Ornis Fennica 100: 17–26. 2023

Chick survival in a high-density Northern Lapwing (*Vanellus vanellus*) population on the river islets of the middle Pripyat River, Belarus

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Received 26 March 2021, accepted 28 October 2022

The field studies were conducted in three ephemeral river islets of the middle Pripyat River, southern Belarus in 2006–2007. Nestlings of the Northern Lapwing (*Vanellus vanellus*) were ringed soon after hatching, and reencountered during subsequent visits. Post-hatching survival was estimated by capture-mark-recapture models. Daily survival rates of the Northern Lapwing chicks were very high, varying between 0.90 and 0.99, and the cumulative survival rates over 35 days between hatching and fledging were 0.54 and 0.70 in 2006 and 2007, respectively. Survival rate was lower in the first ten days of life, which is similar to that reported in other precocial species. The key factor supporting this high breeding success is low predation due to nesting of lapwings on periodic river islets that naturally restrict access by mammalian predators and apparent scarcity of terrestrial and avian predators. River islet habitats with co-occurrence of dry and wet fertile microhabitats provide optimum feeding conditions for the Lapwing chicks with a wide range of aquatic, ground and surface invertebrates. Moreover, semicolonial breeding of the Northern Lapwing (about 30 nests/ha) with other waders, terns and gulls increases the effectiveness of anti-predator behaviour. Consequently as a result of low predation pressure and good foraging conditions, in 2006 and 2007, productivity was 2.1 and 2.8 fledged young per single nest with four chicks respectively, a value hardly reported in Europe, except in managed sites.

1. Introduction

In recent decades the Northern Lapwing *Vanellus vanellus*, (hereafter: lapwing) has, along with many other European ground-nesting waders, experienced a strong decline across Europe (Milsom 2005, Donald *et al.* 2006, Roodbergen *et al.* 2012, Plard *et al.* 2020), including the central and eastern lowlands, which are traditionally known to support strong grassland wader populations (Žídková *et al.* 2007, Ławicki *et al.* 2011, Shydlovskyy & Kuzyo 2016, Mischenko 2020). The European lapwing population is currently estimated at about 1.59–2.58 million pairs, with a substantial decreasing trend of 30–49% over the last 27 years (BirdLife International 2021). The lapwing is therefore listed as near threatened (NT) in the IUCN Red List (IUCN 2020). A vast majority of studies report predation as the main, direct cause of the lapwing nest losses (Baines 1990, Blomqvist & Johansson 1995, MacDonald & Bolton 2008, Bellebaum & Bock 2009) and chicks' mortality (Schekkerman *et al.* 2009, Mason & Smart 2015, Mason *et al.* 2018) and low breeding productivity is considered as the main driver of the decline in the number of breeding pairs of this species (Milsom 2005, Bolton *et al.* 2007, MacDonald & Bolton 2008, Roodbergen *et al.* 2012). Predation pressure may be so high that even in favourable habitat conditions, it may effectively limit breeding success and affect population stability (Milsom 2005, MacDonald & Bolton 2008, Mason & Smart 2015).

Survival estimates for the lapwing mostly refer to nest (Šálek & Šmilauer 2002, Bolton *et al.* 2007, Teunissen *et al.* 2008, Królikowska *et al.* 2016, Berthold *et al.* 2017) or post-fledging survival (Bak & Ettrup 1982, Peach *et al.* 1994), whereas survival during the critical post-hatching period remains poorly known in this and other wader species (*e.g.* Berg 1992, Cohen *et al.* 2009, Schekkerman *et al.* 2009). Estimation of post-hatching mortality in ground-nesting avian precocial species, such as waders, is difficult since chick detectability is low and broods are difficult to track (Lukas *et al.* 2004, McGowan *et al.* 2009). Moreover, the numbers of ringed nestlings are frequently too low to allow modelling of survival with a capture-mark-recapture (CMR) approach, which is the best way to achieve reliable estimates of survival rates (Lukas *et al.* 2004, Colwell *et al.* 2007, Rickenbach *et al.* 2011).

