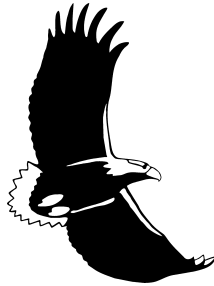


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High adult survival in a northern Eurasian Curlew (*Numenius arquata*) population

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Wetland birds such as waders are in decline across Europe. Information on demography is vital for assessing the causes of population declines, but estimates are needed from multiple populations and time periods. We used capture-recapture data from 2013–2022 including 134 individuals to estimate sex-specific apparent adult survival of Eurasian Curlews from a population breeding on agricultural fields in Finland, a stronghold region for this species in Europe. Using the Cormack–Jolly–Seber Model that considers the recapture probability of individuals, we estimated apparent survival of adults to be 0.89 (SE 0.03) for males and 0.92 (SE 0.03) for females. Our estimates of adult survival are slightly higher than those previously estimated from Fennoscandian breeding grounds in 1980s–1990s (0.82–0.88). Thus, our results suggest that adult survival of populations breeding in northern Europe has not declined during the last decades. Our study supports the view that changes in reproductive success is the main cause of decline in the Eurasian Curlew populations.



1. Introduction

Waders have declined worldwide (Stroud 2003, Morrison *et al.* 2004, Amano *et al.* 2010, Simmons *et al.* 2015, von Numers *et al.* 2020). The causes of their population declines have been associated with changes in reproduction or survival using long-term data on demographic rates (Rönkä *et al.* 2006, Roodbergen *et al.* 2012, Piersma *et al.* 2016, Pakanen & Thorup 2016). Comparing demographic data from declining, stable and growing populations can help test the extent of and reasons behind the declines and plan conservation actions, which warrants research

from numerous population studies (*e.g.*, Green *et al.* 2002).

The curlews (*Numeniini*) include multiple declining and globally threatened species (Pearce-Higgins *et al.* 2017). They are large-bodied long-distance migrants characterised by low fecundity and high survival rates (Piersma & Baker 2000). Curlews are threatened both at their breeding and wintering sites (Pearce-Higgins *et al.* 2017). Habitat changes at wintering grounds are problematic as they may reduce survival and consequently cause dramatic declines in long-lived species (Piersma & Baker 2000). Therefore, information on demographic rates from all

populations, including viable populations, are needed to understand changes in population size and the factors threatening them (Pearce-Higgins *et al.* 2017, Viana *et al.* 2023).

In Europe, the Eurasian Curlew (*Numenius arquata*) is one of the meadow breeding birds that have declined strongly in recent decades (Roodbergen *et al.* 2012, Franks *et al.* 2017). The declines have been strongest in western and southern parts of their distribution in Europe (*e.g.*, Franks *et al.* 2017, Brown *et al.* 2015) with also recent range reductions in central and eastern Europe (Keller *et al.* 2020). The populations in northern Europe also show evidence of decline (*e.g.*, Valkama *et al.* 2011, Lindström *et al.* 2019). The Finnish Eurasian Curlew population was recently categorised as near threatened, which means that the decline in population size does not exceed threshold rates of the threatened IUCN class (*e.g.*, Lehtikoinen *et al.* 2019). Like most grassland breeding waders, their declines have been attributed to changes at the breeding sites, namely agricultural intensification, habitat changes and high nest and chick predation and their interactions (Valkama *et al.* 1999, Grant *et al.* 1999, Valkama & Currie 1999, Douglas *et al.* 2014, Franks *et al.* 2017).

Recent studies on adult survival measured from wintering populations suggest that survival is high and stable, and support the conclusion that the population declines are mainly linked to reproduction (Taylor & Dodd 2013, Mendez *et al.* 2018, Robinson *et al.* 2020, Cook *et al.* 2022). However, further information on survival is needed, including from regions supporting large remaining breeding populations, and also where older estimates are available, to enable comparison with recent survival estimates. Survival estimates from breeding Eurasian Curlews are from the 1980s–1990s (Ylimaunu 1987, Berg 1994, Valkama & Currie 1999) but there is a lack of recent studies that have examined survival from breeding populations in Europe (Roodbergen *et al.* 2012, Viana *et al.* 2023).

We used capture-recapture data collected during 2013–2022 to estimate apparent adult survival of Eurasian Curlews from a population breeding on agricultural fields in northern Ostrobothnia, Finland and compared them to older survival estimates from northern breeding

populations. On the basis of results from European wintering grounds (Robinson *et al.* 2020, Cook *et al.* 2022), we hypothesized that adult survival of Eurasian Curlews breeding in Finland has not declined. As this region is a stronghold of breeding Eurasian Curlews in Europe (Valkama *et al.* 2011, Lindström *et al.* 2019, Keller *et al.* 2020), our results provide valuable information that can be used in assessing causes of population declines.

2. Material and methods

Our study population is located in agricultural areas in northern Ostrobothnia, Finland (Fig. 1 & 2). This area is characterised by various types of fields (*e.g.*, crop, fallow, hay) that have low vegetation and are suitable nesting and chick rearing environments for Eurasian Curlews. Curlew density in this region is among the highest in Europe (Keller *et al.* 2020). We collected data in counties Temmes, Tyrnävä, Muhos and Siikalatva (N64.179–N64.874, E25.507–E26.136). Starting from April, we scanned the breeding sites for Eurasian Curlews and territories multiple times per week and searched for their nests across the breeding season. We visited nests until known nest fate and ringed chicks. We caught incubating adult birds at the nest or when they were with chicks using walk-in traps that have one entrance hole. We replaced eggs with dummy eggs during the capturing of adults. We followed nests until hatching, and there was no evidence that catching causes abandonment. We did not systematically check for delays in resumption of incubation after trapping (Ewing *et al.* 2017), but the parents often changed incubation duties after capturing the other parent from the nest. When catching adults from broods, we waited for the parents to return to their chicks.

We sexed adults based on morphology (Summers *et al.* 2013) and marked them with a metal ring (Finnish ringing scheme) on the tarsus and placed a large plastic ring that included a large easily readable three-digit code formed by letters and numbers above the tarsus (Fig. 1). These codes were readable with a scope and returning birds with coded rings were photographed from a distance enabling their documentation. Verified readings of codes at the breeding sites



Fig. 1. A male Eurasian Curlew with the code ring (CNK) above the tarsus (photo by Reijo Kylmänen). Colour figure is available in the online version of the article at <https://doi.org/10.51812/of.126810>.

were considered as resightings in the data in the following years. Marking and resighting data constituted the capture-recapture data used to study survival.

Our sampling spread out in a large area (measured as polygon of ringing sites 794.1 km²) where effort varied greatly between field areas because the data were gathered entirely by Reijo Kylmänen. Uneven coverage of the study area can cause spatial variation in recapture rates (e.g., Crespin *et al.* 2008). In addition, permanent emigration out of the study area may be more likely from areas situated closer to the edge of the study area or from areas that are covered less thoroughly (e.g., Pakanen *et al.* 2016). Both processes can violate the assumptions of the capture-recapture models by creating heterogeneity in recapture and survival probabilities (Lebreton *et al.* 1992).

Controlling for such spatial variation in recapture or apparent survival probabilities can be done by modelling them in relation a spatial parameter, for example distance to the center or edge of the study area when the study area is uniform (Marshall *et al.* 2004; Pakanen *et al.* 2016).

In order to control for possible spatial variation, we divided our study areas into two parts (variable “Area”, high effort areas vs. low effort areas). The “low effort areas” included large fields with a summed field area of 226.7 km² (Fig. 2). This large area reduced search effort per unit area meaning that these sites that were visited less often. The visiting rate in a given field in the low effort area was on average 3–4 times per week when the Curlews arrived in mid-April, but the rate declined as the spring advanced to about once per week by the end of May. The large area resulted in lower efficiency as there was less time to cover it but also because some areas were less accessible. We searched for Curlews mainly with scopes from the roadside which led to lower coverage in these

large fields that included suitable habitat far away from roads. This could potentially lead into the disappearance of individuals from our sampling, *i.e.*, permanent emigration. In certain years, some of the field roads in the low effort area remained inaccessible for vehicles, for example due to excessive flooding. We checked territories, especially those occupied in the previous year, more closely for Curlews and their nests by walking the fields. Marked Curlews were also searched for when they congregated to feeding groups in the evenings. The low effort area included 79 marked individuals.

The “high effort areas” included fields that were visited more often due to logistical reasons. Most importantly, the fields were small, and therefore search effort per area was high throughout the study (Fig. 3). The summed field area for

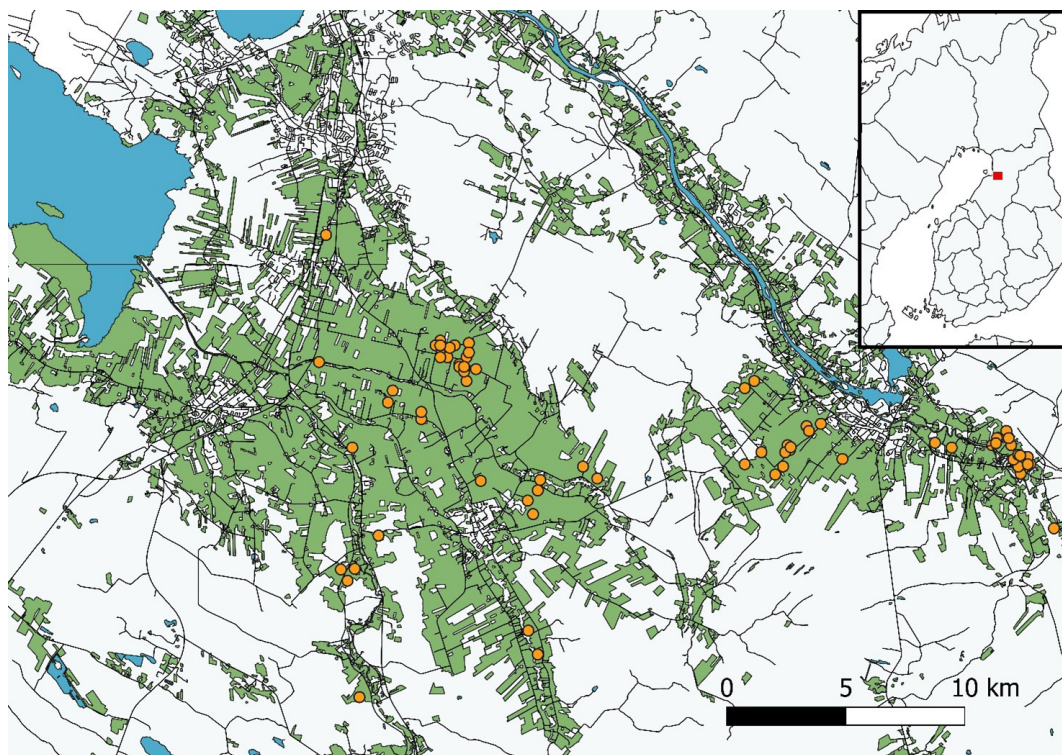


Fig. 1. Map showing the locations of the low effort study areas. Orange dots indicate ringing sites of individuals. Fields that are suitable breeding habitat of Eurasian Curlews area shown in green. Roads are black lines and water is shown in blue. National Land Survey open data, CC 4.0. Colour figure is available in the online version of the article at <https://doi.org/10.51812/of.126810>.

the high effort area was 22.2 km². These field areas were easily accessible due to being near drivable roads which allowed coverage of whole fields and resighting of birds from inside a vehicle. These sites also stayed in the same condition across the study. These factors made visiting the sites easier and resulted in more visits and a more efficient resighting effort. When the Curlews arrived in the spring, our visiting rates per field were up to 2 times per day and the visiting rate continued to be high during the breeding season as these fields were under detailed study on nest success. We searched for territories and nests in all fields throughout the season by walking in the fields and observing parent behaviour from the vehicle or a long enough distance to corner down the nest location. Feeding groups were also searched for in the high effort areas during the evenings. These small field areas were more separated from other field areas (Fig. 3), which likely reduces the

probability of permanent emigration to field areas outside of the study area. We thus expect that recapture rates are higher in the high effort area and that the apparent survival estimates from the high effort area more reliably reflect true survival. The high effort area included 55 marked individuals. Altogether, the data included 134 individuals (males=77; females=57) and 386 observations from 2013 until 2022.

We analysed the data in program MARK using the Cormack–Jolly–Seber Model (White & Burnham 1999, Lebreton *et al.* 1992). Because the data were too scarce and did not allow fitting of complex models, we did not examine temporal variation in survival or recapture rates. In addition to sex of the individual and the Area variable, we examined the effect of transience (permanent emigration after first capture) when estimating survival by using a time since marking variable (Tsm). This variable examines survival separately

after first capture (residents+transients) and after subsequent resightings (residents; Pradel *et al.* 1997). Our starting model thus included Sex, Area and Tsm and their interactions (*) for survival probabilities, and Sex together with Area for recapture probabilities $\Phi(\text{Sex}*\text{Area}*Tsm)$ $p(\text{Sex}*\text{Area})$. This model fit the data (Boostrapping GOF: $p=0.52$, $\hat{c}=1.00$).

We fitted a set of a priori models that were reduced version of the global model. We first

modelled the recapture probabilities and used the best structure when modelling survival probabilities. We used the Akaike's information criterion corrected for small sample size (AICc; Burnham & Anderson 2002) in model selection. We considered models with 2 AICc difference to differ in model and variable support, and we used model averaging (models within 2 ΔAICc units) to control for model selection uncertainty when calculating survival estimates.

