. Similar patterns are observed in the various subsets of lapwings (Figure 5b-d). Also, lapwings preferred short-vegetation habitat types such as tilled field, and avoided tall-vegetation habitat types such as autumn-sown fields. The probability of selecting autumn sown field and >40 cm vegetation height decreased over time, whereas the probability of selecting tilled field, 0 cm and 0-5 cm vegetation height increased over time.

Interestingly, a significant interaction term between the proportion of grass and time was discovered (Table 2). During field visits, both small, uncultivated vegetation islands and large, cultivated grass fields for animal food production were categorised as grass. The probability of selecting small patches of grass increased with time, which suggests that such vegetation islands became more important for lapwings as surrounding vegetation became tall.

The observed preference for short vegetation is in line with findings from other studies. Vegetation height and density has been shown to be an important factor affecting site selection by lapwings (Schmidt et al., 2017). Also, Eggers et al. (2011) recorded a higher number of lapwing territories per hectare in spring sown cereals compared to autumn sown cereals.

Short vegetation is advantageous in multiple ways. For instance, foraging efficiency increases in short vegetation compared to tall vegetation through increased prey detectability and mobility (Butler & Gillings, 2004). Furthermore, predator detectability may be higher in short vegetation (Whittingham & Evans, 2004). The brown colours in fields with no or sparse vegetation may offer camouflage for lapwings as well.

In this study, lapwings showed strong preference for other habitat types than the main categories included in this study. This is a broad category including fields of onion, brussels sprout, raspberry, fallow field, pasture etc. Most notably though, this category includes abnormal habitat types such as roads, and piles of sand or soil. These spots may have served as viewpoints or refuge from the surrounding landscape of tall vegetation, especially late in the breeding period when the vegetation height was tall in general. Such spots are advantageous to lapwings with chickens, so that adults can look out for potential danger while watching their offspring. During field visits, lapwings with chicks were spotted on such atypical patches while looking around, and switching behaviour when potential danger approached (i.e. producing alarm calls and taking to flight; personal observations).

4.2 Hatching success

Another aim of this study was to investigate how hatching success varies in relation to the observed habitat types chosen during nest placement. Although there was not enough data to properly test this, two conclusions can be drawn. First, a high proportion of the nests placed in spring sown fields resulted in hatching success (Table 4), even though lapwings were not selective about this habitat type (Figure 4c). Second, a low proportion of nests placed in fields of faba bean resulted in hatching success, even though lapwings showed a significant preference for this habitat type.

The repeated selection for faba bean suggests that this is a habitat type with good foraging conditions, and which facilitates mobility. The low proportion of hatching success despite the exhibited preference for this habitat type suggests an ecological trap. The selection for faba bean as nesting site could be due to sparse vegetation and favourable soil conditions at nest placement when the crop was short rather than the habitat quality when the crop grew tall. However, more research is needed to establish whether the low hatching success in fields of

faba bean are coincidental or if it reflects a real consequence of this particular nest habitat selection.

Note that because the study period only covers one breeding season, site fidelity is not accounted for. Site fidelity may be as high as 74 % on average (Berg et al., 2002), and may therefore be a confounding factor when studying habitat selection. For instance, lapwings may have chosen the same habitat patch in consecutive years independent of crop rotation.

In the present study, lapwings showed almost no preference for one habitat type over another regarding nest placement. Also, previous findings by Blomqvist and Johansson (1995) show that lapwings showed no apparent preference for arable fields or pastures. This suggests that lapwings are very flexible when it comes to incubation habitat. Habitat selection is perhaps more important after hatching. In fact, lapwings were more selective about habitat occupation when accompanied by their chicks. Johansson and Blomqvist (1996) found that chick-rearing lapwings selected home ranges containing high proportion of preferred foraging habitats for chicks. Such habitats should offer both cover from potential danger, and high foraging quality.

Finally, I investigated the causes for failed breeding attempts. Around 30 % of all nests laid resulted in failed breeding attempts, and 70 % of these nests failed presumably due to predation while 30 % failed due to land use changes (ploughing, specifically). Another 17 % of all nests have uncertain hatching status.

Larger or denser colony size of lapwings in farmland areas has been linked to higher hatching success (Berg et al., 1992). In contrast, I found no relationship between colony size and hatching success. The weak relationship between colony size and hatching success could partly be due to farmland activities. In sites where no failed breeding attempts are caused by farmer activity, but mainly predation, the benefit of common nest defence should increase with larger colony size. On the other hand, in sites where farmland activities are the direct cause of nest loss, there is no strength in numbers.

