

# MASTERARBEIT

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# Important factors for predation of northern lapwing *Vanellus vanellus* nests in a central European lowland pasture system

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# Important factors for predation of northern lapwing *Vanellus vanellus* nests in a central European lowland pasture system

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# Abstract

In the last decades, lapwing populations decreased dramatically all across Europe due to shifts in land use and agricultural intensification. Knowledge of the threats to a species is essential to design appropriate conservation measures. Nest loss and insufficient productivity in the remaining habitats have been a main cause for declines. In this study, the causes for and the factors determining nest loss in the lapwing in the Neusiedler See – Seewinkel National Park were investigated.

Clutches were recorded and monitored until they hatched or failed and the fate of each nest was assessed. Additionally, data on vegetation and ground humidity at the nest site were gathered to test for effects of habitat variables on hatching success. Nest temperatures were recorded through temperature data loggers to record if diurnal or nocturnal predators were involved in nest predations. Artificial nests were deployed at the study site and monitored until they were predated. The results were used to demonstrate the strong anti-predator defense of lapwing colonies. Trail cameras were used to monitor artificial nests to reveal potential predators.

59% of all nests and 97.5% of failed lapwing nests were predated. The average probability for a nest to survive until hatching was 20.3%. Nest survival probabilities differed significantly between different colony sizes (> 5 nests: 55%, 2-5 nests: 14.8%, solitary nests: 3.5%). Colony size was the only statistically valid predictor for nest loss probability. Vegetation cover, sward height and ground humidity at the nest site, as well as rainfall did not prove being significantly related to nest loss. Predation risk of artificial nests was negatively correlated with the distance to the next four lapwing nests.

According to nest temperature data, 14 of 18 monitored nests were predated at night. Thus, nocturnal/mammalian predators are very likely to be the main predators of lapwing nests. Trail cameras recorded 12 predations of artificial nests, all by corvids. Hence, artificial nest exposure experiments can be unreliable when aiming to identify important predators.

Our results emphasize the importance of sufficiently large areas of suitable habitat, where colonies can develop, which have a higher hatching success than solitary nests on small habitat patches.

#### Keywords

pasture, nest, predators, nest loss, hatching success, artificial nests, defense, anti-predator defense, conservation, colony size

# Zusammenfassung

Kiebitz-Populationen erlitten in den letzten Jahrzehnten in ganz Europa dramatische Rückgänge. Hauptgründe sind Änderungen in der Landnutzung und landwirtschaftliche Intensivierung. Es ist essentiell, die Gefährdungsursachen einer Art zu kennen, um angemessene Schutzmaßnahmen ergreifen zu können. Nestverlust und eine unzureichende Produktivität in den verbleibenden Habitaten sind Hauptgründe für die Rückgänge. In dieser Studie wurden Ursachen für Nestverluste beim Kiebitz im Nationalpark Neusiedler See – Seewinkel untersucht.

Gelege wurden erhoben und beobachtet, bis sie geschlüpft oder verloren gegangen waren. Zudem wurde das Schicksal jedes Geleges festgestellt. Auch Vegetation und Bodenfeuchte wurden an den Neststandorten erhoben, um einen möglichen Effekt auf den Schlupferfolg zu testen. Nesttemperaturen wurden mithilfe von Nest-Thermologgern aufgezeichnet, um festzustellen ob tag- oder nachtaktive Prädatoren an den Nestverlusten beteiligt waren. Künstliche Nester wurden im Untersuchungsgebiet ausgebracht und bis zur Prädation beobachtet. Die Ergebnisse wurden genutzt, um den starken Feindabwehr-Effekt von Kiebitz-Kolonien zu zeigen. Kunstnester wurden mit Wildkameras überwacht, um potentielle Nestprädatoren zu bestimmen.

59% aller und 97.5% der verloren gegangenen Kiebitznester wurden prädiert. Die durchschnittliche Überlebenswahrscheinlichkeit eines Nestes bis zum Schlüpfen lag bei 20.3%. Die Überlebenswahrscheinlichkeiten unterschieden sich signifikant zwischen

verschiedenen Koloniegrößen (> 5 Nester: 55%, 2-5 Nester: 14.8%, Einzelnester: 3.5%). Koloniegröße war der einzig statistisch signifikante Prädiktor für die Nestverlustswahrscheinlichkeit. Vegetationsdeckung, -höhe und Bodenfeuchte am Neststandort, sowie Niederschlag zeigten keinen Effekt. Das Prädationsrisiko von Kunstnestern war negativ mit der Distanz zu den vier nächsten Kiebitznestern korreliert. Laut Thermologger-Daten wurden 14 von 18 Nestern in der Nacht prädiert. Folglich waren höchstwahrscheinlich nachtaktive Prädatoren (Säugetiere) die Hauptprädatoren von Kiebitznestern. Wildkameras zeichneten zwölf Prädationen von Kunstnestern auf, alle durch Rabenvögeln verursacht. Kunstnester sind daher nur bedingt geeignet, um wichtige Prädatoren zu identifizieren.

Unsere Ergebnisse unterstreichen die Wichtigkeit ausreichend großer, geeigneter Habitate, auf denen sich Kolonien entwickeln können, die einen höheren Schlupferfolg haben als Einzelnester auf kleinen Habitatinseln.

# Introduction

The northern lapwing (*Vanellus vanellus*; hereafter referred to as lapwing) is a groundnesting wading bird of the familiy Charadriidae, distributed throughout the palearctic. As a breeding habitat it prefers flat, open, treeless landscapes of variable humidity. A short sward plays a major role in habitat selection, especially at the beginning of the breeding season (Bauer et al. 2005). In Austria, the species mainly breeds in various meadow, marsh and pasture systems, as well as arable fields, generally up to 500 m above sea level (Dvorak et al. 1993).

The current population estimate for Austria is 3500-6000 breeding pairs (BirdLife Austria, unpublished data). A decline of 60% has been assessed for both Europe (since 1980; PECBMS 2014) and Austria (since 1996; Probst 2014) and all recent regional studies have found severe declines throughout the country (Kleewein et al. 2013, Puchta et al. 2012, Steiner 2009, Uhl & Wichmann 2013).