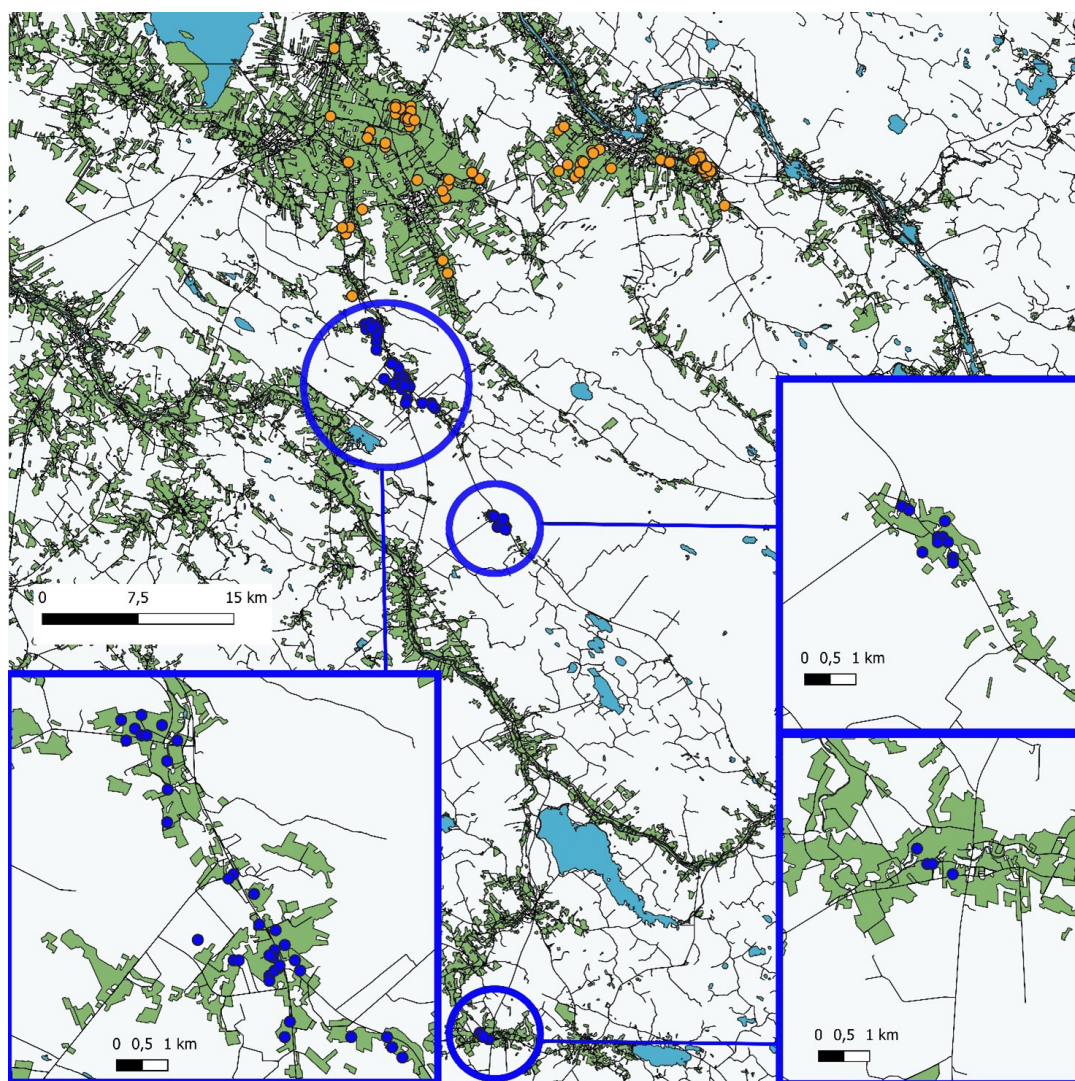


Fig. 2. Map showing the locations of the high effort study areas. Blue dots indicate ringing sites of individuals. Fields that are suitable breeding habitat of Eurasian Curlews area shown in green. Roads are black lines and water is shown in blue. National Land Survey open data, CC 4.0. Colour figure is available in the online version of the article at <https://doi.org/10.51812/of.126810>.

3. Results

The recapture probabilities were higher in males than in females (Table 1, $\Delta\text{AICc}=11.2$ model A1 vs. model A3) and lower in the low effort area (Table 1, $\Delta\text{AICc}=32.1$ model A1 vs. model A4; females 0.289, SE 0.046; males 0.486, SE 0.057)

than in the high effort area (females 0.658, SE 0.047; males 0.817, SE 0.033) being consistent with lower search and resighting effort and possible temporary emigration in the low effort area.

The best models ($\Delta\text{AICc}<2$) for apparent survival probabilities included effects of area,

Table 1. Modelling results for recapture probabilities (p) and survival probabilities (Φ) where: Area = low effort area vs. high effort area; Sex = sex of individual; Tsm = time since marking (two classes); Constant = no variation; + additive effects; * interaction. Models are ranked by the Akaike's information criterion corrected for small sample size (AICc). $\Delta\text{AICc} = \text{iAICc} - \text{minAICc}$; w = Akaike weight; k = number of parameters. Models with two or less interactions are written open in full.

Recapture probabilities					
#	Model	AICc	ΔAICc	w	k
A1	$\Phi(\text{Area}^*\text{Sex}^*\text{Tsm})$ $p(\text{Sex}+\text{Area})$	783.59	0.00	0.728	11
A2	$\Phi(\text{Area}^*\text{Sex}^*\text{Tsm})$ $p(\text{Sex}+\text{Area}+\text{Sex}^*\text{Area})$	785.58	1.99	0.269	12
A3	$\Phi(\text{Area}^*\text{Sex}^*\text{Tsm})$ $p(\text{Area})$	794.76	11.17	0.003	10
A4	$\Phi(\text{Area}^*\text{Sex}^*\text{Tsm})$ $p(\text{Sex})$	815.65	32.06	0.000	10
A5	$\Phi(\text{Area}^*\text{Sex}^*\text{Tsm})$ $p(\text{Constant})$	826.49	42.90	0.000	8
Survival probabilities					
#	Model	AICc	ΔAICc	w	k
B1	$\Phi(\text{Area})$ $p(\text{Sex}+\text{Area})$	778.77	0.000	0.160	5
B2	$\Phi(\text{Sex}+\text{Area}+\text{Tsm}+\text{Area}^*\text{Tsm})$ $p(\text{Sex}+\text{Area})$	779.03	0.264	0.140	8
B3	$\Phi(\text{Sex}+\text{Area}+\text{Sex}^*\text{Area})$ $p(\text{Sex}+\text{Area})$	779.63	0.863	0.104	7
B4	$\Phi(\text{Sex}+\text{Area}+\text{Tsm})$ $p(\text{Sex}+\text{Area})$	779.64	0.871	0.103	7
B5	$\Phi(\text{Area}+\text{Tsm}+\text{Area}^*\text{Tsm})$ $p(\text{Sex}+\text{Area})$	779.98	1.213	0.087	7
B6	$\Phi(\text{Sex}+\text{Area}+\text{Tsm}+\text{Sex}^*\text{Tsm}+\text{Area}^*\text{Tsm})$ $p(\text{Sex}+\text{Area})$	780.31	1.544	0.074	9
B7	$\Phi(\text{Sex}+\text{Area}+\text{Tsm}+\text{Sex}^*\text{Tsm})$ $p(\text{Sex}+\text{Area})$	780.53	1.762	0.066	8
B8	$\Phi(\text{Area}+\text{Tsm})$ $p(\text{Sex}+\text{Area})$	780.82	2.054	0.057	6
B9	$\Phi(\text{Sex}+\text{Area})$ $p(\text{Sex}+\text{Area})$	780.96	2.186	0.054	6
B10	$\Phi(\text{Sex}+\text{Area}+\text{Tsm}+\text{Sex}^*\text{Area}+\text{Area}^*\text{Tsm})$ $p(\text{Sex}+\text{Area})$	781.14	2.369	0.049	9
B11	$\Phi(\text{Sex}+\text{Area}+\text{Tsm}+\text{Sex}^*\text{Area})$ $p(\text{Sex}+\text{Area})$	781.72	2.952	0.037	8
B12	$\Phi(\text{Sex}^*\text{Area}^*\text{Tsm})$ $p(\text{Sex}+\text{Area})^a$	782.32	3.555	0.027	10
B13	$\Phi(\text{Sex}+\text{Area}+\text{Tsm}+\text{Sex}^*\text{Area}+\text{Sex}^*\text{Tsm})$ $p(\text{Sex}+\text{Area})$	782.63	3.861	0.023	9
B14	$\Phi(\text{Sex}^*\text{Area}^*\text{Tsm})$ $p(\text{Sex}+\text{Area})$	783.59	4.820	0.014	11
B15	$\Phi(\text{Sex})$ $p(\text{Sex}+\text{Area})$	787.23	8.462	0.002	5
B16	$\Phi(\text{Constant})$ $p(\text{Sex}+\text{Area})$	788.46	9.686	0.001	4
B17	$\Phi(\text{Sex}+\text{Tsm})$ $p(\text{Sex}+\text{Area})$	789.18	10.411	0.001	6
B18	$\Phi(\text{Sex}+\text{Tsm}+\text{Area}^*\text{Tsm})$ $p(\text{Sex}+\text{Area})$	790.33	11.562	0.000	7
B19	$\Phi(\text{Tsm})$ $p(\text{Sex}+\text{Area})$	790.49	11.717	0.000	5

^a = no three-way interaction.

sex and time since marking. The model with the lowest AIC included only Area. Indeed, apparent survival was clearly higher in the high effort area than in the low effort area ($\Delta AICc=9.7$ model B1 vs. model B16; partial model coefficient on logit scale, β_{AREA} : from model B2: -0.969 , CI -1.533 , -0.405) suggesting that individuals may permanently emigrate more often from the low effort area. Survival of females tended to be higher than that of males but the models including sex were only 0.95 AICc units better than the reduced models (e.g., model B2 vs. model B5) and the confidence interval for the coefficient of sex overlapped zero (partial model coefficient on logit scale, β_{SEX} : from model B2 -0.505 , CI -1.109 , 0.080). The time since marking variable was also included the best models and two models included an interaction with Area. Although the confidence intervals for the coefficients overlapped zero ($\beta_{AREA*TSM}$: from model B2: -1.581 , CI -3.724 , 0.573). Model averaged estimates of apparent survival that consider model selection uncertainty (models B1–B7) indicated possible transience as survival of the first class of the time since marking variable (transients + residents) tended to be lower than survival in the second class of the time since marking variable (i.e., resident individuals) in the low effort area (Fig 4). However, there was no evidence of transience

in the high effort area (Fig 4.). Therefore, we retrieved survival estimates for the high effort area by model averaging models that did not include time since marking as factor. Survival of males was 0.891 (SE 0.032, CI 0.811-0.939) and survival of females was 0.915 (SE 0.030, CI 0.835-0.958) in the high effort area when time since marking was not considered.

4. Discussion

We estimated apparent adult survival of 0.89–0.92 for a Eurasian Curlew population breeding in agricultural fields in Finland. These estimates are in line with an estimate (0.90) derived from recovery data on chicks ringed in European breeding populations during 1968–2016 (Viana *et al.* 2023) and those estimated from wintering populations in Great Britain (0.91–0.92; Taylor & Dodd 2013, Robinson *et al.* 2020, Cook *et al.* 2021). Importantly, our estimate of survival for the last decade is slightly higher than those reported for breeding Eurasian Curlews in Fennoscandia during 1980s and 1990s (0.82–0.88; Ylimaunu *et al.* 1987, Berg 1994, Valkama & Currie 1999), thereby supporting the view that the survival of Eurasian Curlews breeding in northern Europe is high and has not declined during the last decades.

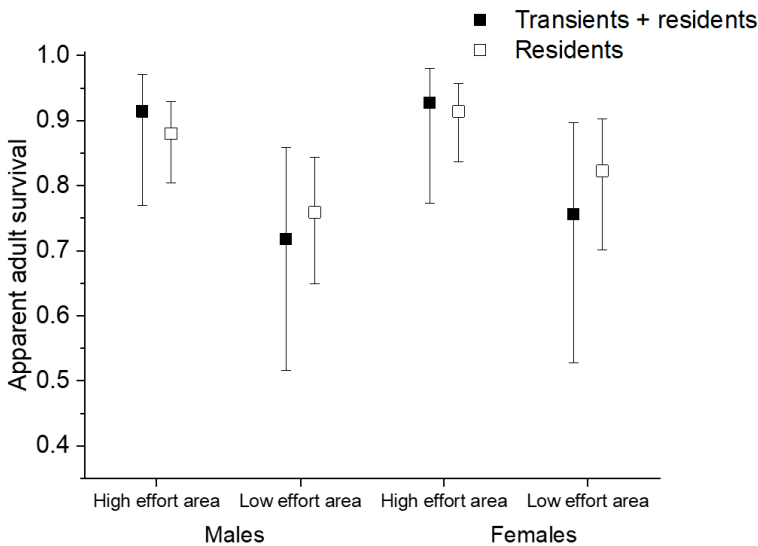


Fig. 4. Apparent survival estimates of male and female Eurasian Curlews separately for the low and high effort areas and for both time since marking classes (1: transients + residents; 2: residents only) derived by model averaging (models with $\Delta AICc < 2$).

We controlled for recapture probabilities when estimating survival whereas the previous survival estimates for breeding Eurasian Curlews in northern Europe were return rates that may have been biased low. The lower survival in the earlier decades could have also resulted from hunting at the wintering grounds in Great Britain and France (Saurola *et al.* 2013, Robinson *et al.* 2020, Spina *et al.* 2022). Hunting was banned from 1982 onwards in Great Britain (Taylor & Dodd 2013) whereas in France a hunting ban was achieved only recently in 2020 with poaching remaining as a possible threat (Jiguet *et al.* 2021). Individuals wintering in France may have been subject to hunting during the 1980s and 1990s, but the number of Finnish-breeding birds reported shot has decreased dramatically in latest decades (Saurola *et al.* 2013, Pearce-Higgins *et al.* 2017). Curlews may also be susceptible to changes in their wintering areas, such as cockle dredging (Taylor & Dodd 2013), but also adverse changes in predation, weather and/or intensification of agricultural practices in wintering areas may reduce survival in particular years (Davidson 1981, Cresswell & Whitfield 1994, Franks *et al.* 2017, Cook *et al.* 2021).

Apparent survival estimates derived from open populations can be biased low by permanent emigration (Sandercock 2006), especially when suitable habitat extends beyond the study area (e.g., Pakanen *et al.* 2015). By using the Area-variable, we attempted to account for spatial heterogeneity in resighting probabilities and movement within the larger fields of the low effort area that likely resulted in permanent emigration. Indeed, both recapture and survival probabilities were higher in the high effort areas. Site fidelity of Eurasian Curlews to our high effort study area was clearly strong as their survival estimate was high. This is in line with reports on breeding site fidelity (Berg 1994, Valkama *et al.* 1998) and resightings/recoveries of breeding Finnish Eurasian Curlews (Saurola *et al.* 2013). At the low effort area, the large fields made it possible for individuals to emigrate out of reach but also other factors such as potential differences in nest predation, Curlew density or lower habitat quality may have affected dispersal (Berg 1994, Valkama *et al.* 1998). Furthermore, we found some evidence of transience (emigration after first capture) in

the low effort area but not in the high effort area supporting the view that survival probabilities in the low effort areas were biased low by permanent emigration.

We found that females tended to have higher apparent survival than males, which contradicts previous studies on Eurasian Curlews (Taylor & Dodd 2013). In general, females are the more dispersive sex in monogamous waders, including the Eurasian Curlew (Berg 1994, Kwon *et al.* 2022), and females should therefore be more likely to permanently emigrate from small study areas. The observed survival difference may, therefore, reflect for example sex-specific differences in predation pressure at the breeding site. Importantly, recapture probabilities were lower for females, which likely results from less conspicuous behaviour during the breeding season or possibly temporary emigration.

Adult survival estimated from this breeding population of the Eurasian Curlew breeding in Finland is high, being clearly within the expectation for a self-sustaining population (Brown *et al.* 2015). This result agrees with earlier studies which suggest that the observed population declines in Europe are not linked to changes in adult survival but rather low reproductive success (Roodbergen *et al.* 2012, Robinson *et al.* 2020). Reproductive success is largely determined by nest survival, chick survival and local recruitment, which are mainly affected by conditions at the breeding sites among grassland breeding shorebirds (Plard *et al.* 2020, Pakanen *et al.* 2020). One of the main factors affecting success of Eurasian Curlews is predation of nests and young (Grant *et al.* 1999, Valkama & Currie 1999, Zielonka *et al.* 2019, Ewing *et al.* 2023). Increased predator numbers and new alien predators such as raccoon dogs (*Nyctereutes procyonoides*) threaten the ground nesting birds in Europe (Roos *et al.* 2018, Brzeziński *et al.* 2010, Holopainen *et al.* 2020; 2021). In our study area, the main nest predators include the raccoon dog, the red fox (*Vulpes vulpes*), corvids (*Corvus* sp.) and the marsh harrier (*Circus aeruginosus*) (own observations). Studies determining which mechanisms and habitat features at the breeding sites affect predation of nests and chicks should be helpful in designing management (e.g., Kentie *et al.* 2013, Laidlaw *et al.* 2017, Kaasiku *et al.* 2022, Pakanen *et al.* 2022, Ewing *et al.* 2023).