Results also showed that hatching success is linked to habitat type selected upon nest placement. Vegetation height upon egg laying could not be linked to hatching success, on the other hand. This implies that the farmland landscape can be altered in order to affect hatching success. For example, higher hatching success has been documented in unsown, tilled fields; so-called lapwing plots (Schmidt et al., 2017).

4.3 Implications for conservation

As previously stated, understanding which mechanisms affect the observed population decline for lapwings can help reveal which conservation efforts should be recommended in order to preserve this species. This study has shown that sward height is perhaps the most important factor influencing habitat choice of lapwings in south-east Norway. Lapwings tended to avoid tall vegetation, especially late in the breeding season.

Tall vegetation height limits mobility and access to forage, and has been linked to population declines in farmland bird species (Bell & Calladine, 2017; Eggers et al., 2011; Hiron et al., 2012). Reduced mobility and foraging access likely escalates as sward height increases because vegetation structure has shown to become more dense in addition to taller as the breeding season progresses (Schmidt et al., 2017). Furthermore, proportion of fields with tall sward height has increased significantly in the past decades (Bell & Calladine, 2017).

Interestingly, Santangeli et al. (2018) proposed that the switch from spring sown cereals to autumn sown cereals would be beneficial both to lapwings and farmers as an adaption to climate change. The timing of farming activities has advanced slower than the timing of nest laying, and consequently, the risk of nest destruction by farming activities increased. They argued that autumn sowing would decrease nest destruction. In lights of the results of the present study, autumn sown cereals were not a preferred habitat type and predation accounted for the most frequent cause of failed breeding. I therefore remain critical to the switch from spring sown cereals to autumn sown cereals as a measure to conserve lapwing populations.

Another measure with potential to increase hatching success is to mark nests upon discovery and avoid these nests during ploughing, sowing and other farming activities. In this study, nest marking was performed in Ski municipality where possible, which resulted in several nests being rescued (Gaathaug & Sakseide, 2019). This could partly explain why nest destruction by farming activities contributed less to nest loss compared to predation. However, it has been shown that nest protection has small effect on population growth rate (Plard et al., 2019). Although hatching success increases with increased nest protection, more efforts are needed to ensure that chicks also survive until independence.

In this study, lapwings were more selective about their habitat after hatching (when in company with chicks) compared to during nest placement. No set-asides or vegetation islands were selecting during nest placement, but such sites could prove to be more important for

lapwings after hatching. Suitable habitat after hatching is critical to ensure optimal growth and survival probability of lapwing chicks.

5 Conclusion

Altoghether, this study has shown that lapwings are generally flexible regarding choice of habitat types. It appears that vegetation height and structure is a more important factor influencing site selection of lapwings in the farmland landscape, particularly late in the breeding season. Furthermore, predation is believed to be the most important cause of nest loss locally, whereas nest protection is valued as a measure to increase hatching success. Agricultural intensification remains the most important factor affecting population trends in lapwings through direct effects such as nest destruction, and indirect effects such as homogenization of the farmland landscape and poor foraging quality (Donald et al., 2001; Kentie et al., 2013; Newton, 2004).

The decline of lapwings may be reduced by locally and comprehensively reviewing the farmland landscape and ensuring patches of good forage quality and vegetation structure which facilitates mobility and lookout throughout the entire breeding season. I recommend three measures in order to protect this species from further population decline: 1) Switching to spring sown cereals instead of autumn sown cereals, because the former is related to high hatching success while the latter is a less preferred habitat type of lapwings. 2) Mark nests upon discovery and actively avoid nest destruction during farming activities in order to maximize hatching success. 3) Create set-asides and vegetation islands in areas with known occurrence of lapwings in order to facilitate forage, mobility, and lookout, and increase the number of chicks reaching independence.

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7 Appendix

Table S1: Observed frequency of selection, selection percentage, expected frequency of selection and mean availability of habitat types and vegetation heights throughout the study period, for total number of lapwings and different sub-sets of lapwings: foraging lapwings, nest placement of lapwings and adult lapwings observed with chicks. Expected frequency of selection is calculated as the sum of the proportion of the given habitat type or vegetation height available. Mean availability is the mean proportion of a habitat type or vegetation height, calculated as the expected frequency of selection divided by total number of observations.