For the state of Burgenland, the latest population estimate was 400-700 breeding pairs (Berg & Dvorak in Puchta et al. 2012), whereas the Neusiedler See – Seewinkel National Park alone hosts around 400 breeding pairs (Kohler in Bieringer et al. 2012) making it a site of high relevance for the Austrian population.

Just as other species of wading birds, the lapwing suffers from habitat loss, habitat degradation and a progressing agricultural intensification (BirdLife International 2014).

Still, nest predation has been identified as an important factor for little breeding success and declines (e.g. Bellebaum & Bock 2009, Evans 2004), since predation rates are unsustainably high in many cases, even in otherwise favourable breeding habitat (MacDonald & Bolton 2008a). Many populations are subject to conservation measures, such as grazing and mowing management, renaturation, nest protection or predator control (e.g. Bellebaum & Bock 2009, Bolton et al. 2007, Langgemach & Bellebaum 2005, MacDonald & Bolton 2008a, Rauer & Kohler 1993).

A large part of the breeding population inside the Neusiedler See – Seewinkel National Park uses pastures, shores of soda lakes and hay meadows as breeding habitats, which are all subject to habitat management measures (B. Kohler pers. comm.).

A well-founded knowledge of threats of a species is an essential base to develop effective conservation measures. The conservation of wading birds on farmland has been treated by a large array of studies all across Europe and especially the lapwing has been subject to a lot of studies dealing with causes of nest loss in various habitats. Their results show, that risks and causes for declines do not only vary regionally, but also inbetween years and habitats (e.g. Beintema & Muskens 1987, Rauer & Kohler 1993, Steiner 2007). The habitat type of dry pastureland, which the present study deals with, has rarely been studied in this respect. From the Seewinkel region, there is one study on the breeding biology of common redshank (*Tringa totanus*) and lapwing, which shed light on phenology, hatching success and causes for nest loss (Rauer & Kohler 1993). Besides the basic knowledge this survey created for the studied species, it also raised questions.

Aim of the present study was to create further knowledge on current nest loss threats of the lapwing in the pastures around the Lange Lacke soda lake. In particular, we studied the importance of nest loss through predators by considering habitat variables and colony size. Different sward heights could be important factors for both the incubating birds and predators. Higher vegetation could hide nests and thus lower the predation pressure. Lower grass swards could help the incubating lapwing to spot potential predators and defend the nest earlier and more effectively. Little vegetation cover could ease ground predator movements and result in higher predation rates, while ground humidity could make nest sites less attractive to ground predators preferring dry habitats. Nest density and colony size were suspected to have an effect on nest predation, because of the lapwings' collective anti-predator defense behaviour.

# Methods

## Study period and area

The study area lies within the "Bewahrungszone Apetlon – Lange Lacke" which is a part of the Neusiedler See – Seewinkel National Park's buffer zone ("conservation zone") in the state of Burgenland, eastern Austria. It is an area north-east of the towns of Illmitz and Apetlon which includes eleven soda lakes of different size, pastures, meadows, fields, reeds and few shelter belts of trees, between 118 and 120 metres above sea level. The pastures inbetween and around the lakes are grazed by a tended herd of roughly 300 cattle in summer, creating habitats for a variety of ground-nesting bird species. The cattle are herded by two shepherds and around five dogs, the latter attending the herd by day, staying at the stable by night.

The study was carried out on pastureland between and around the lakes Darscho, Östliche Wörthenlacke, Westliche Wörthenlacke and Lange Lacke between 47°46'37" -47°45'11" N and 16°50'12" - 16°53'12" E (see Fig. 1). The area is particularly prone to changes in ground humidity and water levels in lakes and the amount of flooded pastures can vary heavily inbetween weeks, months and years. During the study period, the grassland was mostly dry. As the search for incubating adults was the chosen method to find nests, the study area was restricted to those parts of the pastures that could be scanned from the existing road network and raised hides, resulting in an study area of roughly 1.7 km<sup>2</sup>.

Most of the study area was confined by water or unsuitable habitats, so that the lapwing nests and full extent of colonies could be thoroughly recorded from trails. The only exception was an area between the northern shore of Lange Lacke soda lake and Katschitzellacke (compare Fig. 1), which could not be monitored. However, these parts were more than 150 m from the nearest nests and also separated by unsuitable habitat, so that the risk of a bias due to adjacent, not recorded nests was considered to be very little.



*Fig. 1* Study area (orange outline), lapwing nests (white rings), and exposed artifical nests (yellow stars). Image source: Google Earth

#### Fieldwork period and weather conditions

All fieldwork was carried out in spring and summer of 2014, between 8 March, when proforma searching for nesting lapwings was started and 3 July, when the data logger of the last monitored nest was collected.

The spring of the study period was the seventh warmest of all time in Austria, despite the wet and rather cool May. The month of March was unusually warm and dry in the state of Burgenland (deviation from annual mean: +3.8°C temperature, +58% sunshine, -60% precipitation). April was still warm but with less sunshine and more rain than in average years (+1.9°C temperature, ±0% sunshine, +50% precipitation). May had lots of rain (-0.7°C temperature, -2% sunshine, +92% precipitation) and June was hot and dry again (+1.0°C temperature, +25% sunshine, -48% precipitation; data courtesy of Zentralanstalt für Meteorologie und Geodynamik, http://www.zamg.ac.at).

Rainfall during the breeding season (25 March to 25 June) was slightly above the average of 173.3 mm of the last ten years (data from Apetlon, ca. 3 km from the study site, courtesy of Hydrographischer Dienst, Amt der Burgenländischen Landesregierung, http://wasser.bgld.gv.at).

#### Nest search, nest controls and assessment of nest site variables

Pastures and shores of soda lakes were scanned for incubating adult lapwings every two to four days from the roads and paths by bare eye, binoculars (10x magnification) and spotting scope (25x magnification). When a bird was seen lying on the ground, it was observed for 1-3 minutes to make sure if it was really incubating. The birds exact location was then fixed with the help of landmarks on the horizon or nearby the bird and the nest was approached in a straight way. Helpers were sometimes directing the searcher from the road by mobile phone. In the rare case that no nest was found, the search was aborted after about one minute to keep disturbance as limited as possible. When the nest was found, the exact location was stored on a GPS device (Garmin Dakota 20), no visible mark (e.g. flag or stick) was used. From each nest the following data was collected: finding date, number of eggs, height of vegetation and ground humidity at the nest site, estimated average height and cover of vegetation in a 10 m radius around the nest. Digital photos were taken of the clutch and surroundings of the nest. Values for average vegetation height were estimated and noted in four categories (1: < 5 cm, 2: 5-10 cm, 3: 10-20 cm, 4: 20-30 cm) and in three categories (1: dry, 2: humid, 3: wet/flooded) for humidity.