Suomessa pesivien isokuovien aikuissäilyvyys

Kahlaajapopulaatiot ovat vähentyneet Euroopassa laajalti. Demografinen tieto on hyvin tärkeässä osassa, kun arvioidaan populaatioiden vähenemisen syitä. Vähenemisen syiden selvittämiseen tarvitaan tietoa useista populaatioista ja eri aikajaksoilta. Isokuovi (*Numenius arquata*) on vähentynyt etenkin Länsi- ja Etelä-Euroopassa. Vähenemisen pääsyyinä pidetään lisääntymismenestyksessä tapahtuneita muutoksia eikä aikuisten säilyvydessä ole havaittu muutoksia talvehtimisalueilla tehdyissä tutkimuksissa. Pesivien populaatioiden aikuissäilyvyydestä on kuitenkin hyvin vähän viimeaikaista tietoa, jota voidaan verrata vanhempiin tutkimuksiin selvittääksemme mahdollisia ajallisia muutoksia, varsinkin isokuovien pääpesimäpaikoilta Pohjois-Euroopasta. Me tutkimme Pohjois-Pohjanmaalla pesivän isokuovipopulaation aikuissäilyvyyttä lukurengasaineiston avulla vuosina 2013–2022 (134 rengastettua yksilöä). Analysoimme merkintä-takaisinpyyntiaineiston Cormack–Jolly–Seber-mallin avulla, jossa otettiin huomioon sukupuoli säilyvydessä ja yksilöiden kiinnijäämistodennäköisyydessä. Aikuisten isokuovikoiraiden vuodenaikainen säilyvyys oli 0.89 ja naaraiden säilyvyys oli 0.92. Säilyvysestimaatit ovat hieman korkeampia kuin 1980- ja 1990-luvuilla havaitut säilyvytykset (0.82–0.88). Nämä vanhempien tutkimusten tulokset voivat olla aliarvioita, koska niitä arvioitaessa ei huomioitu kiinnijäämistodennäköisyyttä. Tästä huolimatta näyttää siltä, että isokuovien aikuissäilyvyys ei ole vähentynyt viime vuosikymmeninä. Meidän tutkimustulostemme avulla voidaan arvioida isokuovien vähenemisen syitä Euroopassa. Ne tukevat aikaisempien tutkimusten tuloksia. Isokuovien väheneminen johtunee pääosin lisääntymiseen liittyvien vaiheiden (pesä- ja poikassäilyvyys) heikentymisestä.

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References

- Amano, T., Székely, T., Koyama, K., Amano, H. & Sutherland, W.J. 2010: A framework for monitoring the status of populations: an example from wader populations in the East Asian-Australasian flyway. — *Biological Conservation* 143: 2238e2247. <https://doi.org/10.1016/j.biocon.2010.06.010>
- Berg, A. 1994: Maintenance of populations and causes of population changes of curlews *Numenius arquata* breeding on farmland. — *Biological Conservation* 67: 233–238. [https://doi.org/10.1016/0006-3207\(94\)90614-9](https://doi.org/10.1016/0006-3207(94)90614-9)
- Brzeziński, M., Żmihorski, M. & Barkowska, M. 2010: Spatio-temporal variation in predation on artificial ground nests: a 12-year experiment. *Annales Zoologici Fennici* — 47:173–183. <http://dx.doi.org/10.5735/086.047.0302>
- Brown, D.J. 2015: International single species action plan for the conservation of the Eurasian Curlew *Numenius arquata arquata*, *N. a. orientalis* and *N. a. suschkini*. — AEWA Technical Series No. 58. Bonn, Germany.
- Burnham, K. P. & Anderson, D. R. 2002: Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York.
- Cook, A.S.C.P., Burton, N.H.K., Dodd, S.G., Foster, S., Pell, R.J., Ward, R. M., Wright, L.J. & Robinson, R.A. 2021: Temperature and density influence survival in a rapidly declining migratory shorebird. — *Biological Conservation* 260: 109198. <https://doi.org/10.1016/j.biocon.2021.109198>
- Crespin, L., Choquet, R., Lima, M., Merritt, J. & Pradel, R. 2008: Is heterogeneity of catchability in capture–recapture studies a mere sampling artefact or a relevant feature of the population? — *Population Ecology* 50:247–256. <https://doi.org/10.1007/s10144-008-0090-8>
- Cresswell, W. & Whitfield, D. P. 1994: The effects of raptor predation on wintering wader populations at the Tynninghame estuary, southeast Scotland. — *Ibis* 136: 223–232. <https://doi.org/10.1111/j.1474-919X.1994.tb01088.x>
- Davidson, N.C. 1981: Survival of shorebirds (*Charadrii*) during severe weather: The role of nutritional reserves. In *Feeding and survival strategies of estuarine organisms*. (ed. Jones N.V. & Wolff W.J.). — *Marine Science* vol 15. Springer, Boston, MA.
- Douglas, D.J., Bellamy, P.E., Stephen, L.S., Pearce-Higgins, J.W., Wilson, J.D. & Grant, M.C. 2014: Upland land use predicts population decline in a globally near-threatened wader. — *Journal of Applied Ecology* 51: 194–203. <https://doi.org/10.1111/1365-2664.12167>
- Ewing, S.R., Scragg, E.S., Butcher, N., & Douglas, D.J.T. 2017: GPS tracking reveals temporal patterns in breeding season habitat use and activity of a globally Near-Threatened wader, the Eurasian Curlew. — *Wader Study* 124: 206–214. <http://dx.doi.org/10.18194/ws.00090>
- Ewing, H., Franks, S., Smart, J., Burton, N. & Gill, J.A. 2023: Nest survival of threatened Eurasian Curlew (*Numenius arquata*) breeding at low densities across a hu-

- man-modified landscape. — *Ibis* 165: 753–766. <https://doi.org/10.1111/ibi.13180>
- Franks S.E., Douglas D.J.T., Gillings, S. & Pearce-Higgins, J.W. 2017: Environmental correlates of breeding abundance and population change of Eurasian Curlew *Numenius arquata* in Britain. — *Bird Study* 64: 393–409. <https://doi.org/10.1080/00063657.2017.1359233>
- Grant, M.C., Orsman, C., Easton, J., Lodge, C., Smith, M., Thompson, G., Rodwell, S. & Moore, N. 1999: Breeding success and causes of breeding failure of curlew *Numenius arquata* in Northern Ireland. — *Journal of Applied Ecology* 36: 59–74. <https://doi.org/10.1046/j.1365-2664.1999.00379.x>
- Green, R.E. 2002: Diagnosing causes of population declines and selecting remedial actions. — In *Conserving Bird Biodiversity* (ed. Norris, K. & Pain, D.J.): 139–156. Cambridge University Press, Cambridge.
- Holopainen, S., Väänänen, V.-M. & Fox, A. 2020: Landscape and habitat affects frequency of native but not alien predation of artificial duck nests. — *Basic and Applied Ecology* 48:52–60. <https://doi.org/10.1016/j.baae.2020.07.004>
- Holopainen, S., Väänänen, VM., Vehkaoja, M. & Fox, A. 2021: Do alien predators pose a particular risk to duck nests in Northern Europe? Results from an artificial nest experiment. — *Biological Invasions* 23: 3795–3807. <https://doi.org/10.1007/s10530-021-02608-2>
- Jiguet, F., Duby, D., Bourgeois, A., Robin, F., Rousseau, P., Nijs, G., Fuchs, J., Lorrillière, R. & Bocher, P. 2021: Investigation into the illegal killing of a tagged Eurasian Curlew. — *Forensic Science International: Animals and Environments* 1:100005. <https://doi.org/10.1016/j.fsi-ae.2021.100005>
- Kaasiku, T., Rannap, R. & Männil, P. 2022: Predation-mediated edge effects reduce survival of wader nests at a wet grassland-forest edge. — *Animal Conservation* 25: 692–703. <https://doi.org/10.1111/acv.12774>
- Keller, V., Herrando, S., Vorisek, P. *et al.* 2020: European Breeding Bird Atlas 2: Distribution, abundance and change. — European bird census council & Lynx Editions, Barcelona.
- Kentie, R., Hooijmeijer, J.C., Trimbos, K.B., Groen, N.M. & Piersma, T. 2013: Intensified agricultural use of grasslands reduces growth and survival of precocial shorebird chicks. — *Journal of Applied Ecology* 50: 243–251. <https://doi.org/10.1111/1365-2664.12028>
- Kwon, E., Valcu, M., Cragolini, M., Bulla, M., Lyon, B. & Kempenaers, B. 2022: Breeding site fidelity is lower in polygamous shorebirds and male-biased in monogamous species. — *Behavioral Ecology* 33: 592–605. <https://doi.org/10.1093/beheco/arac014>
- Laidlaw, R.A., Smart, J., Smart, M.A. & Gill, J.A. 2017: Scenarios of habitat management options to reduce predator impacts on nesting waders. — *Journal of Applied Ecology* 54: 1219–1229. <https://doi.org/10.1111/1365-2664.12838>
- Lebreton, J.-D., Burnham, K.P., Clobert, J. & Anderson, D.R. 1992: Modelling survival and testing biological hypothesis using marked animals: a unified approach with case studies. — *Ecological Monographs* 62:67–118. <https://doi.org/10.2307/2937171>
- Lehikoinen, A., Jukarainen, A., Mikkola-Roos, M., Below, A., Lehtiniemi, T., Pessa, P., Rajasärkkä, A., Rintala, J., Rusanen, P., Sirkkiä, P., Tiainen, J. & Valkama, J. 2019: Birds. — In *The 2019 Red List of Finnish Species* (ed Hyvärinen, E., Juslén, A., Kemppainen, E., Uddström, A. & Liukko, U.-M.): 560–570. Ministry of the Environment & Finnish Environment Institute. Helsinki.
- Lindström, Å., Green M., Husby M., Kälås J.-A., Lehikoinen, A. & Stjernman, M. 2019: Population trends of waders on their boreal and arctic breeding grounds in northern Europe. — *Wader Study* 126: 200–216. <https://doi.org/10.18194/ws.00167>
- Marshall, M.R., Diefenbach, D., Wood, L.A. & Cooper, R.J. 2004: Annual survival estimation of migratory songbirds confounded by incomplete breeding site-fidelity: study designs that may help. — *Animal Biodiversity and Conservation* 27: 59–72.
- Méndez, V., Alves, J.A., Gill, J.A. & Gunnarsson, T.G. 2018: Patterns and processes in shorebird survival rates: a global review. — *Ibis* 160: 723–741. <https://doi.org/10.1111/ibi.12586>
- Morrison, R. I. G., Downes, C. & Collins, B. 1994: Population trends of shorebirds on fall migration in eastern Canada 1974–1991. — *Wilson Bulletin* 106: 431–447.
- Pakanen, V.-M., Lampila, S., Arppe, H. & Valkama, J. 2015: Estimating sex specific apparent survival and dispersal of Little Ringed Plovers (*Charadrius dubius*). — *Ornis Fennica* 92: 172–186.
- Pakanen, V.-M. & Thorup, O. 2016: Apparent adult survival of the critically endangered Baltic Dunlin (*Calidris alpina schinzii*) during a period of strong population decline. — *Bird study* 63: 293–302. <https://doi.org/10.1080/00063657.2016.1214812>
- Pakanen, V.-M., Orell, M., Vatka, E., Rytkönen, S. & Broggi, J. 2016: Different ultimate factors define timing of breeding in two related species. — *PlosOne* 11(9): e0162643. <https://doi.org/10.1371/journal.pone.0162643>
- Pakanen, V.-M., Hagstedt, R., Pauliny, A. & Blomqvist, D. 2020: Survival during the pre-fledging period rather than during post-fledging drives variation in local recruitment of an endangered migratory shorebird, the Southern Dunlin *Calidris alpina schinzii*. — *Journal of Ornithology* 162: 119–124. <https://doi.org/10.1007/s10336-020-01814-4>
- Pakanen, V.-M., Tornberg, R., Airaksinen, E., Rönkä, N. & Koivula, K. 2022: The abundance of small mammals is positively linked to survival from nest depredation but negatively linked to local recruitment of a ground nesting precocial bird. — *Ecology and Evolution* 12: e9292. <https://doi.org/10.1002/ece3.9292>
- Pearce-Higgins, J., Brown, D., Douglas, D., Alves, J., Bellio, M., Bocher, P., . . . Verkuil, Y. 2017: A global threats overview for Numeniini populations: Synthesising ex-