The seasonally flooded lowland valley of the middle Pripyat River is the best preserved part of the Pripyat river valley, under law protection as the Mid-Pripyat State Landscape Zakaznik Ramsar site (Kozulin *et al.* 2002). It is known as an Important Bird Area in semi-natural conditions offering supreme habitats for waders and wildfowl either during breeding or migration (Pinchuk *et al.* 2005, Meissner *et al.* 2011, Pinchuk & Karlionova 2011, Pinchuk *et al.* 2016). Each year up to 13 species of waders and more than 20 species of other waterbirds breed in this area (Luchik *et al.* 2017a,b, 2019) with *ca.* 1200–1500 breeding pairs of lapwings found in a 420 km long middle section of the river (Luchik *et al.* 2017b). The highest abundance of waders was in Turov meadow, where the number of the lapwing remained high and quite stable between 2005 and 2008 with about 200–350 nests (Luchik *et al.* 2017b, authors unpublished data). We investigated the post-hatching survival of lapwing chicks at Turov and hypothesized that due to unique breeding habitat conditions, *i.e.*, ephemeral river islets, and semi-colonial breeding of a group of waders, gulls and terns, the post-hatching lapwing chick survival should be high.

2. Methods

2.1. Study area

The studies were conducted in the middle part of the Pripyat river valley in the vicinity of Turov city, southern Belarus (52°04'N, 27°44'E) from late April until mid-June in 2006 and 2007. The study area covered natural, riparian meadows on the right bank of the Pripyat river. Every spring this river valley is flooded (Mongin & Pinchuk 1999, Meissner *et al.* 2011) and the highest parts of the flooded meadows form the islets. In April–May a single islet typically covers an area of about 0.5–2 ha. These periodic islets consist of a mosaic of microhabitats from neutral, fertile aquatic and wetland habitats, fertile and slightly acidic mesic to poor and acidic dry land. The islets are covered by dense and low vegetation of fresh and wet meadow plant species represented mostly by grasses (Afranowicz-Cieślak *et al.* 2014) reaching a maximum height of 0.5 m in some parts. The occurrence of dry and wet habitats with a wide spectrum of plants provides optimum conditions for aquatic and terrestrial invertebrates (Afranowicz-Cieślak *et al.* 2014, Hajdamowicz *et al.* 2015). Due to spring floods and high water levels islets remain inaccessible from the main land until the end of May or beginning of June and therefore, human and mammalian predators' pressure in this area is negligible.

2.2. Field study

The fieldwork was carried out on three islets of which a total area of 3–5 ha in the beginning of May (A. Szurlej-Kielańska, pers. comm.). Despite seasonal variation in water level, similar area remains available for breeding waders and is quite constant each year. The number of the lapwing nests on these three islets was 117 and 122 in 2006 and 2007, respectively. In April, when the highest water level limited the size of the islets to its minimum, lapwing breeding density was extremely high, reaching about 30 nests/ha. Also about 50 pairs of Black-headed Gulls (*Chroicocephalus ridibundus*), 50 pairs of Common Terns (*Sterna hirundo*), and 10 pairs of Little Terns (*Sternula albifrons*) nested on those islets. Due to the limited area of the islets, the nests were located close to each other, which resembled the conditions of a bird colony including typical antipredator behaviour, like simultaneous reaction of most birds to the potential danger.

We monitored lapwing nests and chicks twice a week by carefully inspecting the entire area. Nests with eggs were marked with numbered sticks that according to Galbraith (1987) and Zámečník *et al.* (2018) does not significantly increase nest predation risk. The dates of clutch initiation and hatching were estimated by egg flotation method (Hays & Le Croy 1971). Chicks were ringed with a metal ring. Only chicks with known date of hatching were included in this study. In the second part of the season the field inspections were carried out every 1–4 days. Both the frequency of inspections and their extent (entire or part of the area) depended mainly on weather conditions and availability of volunteers. Each control was carried out by at least 3–4 experienced volunteers to minimize the time and disturbance to birds. During subsequent visits, newly hatched chicks were ringed and all recaptures were noted. Mobility of chicks was limited and did not affect the effectiveness of field checks since chicks were not able to leave the islets.