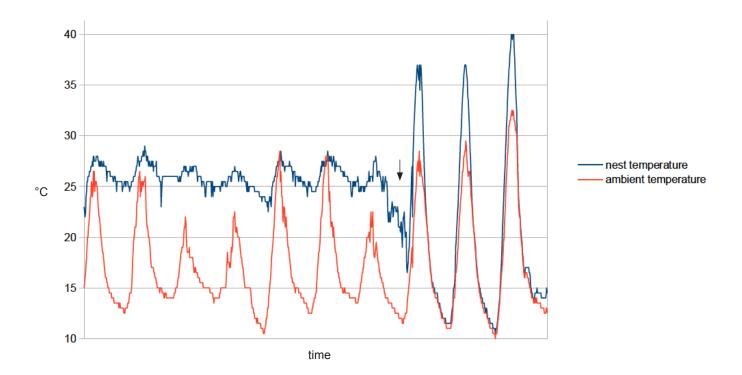
Nests were checked every two to four days from a distance without disturbing the incubating adult. When the bird was seen on the nest, it was noted as being active. Only if there was no incubating lapwing to be seen, the nest was approached and checked. Whenever a close check of a nest was performed, the same data as on the finding date plus the outcome of the clutch (hatching or predation) were noted.

#### Rainfall

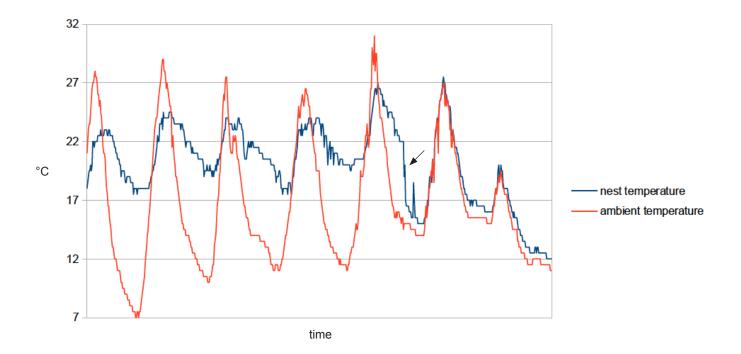
To assess the effect of rainfall on nest loss, precipitation data of the two days prior to each nest control from a measuring station close to the study site (Apetlon) was used (data courtesy of Hydrographischer Dienst, Amt der Burgenländischen Landesregierung). Rainfall was classified as none (0 mm), weak (0-10 mm) or strong (>10 mm) for each day.

#### Nest temperature data loggers

Small nest temperature loggers (1-Wire/iButton DS1921G-F5) were placed in 58 nests to constantly record nest temperature at intervals of five or 15 minutes. The loggers were placed beneath the eggs when finding the nest and removed after eggs had



*Fig. 2* Example temperature curve from a nest temperature data logger in a hatched nest and ambient temperature. The stepwise fall in nest temperature (arrow) until it joins the ambient temperature curve is diagnostic for hatched nests.



*Fig.* 3 Example temperature curve from a nest temperature data logger in a depredated nest and ambient temperature. The sharp drop in nest temperature (arrow) and quick approximation to the ambient temperature curve marks the time of predation, the small rise soon later might mark the return of a lapwing or the predator. hatched or were predated. It proved to be important to push loggers into the soil to fix their position, as the devices were somewhat prone to being displaced. Lapwings apparently removed loggers from the nest three times during incubation and loggers were found up to two metres outside the nest four times after predation. Eggs were only handled using disposable gloves to avoid human scent getting attached to the nest or eggs. One data logger was used to record ambient temperature. This proved to be very useful to judge nest fates using nest temperature curves.

According to nest temperature logger data revealing the exact time of predation, predators were classified as nocturnal (very likely to be mammals) or diurnal (more likely to be birds).

Predation events between 20 minutes after sunset and 20 minutes before sunrise were classified as nighttime predations.

Temperature data loggers allowed obtaining information of nest fates and exact times of nest loss. They also helped to correct potential mis-interpretations of nest fates. In three cases, the initially noted outcome had to be revised after reviewing nest temperature logger data.

It proved to be very important to have observations of nest fates combined with the logger data. For example, data from nests where chicks were seen hatching helped to learn the typical course of temperature curves of hatched clutches.

#### Assessing nest fate

Whenever a nest was found not to be incubated anymore, it was assessed whether the eggs had hatched or the nest had been predated, by searching the nest location and the near surroundings. The nest lining was searched for small egg shell fragments that typically are produced by the hatching chicks when pecking from the in- to the outside (Fig. A1, A3-A4).

Completely empty nests without any egg shell fragments, as well as nests with obvious traces of predation (such as empty eggs, large egg shell fragments with traces of yolk, destroyed nest scrapes) were noted as having been predated (Fig. A2, A5-A6). Intact nests with many small egg shell fragments were classified as hatched. Egg shell remains were not used for further analysis. Predators have been found to be not reliably identifiable from egg shells and fragments, since mammals, birds and reptiles all can leave all types of remains and there is great overlap (Larivière 1999, Marini & Melo 1998).

From nests equipped with temperature data loggers, temperature curves were analyzed. They were used to assess the exact time of nest loss and as a validation in judging nest fates. Predation events could be well read from the temperature curves, as quick adjustment to the ambient temperature after the incubating adult had left the nest. These adjustments were most obvious in the night as very steep drops, when there was a large difference between temperatures inside the incubated nest and the outside (Fig. 2). Still, daytime predations could also be easily told with the help of the ambient temperature curves of hatched nests also show a typical course, with a slow and stepwise drop until they join the outside temperature curve.

#### **Artificial nest experiments**

A total of 37 artifical nests containing three brown hen's eggs were used to carry out experiments on anti-predatory effects of lapwing colonies and to identify predator species within the study site by attracting them close to trail cameras. It was not intended to accurately imitate lapwing eggs (which would be smaller and of different coloration) but to use attractive and easily findable clutches to obtain clear results. Potential predators were assumed to predate on lapwing and hen's eggs alike.