- pert knowledge for a group of declining migratory birds. — *Bird Conservation International* 27: 6–34. <http://dx.doi.org/10.1017/S0959270916000678>
- Piersma, T. & Baker, A.J. 2000: Life history characteristics and the conservation of migratory shorebirds. — In *Behaviour and conservation*. (ed Gosling L.M. & Sutherland W.J.): 105–124. Cambridge, Cambridge University Press.
- Piersma, T., Lok, T., Chen, Y., Hassell, C.J., Yang, H.-Y., Boyle, A., Slaymaker, M., Chan, Y.-C., Melville, D.S., Zhang, Z.-W. & Ma, Z. 2016: Simultaneous declines in summer survival of three shorebird species signals a flyway at risk. — *Journal of Applied Ecology* 53: 479–490. <https://doi.org/10.1111/1365-2664.12582>
- Plard, F., Bruns, H.A., Cimiotti, D.V., Helmecke, A., Hötter, H., Jeromin, H., Roodbergen, M., Schekkerman, H., Tenissen, W., van der Jeugd, H. & Schaub, M. 2020: Low productivity and unsuitable management drive the decline of central European lapwing populations. — *Animal Conservation* 23: 286–296. <https://doi.org/10.1111/acv.12540>
- Robinson, R.A., J.D. Sanders & Rees, E.C. 2020: Survival of Eurasian Curlew *Numenius arquata* differs by season but not breeding origin. — *Wader Study* 127: 25–30. <http://dx.doi.org/10.18194/ws.00176>
- Roodbergen, M., van der Werf, B. & Hötter, H. 2012: Revealing the contributions of reproduction and survival to the Europe-wide decline in meadow birds: review and meta-analysis. — *Journal of Ornithology* 153: 53–74. <https://doi.org/10.1007/s10336-011-0733-y>
- Roos, S., Smart, J., Gibbons, D.W. & Wilson, J.D. 2018: A review of predation as a limiting factor for bird populations in mesopredator-rich landscapes: a case study of the UK. — *Biological Reviews* 93: 1915–1937. <https://doi.org/10.1111/brv.12426>
- Rönkä, A., Koivula, K., Ojanen, M., Pakanen, V.-M., Pohjoismäki, M., Rannikko, K. & Rauhaluoma, P. 2006: Increased nest predation in a declining and threatened Temminck's stint (*Calidris temminckii*) population. — *Ibis* 148: 55–65. <https://doi.org/10.1111/j.1474-919X.2006.00481.x>
- Taylor, R.C. & Dodd, S.G. 2013: Negative impacts of hunting and suction-dredging on otherwise high and stable survival rates in Curlew *Numenius arquata*. — *Bird Study* 60: 221–228. <https://doi.org/10.1080/00063657.2013.775215>
- SandercocK, B.K. 2006: Estimation of demographic parameters from live encounter data: a summary review. — *Journal of Wildlife Management* 70: 1504–1520.
- Saurola, P., Valkama, J., & Velmala, W. 2013: The Finnish Bird Ringing Atlas, vol I. — Finnish Museum of Natural History and Ministry of Environment, Helsinki.
- Simmons, R. E., Kolberg, H., Braby, R. & Erni, B. 2015: Declines in migrant shorebird populations from a winter-quarter perspective. — *Conservation Biology* 29: 877–887. <https://doi.org/10.1111/cobi.12493>
- Spina, F., Baillie, S.R., Bairlein, F., Fiedler, W. and Thorup, K. 2022: The Eurasian African bird migration Atlas. <https://migrationatlas.org>. — EURING/CMS.
- Stroud, D. 2003: Are waders world-wide in decline? Reviewing the evidence. A workshop summary. — *Wader Study Group Bulletin* 101/102: 8–12.
- Summers, R.W., Pålsson, S., Etheridge, B., Foster, S. & Swann, R.L. 2013: Using biometrics to sex adult Eurasian Curlews *Numenius a. arquata*. — *Wader Study Group Bulletin* 120: 71–74.
- Valkama, J. & Currie, D. 1999: Low productivity of Curlews *Numenius arquata* on farmland in southern Finland: causes and consequences. — *Ornis Fennica* 76: 65–70.
- Valkama, J., Currie, D. & Korpimäki, E. 1999: Differences in the intensity of nest predation in the curlew *Numenius arquata*: A consequence of land use and predator densities? — *Ecoscience* 6: 497–504. <https://doi.org/10.1080/11956860.1999.11682552>
- Valkama, J., Robertson, P. & Currie, D. 1998: Habitat selection by breeding curlew (*Numenius arquata*) on farmland: the importance of grassland. — *Annales Zoologici Fennici* 35: 141–148.
- Valkama, J., Vepsäläinen, V. & Lehikoinen, A. 2011: The third Finnish breeding bird atlas. — Finnish Museum of Natural History and Ministry of Environment. Accessed at <<http://atlas3.lintuatlas.fi/english>>.
- Viana, D.S., Santoro, S., Soriguer, R.C. & Figuerola, J. 2023: A synthesis of Eurasian Curlew (*Numenius arquata arquata*) demography and population viability to inform its management. — *Ibis* 165: 767–780. <https://doi.org/10.1111/ibi.13184>
- von Numers, S., Öst, M. & von Numers, M. 2020: Population changes in the declining Turnstone (*Arenaria interpres*) and other waders in the northern Baltic Sea based on past and current breeding observations. — *Ornis Fennica* 97: 149–164.
- Ylimaunu, O., Ylimaunu, O., & Liehu, H. 1987: Isokuovin pesimäekologiasta ja kannasta Suomessa. — *Lintumies* 22: 98–103. (In Finnish)
- White, G.C. & Burnham, K.P. 1999: Program MARK: survival estimation from populations of marked animals. — *Bird Study* 46: 120–139. <https://doi.org/10.1080/00063659909477239>
- Zielonka, N.B., Hawkes, R.W., Jones, H., Burnside, R.J. & Dolman, P.M. 2019: Placement, survival and predator identity of Eurasian Curlew *Numenius arquata* nests on lowland grass-heath. — *Bird Study* 66:471–483. <https://doi.org/10.1080/00063657.2020.1725421>

Assessing timing of fledging in a cavity-nesting passerine using temperature data loggers

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In altricial birds, the length of the nestling period, *i.e.* time from hatching until fledging (young leaving the nest) varies within and between species. In general, however, variation in the time of fledging and factors mediating such variation remain largely unexplored. To assess the time of nestlings leaving the nest, daily observer visits to the nest are usually done in the predicted fledging period. However, this might initiate premature fledging of young and/or increase the predation risk. The application of iButtons – coin-sized temperature data loggers, which are increasingly used in ornithological studies – may help to overcome these obstacles. We tested whether nest temperatures recorded with iButtons might be used to identify the date and hour of young fledging, *i.e.* when the last nestling in the brood left the nest, in a small cavity-nesting passerine – the Great Tit (*Parus major*). We installed iButtons in 38 nests when nestlings were 14–15 days old (hatching day = day 0) and verified the presence of nestlings during daily inspections starting on day 17 post-hatching or later. We found that the day of fledging could be accurately determined based on the difference between the temperature of the nest cup and the outside. The age of nestlings ranged between 17 and 22 days at fledging, with nearly 58% of broods fledging at the age of 20 and 21 days. The majority (81.6%) of broods fledged within 6 h after sunrise. We discuss the advantages and disadvantages of using iButtons to identify fledging time in altricial birds.



1. Introduction

Offspring of altricial species hatch undeveloped and, therefore, are confined to the nest until they reach the stage of growth that allows them to leave the nest. The length of the period between hatching and fledging (leaving the nest) varies to a great extent among bird species (Remeš & Martin 2002, Cooney *et al.* 2020, Merrill *et al.*

2021). In altricial, open-nesting species, like the Eurasian Skylark (*Alauda arvensis*), the nestling period lasts for 7–11 days, while nestlings of other, often larger species, require more time to develop and leave the nests, even up to 58–64 days (White Stork, *Ciconia ciconia*) (Billerman *et al.* 2022). The length of the nestling period varies also within species, both from the same or

different populations (Michaud & Leonard 2000, Johnson *et al.* 2004). For example, the length of the nestling period varied by nearly 100% (7–13 days) between the nests of the Horned Lark (*Eremophila alpestris*) in an alpine population (Zwaan *et al.* 2019). In general, however, the intra-specific variation in fledging age, and potential factors mediating such variation, remain largely unexplored (but see Stodola *et al.* 2010, Yoda *et al.* 2017, Moreno 2020, 2022).

To accurately determine the age of nestlings leaving the nest, most commonly nests are visited daily around the expected fledging time (Bowers *et al.* 2013; *e.g.*, Michaud & Leonard 2000, Stodola *et al.* 2010, Moreno 2020, 2022). However, the increased frequency of observer visits to the nests close to fledging time might initiate premature fledging (Michaud & Leonard 2000, McCarty 2001, Pietz *et al.* 2012), which may decrease the probability of post-fledging survival due to impaired flight capacity (*e.g.*, Jones *et al.* 2017, Martin *et al.* 2018; but see Streby *et al.* 2013 for no or a positive effect of forced and premature fledging on fledgling survival of two songbird species). Moreover, frequent visits to the nests by observers might increase the risk of nest predation (Major 1990), although the opposite or no effect has also been observed (Weidinger 2008, Jacobson *et al.* 2011).

The application of temperature data loggers, which are increasingly used in ornithological studies (*e.g.*, Hartman & Oring 2006), might help to overcome the obstacle of frequent nest visitation to determine the nestlings' age at fledging. Temperature data loggers measure and record temperature, according to the set frequency of data logging, for an extended time, limited by memory capacity. To date, temperature data loggers have been commonly used to examine nest attendance during incubation (Ardia *et al.* 2009, Nord & Nilsson 2012, Podlas & Richner 2013, Arct *et al.* 2022), or to determine the events associated with temporary nest desertion or permanent termination of breeding attempts in response to predation or flooding (Arnold *et al.* 2006, Bayard & Elphick 2011, Betuel *et al.* 2014, Taylor 2015, Hunter *et al.* 2016). Other studies included an examination of air temperature within artificial and natural cavities (Ardia *et al.* 2006, Fairhurst *et al.* 2012, Maziarz *et al.* 2017, Pattinson *et al.* 2022) and

an assessment of insulatory properties of bird nests (Deeming & Campion 2018, Deeming *et al.* 2020).

Altricial nestlings are poikilothermic at hatching, but develop endothermy during the nestling period (Dunn 1975). At the end of the nestling period, the body temperature of young is close to that of adult birds (at the active phase *ca.* 41 °C) (Mertens 1977, Prinzing *et al.* 1991). Consequently, due to the endothermic activity of older nestlings, the temperatures of active nests are usually higher than in vacant nests, from which nestlings have fledged (Maziarz *et al.* 2020). As such, nest temperatures could be a good indicator for monitoring the status of nests and the presence/absence of live nestlings in them. Following nestling departure, the nest temperatures should be similar to ambient temperatures, so the difference between internal (within a nest) and ambient temperatures would allow to pinpoint the date and hour of young fledging. Thus, collecting the data on nest temperatures would require only two visits to the nest: the first one – in advance of the expected fledge date to install a temperature data logger in the nest, and the second one – a few days later to check the content of the nest for the presence of nestlings and to retrieve the data logger if young were absent. Despite the advantages of this method, such as low time investments and cost, the method is rarely used specifically for assessing the time of young fledging in altricial birds (Ballance 2018). Given the scarcity of data, it is unclear to what extent the method could be successfully applied across different species.

We aimed to verify whether the moment of fledging could be accurately assessed by measuring the temperatures of nests with data loggers in a small cavity-nesting passerine – the Great Tit (*Parus major*). To establish nest temperatures, we used iButton temperature data loggers (Maxim Integrated, USA; referred to hereafter as iButtons), which are stand-alone coin-sized loggers. By using the data collected with iButtons, we describe the variation in fledging age and the diel pattern of fledging in the study population. Great Tit nestlings usually fledge between 16 and 22 days after their hatching, most of them during mornings (Radersma *et al.* 2015, Gosler *et al.* 2020).

2. Materials and methods

We collected data in a nestbox breeding population of Great Tits during April–June 2017 in the Sekocin Forest in central Poland, *ca.* 10 km south-west of Warsaw (52°05'N, 20°52'E) (see Harnist *et al.* 2020 for a description of nestboxes and the study area). From early April we checked nestboxes every few days to record the laying of the first egg and clutch size, and daily around the expected hatching day to record hatching date (day when at least one nestling was observed during the nestbox inspection, day=0). On day 14–15 post-hatching, we ringed nestlings with a numbered aluminium ring, and placed one iButton in nesting material of 38 nests. We chose the age of 14–15 days based on the developmental stage reached by Great Tit nestlings two weeks after hatching. Specifically, at this age, feathers of Great Tit nestlings are not sufficiently developed to support premature fledging. All except five loggers were first mounted in a plastic iButton holder (DS9093S+, Maxim Integrated, USA; oval-shaped with dimensions of 46.9 mm × 30.9 mm) to help to immobilize the loggers within the nests. We positioned each iButton within the central part of the nest cup buried under *ca.* 1–2 mm of nesting material. Because the study aimed to verify whether fledging date and hour may be identified based on the comparison of nest and ambient temperatures, we deployed one logger (mounted in a plastic holder) to collect data on ambient temperature. We attached this logger to the outer side of the floor of the nestbox placed *ca.* 3.5 meters above the ground in the central part of the study area. The ambient temperature logger was positioned at an average distance of approximately 550 meters from the nestboxes where nest loggers were deployed. We chose the position of the logger to keep it in shade during the daytime. Only first broods were used in this study.

We used two models of iButtons: DS1921G-F5 and DS1922L (diameter: 17.35 mm, thickness: 5.89 mm). DS1921G-F5 measures temperature from –20 °C to +85 °C with an accuracy of 1 °C and resolution of 0.5 °C, and DS1922L — from –10 °C to +65 °C with an accuracy of 0.5 °C and resolution of 0.0625 °C. The use of two models

was necessitated by the insufficient number of loggers of one type to record temperature in highly synchronic broods (hatching dates ranged between April 26th and May 15th, with 57.9% of broods hatching over a span of 5 consecutive days). We found that the difference in measurement accuracy between the two iButton models did not affect our ability to determine the date and hour of fledging based on the comparison of nest and ambient temperature profiles. For both logger models the success rate of determining the timing of fledging was 100%.

We programmed nest loggers and the ambient temperature loggers to measure and record temperature synchronously (± 2 min) every 10 minutes. We chose the frequency of logging based on the maximum number of temperature readings that could be stored in a logger with a lower storing capacity (DS1921G-F5, up to 2048 readings) without the need for replacement of nest loggers, and considering the length of the nestling period of the study species. Chosen logging frequency allowed to record temperature for 14 days, which corresponds to day 28 or 29 post-hatching depending on the day of logger installation. Based on literature data such a logging limit captures all fledging events in the study species (Verhulst & Tinbergen 1997, Gosler *et al.* 2020). Given the time span of a few weeks between placing the logger in the earliest monitored brood and removing the logger after the nestlings fledged from the latest monitored brood, we had to exchange the ambient temperature logger due to its storage capacity limitations. Loggers were programmed and temperature records were downloaded using OneWireViewer version 0.3.15.49 (Maxim Integrated Products, Sunnyvale, CA, USA).

To verify whether information on the nest activity status ('active – nestlings present' vs. 'non-active – no live nestlings') may be reliably derived from the difference between the nest and ambient temperatures, the content of nest boxes was checked daily in the afternoon (after 1 pm) starting from day 17 post-hatching. Due to logistic constraints, in the subset of nests inspections started on day 18 post-hatching or later. The presence of nestlings was assessed through an entrance hole using a handheld flashlight with a flexible neck (Uni-max, Czech Republic) and a

magnifying dental mirror. This method is used in studies on birds nesting in natural cavities (e.g., Wesołowski & Rowiński 2014). The method minimizes the level of disturbance experienced by nestlings and prevents premature fledging. During nest-checks, we recorded the date, hour and outcome: nestlings present or absent. On the day we found that nestlings were absent, the logger was retrieved. We recorded the date and hour of logger retrieval, the number of dead nestlings, and in a subset of nests also a crude estimation of the distance (in mm) between the bottom of the nest cup and the logger location. We collected data on dead nestlings, because their presence may affect temperature recorded by the logger in the nest. First, if some nestlings die before the last successful fledging event in a brood, their bodies, located at the bottom of the nest cup, may interfere with the transfer of the heat produced by live nestlings towards the logger. Second, when some nestlings die after the last successful fledging event in a brood, the moment when nest and ambient temperatures level out should be shifted in time, until the death of nestlings which failed to fledge. In both cases the drop in nest temperature following the last successful fledging event may be less distinct and consequently more difficult to detect than in nests without nestling mortality. We recorded the logger-bottom of the nest cup distance to verify whether the chosen method of logger installation (mounting in a plastic holder) successfully prevents extensive relocation of loggers within the nesting material.

2.1. Data analyses

To identify the time of the last successful fledging event in the nest, we compared the nest and ambient temperatures. As the time of fledging, we selected the hour corresponding to the start of a steady drop in the nest temperature until the nest and ambient temperatures leveled out. To compare nest and ambient temperatures, we plotted temperature records against time (Fig. 1, Hartman & Oring 2006). Moreover, for each nest, we retrieved the minimum and mean difference between the nest and ambient temperatures over the period between midnight

on the day the logger was placed in the nest and the hour identified as the moment of departure of the last nestling. The time of fledging was expressed as the number of hours since sunrise. Data on sunrise at the study site were obtained at <https://www.timeanddate.com>. In the next step, we verified whether the date of fledging assessed with temperature data loggers corresponded with the outcome of the visual inspection of the nest activity status.