2.3. Statistical analysis

We initially tested daily survival models on raw data, but none of the models passed goodness of fit tests (nonparametric bootstrap in MARK, White & Burnham 1999). For this reason, raw data were pooled into five- and six-day long periods covering 38 and 43 days in total, in 2006 and 2007, respectively, depending on the numbers of controls and the time intervals between them to maximize regular distribution of controls (*i.e.*, shorter pooling periods, while desirable, would result in no controls in some of them). After pooling, the final datasets included eight recapture 'occasions'. Due to the differences in breeding phenology, they covered periods from 8th May to 15th June 2006 and from 24th April to 6th June 2007; the extremes represent the dates when the earliest chick was ringed and the last survey was performed. Uneven intervals between successive occasions were accounted for in the model in MARK (White & Burnham 1999) by setting interval lengths to the desired number of days to get reliable daily survival estimates.

We used standard Cormack-Jolly-Seber models (CJS models), in which two types of parameters were estimated: the survival probability Φ and recapture probability p. In the first step, the model with both parameters, fully time-dependent model $\{\Phi_t, p_t\}$ (a global model) and its reduced versions were fitted, with constant parameters $\{\Phi_t, p.\}$, $\{\Phi., p_t\}$ and $\{\Phi., p.\}$. Then to address possible dependence of the survival rate on the age of chicks, we implemented age-structure in the survival parameter, fitting models with 2 and 3 age classes. An age class spans one occasion, so a model with two age classes estimates two survival parameters: one for chicks aged 1–5 (6) days and the second one for all older chicks. A model with three age classes is similar, but estimates three separate parameters: for chicks aged 1–5, 6–10 and all older. These models reflect the scenario in which the survival rate is different (most likely lower, as expected for most precocial species) in the youngest chicks (age 1–5 and 6–10 days) and then stabilizes (at a different, most likely higher value) at older age (≥11 days). We do not have reliable data on the mean clutch size in the studied lapwing population and, in assessing the number of young surviving to fledging, we assumed that three or four eggs hatched in the nest. The recapture probability in our models was treated as time-dependent, constant or had a linear (on a logit scale) trend imposed, assuming that it could constantly decline (or increase) with time (*e.g.*, due to vegetation growth). We calculated the cumulative survival, simulating daily model-averaged parameter estimates (considering age-structure) for the period of 35 days, roughly between hatching and fledging.

The goodness of fit tests were performed by parametric bootstrapping procedure in MARK with 1,000 simulations and assessed by the quasi-likelihood parameter, $\hat{c}$, based on deviance). In this approach, the observed $\hat{c}$ from the global models is divided by the $\hat{c}$ from simulations (White & Burnham 1999). In both years, $\hat{c}$ indicated moderate to slight overdispersion in the data (2006: mean $\hat{c}$=1.53, min-max range: 1.23−2.31, 2007: mean $\hat{c}$=1.36, min-max range: 0.81−2.20) and thus model ranking was adjusted by these mean values. Then these adjusted models were ranked by the Akaike's information criterion (AIC) corrected for small sample sizes (AICc). As model rankings were relatively balanced in these two years, averaged parameters were used for inference (Burnham & Anderson 2002).

The effect of multiple visits in the field that potentially may increase the chance of an individual not surviving (*e.g.*, chick being predated) was assessed by TEST 3, which is a part of the goodness of fit tests performed in RELEASE run under MARK (White & Burnham 1999). This test checks for violations of one of the CJS model assumptions, saying that all individuals marked at an occasion *i* have the same probability of surviving to occasion *i*+1, regardless of whether they were marked at occasion *i* or before. This test contrasts groups of individuals caught for the first time to those which were caught before, thus testing for the effect of previous catching on the probability of survival. There was no evidence for violations of this assumption and, thus, for the effect of previous catching on survival, as the overall results of this test were not significant (2006: χ^2=3.035, df=6, p=0.804, 2007: χ^2=11.547, df=6, p=0.07). Model construction and fitting, as well as GOF tests were all performed in MARK 7.2 (White & Burnham 1999).

3. Results

In the two study years, a total of 403 chicks were ringed, mainly during the first two days of their life: 250 chicks (62%) on the day of hatching and 43 (11%) on the next day. Of these, 182 were recaptured at least once before fledging. The oldest chicks recaptured were 36 days old, and there were several cases of ringed chicks recaptured at the age of 25 days or more (16 in 2006 and 26 in 2007).