Eggs were placed in potential or actual lapwing habitat (flat areas with grass sward of < 5-10 cm) in handmade scrapes lined with dry grass between 3 April and 17 June. 19 artifical nests were monitored by motion detector triggered trail cameras (Maginon WK 1) that were fixed on small bushes (see Fig. A57) or poles of 30 cm height, 1-2 m away from the nest. Four clutches of four quail eggs were also used with the trail cameras, but not included in further analysis.

#### Colonies

Colonies were defined similar to Berg et al. (1992). Nests were counted as belonging to a colony when there was another active nest (being incubated on at least one identical day) in < 150 m distance. Small colonies were aggregations of 2-5 nests, large colonies of more than 5 nests. Not all nests of a colony had to be in a distance of < 150 m to each other. For example: A colony comprises three nests. Nests A and B are located 220 m apart of each other, while nest C is located 105 m from A and 147 m from B. All three nests have been incubated for at least one identical day and are linked by C, making them a small colony. If there was no simultaneously incubated nest in < 150 m distance, nests were categorized as solitary.

#### **Statistics**

Daily survival rates and nest survival probabilities were calculated following Mayfield (1961, 1975) to obtain more realistic values for nest survival probability than just the percentages of hatched and lost nests do give. The latter approach underestimates nest loss, because it doesn't take nests into account which are not found before they are lost.

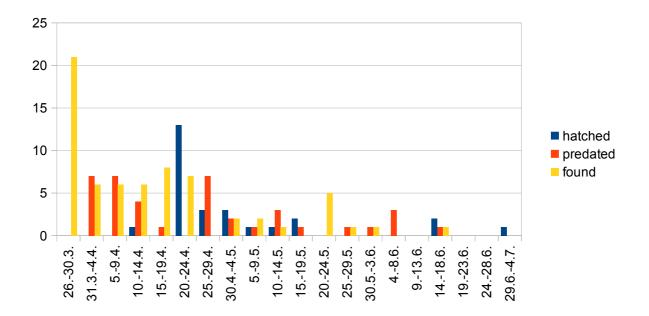
An average incubation period of 30 days was assumed for the lapwing (including the egg-laying period of three days, until the clutch is completed) following Glutz von Blotzheim & Bauer (1999). Nest survival probabilities were calculated for the whole nesting period, including laying. To test for effects of colony size on predated vs. hatched clutches, a Chi-square test was calculated using the software Statistica v. 7.1.

Effects of nest site parameters, colony size and rainfall on predation risk were evaluated using a generalized linear mixed model (GLMM) with binomial error distribution and logit-link function, calculated with SPSS Statistics vers. 21. When nests were controlled more than once, all variables were measured again and all these data were used as new data sets in the GLMM. To reduce effects of pseudoreplication by using data of the same nest re-checked several times, the nest identification number was included as random effect in our calculated GLMM.

# Results

#### Data volume, breeding phenology and clutch size

67 lapwing nests were found during the study period. Of those, 27 hatched (40.9%), 39 were predated (59%), one was either flooded or predated, none were trampled by cattle or destroyed otherwise. The first clutch was found on 26 March, the last on 15 June. 21 clutches (31.4%) were found in the pentade of 26-30 March, which also marked the highest number of simultaneousely incubated nests. 55% of nests were found before 15 April. Nine nests were found before clutches were complete. The first clutch hatched on 13 April, thus must have been laid around 18 March. An overview of the phenology of the recorded nests is given in Fig. 4. The average clutch size ( $\pm$  SD) was 3.92 eggs ( $\pm$  0.28) per nest (n=59; 54 with four eggs, five with three eggs). Only clutches that have been observed longer than one week have been included in this number to avoid incomplete clutches recorded in the laying period to flow in.



*Fig. 4* Numbers of new-found nests, predation events and hatched clutches in the respective pentades of finding.

### **Nest site selection**

Basic data on nest sites were collected when nests were found. Most nests were situated at dry, well vegetated sites with short grass sward (compare Table 1-3; Fig. A11-A22).

Tab. 1 Observed sward heights at nest sites (n=64).

| <u>cat.</u> | sward height | nests | %     |
|-------------|--------------|-------|-------|
| 1           | < 5 cm       | 33    | 51.56 |
| 2           | 5-10 cm      | 29    | 45.31 |
| 3           | 11-20 cm     | 2     | 3.13  |

Tab. 2 Observed values for humidity at nest sites (n=64).

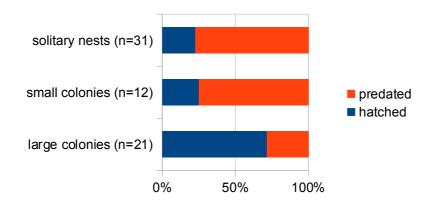
| <u>cat.</u> | humidity    | nests | %     |
|-------------|-------------|-------|-------|
| 1           | dry         | 52    | 81.25 |
| 2           | moist       | 11    | 17.19 |
| 3           | wet/flooded | 1     | 1.56  |

Tab. 3 Observed values for vegetation cover in a 10 m radius around nest sites (n=63).

| <u>cat.</u> | cover (%) | nests | %     |
|-------------|-----------|-------|-------|
| 1           | 0-50      | 11    | 17.46 |
| 2           | 55-80     | 21    | 33.33 |
| 3           | 85-100    | 31    | 49.2  |

# Colony size related to predation rate

Of 67 nests, 40 failed to hatch with 39 having been predated (59%) and 27 hatched. 71.4% of nests in large colonies hatched, 25% in small colonies and 22.6% in solitary nests. Colony size significantly affected nest predation risk (Chi-square test:  $\chi^2$ = 13.78, df = 2, p = 0.001). A much smaller percentage (28.6%) of nests located in larger colonies was predated compared to single nests (77.4%) and smaller colonies (25%).



*Fig.* 5 Percentages of failed and predated solitary nests and nests in small (2-5 nests) and large colonies (> 5 nests).

Daily and overall nest survival probabilities after Mayfield (1975) were highest for nests in large colonies, intermediate for nests in small colonies and lowest for solitary nests (Table 4).

*Tab. 4* Daily and overall nest survival probabilities of solitary lapwing nests and nests established in small (2-5 nests) and large colonies (> 5 nests). n=total number of nests; f=number of failed nests.