Temperature records of the nest cup were available for 38 broods. However, in 7 broods inspection of the nestbox for the presence of nestlings was not carried out on a daily basis or nestlings fledged before the first inspection. Since in such cases it was not possible to verify whether the temperature profiles of the nest cup corresponded with the presence of nestlings in the nestbox, such broods were excluded from the validation of the suitability of iButton temperature loggers for identifying the time of fledging. However, following the validation of the method, we used data from all 38 broods to assess fledging age and the diel pattern of fledging in the study population.

3. Results

3.1. Validation of the method

In all but one case, we retrieved the logger from the nesting material beneath the bottom of the nest cup. In one nest we found the logger on the rim of the nest, while the logger holder was in the nesting material. However, despite logger relocation, it was possible to identify fledging time based on recorded temperature. Some loggers, whether mounted in holders or positioned within nests without holders, displayed movement within the nesting material. This was evident in the variation observed among nests in the distances between the nest cup's bottom and the logger's location within the nest base during logger retrieval. These distances ranged from 0 to approximately 20 mm.

In all 31 broods, the date of fledging could be accurately determined based on the comparison of the nest cup and ambient temperatures, as confirmed by the outcome of the visual inspection

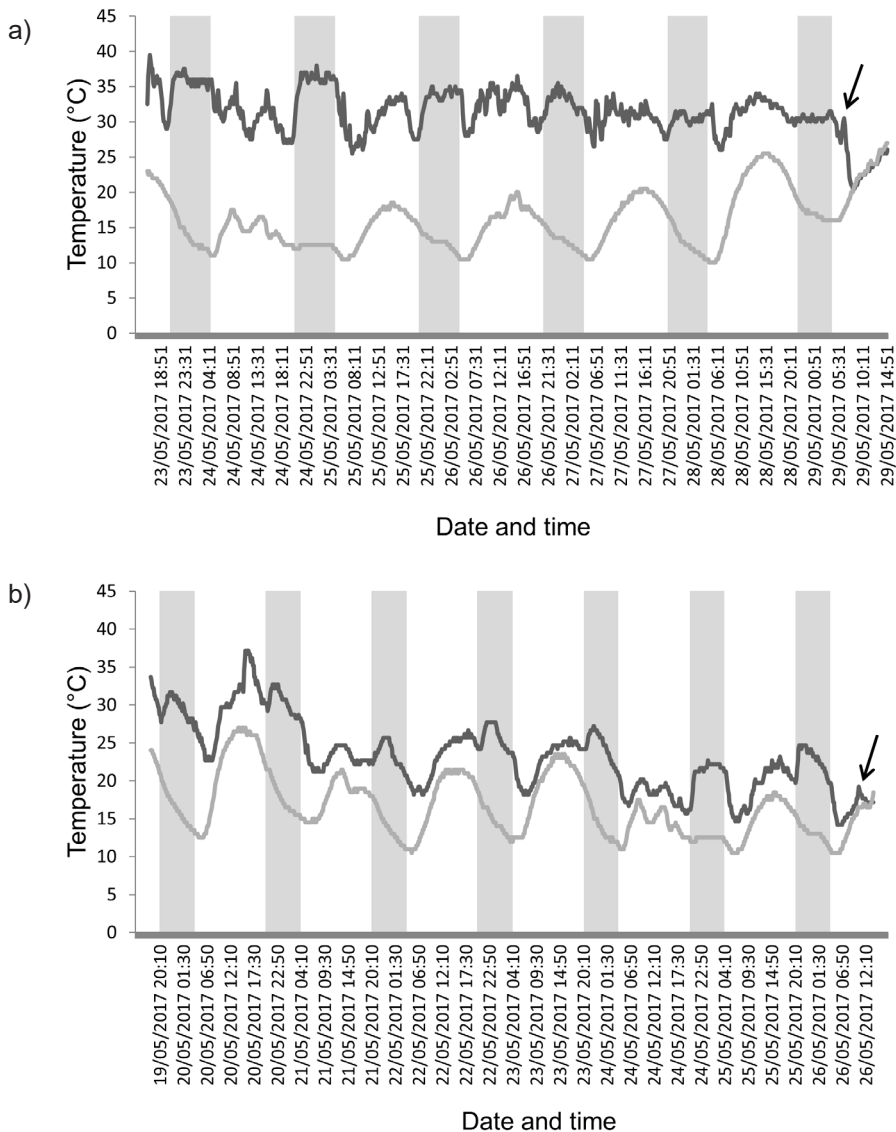


Fig. 1. Records of the nest cup (black) and ambient (grey) temperatures between day 14 post-hatching (hatching day = day 0) and fledging day in two Great Tit nests in the Sekocin Forest in central Poland. Data for the nest with no (a) and partial (b) nestling mortality after day 14 post-hatching is presented. Nest cup and ambient temperatures were synchronously (± 2 min) recorded every 10 minutes. The arrow marks the time point of the presumed last successful fledging event in a brood. Periods of nighttime (between sunset and sunrise) are shaded.

of nests for the presence of nestlings. This also applied to eight nests with dead nestlings (1–5 young over 14 days old) which were found on the day of the logger retrieval. In all nests, we identified the temperature record corresponding to the start of a gradual decrease in the nest temperature,

which was followed by the nest and ambient temperatures leveling out (Fig. 1). On average, the minimum and mean per nest difference between the nest and ambient temperatures was 5.6 °C (range: 0.5–7.7 °C) and 12.4 °C (range: 6.2–17.7 °C), respectively.

3.2. Age and the diel pattern of fledging

Fledging of entire broods was completed between days 17 and 22 post-hatching. Most broods fledged on days 20 and 21, 28.9% ($n=38$) on each of these days. The average fledging age was 20.1 days (± 1.3 SD), while the median fledging age was 20 days (Fig. 2). The last nestlings in the brood departed from the nests between 26 minutes before and 14 h 18 minutes after sunrise, which corresponds to 4:01 am and 6:49 pm local time, respectively (Fig. 3). The mean and median time of fledging after sunrise were approximately 3 h 57 min and 2 h 46 min, which corresponds to 8:26 am and 7:15 am local time, respectively. The highest number of broods fledged between 2 h and 2 h 29 min after sunrise. Out of 38 monitored broods, 52.6% fledged within 3 h and 81.6% — within 6 h after sunrise.

4. Discussion

We show that iButton temperature data loggers may be successfully used to determine fledging age and the diel pattern of fledging in a cavity-nesting species that builds nests of dense structure (Gosler *et al.* 2020). In the study population of Great Tits, this method allowed for 100% accuracy in identifying the day when

the last nestling(s) left the nest, as confirmed by daily nest visits around the predicted fledging day.

The two main advantages of this method over traditionally used frequent nest visitations are time and observer effort effectiveness, and avoidance of disturbance of nestlings at the end of the nestling period when they might be provoked to leave the nest prematurely. Alternative remote methods such as radio-frequency identification technology (RFID) and video or trail cameras (Johnson *et al.* 2004, 2013, 2017, Pietz *et al.* 2012, Brandis *et al.* 2014, Iserbyt *et al.* 2018, Ribic *et al.* 2019, Surmacki & Podkowa 2022) allow precise determination of timing of fledging, and, especially in the case of RFID technology, also fledging order (Radersma *et al.* 2015; Schlicht *et al.* 2012). However, given the much lower cost and easier installation, iButton temperature data loggers may be a method of choice in many studies focusing on the identification of fledging age in altricial birds.

When using iButtons to assess the time of fledging, one must consider the nestling's age at which to deploy loggers and how to install the logger in the nest. Because inserting the temperature logger into the nest material is associated with a certain amount of disturbance, this manipulation should not be conducted during the very advanced stages of the nestling period, even

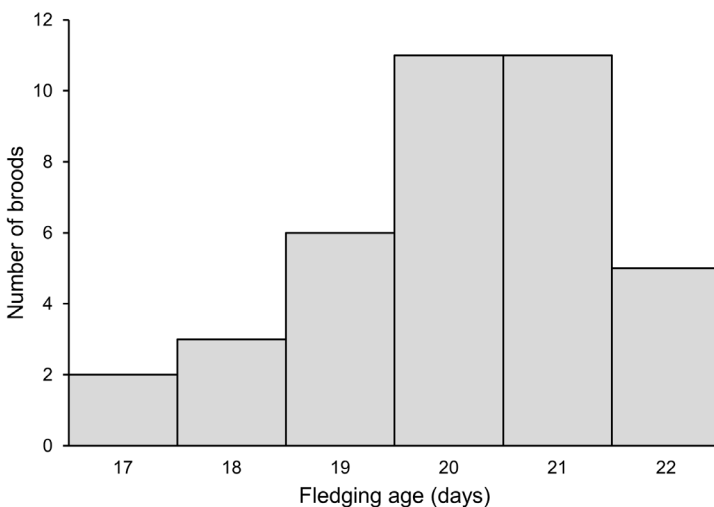


Fig. 2. Frequency distribution of fledging age (in days) of Great Tit nestlings from first broods in the Sekocin Forest in central Poland in 2017. Fledging age was identified based on nest temperature records logged with iButtons.

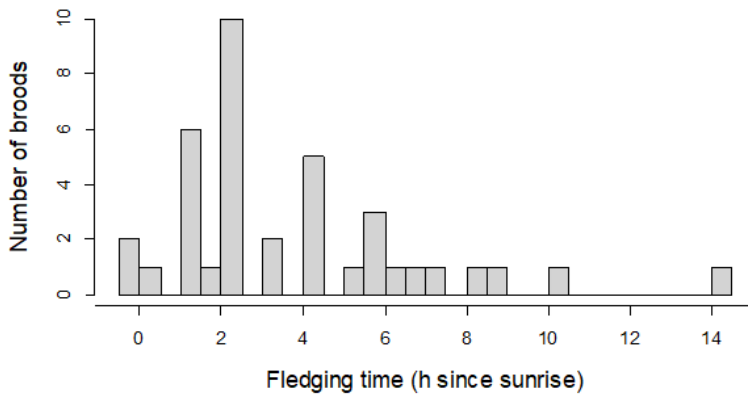


Fig. 3. Frequency distribution of the time of fledging expressed as the difference in hours between sunrise and the moment of fledging of last nestling(s) in the nest.

if it results in a reduced frequency of temperature logging due to logger storage capacity limitations. As for the methods of inserting the logger into the nest material, it is important to note that when unsecured, the logger may change its location in the nest. This may occur in response to nestling locomotor activity or when adult birds move the logger to other parts of the nest, such as the nest rim (as observed in this study). With increasing distance from the nest cup containing nestlings, temperatures recorded by the logger should less accurately mirror temperatures of the nest cup. Such a reduction in temperature resolution in relation to the relocation of loggers in the nesting material has been previously observed in the Great Tit during the incubation stage when the main source of the heat is an incubating female (Smith *et al.* 2015). Second, iButton loggers may be removed by the parent(s) to the outside of the nest. Smith (2011) reported frequent removal of unsecured iButtons during incubation by Great Tit females, while Nord & Nilsson (2012) reported such behaviour in incubating Pied Flycatchers (*Ficedula hypoleuca*), although in this species it was sporadic. To the best of our knowledge, no study so far looked into the frequency of iButton removal during different nesting stages. However, it is possible that such behaviour is more common during egg laying and incubation, when a logger may be perceived by parents as a parasitic egg, than during the nestling period. To reduce relocation and/or prevent removal of iButton loggers from the nest it is recommended that they are secured. This may be

achieved by attaching strings/wire to the logger and wrapping them around the nesting substrate or *e.g.*, a wooden stick placed beneath the nest (Smith 2011, Weintraub *et al.* 2016, Schöll *et al.* 2020). In our study, we secured iButtons against relocation and removal by adult birds by mounting the logger in a plastic holder. Because almost all loggers were recovered no deeper than approximately 10 mm from the bottom of the nest cup, this method may be recommended in species building nests of dense structure. Moreover, only in one nest, the logger was removed by the adult bird from its location beneath the bottom of the nest cup by removing it from the plastic holder and placing it on the nest rim. By applying additional measures to secure logger position in the holder, such a method should ensure full protection against relocation of loggers by parents in small bird species. In species that build nests of less dense structures and/or are larger, other methods may be preferred. For example, to monitor nest activity in the Tricolored Blackbird (*Agelaius tricolor*), an open-cup nester, that builds nests from leaves woven around plant stems, Weintraub *et al.* (2016) secured iButtons by sewing them into pieces of brown nylon stocking, which was then attached to green floral wire put through the bottom of the nest and wrapped around the nesting substrate.

While iButtons offer some advantages over other techniques of monitoring the nest activity (either remote or direct), this method has several limitations. First, with iButtons it is not possible to identify fledging age of individual nestlings.

Temperature data loggers will only pinpoint the moment when the last nestling from the brood leaves the nest. In consequence, in multiparous species with brood fledging asynchrony, *i.e.*, when fledging of nestlings from the same brood is extended over time, this will result in the overestimation of the mean brood fledging age. However, the magnitude of such overestimation will depend on the degree of fledging asynchrony and the frequency of this phenomenon in the population. In species with narrow fledging asynchrony, *i.e.*, when fledging of the entire brood spans across several hours but finishes on the same day, or is limited to a small proportion of broods in the population, the overestimation of the brood fledging age defined as the day when the last nestling left the nest, may be treated as negligible. In many songbirds all nestlings in the majority of broods complete fledging within 1 day, for example, in the Blue Tit (*Cyanistes caeruleus*) – in 55% (Schlicht *et al.* 2012), in the House Wren (*Troglodytes aedon*) – in 65% (Johnson *et al.* 2004) and in the Mountain Bluebird (*Sialia currucoides*) – in 83% of broods (Johnson *et al.* 2013). Also in the Great Tit in the majority of cases, the entire brood fledges on the same day (Verhulst & Tinbergen 1997). Radersma *et al.* (2011) found that in this species fledging asynchrony within a brood ranged from 7 min 13 s to 2637 min (about 44 h) with an average of about 136 min.

Second, with temperature records, it is not possible to distinguish between successful and depredated broods (either depredated fully or partially) if the predation event leaves no traces, such as feathers or disturbed nesting material (Weidinger 2006). For example, Ball & Bayne (2012) monitoring 127 shrub–subcanopy nests representing 13 species found that among 78 nests that were classified as successful based on cues at the nest, 21 were in fact partially (14 nests) or entirely (7 nests) depredated based on video records. And among 49 nests classified as depredated based on nest cues, in 5 nests 1 or more nestlings fledged. However, if nesting places are well secured against predators, for example, some types of nestboxes, the lack of live nestlings in the nest after the predicted fledging age may be relatively safely interpreted as a sign of successful fledging. For example, in the study population

of Great Tits in the Sekocin Forest, no evident signs of nestling depredation were recorded over the whole period of population monitoring, *i.e.*, for over 10 breeding seasons (own observation).

Third, without video or trail camera records iButtons, similarly to fledging status assessed based on regular nest visits, do not allow to distinguish between unforced and forced fledging, either of the entire brood or some nestlings from the brood (Ball & Bayne 2012).