Models including age-structure in survival had the highest support in both seasons (Table 1). The relative importance of age structure (*i.e.*, the cumulative weight of models including any age-structure) was ω=1.0 in 2006 and ω=0.98 in 2007, strongly indicating that the survival rate of the lapwing chicks is related to age. Survival rate was lowest in the youngest chicks (1–10 days of age). Model-averaged daily survival probabilities in both years ranged from 0.91 to 0.99 (Table 2). Over 35 days between hatching and fledging, the cumulative daily survival rate was 0.54 (CI: 0.28–0.72) in 2006 and 0.70 (CI: 0.42–0.82) in 2007. Model-averaged recapture probabilities varied greatly (0.17–0.99 and 0.04–0.44 in 2006 and 2007, respectively) and were generally higher earlier in the season (Table 2). The number of young surviving to fledging time was estimated at 2.1 and 1.6 fledglings per nest in 2006 and 2.8 and 2.1 in 2007 for the four and three chicks hatched in the lapwing nest respectively (Table 3).

4. Discussion

The breeding density of the lapwing on river islets in the middle Pripyat river was much higher than maximum densities reported in other areas, *i.e.*, in England and Wales in 1995–1997 (0.8 nest/ha,

Table 1. Models fitted to the lapwing chicks capture-recapture data from Turov, Prypyat river, Belarus, 2006–2007. Models are ranked according to the Akaike Information Criterion corrected for small sample size (AICc). Δ AICc – difference in AIC units between the best-supported model and a given model, ω AICc – model weight, NPar – number of parameters in a model. (.) – parameter constant in time, (t) – parameter time-dependent, (trend) – parameter with a linear trend. (a2) and (a3) denote for 2 and 3 age-classes in the survival parameter.

Model	AICc	Δ AICc	ω AICc	Model likelihood	NPar	Deviance
2006						
Phi(a3) p(trend)	651.612	0.000	0.977	1.000	4	129.934
Phi(a3) p(t)	659.224	7.613	0.022	0.022	10	124.908
Phi(a2) p(t)	665.693	14.082	0.001	0.001	8	135.649
Phi(.) p(t)	665.805	14.193	0.001	0.001	8	135.760
Phi(.) p(trend)	676.277	24.666	0.000	0.000	3	156.655
Phi(a2) p(trend)	678.075	26.464	0.000	0.000	4	156.398
Phi(a3) p(.)	683.600	31.988	0.000	0.000	4	161.922
Phi(.) p(.)	690.792	39.181	0.000	0.000	2	173.212
Phi(a2) p(.)	692.170	40.558	0.000	0.000	3	172.548
2007						
Phi(a2) p(t)	843.913	0.000	0.603	1.000	9	96.011
Phi(a3) p(t)	846.026	2.113	0.210	0.348	10	96.011
Phi(a2) p(trend)	847.236	3.323	0.115	0.190	3	111.771
Phi(a3) p(trend)	848.962	5.049	0.048	0.080	4	111.452
Phi(.) p(t)	850.536	6.623	0.022	0.037	8	104.735
Phi(.) p(trend)	855.425	11.512	0.002	0.003	3	119.959
Phi(.) p(.)	880.984	37.071	0.000	0.000	2	147.552
Phi(a2) p(.)	882.288	38.375	0.000	0.000	3	146.823
Phi(a3) p(.)	884.333	40.420	0.000	0.000	4	146.823

Hart *et al.* 2002), in South Bohemia, Czech Republic in 1988–1998 (0.2 nest/ha, Šálek & Šmilauer 2002) or in the Lviv region, western Ukraine in 2008–2014 (2.5 nest/ha, Shydlovskyy & Kuzyo 2016). A very high number of breeding pairs along with the mobility of chicks limited to islets provided very good conditions for the study on the post-hatching survival using CJS models. To our best knowledge, no similar studies have been carried out in such a dense lapwing population before.