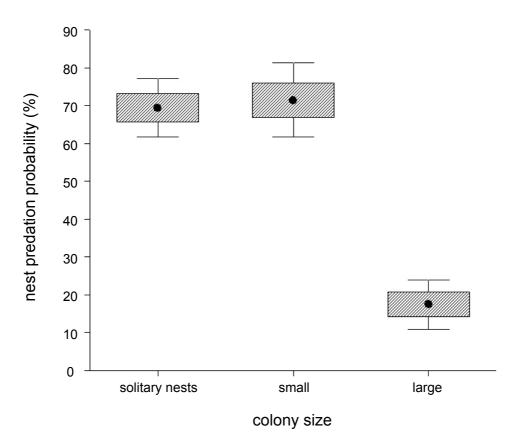
| categories                  | nest days | daily surv. prob. | nest surv. Prob. |
|-----------------------------|-----------|-------------------|------------------|
| all nests (n=67, f=40)      | 754.5     | 0.95              | 0.20             |
| large colonies (n=21, f=6)  | 305.0     | 0.98              | 0.55             |
| small colonies (n=12, f=9)  | 146.0     | 0.94              | 0.15             |
| solitary nests (n=32, f=24) | 303.5     | 0.89              | 0.04             |

#### Habitat parameters, rainfall and colony size in relation to predation rate

The effects of habitat parameters (vegetation cover, sward height and ground humidity at the nest site), rainfall and colony size on nest predation risk were tested using a GLMM. Only colony size has a significant impact on nest loss (Table 5) with nests located in large colonies having a much lower predation risk than all other nests (Fig. 7).

*Tab. 5* Results of a GLMM testing for effects of nest site variables (vegetation cover, humidity and sward height), rainfall and colony size on nest predation. Significant effects are printed bold.

| variables        | F     | df1_ | df2_ | р       |
|------------------|-------|------|------|---------|
| corrected model  | 2.503 | 9    | 80   | 0.014   |
| rainfall         | 0.373 | 2    | 80   | 0.690   |
| colony size      | 8.624 | 2    | 80   | < 0.001 |
| vegetation cover | 0.895 | 1    | 80   | 0.247   |
| humidity         | 0.510 | 1    | 80   | 0.477   |
| sward height     | 0.584 | 3    | 80   | 0.627   |

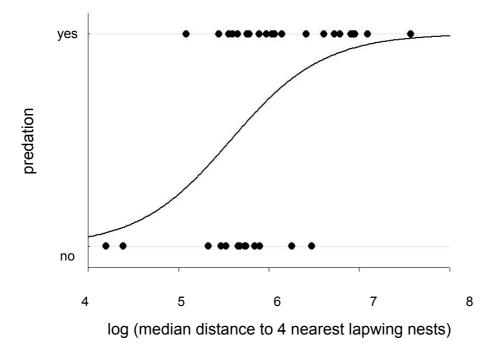


*Fig.* 7 Mean nest predation probabilities  $\pm$  SE (box) and 95% CI (whiskers) predicted by a GLMM (compare Table 5) for solitary nests, nests in small (2-5 nests) and large colonies (> 5 nests).

# Artificial nest survival in relation to distance to lapwing colonies

Predation risk of artificial nests was tested in relation to the median distance to the nearest four active lapwing nests. Predation risk increased significantly with distance to lapwing nests (Fig. 8). The nest predation probability was not related to the exposure duration of artificial nests.

Exposure lengths of predated and non-predated artificial nests did not differ significantly (Mann-Whitney U test: U = 138.00, p = 0.5669).



*Fig. 8* Relationship between artificial nest predation risk and lapwing nest density visualized by a logistic regression ( $\chi^2 = 9.08$ , df = 1, *p* = 0.0026).

#### **Predator species**

Predators of lapwing nests could generally not be identified to species level. In many cases, predated nests were completely empty and no signs or traces could be found at or around the nest. Empty egg shells and large fragments were found four times near the nest scrape. No useful clues regarding predator identity could be found on those remains.

#### Predators of lapwing nests revealed by nest temperature data loggers

The data of 18 nest temperature loggers revealed exact times of predation. Of those, 14 predation events happened at night (presumably mammalian predators) and four during the day (considered more likely to have been robbed by birds). All of the latter happened at the very beginning or end of the defined "daytime" (20 minutes before sunrise to 20 minutes after sunset) and could thus maybe account to mammals (such as diurnal mustelids) as well. In just one case, the nest fate could not be determined due to flooding of the nest site (Fig. A9). It could not be told from nest temperature logger data with certainty if the nest was predated prior to flooding or not.

#### Predators of artificial nests revealed by trail cameras

Predators of artificial nests could be identified from trail camera footage in twelve cases, being hooded crows (*Corvus cornix*) in eleven and rook (*C. frugilegus*) in one (Fig. A47-A52). One nest was trampled by cattle and in one case the predator could not be identified from the photos.

In one case, a European ground squirrel (*Spermophilus citellus*) tried to open a hen's egg but failed. In two cases, when eggs had been opened by crows, squirrels were feeding on egg remains after the crows had left (Fig. A53-A55).

In one case, a badger (*Meles meles*) showed up ca. 50 cm from the artificial nest but didn't eat the eggs, as did other species of mammals and birds (Fig. A41-A46).

Though crows are likely to have found the eggs more quickly because they were deposited during the day, eleven of 37 artificial clutches survived more than four days, giving nocturnal predators opportunities to feed on them. Trail camera footage showed that crows often took more than one day to discover the nests.