Fourth, iButtons may be used to correctly determine fledging time only under the condition that a difference between the nest and ambient temperatures is measurable. This may not be the case in regions with very high daytime ambient temperatures or when the nest is under direct sun exposure (Sutti & Strong 2014, Andersen & Freeman 2022). For example, Andersen & Freeman (2022) showed that in the Botteri's Sparrow (*Peucaea botterii*), a species that nests in hot, semiarid grasslands, during the hot period of the day the cessation of nest activity was correctly identified only in 46% of nests, while during the cooler period of the day (when nest temperature was on average 3.9 °C higher than ambient temperature), termination of the nest activity was correctly assigned in all nests. However, even though the hour of termination of the nest activity may not always be correctly assigned, a distinct difference between nest and ambient temperatures during the coolest parts of the day (night, early morning, late evening) should still allow for correct identification of the day of fledging.

The average fledging age in the study population was 20.1 days and in the broods with the longest nestling period nestlings departed from the nest 5 days later than in nests with the shortest nestling period. Great Tit nestlings in central Poland fledged approximately a day later than in the populations on the island of Vlieland (the Netherlands) and near Bern (Switzerland) and half a day later than in the population in Lauwersmeer in the north of the Netherlands (Verhulst & Tinbergen 1997, Radersma *et al.* 2011, Basso & Richner 2015). However, in order not to introduce any bias in the comparison of fledging ages among populations, data should be preferably collected with the use of the same method and use the same definition of

fledging age. For example, while in the studies in the Sekocin Forest and Vlieland populations fledging age was defined as the day when the last nestlings left the nest, the study in the Lauwsmeer population, which applied RFID technology, defined fledging age at the brood level as the average of fledging age of individual nestlings. Because of that, in broods with extended fledging asynchrony, such an approach introduces an underestimation in fledging age when compared to this parameter expressed as the day when the last nestling left the nest. The majority of Great Tit broods fledged early in the morning with 52.6% of broods fledging within 3 h, and 81.6% within 6 h after sunrise. Fledging at this time of the day is typical for the Great Tit (Lemel 1989, Verhulst & Hut 1996, Radersma *et al.* 2015) as well as for other passerines and is being associated with the developmental stage of nestlings and predation risk (Schlicht *et al.* 2012, Chiavacci *et al.* 2015, Santema *et al.* 2021 and references therein).

Summing up, this study shows that iButton temperature data loggers may be used to correctly determine fledging age of whole broods, as well as the hour of fledging, in an altricial cavity-nesting species. To increase the accuracy of assessment, iButtons are recommended for populations with low predation risk. In general, it is also recommended that iButtons are secured in the nest to prevent their removal and/or relocation within the nest by adult birds. Using iButtons, we showed that in the study population there is substantial variation in the age when nestlings leave the nest, which may potentially translate into differences in such fitness-related traits as survival.

Kolopesijän pesäpoikasten lentoonlähden määrittäminen lämpödataloggereilla

Pesäpoikasaika, eli aika kuoriutumisesta lentoonlähtoon, vaihtelee sekä lajien sisällä että lajien välillä. Lentoonlähden ajoituksen vaihtelusta ja siihen vaikuttavista tekijöistä tiedetään hyvin vähän. Yleensä lentoonlähden ajankohdan arvioimiseksi tehdään päivittäisiä tarkastuskäyntejä pesälle arvioidun lentoonlähden aikana. Tämä saattaa kuitenkin aiheuttaa poikasten ennenaikaista lentoonlähtöä ja/tai lisätä saalistuksen riskiä. Testasimme, että voiko

iButton-lämpödataloggereilla tallennettuja pesän lämpötiloja käyttää poikasten lentoonlähden päivämäärän ja kellonajan määrittämisessä. Pesän lämpötilan odotetaan viilenevän, kun viimeinen pesäpoikanen jättää pesän. Asensimme iButton-lämpödataloggereita 38 talitiaispesään (*Parus major*), kun poikaset olivat 14–15 päivän ikäisiä (kuoriutumispäivä = päivä 0), ja varmistimme poikasten läsnäolon päivittäisillä tarkastuskäynneillä alkaen 17. päivästä kuoriutumisen jälkeen tai myöhemmin. Havaitimme, että lentoonlähden päivää voitiin määrittää tarkasti pesäkupin ja ulkona vallitsevan lämpötilan eron perusteella. Poikasten ikä vaihteli 17 ja 22 päivän välillä lentoonlähden aikana, ja lähes 58% pesueista lähti lentoon 20 ja 21 päivän ikäisinä. Enemmistö (81.6%) pesueista lähti lentoon kuuden tunnin sisällä auringonnousun jälkeen. Tutkimuksessa käsittelemme myös iButton-loggereiden käytön etuja ja haittoja lentoonlähtöajan määrittämisessä kolopesijälinnuilla.

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Conflict of interest. Authors declare that they have no conflict of interest.

Ethics Statement. All applicable national and institutional guidelines for the care and use of animals were followed. The procedures were carried out under the permit issued by the Regional Directorate for Environmental Protection in Warsaw, Poland (permit no. WPN-I.6401.159.2017. LM).

References

- Andersen, E.M. & Freeman, S.L. 2022: Use of thermal data loggers to evaluate nest survival in a grassland songbird. — *Wilson Journal of Ornithology* 134: 390–397. <https://doi.org/10.1676/21-00005>
- Arct, A., Martyka, R., Drobniak, S.M., Oleś, W., Dubiec, A. & Gustafsson, L. 2022: Effects of elevated nest box temperature on incubation behaviour and offspring fitness-related traits in the Collared Flycatcher *Ficedula albicollis*. — *Journal of Ornithology* 163: 263–272. <https://doi.org/10.1007/s10336-021-01944-3>
- Ardia, D.R., Pérez, J.H., Chad, E.K., Voss, M.A. & Clot-

- felter, E.D. 2009: Temperature and life history: experimental heating leads female Tree Swallows to modulate egg temperature and incubation behaviour. — *Journal of Animal Ecology* 78: 4–13. <https://doi.org/10.1111/j.1365-2656.2008.01453.x>
- Ardia, D.R., Pérez, J.H. & Clotfelter, E.D. 2006: Nest box orientation affects internal temperature and nest site selection by tree swallows. — *Journal of Field Ornithology* 77: 339–344. <https://doi.org/10.1111/j.1557-9263.2006.00064.x>
- Arnold, J.M., Sabom, D., Nisbet, I.C.T. & Hatch, J.J. 2006: Use of temperature sensors to monitor patterns of nocturnal desertion by incubating Common Terns. — *Journal of Field Ornithology* 77: 384–391. <https://doi.org/10.1111/j.1557-9263.2006.00068.x>
- Ball, J.R. & Bayne, E.M. 2012: Using video monitoring to assess the accuracy of nest fate and nest productivity estimates by field observation. — *The Auk* 129: 438–448. <https://doi.org/10.1525/auk.2012.11224>
- Ballance, T.E. 2018. Effects of nest quality on incubation and reproductive success in Carolina Chickadees (*Poecile carolinensis*) (MSc dissertation). — Western Carolina University.
- Basso, A. & Richner, H. 2015: Effects of nest predation risk on female incubation behavior and offspring growth in Great Tits. — *Behavioural Ecology and Sociobiology* 69: 977–989. <https://doi.org/10.1007/s00265-015-1910-4>
- Bayard, T.S. & Elphick, C.S. 2011: Planning for sea-level rise: quantifying patterns of Saltmarsh Sparrow (*Ammodramus caudacutus*) nest flooding under current sea-level conditions. — *The Auk* 128: 393–403. <https://doi.org/10.1525/auk.2011.10178>
- Betuel, A., Tuttle, E.M. & Gonser, R.A. 2014: Predation by a Sharp-shinned Hawk on a ground-nesting bird, the White-throated Sparrow. — *Wilson Journal of Ornithology* 126: 161–165. <https://doi.org/10.1676/13-094.1>
- Billerman, S.M., Keeney, B.K., Rodewald, P.G. & Schulenberg, T.S. (eds.) 2022. *Birds of the World*. — Cornell Lab of Ornithology, Ithaca, NY, USA.
- Bowers, E.K., Sakaluk, S.K. & Thompson, C.F. 2013: Sibling cooperation influences the age of nest leaving in an altricial bird. — *The American Naturalist* 181: 775–786. <https://doi.org/10.1086/670244>
- Brandis, K.J., Koeltzow, N., Ryall, S. & Ramp, D. 2014: Assessing the use of camera traps to measure reproductive success in Straw-necked Ibis breeding colonies. — *Australian Field Ornithology* 31: 99–106. <https://search.informit.org/doi/10.3316/informit.353309584632596>
- Chiavacci, S.J., Ward, M.P. & Benson, T.J. 2015: Why fledge early in the day? Examining the role of predation risk in explaining fledging behavior. — *Behavioural Ecology* 26: 593–600. <https://doi.org/10.1093/beheco/aru236>
- Cooney, C.R., Sheard, C., Clark, A.D., Healy, S.D., Liker, A., Street, S.E., Troisi, C.A., Thomas, G.H., Székely, T., Hemmings, N. & Wright, A.E. 2020: Ecology and allometry predict the evolution of avian developmental durations. — *Nature Communications* 11: 2383. <https://doi.org/10.1038/s41467-020-16257-x>
- Deeming, D.C. & Campion, E. 2018: Simulated rainfall reduces the insulative properties of bird nests. — *Acta Ornithologica* 53: 91–97. <https://doi.org/10.3161/00016454AO2018.53.1.009>
- Deeming, D.C., Dickinson, A.M., Broughton, R.E., Locke, E., Gray, L.A., Bennett, S.L., Gilchrist, R., Muniz, S., Goodman, A.M. & Biddle, L.E. 2020: Factors affecting thermal insulation of songbird nests as measured using temperature loggers. — *Physiological and Biochemical Zoology* 93: 488–504. <https://doi.org/10.1086/711959>
- Dunn, E.H. 1975: The timing of endothermy in the development of altricial birds. — *Condor* 77: 288–293.
- Fairhurst, G.D., Treen, G.D., Clark, R.G. & Bortolotti, G.R., 2012: Nestling corticosterone response to microclimate in an altricial bird. — *Canadian Journal of Zoology* 90: 1422–1430. <https://doi.org/10.1139/cjz-2012-0096>
- Gosler, A., Clement, P. & Christie, D.A. 2020: Great Tit (*Parus major*), version 1.0. — In Billerman, S.M., Keeney, B.K., Rodewald, P.G., Schulenberg, T.S. (Eds.), *Birds of the World*. Cornell Lab of Ornithology, Ithaca, NY, USA.
- Harnist, I., Dubiec, A. & Mazgajski, T.D. 2020: Changes of nest mass in relation to nesting stages in the Great Tit *Parus major*. — *Bird Study* 67: 292–299. <https://doi.org/10.1080/00063657.2020.1864283>
- Hartman, C.A. & Oring, L.W. 2006: An inexpensive method for remotely monitoring nest activity. — *Journal of Field Ornithology* 77: 418–424. <https://doi.org/10.1111/j.1557-9263.2006.00073.x>
- Hunter, E.A., Nibbelink, N.P. & Cooper, R.J. 2016: Threat predictability influences seaside sparrow nest site selection when facing trade-offs from predation and flooding. — *Animal Behaviour* 120: 135–142. <https://doi.org/10.1016/j.anbehav.2016.08.001>
- Iserbyt, A., Griffioen, M., Borremans, B., Eens, M. & Müller, W. 2018: How to quantify animal activity from radio-frequency identification (RFID) recordings. — *Ecology and Evolution* 8: 10166–10174. <https://doi.org/10.1002/ece3.4491>
- Jacobson, M.D., Tsakiris, E.T., Long, A.M. & Jensen, W.E. 2011: No evidence for observer effects on Lark Sparrow nest survival. — *Journal of Field Ornithology* 82: 184–192. <https://doi.org/10.1111/j.1557-9263.2011.00321.x>
- Johnson, L.S., Hebert, R.M., Napolillo, F.M. & Allen, A. 2013: The process of fledging in the Mountain Bluebird. — *Journal Field of Ornithology* 84: 367–376. <https://doi.org/10.1111/jof.12036>
- Johnson, L.S., Nguyen, A.V. & Connor, C.L. 2017: Do parents play a role in the timing and process of fledging by nestling Mountain Bluebirds? — *Journal of Field Ornithology* 88: 39–46. <https://doi.org/10.1111/jof.12174>
- Johnson, L.S., Rauch, R.L. & Dellone, S.N. 2004: The process and causes of fledging in a cavity-nesting