We also documented a very high survival of the lapwing chicks in the Pripyat river floodplain. Cumulative survival probability from hatching to fledging varied between years, 0.54 in 2006 and 0.70 in 2007, and these are exceptionally high values, hardly reported in Europe, except at managed sites (Roodbergen *et al.* 2012, Plard *et al.* 2020). In the studies considering the lapwing chicks' survival, none have reported survival rate prior to fledging reaching or exceeding 35% without predator removal or applying electric fences as a ground predator exclusion method (Schekkerman *et al.* 2009, Fletcher *et al.* 2010, Rickenbach *et al.* 2011, Roodbergen *et al.* 2012, Malpas *et al.* 2013). The approximate minimum productivity threshold needed to maintain a stable population of Northern Lapwings is estimated at 0.6–0.8 chicks per pair per year in Central and Western Europe (MacDonald & Bolton 2008). In comparison, the productivity of 2.1 and 2.8 fledged young per nest found in this study in

Table 2. Model-averaged daily survival rates (A) and recapture probabilities (B) (± SE) of the lapwing chicks near Turov, Prypyat river, Belarus in 2006 and 2007.

A	Parameter	Age		
	Daily survival	1–5 days	6–10 days	11 days and older
	2006	0.973 ± 0.014	0.907 ± 0.024	0.999 ± 0.001
	2007	0.935 ± 0.017	0.998 ± 0.007	0.999 ± 0.004

B	Parameter	Occasion						
	Recapture rate	2	3	4	5	6	7	8
	2006	0.99 ± 0.01	0.42 ± 0.06	0.36 ± 0.04	0.31 ± 0.03	0.26 ± 0.03	0.21 ± 0.03	0.17 ± 0.04
	2007	0.44 ± 0.07	0.25 ± 0.04	0.20 ± 0.04	0.09 ± 0.03	0.14 ± 0.04	0.04 ± 0.02	0.04 ± 0.02

2006 and 2007 largely exceeds this threshold and indicates that the population at Turov is highly productive. The high survival rate of chicks seems to be the main factor resulting in high recruitment to the breeding population and stable, abundant breeding population in this area.

We found that the survival rate of lapwing chicks was lowest in their first ten days of life. This age-dependent survival supports the results of previous studies on the lapwing and other precocial species (*e.g.*, Flint *et al.* 1995, Chouinard & Arnold 2007, Colwell *et al.* 2007, Schekkerman *et al.* 2009). However, an exception with relatively high survival rate during the first days post-hatching was noted in southwest Norway (Grønstøl *et al.* 2013). The survival of precocial chicks is related to the development of thermal independence from adults, and the capability of evading predators. Younger chicks tend to lie motionless when approached by humans or terrestrial predators, whereas older chicks respond by running to evade danger (Colwell *et al.* 2007, authors' unpublished data), which might also contribute to a higher chance of survival in the latter. The predation pressure in the study area was low, but small lapwing chicks seem to be more vulnerable to trampling by horses and cows than larger chicks. Moreover, as they age, chicks become more proficient in thermoregulation and foraging (Kersten & Brenninkmeijer 1995, Schekkermann & Visser 2001).

Table 3. Estimated number of lapwing chicks surviving to fledging near Turov, Prypyat river, Belarus in 2006 and 2007.

Number of chicks hatched	Mean	95% confidence interval
2006		
3	1.6	0.83–2.15
4	2.1	1.12–2.87
2007		
3	2.1	1.25–2.47
4	2.8	1.67–3.29

Nesting on periodic river islets naturally restricts access by mammalian predators and this is likely the key factor supporting such high breeding success of the studied species. Although there were no studies on the populations of main predators, their numbers in the study area seem to be very low. The only species of terrestrial predator observed during intensive field studies was the red fox (*Vulpes vulpes*), but we found no signs of its presence on the islets. The red fox avoids crossing water, and this limits its distribution (Mullins *et al.* 2014, but see Storm *et al.* 1976). Among avian predators, the Hooded Crow (*Corvus cornix*) and the Marsh Harrier (*Circus aeruginosus*) were observed, but only occasionally. Moreover, foxes and crows were significantly limited by Turov inhabitants as domestic ducks and geese are raised free-range without cages there. As foxes and crows steal chickens, locals try to get rid of crows' nests or chicks at an early stage of incubation and kill adult foxes using traps around fox dens. As a result, during the field study, there were only about five nests of the Carrion Crow in the area and, in early spring, one fox den within a distance of 1 km from the study site.