#### Observations of predators in the study area

During the study period, there was a large diversity of potential nest predators observed in the study area, of which none was very numerous except for black-headed gulls (Larus ridibundus) which were breeding in a colony of 150-200 breeding pairs in the study area (B. Wendelin, M. Dvorak pers. comm.). Although the gulls were foraging in lapwing territories, there was no interaction observed and lapwings seemed to tolerate the presence of black-headed gulls even in the close vicinity of their nests. Hooded crows were frequently observed in pairs and groups of up to 50 rooks were seen foraging within lapwing colonies, but were not attacked by lapwings. Common buzzard (Buteo buteo), marsh harrier (Circus aeruginosus) and Montagu's harrier (C. pygargus) were seen frequently but only in single individuals and not at every visit to the study area. Stoat (Mustela erminea), least weasel (M. nivalis) and steppe polecat (M. eversmanni) were observed once at daytime each and are known to occur in rather low densities. Red fox (Vulpes vulpes) was not observed but is known to be common in the area. 2014 marked a record year for this species in the hunting statistics, with 56 individuals bagged by the local hunters in a ca. 3 km radius including the study site (hunting district "Apetlon I" 2013: 42 individuals, 2012: 36, 2011: 29, 2010: 27, 2009: 28, 2008: 43). European badger is generally rare in the region (K. Gelbmann pers. comm.). One individual was recorded on a trail camera once near the only known burrow in the

study area. Both European hedgehog (*Erinaceus europaeus*) and European ground squirrel occur in the study area, the latter populating the pastures rather densely (E. Schmelzer pers. comm., pers. obs.). The two species are known to eat eggs but there were no cues that they are actual predators of lapwing nests.

A dog track (Fig. A10) recorded near one predated nest on 6 April is not likely to origin from the shepherd's dogs that tend the local cattle herd, as grazing started on May 1. It can not be said if the nearby nest was robbed by this dog and where the animal came from. However, there were no other observations of straying dogs in the study area.

It's considered unlikely that the shepherd's dogs play a role as lapwing nest predators, since they stay at the stable at night, have never been seen straying and nearly all predation events with known time of predation happened at night.

Domestic cats were very rarely seen in the pastures (outside the study area) and always very close the nearby village.

# Discussion

Egg-laying dates of the lapwing are known to vary geographically and inbetween years, depending on weather (Glutz von Blotzheim & Bauer 1999). The observed egg-laying dates recorded in our study in 2014 fit well into the pattern described by Rauer & Kohler (1993) for the same region, who recorded 50% of egg-laying dates within the last ten days of March. Note that the exact figures can not be compared, as the laying dates of found clutches were not calculated in the present study. Another study that was carried out in Upper Austria in the same year gave similar results regarding phenology (Uhl 2014). The ratio of clutches with four eggs (91.53%) was in the expected range (e.g. Baines 1989, Glutz von Blotzheim & Bauer 1999).

Used nest site habitats were expectably characterized by a sward height of less than 10 cm in height (cf. Durant et al. 2008, Glutz von Blotzheim & Bauer 1999). Lapwings are known to build nests on a wide range of different ground types, from densely covered meadows to bare gravel banks and mudflats (Glutz von Blotheim & Bauer 1999; Fig. A11-A48). Still, no comparable figures could be found in the available literature for preferred vegetation cover of the surroundings of the nest.

Studies on lapwing nest success have come up with extremely varying results for different habitats and land-use systems (Shrubb 2007). Thus, it seems important not to rely on single results but to study areas of conservation concern in detail to choose

appropriate conservation measures. In the case of the site and habitat of the present study, which holds an important part of the Austrian population of lapwing, no detailed information on nest predation rates, nest loss causes and predator species had been available so far.

Nest predation rates in lapwing have been shown to vary considerably between years, habitats and populations (e.g. Baines 1990, Bellebaum & Bock 2009, Berg et al. 1992, MacDonald & Bolton 2008b, Rauer & Kohler 1993) but none of the tested habitat variables proved to have an effect on predation rate. Also linear habitat structures and and elevated perches, such as trees can be drivers of nest predation (Berg et al. 1992, Eglington et al. 2009, MacDonald & Bolton 2008). The study area hosts extremely few elevated perches, such as larger bushes, trees, raised observation hides and draw wells. Only six nests had elevated perches higher than 2 m in the vicinity of less than 100 m, of which two were predated and four hatched. The distance of each nest to the next footpath or road was also measured. Six nests were located closer than 50 m to a footpath, of which five were predated and one hatched.

Naturally, predator species also vary inbetween habitats, but nest temperature logger data suggest that nocturnal/mammalian predators play a key role in many populations (cf. Bolton et al. 2007, Langgemach & Bellebaum 2005, MacDonald & Bolton 2008b). So the finding that nocturnal predators predominantly account for nest predations in our study area is not surprising. Still, for the region and habitat, this marked result is new. Rauer & Kohler (1993), who didn't focus on predator identities, found six nests to have been predated by mammals and birds each during their work in the region, judging on egg remains.

Overall predation rate (59%) in our study area was high compared to an average of 57.7% of ten studies of lapwing from across Europe (MacDonald & Bolton 2008a) and 47% on unimproved pastures in Great Britain (Baines 1990) but these values should be compared with great care if at all, as they inherit huge possibilites for bias pointed out by Mayfield (1975). The more reliable daily survival rate (0.95 for all nests) as introduced by the same author was similar to results from Dutch agricultural grasslands (0.96; Beintema & Muskens 1987), wet grasslands in north-eastern Germany (averages of 0.95 and 0.94 from multiple study years and different sites; Bellebaum & Bock 2009) but lower than in Swedish grassland (0.99; Berg et al. 1992). Note that daily survival rates in the cited studies varied between habitats and no comparable values for the studied habitat type were available.

The strong anti-predator effect and significantly increased nest survival of lapwings breeding in colonies or in high densities has been reported and discussed in several studies and was recognized as a main predictor for predation risk (e.g. Berg et al. 1992, Berg 1996, MacDonald & Bolton 2008b, Šálek & Šmilauer 2002, Seymour et al. 2003) although not universally (e.g. Galbraith 1988).

Combined with the results from nest temperature data loggers and trail cameras, which revealed nocturnal mammalian predators as the main threat to lapwing nests, the question can be raised, why lapwings are able to defend their nests against diurnal avian predators independently of the size of their colony, whereas nocturnal predators are far more successful in predating on single nests outside lapwing colonies.

According to Elliot (1982, 1985a) lapwing anti-predator response to crows is both very intense and effective, whereas predators which pose a higher risk to the adults themselves, like foxes, are generally not attacked with the same intensity, e.g. without striking the predator. He concluded, that defensive behaviour works better in groups when attacking a crow, but that there is no benefit of group defence against foxes, which are not directly attacked. Seymour et al. (2003) even suggested that negative density dependent predation could be a typical feature of populations under carrion crow nest predation and expected that heavy nest predation by mammals would obscure this pattern. Regarding the evidence of this study, this assumption seems to be disconfirmed. Lapwing colonies are apparently able to defend their nests against mammalian predators at night to some higher degree than single pairs.