- passerine bird, the House Wren (*Troglodytes aedon*). — *Ethology* 110: 693–705. <https://doi.org/10.1111/j.1439-0310.2004.01001.x>
- Jones, T.M., Ward, M.P., Benson, T.J. & Brawn, J.D. 2017: Variation in nestling body condition and wing development predict cause-specific mortality in fledgling dickcissels. — *Journal of Avian Biology* 48: 439–447. <http://dx.doi.org/10.1111/jav.01143>
- Lemel, J. 1989: Body-mass dependent fledging order in the Great Tit. — *Auk* 106: 490–492.
- Major, R.E. 1990: The effect of human observers on the intensity of nest predation. — *Ibis* 132: 608–612. <https://doi.org/10.1111/j.1474-919X.1990.tb00285.x>
- Martin, T.E., Tobalske, B., Riordan, M.M., Case, S.B. & Dial, K.P. 2018: Age and performance at fledging are a cause and consequence of juvenile mortality between life stages. — *Science Advances* 4: eaar1988. <https://doi.org/10.1126/sciadv.aar1988>
- Maziarz, M., Broughton, R.K., Casacci, L.P., Dubiec, A., Maák, I. & Witek, M. 2020: Thermal ecosystem engineering by songbirds promotes a symbiotic relationship with ants. — *Scientific Reports* 10: 20330. <https://doi.org/10.1038/s41598-020-77360-z>
- Maziarz, M., Broughton, R.K. & Wesolowski, T. 2017: Microclimate in tree cavities and nest-boxes: Implications for hole-nesting birds. — *Forest Ecology and Management* 389: 306–313. <https://doi.org/10.1016/j.foreco.2017.01.001>
- McCarty, J.P. 2001: Variation in growth of nestling Tree Swallows across multiple temporal and spatial scales. — *The Auk* 118: 176–190. <https://doi.org/10.1093/auk/118.1.176>
- Merrill, L., Jones, T.M., Brawn, J.D. & Ward, M.P. 2021: Early-life patterns of growth are linked to levels of phenotypic trait covariance and postfledging mortality across avian species. — *Ecology and Evolution* 11: 15695–15707. <https://doi.org/10.1002/ece3.8231>
- Mertens, J.A.L. 1977: Thermal conditions for successful breeding in Great Tits (*Parus major* L.). — *Oecologia* 28: 1–29. <https://doi.org/10.1007/BF00346834>
- Michaud, T. & Leonard, M. 2000: The role of development, parental behavior, and nestmate competition in fledging of nestling Tree Swallows. — *Auk* 117: 996–1002. <https://doi.org/10.1093/auk/117.4.996>
- Moreno, J. 2020: Effects of food availability and parental risk taking on nestling period duration: a field experiment on the Pied Flycatcher *Ficedula hypoleuca*. — *Ardeola* 67: 29–38. <https://doi.org/10.13157/arla.67.1.2020.ra3>
- Moreno, J. 2022: Food supplementation of parents before hatching of the young prolongs the nestling period in European pied flycatchers (*Ficedula hypoleuca*). — *Ibis* 164: 1252–1256. <https://doi.org/10.1111/ibi.13074>
- Nord, A. & Nilsson, J.-Å. 2012: Context-dependent costs of incubation in the Pied Flycatcher. — *Animal Behaviour* 84: 427–436. <https://doi.org/10.1016/j.anbehav.2012.05.017>
- Pattinson, N.B., van de Ven, T.M.F.N., Finnie, M.J., Nupen, L.J., McKechnie, A.E. & Cunningham, S.J. 2022: Collapse of breeding success in desert-dwelling hornbills evident within a single decade. — *Frontiers in Ecology and Evolution* 10: 842264. <https://doi.org/10.3389/fevo.2022.842264>
- Pietz, Pamela J., Granfors, D.A. & Grant, T.A. 2012: Hatching and fledging times from grassland passerine nests. — In Ribic, C.A., Thompson III, F.R., Pietz, P. J. (Eds.), *Video Surveillance of Nesting Birds. Studies in Avian Biology*: 47–60. University of California Press, Berkeley, CA, USA.
- Podlas, K. & Richner, H. 2013: Partial incubation and its function in Great Tits (*Parus major*) – an experimental test. — *Behavioural Ecology* 24: 643–649. <https://doi.org/10.1093/beheco/ars224>
- Prinzinger, R., Preßmar, A. & Schleucher, E. 1991: Body temperature in birds. — *Comparative Biochemistry and Physiology Part A: Physiology* 99: 499–506. [https://doi.org/10.1016/0300-9629\(91\)90122-S](https://doi.org/10.1016/0300-9629(91)90122-S)
- Radersma, R., Komdeur, J. & Tinbergen, J.M. 2015: Early morning fledging improves recruitment in Great Tits *Parus major*. — *Ibis* 157: 351–355. <https://doi.org/10.1111/ibi.12230>
- Radersma, R., Tinbergen, J.M. & Komdeur, J. 2011: Do brood sex ratio, nestling development and sex affect fledging timing and order? An experimental study on Great Tits. — *Animal Behaviour* 81: 69–75. <https://doi.org/10.1016/j.anbehav.2010.09.007>
- Remeš, V. & Martin, T.E. 2002: Environmental influences on the evolution of growth and developmental rates in passerines. — *Evolution* 56: 2505–2518. <https://doi.org/10.1111/j.0014-3820.2002.tb00175.x>
- Ribic, C.A., Rugg, D.J., Koper, N., Ellison, K. & Ng, C.S. 2019: Behavior of adult and young grassland songbirds at fledging. — *Journal Field Ornithology* 90: 143–153. <https://doi.org/10.1111/jof.12289>
- Santema, P., Schlicht, L., Beck, K.B., Sheldon, B.C. & Kempenaers, B., 2021: Why do nestling birds fledge early in the day? — *Animal Behaviour* 174: 79–86. <https://doi.org/10.1016/j.anbehav.2021.01.026>
- Schlicht, L., Girg, A., Loës, P., Valcu, M. & Kempenaers, B. 2012: Male extrapair nestlings fledge first. — *Animal Behaviour* 83: 1335–1343. <https://doi.org/10.1016/j.anbehav.2012.02.021>
- Schöll, E.M., Aparisi, M.P. & Hille, S.M. 2020: Diurnal patterns of ambient temperature but not precipitation influence incubation behavior in Great Tits. — *Journal of Ornithology* 161: 529–538. <https://doi.org/10.1007/s10336-019-01737-9>
- Smith, J., Cooper, C. & Reynolds, S. 2015: Advances in techniques to study incubation. — In Deeming, D.C., Reynolds, S.J. (Eds.), *Nests, Eggs, and Incubation: New Ideas about Avian Reproduction*: 179–195. Oxford University Press, Oxford, UK.
- Smith, J.A. 2011: From nest building to life-history patterns: does food supplementation influence reproductive be-

- haviour of birds? (PhD dissertation). — University of Birmingham.
- Stodola, K.W., Buehler, D.A., Kim, D.H., Franzreb, K.E., Linder, E.T., 2010: Biotic and abiotic factors governing nestling-period length in the Ovenbird (*Seiurus aurocapilla*). — *Auk* 127: 204–211. <https://doi.org/10.1525/auk.2009.09151>
- Streby, H.M., Peterson, S.M., Lehman, J.A., Kramer, G.R., Iknayan, K.J. & Andersen, D.E. 2013: The effects of force-fledging and premature fledging on the survival of nestling songbirds. — *Ibis* 155: 616–620. <https://doi.org/10.1111/ibi.12051>
- Surmacki, A. & Podkova, P. 2022: An extreme type of brood overlapping in wild-living birds. — *European Zoology Journal* 89: 527–534. <https://doi.org/10.1080/24750263.2022.2058100>
- Sutti, F. & Strong, A.M. 2014: Temperature loggers decrease costs of determining bird nest survival. — *Wildlife Society Bulletin* 38: 831–836. <https://doi.org/10.1002/wsb.473>
- Taylor, J.A., 2015: Determinants of variation in productivity, adult survival and recruitment in a declining migrant bird: the Whinchat (*Saxicola rubetra*) (PhD dissertation). — Lancaster University.
- Verhulst, S. & Hut, R.A. 1996: Post-fledging care, multiple breeding and the costs of reproduction in the Great Tit. — *Animal Behaviour* 51: 957–966. <https://doi.org/10.1006/anbe.1996.0099>
- Verhulst, S., Tinbergen, J.M., 1997: Clutch size and parental effort in the Great Tit *Parus major*. — *Ardea* 85: 111–126.
- Weidinger, K. 2006: Validating the use of temperature data loggers to measure survival of songbird nests. — *Journal of Field Ornithology* 77: 357–364. <https://doi.org/10.1111/j.1557-9263.2006.00063.x>
- Weidinger, K. 2008: Nest monitoring does not increase nest predation in open-nesting songbirds: inference from continuous nest-survival data. — *Auk* 125: 859–868. <https://doi.org/10.1525/auk.2008.07016>
- Weintraub, K., George, T.L. & Dinsmore, S.J. 2016: Nest survival of Tricolored Blackbirds in California's Central Valley. — *Condor* 118: 850–861. <https://doi.org/10.1650/CONDOR-16-56.1>
- Wesołowski, T. & Rowiński, P. 2014: Do Blue Tits *Cyanistes caeruleus* synchronize reproduction with caterpillar peaks in a primeval forest? — *Bird Study* 61: 231–245. <https://doi.org/10.1080/00063657.2014.899307>
- Yoda, K., Shiozaki, T., Shirai, M., Matsumoto, S. & Yamamoto, M. 2017: Preparation for flight: pre-fledging exercise time is correlated with growth and fledging age in burrow-nesting seabirds. — *Journal of Avian Biology* 48: 881–886. <https://doi.org/10.1111/jav.01186>
- Zwaan, D.R. de, Camfield, A.F., MacDonald, E.C. & Martin, K. 2019: Variation in offspring development is driven more by weather and maternal condition than predation risk. — *Functional Ecology* 33: 447–456. <https://doi.org/10.1111/1365-2435.13273>

Brief report

Are Grey Plovers true Jelly Bon lovers? First record of Grey Plovers (*Pluvialis squatarola*) deliberately feeding on barrel jellyfish (*Rhizostoma pulmo*) in the Western Palearctic

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Coelenterates are not considered important food items for waders such as Grey Plovers (*Pluvialis squatarola*), although this has rarely been investigated in detail. During three days of fieldwork on the Bulgarian Black Sea coast in October 2020 Grey Plovers were documented deliberately choosing and swallowing barrel jellyfish *Rhizostoma pulmo* (Scyphozoa: Rhizostomatidae) while foraging on sand seashore where Scyphozoan jellyfish are often stranded. According to peer-reviewed literature, there is to-date no evidence of Grey Plovers consuming scyphozoan medusae, particularly as a specific choice for their food components. As a result of the present study, it is concluded that barrel jellyfish is part of the diet of Grey Plovers on the Black Sea coast and is purposely chosen by them. So far, this is the first video-recorded observation and published record of such an event in Europe and Western Palearctic. It suggests that coelenterates may be more important food items for waders than previously believed and shows the potential of medusae to become an important food alternative for them.

1. Introduction

The Grey Plover (*Pluvialis squatarola*, Linnaeus, 1758) is a cosmopolitan long-distance migratory bird. It visits the Bulgarian Black Sea coast mostly in spring, autumn and winter on the way to its African winter quarters and back to its Arctic breeding grounds (Michev & Profirov 2003, Nankinov *et al.* 2016). The world population of Grey Plovers shows a decreasing trend according to the IUCN Red List of Threatened Species

2019 (BirdLife International 2019). The species is protected by Bulgarian biodiversity legislation. In Bulgaria, Nankinov (1989) reported the species to be usually encountered singly or in gatherings of less than ten birds. However, gatherings of Grey Plovers of 421 and 344 birds were counted in November 1979 and November 1981 at Lake Atanasovsko (near Burgas Bay). The 1996–2002 assessment of the Grey Plover population in the Burgas wetland area yielded stable numbers, with an absolute maximum of

159 birds recorded in winter stages, including 149 at Lake Atanasovsko in January 1999 and 41 at Lake Pomorie in January 2001 (Dimitrov *et al.* 2005). Kostadinova & Gramatikov (2007) reported a wintering population in Bulgaria reaching 171 individuals.

Already in the 19th Century, Mackay (1892) described the Grey Plover primarily as a tideline bird, seeking a large proportion of its food on the extensive sand flats left by the receding waters which may be adjacent to marshes. Grey Plovers are known to feed on insects and other terrestrial invertebrates on their arctic tundra breeding grounds (Cramp & Simmons 1983). The species seems to be a generalist rather than a specialist on a particular prey type (Pienkowski 1982). The main foraging strategy of the Grey Plover is a visual inspection of the substrate, with running, stopping and pecking, as well as occasionally probing (Pienkowski 1982, Message & Taylor 2005). Outside the breeding season the main prey includes polychaetes, molluscs, and crustaceans along with small quantities of plant materials (Cramp & Simmons 1983). Poole *et al.* (2020) presented polychaetes and small bivalves as the favourite foods of the species, but also suggested that its diet is variable. They concluded that insects are the main prey at breeding grounds consisted of adult and larval Diptera (Tipulidae, Chironomidae, Culicidae), Coleoptera (Carabidae, Dytiscidae, Curculionidae), larval Lepidoptera (Tortricidae), Ephemeroptera, Trichoptera, and on rare occasions also Hemiptera, Hymenoptera, amphipods, isopods, and other freshwater crustaceans. On the other hand, polychaetes (especially slender worms), bivalves, and crustaceans were described as the main prey on wintering quarters, with diet variations depending on location and substrate (Poole *et al.* 2020).

Polychaetes, crustaceans and bivalves have been reported as the Grey Plover's most common prey during the non-breeding season in studies in Western Europe (Goss-Custard *et al.* 1977, Pienkowski 1982, Dit Durell & Kelly 1990, Moreira 1996, De Smet *et al.* 2013). Additionally, Perez-Hurtado *et al.* (1997) found Coleoptera remains in pellets collected in Spain.

In the Western Black Sea, Kirikova (2017) reported Grey Plovers intensively forage for ragworm (*Hediste diversicolor*) and lagoon sand

shrimp (*Gammarus insensibilis*) when their densities are high. Polychaetes, bivalves, gastropods, dipteran larvae, amphipods and isopods were determined to be the main prey for the Grey Plover in Sivash brackish lagoon, bordered by the Black and the Azov Seas (Verkuil *et al.* 1993).

Wader diet composition information from Bulgaria is still scarce (Nankinov *et al.* 2016). Prostov (1964) found remains of Coleoptera (Hydrophilidae), Mollusca and gastroliths in stomach contents of three Grey Plovers shot in the Burgas region. Nankinov *et al.* (2016) listed insects (adults and larvae), worms, molluscs, seeds, and small berries as part of the Grey Plover diet, but did not name specific taxa. Grey Plover has been found searching for food on sandy, muddy, or shell shores of both sea and inland bodies of water, being most frequently recorded on lakes near Burgas (Nankinov 1989).

Jellyfish and their coelenterate relatives are reported as part of the diet of multiple invertebrate and vertebrate species (Ates 1991, Arai 2005, Ates 2017, Hays *et al.* 2018). A recent review on the predation on pelagic coelenterates suggested that coelenterates may provide a source of energy comparable to better recognized prey such as arthropods (Arai 2005). Arai (2005) listed numerous vertebrate predators, such as fish, marine turtles, birds and mammals. From 23.5% (Short-tailed Shearwater *Puffinus tenuirostris*) to 27.27% (Fork-tailed Storm-petrel *Oceanodroma furcata*) to more than 42% (Northern Fulmar *Fulmarus glacialis*) in some bird species stomachs contented scyphozoan tissues, which is to be considered as a quite large extent. Harrison (1984) examined stomach contents of 17 marine bird species and found that 11 of them had eaten scyphozoan jellyfish.

There are several observations in the literature on various wader species feeding on coelenterates, for example Variable Oystercatchers (*Haemotopus unicolor*) and Pied Oystercatchers (*H. finschi*) feeding on Lion's Mane jellyfish (*Cyanea* spp.) (Melville 2013), and Sanderlings (*Calidris alba*) feeding on common jellyfish (*Aurelia aurita*, Linnaeus, 1758) in the Baltic Sea (Grimm 1984, Ates 1991). Multiple photographs of this wader species feeding on jellyfish were found on photo stocks (Ouwerkerk 2008, Cottele n.d., Ellington n.d.). Rock Sandpipers (*Calidris*

ptilocnemis) feeding on gonads of beached hydromedusae in Alaska (Gill *et al.* 2002), and Grey Plovers feeding on beached hydromedusae on the Alaskan Peninsula (Robinson 2016).

A more detailed literature search revealed that Fraser (1933) (mistakenly cited as 1939 in some publications) actually reported remains of *Sertularia pumila* (Cnidaria: Hydrozoa) found in Grey Plovers stomachs in Pine point, Maine, in September 1914. *Sertularia pumila* is part of Hydrozoan Class and its valid species name today is *Dynamena pumila*. As the phylum Cnidaria is made up of six different accepted classes: Hydrozoa (hydrozoans), Scyphozoa (scyphozoans), Anthozoa (anthozoans), Cubozoa (cubozoans), Myxozoa (Myxozoans) and Staurozoa (Staurozoans) (WoRMS Editorial Board 2022), Fraser's data were unfortunately wrongly interpreted in Melville's (2013) Short note as scyphozoan jellyfish (instead of hydrozoan) while citing Ates 1991 (Ates 1991, Melville 2013).

Visual observations and prey sampling from the littoral and supralittoral Western Black Sea

coast in 2019–2021 suggest that Grey Plovers feed mainly on amphipods and bivalves (*Donacilla cornea*) (unpublished data). However, the information provided in the present study is focused specifically on the scyphozoan jellyfish as food diet composition for this wader species, which can contribute to widen Grey Plover's diet composition knowledge. Further investigation into the annual and seasonal variation in the abundance of jellyfish washed up on the Black Sea beaches, and how that influences Grey Plover use of these beaches and their diet, would help quantify the importance of jellyfish as a dietary component and its importance as a resource for migratory waders visiting the Black Sea, such as the Grey Plover.