	Lapwings in total				Foraging			
Habitat type	Observed frequency of selection	Selection percentage (%)	Expected frequency of selection	Mean availability (%)	Observed frequency of selection	Selection percentage (%)	Expected frequency of selection	Mean availability (%)
Spring sown cereal	252	45.5	265.2	47.9	149	49.5	158.9	52.8
Autumn sown cereal	78	14.1	124.4	22.5	41	13.6	60.7	20.2
Faba bean	49	8.8	37.0	6.7	31	10.3	17.5	5.8
Tilled field	40	7.2	29.3	5.3	20	6.6	17.0	5.6
Grass	34	6.1	23.0	4.1	13	4.3	10.4	3.5
Kale	27	4.9	36.3	6.6	14	4.7	16.5	5.5
Stubble field	20	3.6	15.8	2.9	15	5.0	9.8	3.3
Other	54	9.7	23.0	4.2	18	6.0	10.2	3.4
Fallow field	12	2.2	9.5	1.7	5	1.7	4.7	1.6
Brussels sprout	7	1.3	2.85	0.5	2	0.7	1.3	0.4
Raspberry	3	0.5	1.5	0.3	3	1.0	1.2	0.4
Total	554	100	554	100	301	100	301	100
Vegetation height								
0 cm	58	12.6	73.5	14.6	20	7.94	17.1	6.5
0-5 cm	78	17.0	60.6	12.0	53	21.0	48.1	18.3
5-10 cm	61	13.3	104.0	20.6	35	13.9	33.9	12.9
10-20 cm	103	22.4	95.2	18.9	68	27.0	62.6	23.9
20-30 cm	88	19.1	91.8	18.2	51	20.2	53.7	20.4
30-40 cm	33	7.2	46.0	9.1	11	4.37	18.5	7.1
>40 cm	39	8.5	33.7	6.7	14	5.56	28.5	10.8
Total	460	100	504.8	100	252	100	262.4	100

Table S1 (continued): Observed frequency of selection, selection percentage, expected frequency of selection and mean availability of habitat types and vegetation heights throughout the study period, for total number of lapwings and different sub-sets of lapwings: foraging lapwings, nest placement of lapwings and adult lapwings observed with chicks. Expected frequency of selection is calculated as the sum of the proportion of the given habitat type or vegetation height available. Mean availability is the mean proportion of a habitat type or vegetation height, calculated as the expected frequency of selection divided by total number of observations.

	Nest placement					Adult lapwin		
Habitat type	Observed frequency of selection	Selection percentage (%)	Expected frequency of selection	Mean availability (%)	Observed frequency of selection	Selection percentage (%)	Expected frequency of selection	Mean availability (%)
Spring sown cereal	24	44.4	24.6	45.6	22	56.4	22.0	56.3
Autumn sown cereal	5	9.3	9.4	17.4	1	2.6	4.9	12.5
Faba bean	9	16.7	4.5	8.2	1	2.6	0.7	1.8
Tilled field	6	11.1	5.2	9.6	4	10.3	1.9	4.9
Grass	3	5.6	3.8	7.0	0	0.0	2.5	6.5
Kale	3	5.6	2.3	4.3	0	0.0	4.3	10.9
Stubble field	4	7.4	3.0	5.5	0	0.0	0.1	0.1
Other	0	0	1.3	2.4	11	28.2	2.7	6.9
Fallow field	0	0	0.8	1.5	2	5.1	1	2.6
Brussels sprout	0	0	0	0	0	0	0	0
Raspberry	0	0	0.2	0.3	0	0	0.3	0.6
Total	54	100	54	100	39	100	39	100
Vegetation height								
0 cm	6	12	5.3	11	8	24.2	2.0	5.6
0-5 cm	26	52	21.2	44.4	1	3.0	1.1	2.9
5-10 cm	13	26	12.4	25.9	0	0.0	1.7	4.7
10-20 cm	3	6	6.8	14.3	8	24.2	6.0	16.4
20-30 cm	0	0	0.8	1.6	7	21.2	8.3	22.7
30-40 cm	0	0	0	0	7	21.2	6.6	18.2
>40 cm	2	4	1.4	2.8	2	6.1	10.8	29.6
Total	50	100	47.9	100	33	100	36.5	100