Some authors proposed that lapwings could knowingly select nest sites with lower predation risk (Berg 1996, MacDonald & Bolton 2008b). At the studied site, I consider this rather unlikely, as the presumed predator species are not restricted in their movements and are capable of searching larger areas.

The solution offered by MacDonald & Bolton (2008b) seems possible: Lapwings may select areas of low predation pressure *and* be more successful at excluding nest predators from such sites. Further research including detailed data on predator distribution and densities could help to unravel this mystery.

Our results emphasize the significance of colony size for nest survival, while other factors such as nest site variables did not prove to affect nest loss probability. Predation risk was also tested in relation to rainfall in the two days prior to predation. Heavy rain in the study area causes an immediate rise of water levels in soda lakes and pastures, due to a damming clay layer in the soil and the lack of a direct drainage (e.g. streams)

of surface water. Bellebaum & Bock (2009) suggested that water tables in inundated areas could have some effect on nest predation e.g. by reducing predator densities and it seems imaginable that nests are harder to reach for predators in partly flooded areas. Water levels in our study area were certainly not high and changes in water levels not numerous enough during the breeding season 2014 to conclude that they are of minor importance for nest survival. In fact, they could prove to be important in years with heavy rain in spring causing a rise of water levels in the soda lakes and a local flooding of adjacent pastures.

However, our results confirm the findings of MacDonald & Bolton (2008b), who also found nest density to be the strongest predictor for lapwing nest predation. Rauer & Kohler (1993) found no relation between habitat variables and nest predation for the redshank in our study area, but unfortunately they didn't test for effects on nest loss in the lapwing.

Our results of artificial nest experiments underline the protective effect of defending adult lapwings to the surroundings of their nests.

Although the main lapwing nest predator in our study area remains unknown, diurnal predatory birds can be largely excluded. The nest temperature logger data provide clear evidence for a predominantly nocturnal nest predation. Hence, red fox, mustelids like steppe polecat, least weasel and stoat as well as hedgehog remain as the most likely candidates. Badger which had been suggested as main predator of wader nests (MacDonald & Bolton 2008a), may also play a smaller role. European ground squirrel, an exclusively diurnal species, can be eliminated as a main predator as well.

It has been discussed that artificial nest experiments can produce bias in nest predation studies regarding both predation rate (Berg 1996, Moore & Robinson 2004) and predator identification (Langgemach & Bellebaum 2005). Artificial nests in this study were used as a second method to verify the protective effect of lapwings towards other nests and to receive clues towards the nest predators present in the study area. Whereas the first aim was convincingly achieved, the second was not and a severe bias of artificial nest experiments using hen's eggs can be confirmed. No artificial nest under camera surveillance was robbed by a predator who could also act as a main predator of lapwing nests. It seems that the mistake of identifying crows as predators of lapwing nests from artificial nests alone could have been made in the past (cf. Šálek & Šmilauer 2002).

The anti-predator effect of lapwing colonies could be shown from the artificial nest

experiments as well. Predation rates in colonies are not only reduced for lapwing but also for other nests, as became obvious from these experiments. The same effect has been shown in the past (Elliot 1982, 1985b, Göransson et al. 1975) and it was suggested that passerine birds and redshanks could breed in vicinity of lapwings to benefit from their efficient anti-predator response (Eriksson & Götmark 1982, Rauer & Kohler 1990).

It appears unexpected that results of nest temperature loggers and artificial nests with trail cameras are so wide apart and not a single nocturnal/mammalian predator was caught on camera. Reasons for this can so far only be guessed. The possibility that crows found and robbed artificial nests before the night was ruled out (see results). If hen's eggs' shells were too thick to break for mustelids, they would have been caught on camera, trying to feed on eggs at least. Also, there were no scratch or bite marks noticed on the eggs. An option could be that mammalian predators using olfactory cues depend on the smell emitted from active nests.

## **Conclusions and management implications**

Rauer & Kohler (1990) presented suggestions for the national park's management of extensively grazed pastureland, regarding optimal treatment for lapwing and redshank. Although no suggestions in regard of the lapwing had been given for the exact study site, the general idea of measures can be assumed to correspond for similar areas. The contents of some of their proposals have been touched by the present study.

The presented results implicate an alarmingly little breeding success of lapwing in the studied area. The overall nest survival probability of only 20% gives a good clue about the current situation, despite the only one-year study period and the known fluctuations of nest loss rates. This figure does not incorporate the expectably high chick mortality, which affected up to 50-100% of the offspring in Dutch populations (Schekkerman et al. 2009, Teunissen et al. 2005). Figures are lacking from the studied region and habitat. A declaredly rough calculation of the number of nests, their recorded hatching success and a very conservative chick mortality of 50% results in 0.3 chicks per pair for the studied lapwings. Nests were equated with pairs and the number thus includes replacement clutches of the same pairs. Still, the figure shows that the studied population was far from being self-sustaining in an average year, regarding water tables

and weather. In lapwing, one chick per pair is assumed to be the minimum reproductive success for a viable population (Baines 1989). The lapwings in the studied habitat and area are most likely a non-productive sink population of currently little or no supraregional value.

Cattle herding could be confirmed to have no impact on lapwing nesting performance.

The only proven factor driving nest survival was colony size. It became clear during the field work that, despite the areas large size, few optimal habitat patches are of sufficient size for larger lapwing colonies. The preferred habitat, flat, dry, densely covered meadows with very short sward was rather rare in sufficient extent, compared to less intensively grazed areas with higher sward, unsuitable for lapwing. Most lapwing pairs seemed to be pushed to narrow habitat margins, where they were forced to breed solitarily. Nearly half of all the nests recorded were solitary, with a calculated nest survival probability of only 3.5%.

Due to its large number of breeding pairs, the pastures of the Seewinkel region are still of high relevance for the species on a national scale. Hence, the importance for the lapwing has to be maintained by applying adequate management measure to increase the species' breeding success. More intensive grazing in early spring and fall could be one potential measure for improving habitat quality for the next season (cf. Durant et al. 2008) and thus could raise the number of larger colonies with higher hatching success.

### Permits

During the field work for this study, the conservation zones of the Neusiedler See – Seewinkel were entered by permission of the state of Burgenland – Abteilung 5. All work was carried out in accordance with the national park's administration.