Waders and terns that breed close to each other exhibit communal nest defence against predators (Göransson *et al.* 1975, Dyrcz *et al.* 1981, Houde 1983, Elliot 1985). In the study area, chicks hatched in high numbers on river islets remained in that area and none of them have ever been observed out of the islet areas, even when the islets were partially connected to the mainland in late May and early June. Every time appearance of a predator or human caused a strong anti-predator reaction of numerous adult lapwings, gulls and terns, which we observed also in the pre-hatching period. Such collective nest defence usually results in lower predation rate in the areas with the highest densities of breeding waders (Houde 1983, Elliot 1985, Kis *et al.* 2000, Seymour *et al.* 2003). Furthermore, in the Lapwing, brood survival is negatively correlated with the distance between the natal and feeding sites (Blomqvist & Johansson 1995). In our study area, chicks moved only within the relatively small area of the islet and this may have contributed to the observed high survival rate. In addition, the islets were connected to the mainland only after the water level in the river got lower, which was in the turn of May and June, *i.e.*, just before or after fledging in most chicks. Hence, predation might not be an important factor limiting breeding success of the Lapwing in this area. The highest losses were recorded during the egg laying and incubation periods due to trampling by livestock (mainly horses) that sometimes crossed the river and entered the islets, or due to flooding by the river (authors' unpublished data).

Survival of precocial chicks depends also on suitable habitat with patches of vegetation enabling them to hide and patches of invertebrate-rich foraging habitats (Johansson & Blomqvist 1996). The gradual lowering of the water level in spring creates a mosaic of unflooded and flooded small patches of grassland with higher vegetation in the centre of the islet, suitable for hiding, and bare soil with low grass on the outskirts, allowing chicks to access food easily. Hence, river islet habitats composed of dry and wet fertile microhabitats provide optimum feeding conditions with a wide range of aquatic and terrestrial invertebrates and co-occurrence of various microhabitats (Afranowicz-Cieślak *et al.* 2014, Hajdamowicz *et al.* 2015). The combination of a low predation pressure and optimal habitats for chick rearing results in high chick survival rate that is likely to maintain the stability of the local Lapwing breeding population.

Ungöverlevnad i en tät population av tofsvipor (*Vanellus vanellus*) på flodholmar vid mellersta delen av floden Pripyat i Belarus

Fältstudierna gjordes vid tre efemära flodholmar i mellersta delarna av floden Pripyat i södra Belarus åren 2006–2007. Tofsvipeungar ringmärktes efter att de kläckts och observarades därefter med jämna mellanrum under återkommande besök. Vi uppskattade överlevnaden efter kläckning med märknings-återfångst modeller. De dagliga överlevnadsuppskattningarna hos tofsvipeungarna var väldigt höga, mellan 0.90 och 0.99 och den kumulativa överlevnaden till 35 dagars ålder, från kläckning till flygfärdighet, var 0.54 under 2006 och 0.70 under 2007. Överlevnaden var lägre de 10 första levnadsdagarna, vilket motsvarar uppskattningar hos andra precociala arter. Nyckelfaktorn till den observerade höga häckningsframgången är låg predationsrisk vid dessa periodiska flodholmar som på ett naturligt sätt begränsar tillgängligheten för rovdäggdjur och minskar tätheten av rovfåglar. Flodholmarnas habitat med både torra och fuktiga mikrohabitat utgör optimala furageringsomständigheter för tofsvipeungarna med ett brett utbud av akvatiska, jordlevande och ytlevande evertebrater. Dessutom utgör det semikoloniala häckningsbeteendet hos tofsvipan (*ca.* 30 häckningar / ha) tillsammans med andra vadare, tärnor och måsfåglar ett effektivt skydd mot rovdjur. Tack vare ett lågt predationstryck och goda furageringsomständigheter under studien var antalet flygga ungar per häckning 2.1 under 2006 och 2.8 under 2007, vilket är ovanligt höga värden i Europa.

Acknowledgements. We are grateful to all volunteers taking part in this study, particularly to Ivan Bogdanovich and Dmitry Zhuravliou for their help in the field work and to Agnieszka Ożarowska for language correction. Aleksandra Szurlej-Kielańska kindly provided data on the size of the river islets and supported the field work. This study was a part of L.P. PhD project at the University of Gdańsk, financially supported by the grant of the State Committee for Scientific Research KBN 3395/PO1/2008/34 and grant of the University of Gdańsk for young scientists BW 1440-5-0405-6.

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