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# Appendix I – Photos

# Nest fates



*Fig. A1* Typical hatched nest with many egg shell fragments in the nest scrape.

*Fig. A2* Visible thermologger after predation, with typical empty nest scrape.



*Fig. A3* Hatched nest with one remaining, unfertilized (?) egg.

*Fig. A4* Detail of the same nest with egg shell fragments hidden in the lining, under the remaining egg.



Fig. A5 Predated nest with empty egg shell nearby.

Fig. A6 Predated lapwing egg.

# **Nest fates**



Fig. A7 Lapwings hatching.

Fig. A8 Recently hatched juvenile lapwings.



Fig. A9 Predated and flooded nest.

*Fig. A10* Trace of a dog found near nest 27 after predation.



Fig. A11 Nest 38, 10.4.2014, sward 1, cover 5%.

Fig. A12 Nest 51, 29.3.2014, sward 1, cover 10%.



Fig. A13 Nest 46, 15.4.2014, sward 1, cover 20%.

Fig. A14 Nest 73, 23.4.2014, sward 1, cover 30%.



Fig. A15 Nest 17, 30.3.2014, sward 1, cover 40%.

Fig. A16 Nest 44, 15.4.2014, sward 2, cover 50%.



Fig. A17 Nest 40, 10.4.2014, sward 3, cover 50%.

Fig. A18 Nest 35, 10.4.2014, sward 1, cover 60%.



Fig. A19 Nest 51, 23.4.2014, sward 1, cover 70%.

Fig. A20 Nest 36, 10.4.2014, sward 1, cover 80%.



*Fig. A21* Nest 25, 23.4.2014, sward 2, cover 90%.

Fig. A22 Nest 54, 23.4.2014, sward 2, cover 100%.

## Nests

Variations in egg color and pattern



Fig. A23 Nest 53, 23.4.2014.

*Fig. A24* Nest 47, 15.4.2014, clutch not yet complete.

Fig. A25 Nest 55, 23.4.2014.



*Fig. A26* Nest 54, 23.4.2014, complete *Fig. A27* Nest 11, 30.3.2014. clutch with three eggs.

Fig. A28 Nest 31, 8.4.2014.



Fig. A29 Nest 56, 23.4.2014.

Fig. A30 Nest 4, 29.3.2014.

Fig. A31 Nest 39, 10.4.2014.

## Nests

Variation in amount of nest-building



Fig. A32 Nest 75, 31.5.2014.

Fig. A33 Nest 70, 27.5.2014.

Fig. A34 Nest 74, 27.5.2014.



Fig. A35 Nest 54, 23.4.2014.

- *Fig. A36* Nest 46, 15.4.2014.
- Fig. A37 Nest 48, 23.4.2014.



Fig. A38 Nest 11, 30.3.2014.

Fig. A39 Nest 31, 8.4.2014.

Fig. A40 Nest 48, 15.4.2014.

# **Trail camera footage** Visitors of artifical nests



Fig. A41 Badger (Meles meles).

Fig. A42 Roe Deer (Capreolus capreolus).



Fig. A43 European Hares (Lepus europaeus)

Fig. A44 Greylag Geese (Anser anser).



Fig. A45 Greylag Geese.

Fig. A46 Eurasian Curlew (Numenius arquata).

# **Trail camera footage** Predators of artificial nests



*Fig. A47* Hooded crows (*Corvus cornix*) feeding on hen's *Fig. A48* Hooded crow opening a hen's egg. eggs.



Fig. A49 Hooded crow opening a hen's egg.

Fig. A50 Rooks (Corvus frugilegus) feeding on hen's eggs.



Fig. A51 Rook taking quail egg.

Fig. A52 Rook with two quail eggs in its throat pouch.

# **Trail camera footage** Predators of artificial nests



*Fig. A53* European ground squirrel (*Spermophilus citellus*) feeding on hen's eggs opened by hooded crow.

*Fig. A54* European ground squirrel feeding on hen's eggs opened by hooded crow.



*Fig. A55* European ground squirrel lifting hen's egg shell opened by hooded crow.

*Fig. A56* Shepherd closely missing an artifical nest of quail eggs.



*Fig. A57* Trail camera monitoring artificial nest, fixed on a small bush.

# Appendix II - Curriculum vitae

Name: Markus-Leander Khil

Place of birth: Graz, Austria

Education

Since November 2012

October 2007 – June 2010

Master Programme 'Conservation Biology and Biodiversity Management' University of Graz Bachelor Studies 'Biodiversity and Ecology' Bachelor theses: Fall migration of the White Stork (*Ciconia ciconia*) on the East European flyway and observations over Bourgas/Bulgaria; Morphological changes of chicks of the Eurasian Oystercatcher (*Haematopus ostralegus*) and selected behavioral observations from North Frisia

University of Vienna

| September 1998 – June 2006 | Akademisches Gymnasium Graz |  |
|----------------------------|-----------------------------|--|
|                            |                             |  |

#### September 1994 – July 1998 Volksschule Ferdinandeum Graz

#### Education-related work experience and stays abroad (selection)

| September – October 2013 | 4-week tutorial in rapid biodiversity assessment in Indonesia (Krakatoa archipelago) with the University of Vienna   |
|--------------------------|--|
| Since December 2012      | Bird and wildlife guide with St. Martins Lodge, Frauenkirchen, Austria   |
| April – June 2012<br>for | 10-week monitoring of daytime migration for wind farm risk assessments, breeding bird census and migratory bird census on Föhr island, Germany Schutzstation Wattenmeer e.V. |
| March 2012               | 3-week monitoring of daytime migration for wind farm risk assessments in the western desert, Egypt for ecoda Umweltgutachten, Dortmund                                       |
| May – September 2010     | 4-month internship on Hamburger Hallig, Germany with the Wadden Sea National Park, Schleswig Holstein  |
| February 2010            | 3-week zoological excursion to Costa Rica with the University of Graz  |
| April 2009 – June 2011   | Ornithological mappings for institutions in Styria, Lower Austria and<br>Tyrol e.g. on European Honey Buzzard, Black Stork, Black Grouse,<br>Capercaillie, Bluethroat        |
| August – September 2008  | 5-week internship at Poda nature reserve, Burgas, Bulgaria with the Bulgarian Society for the Protection of Birds  |