2. Material and methods

The study area (42°36'17.9"N 27°37'50.0"E, Fig. 1) is situated at the Pomorie sand shore between Lake Pomorie (or Pomoriysko Lake)



Fig. 1. The study area in relation to Europe and Bulgaria (Esri Topographic Basemap). Colour figure is available in the online version of the article at <https://doi.org/10.51812/of.12124>.

and the Black Sea. Lake Pomorie is a salt lagoon located at Burgas Bay, between the towns of Pomorie and Aheloy, about 25 km north-east from the town of Burgas. It covers a surface of 921.5 ha and is part of the Burgas lake complex (Kostadinova & Gramatikov 2007). An artificial dyke and natural sand dunes separate the lake and the salt pans from the sea.

Lake Pomorie is a Ramsar site of international importance since 2003 (code 3BG009), and a Corine site since 1998 (code F00007800), as well as an Important Bird Area in the BirdLife International system (code BG037) (Kostadinova & Gramatikov 2007). The wetland has a designated protected area status since 2001 and is part of the Bulgarian national ecological network Natura 2000 since 2007 (code BG0000620 under the Habitat Directive, and BG0000152 under the Birds Directive) (Natura 2000 protected areas 2022). The sand shore and the adjacent marine area are part of the protected site.

According to the Red Data Book of the Republic of Bulgaria (Biserkov *et al.* 2015) the natural habitats on the studied area are as follows: Pal. Class.: 44.8141 Pontic *Tamarix* stands; Pal. Class.: 16.2124 Pontic white dunes; Pal. Class.: 16.2113 Pontic embryonic dunes; Pal. Class.:

11.27 Soft sediment littoral communities, 14.1 Mud flats and sand flats.

Photographs and video material for this article were collected during three days in October 2020, during an autumn survey and data collection for a PhD project. Wader species were observed and video recorded since August 2019 on a larger scale to assess their time budget and diet composition during migration time (spring and autumn).

Two parallel transects were walked for the whole length of the sand shore at daylight: one on the dyke and the second one on the sand strip itself. Transect length is approximately seven to eight kilometres long.

Video data were recorded with a Canon PowerShot SX70 HS digital camera with 65x optical zoom and Full HD (1920 x 1080), 50 fps. A tripod was used for stability because of strong winds. Some of the events were photographed on a cell phone Lenovo Vibe Shot (Z90a40).

3. Results

Grey Plovers (*Pluvialis squatarola*) foraging on stranded barrel jellyfish (*Rhizostoma pulmo*, Macri, 1778) on the sand shore were observed



Fig. 2. The barrel jelly (*Rhizostoma pulmo*) stranded on the shore and already consumed by birds; smaller orange arrows indicate Grey Plover's footprints; larger green arrows indicate barrel jelly remains. Colour figure is available in the online version of the article at <https://doi.org/10.51812/of.12124>.

and filmed on three separate days (October 23, 26 and 28 in 2020).

The first observation on October 23 was on a single bird ripping apart washed ashore jellyfish remains. It was clearly seen that the bird was tearing apart fragments of the jellyfish remains (Fig. 2). The second observation was documented on October 26 when two plovers scavenged two separate freshly stranded jellies. On a separate video, one bird dismembers multiple times and washes the prey in the sea before swallowing it (Fig. 3). The third record was taken on October 28, when one of two birds dismembered and swallowed parts of different *Rhizostoma* specimens spread on the sand shore (Fig. 4).

Additional video material can be found as supplemental material. Eleven video clips demonstrating Grey Plovers feeding on barrel

jellyfish are deposited to Zenodo open repository (Vassileva 2023).

4. Discussion

Prey quality and availability is vital for bird survival. Hence, foraging behaviour and diet composition are of key importance for understanding the ecological role and trophic relations of birds. The multiple video-documented observations in the present study provide evidence that scyphozoan jellyfish *Rhizostoma pulmo* are deliberately chosen and taken by Grey Plovers as food items. Therefore, true jellies can be considered part of the diet of Grey Plovers on the Black Sea coast. This is the first report of proven consumption of



Fig. 3. Screenshots from video, depicting how a Grey Plover is feeding on barrel jellyfish. Colour figure is available in the online version of the article at <https://doi.org/10.51812/of.12124>.



Fig. 4. Specimens of barrel jellyfish partially eaten by a Grey Plover. Colour figure is available in the online version of the article at <https://doi.org/10.51812/of.12124>.

scyphozoan medusae by Grey Plovers in the Western Palearctic.

The Black Sea is known to have small insignificant daily level tidal fluctuations. Tidal range is between 4 cm and 9 cm (Valkanov & Rozhdestvenski 1978). Wind waves have their registered maximums in February, October and December (Grozdev 2006). Consequently, wind-tides and storms, caused by coastal winds, produce beach wrack on the drift line. The two species of the Black Sea scyphozoan jellyfish: the barrel and the common jellyfish (or moon jelly) *Aurelia aurita* (Linnaeus, 1758) are often part of the wrack (Valkanov & Marinov 1978, Zaitsev 2008). It is likely that this small tidal range may affect the abundance and availability of benthic invertebrate prey relative to other sites where Grey Plover diet has been studied. Further work is required to quantify prey availability at the Black Sea coasts and to compare their findings with data from other sites. This would enable us to understand whether the foraging on beached jellyfish is related to a potentially low abundance of other potential prey compared to other sites, or simply reflects opportunistic foraging on a novel unknown prey.

Knowledge of the distribution, phenology, life cycle and abundance of barrel jellyfish on a local and global scale, will aid in building hypotheses about its importance as a food resource for Grey Plovers and other similar wader species. The barrel jellyfish is distributed in the Mediterranean and the Black Sea from the Alboran Sea to Libya in the Mediterranean, east to Russia and north to Ukraine, the Black Sea (Göthel 1992, Palomares & Pauly 2022). Campbell (2004) stated far wider distribution of the species: the Mediterranean, the Atlantic, the North Sea and the West Baltic, providing that he considered *R. pulmo* same as *Rhizostoma octopus*. Additionally, the species was first recorded in Pakistani waters in 2008 (Muhammed & Sultana 2008).

The barrel jellyfish is considered the biggest bloom-forming jellyfish inhabiting southern European seas: the Mediterranean Sea, the Black Sea and the Sea of Marmara (Leoni *et al.* 2021). Leoni *et al.* (2021) provide evidence that bloom events are favoured by coastal eutrophication and climate warming, due to higher food abundance and enhanced reproduction rates. Over the long term, Leoni *et al.* (2021) expected that the

rising temperatures in the region will alter the timing of bloom events, promoting earlier and possibly massive blooms under high temperature regimes.

This study thus brings reason to believe that jellyfish as a growing sea resource will become an important food alternative for seastrand-feeding waders. More studies are needed in this direction. Given recently developed methods, such as stable isotope analysis, DNA metabarcoding and animal-borne cameras, assessing the jellyfish content and its nutritive importance in wader diet will provide valuable data for future ecological studies (Sato *et al.* 2015, Hays *et al.* 2018).

Herkuttelevatko tundrakurmitsat (*Pluvialis squatarola*) meduusoilla? Ensimmäinen havainto tundrakurmitsoista ruokailemassa tynnyrimeduusoilla (*Rhizostoma pulmo*) Länsi-Palearktisella alueella

Meduusoja ei tavallisesti pidetä tärkeänä ravintona kahlaajille, kuten esimerkiksi tundrakurmitsoille (*Pluvialis squatarola*). Ilmiötä ei ole kuitenkaan juuri tutkittu aiemmin. Lokakuussa 2020 havaitsin ja dokumentoin kolmena päivänä tundrakurmitsojen tietoisesti valitsevan ja käyttävän ravintonaan tynnyrimeduusaa (*Rhizostoma pulmo*). Tein havainnot Bulgarian Mustanmeren rannikolla, missä tundrakurmitsat etsivät ravintoa hiekkarannalta. Rannalle ajautuu usein Scyphozoa-luokkaan kuuluvia meduusoja (joihin myös tynnyrimeduusa kuuluu), esimerkiksi voimakkaiden tuulien seurauksena. Tutkimuskirjallisuudessa ei tähän päivään mennessä ole todisteita siitä, että tundrakurmitsat käyttäisivät tynnyrimeduusoja tarkoituksenmukaisesti ravintonaan. Mustanmeren rannikolla tehtyjen havaintojen perusteella kuitenkin päätellen, että tundrakurmitsat hyödyntävät niitä osana ravintonaan. Tietämykseni mukaan tämä on ensimmäinen Euroopassa ja Länsi-Palearktisella alueella videoitu ja julkaistu havainto. Tutkimuksen tulokset viittaavat siihen, että onteloeläimet voivat olla tärkeämpää ravintoa kahlaajille kuin aiemmin on uskottu, ja lisäksi tutkimus myös osoittaa meduusojen potentiaaloin osana kahlaajien ravintoa.

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References

- Arai, M. N. 2005: Predation on pelagic coelenterates: a review. — *Journal of the Marine Biological Association of the United Kingdom* 85(3): 523–536. <https://doi.org/10.1017/S0025315405011458>
- Ates, R. M. L. 1991: Predation on Cnidaria by vertebrates other than fishes. — *Coelenterate Biology: Recent Research on Cnidaria and Ctenophora* 216/217: 305–307. https://doi.org/10.1007/978-94-011-3240-4_44
- Ates, R. M. L. 2017: Benthic scavengers and predators of jellyfish, material for a review. — *Plankton and Benthos Research* 12(1): 71–77. <https://doi.org/10.3800/pbr.12.71>
- BirdLife International 2019: *Pluvialis squatarola*. — Available at: <https://www.iucnredlist.org/species/22693749/154513104#assessment-information>. Accessed 25 April 2021.
- Biserkov, V., Gushev, C., Popov, V., Hibaum, G., Roussakova, V., Pandurski, I., Uzunov, Y., Dimitrov, M., Tzonev, R. & Tsoneva, S. (eds.) 2015: Natural Habitats. — In *Red Data Book of the Republic of Bulgaria*: 458. BAS and MoEW, Sofia.
- Campbell, A. 2004: *Seashores and shallow seas of Britain and Europe*. — Bounty Books, London.
- Cottele, B. n.d.: Sanderling (*Calidris alba*) eating a jellyfish at the beach of Texel (The Netherlands). — Shutterstock. Available at: <https://www.shutterstock.com/image-photo/sanderling-calidris-alba-eating-jellyfish-beach-1845442180>. Accessed 23 October 2021.
- Cramp, S. & Simmons, K. E. L. (eds.) 1983: *The Birds of the*

- western Palearctic, Waders to gulls. — Oxford University Press, Oxford.
- De Smet, B., Godet, L., Fournier, J., Desroy, N., Jaffré, M., Vincx, M. & Rabaut, M. 2013: Feeding grounds for waders in the Bay of the Mont Saint-Michel (France): the *Lanice conchilega* reef serves as an oasis in the tidal flats. — *Marine Biology* 160(4): 751–761. <https://doi.org/10.1007/s00227-012-2130-3>
- Dimitrov, M., Michev, T., Profirov, L. & Nyagolov, K. 2005: Waterbirds of Bourgas Wetlands. Results and Evaluation of the Monthly Waterbird Monitoring 1996–2002. — Bulgarian Biodiversity Foundation and Pensoft Publishers, Sofia–Moscow.
- Dit Durell, S. E. A. L. V. & Kelly, C. P. 1990: Diets of Dunlin *Calidris alpina* and Grey Plover *Pluvialis squatarola* on the Wash as determined by dropping analysis. — *Bird Study* 37(1): 44–47. <https://doi.org/10.1080/0006359009477037>
- Ellington, K., n.d.: Sanderling eating a jellyfish on seashore — Dreamstime. Available at: <https://www.dreamstime.com/stock-photo-sanderling-bird-eating-jellyfish-beach-seashore-image63234506>. Accessed 23 October 2021.
- Fraser, C. M. 1933: Hydroids as a food supply. — *Proceedings and transactions of the Royal Society of Canada* 27(5): 259–264.
- Gill, R. E., Tomkovich, P. S. & McCaffery, B. J. 2002: Rock Sandpiper (*Calidris ptilocnemis*). — In *The birds of North America*. (eds. A. Poole & F. Gill): 686. The Academy of Natural Sciences, Philadelphia, and the American Ornithologists' Union, Washington DC. <http://dx.doi.org/10.2173/bna.686>
- Goss-Custard, J. D., Jones, R. E. & Newbery, P. E. 1977: The ecology of the Wash. I. Distribution and diet of wading birds (Charadrii). — *Journal of Applied Ecology*: 681–700. <https://doi.org/10.2307/2402803>
- Göthel, H. 1992: Guide de la faune sous-marine: La Méditerranée. Invertébrés marins et poissons. — Eygen Ulmer GmbH & Co.
- Grimm, P. 1984: Gonaden der Ohrenqualle (*Aurelia aurita*) als Nahrung des Sanderlings (*Calidris alba*). — *Seevögel* 5(2): 24. (In German)
- Grozdev, D. 2006: Wind wave climate along the Bulgarian Black Sea coast. — *s.l., s.n.*: 296–299. (In Bulgarian)
- Harrison, N. M. 1984: Predation on jellyfish and their associates by seabirds. — *Limnology and Oceanography*, 29(6): 1335–1337.
- Hays, G. C., Doyle, T. K. & Houghton, J. D. R. 2018: A paradigm shift in the trophic importance of jellyfish? — *Trends in Ecology & Evolution* 33(11): 874–884. <https://doi.org/10.1016/j.tree.2018.09.001>
- Kirikova, T. A. 2017: On the Diet and Foraging Strategy of Tundra Waders at Sivash. — *Vestnik zoologii* 51(6): 509–516. <http://dx.doi.org/10.1515/vzoo-2017-0061>
- Kostadinova, I. & Gramatikov, M. (eds.) 2007: Important Bird Areas in Bulgaria and Natura 2000. — Conservation Series. Bulgarian Society for the Protection of Birds, Sofia.
- Leoni, V., Bonnet, D., Ramírez-Romero, E. & Molinero, J. C. 2021: Biogeography and phenology of the jellyfish *Rhizostoma pulmo* (Cnidaria: Scyphozoa) in southern European seas. — *Global Ecology and Biogeography* 30(3): 622–639. <https://doi.org/10.1111/geb.13241>
- Mackay, G. H. 1892: Habits of the Black-Bellied Plover (*Charadrius squatarola*) in Massachusetts. — *The Auk*: 143–152.
- Melville, D. S. 2013: Variable (*Haematopus unicolor*) and Pied Oystercatchers (*H. finschi*) feeding on Lion's Mane jellyfish (*Cyanea* sp.). — *Notornis* 60: 309–310.
- Message, S. & Taylor, D. 2005: Waders of Europe, Asia and North America. — *Gardners Books*.
- Michev, T. & Profirov, L. 2003: Mid-winter Numbers of Waterbirds in Bulgaria (1977–2001): Results from 25 Years of Mid-winter Counts Carried Out at the Most Important Bulgarian Wetlands. — Pensoft.
- Moreira, F. 1996: Diet and feeding behaviour of Grey Plovers *Pluvialis squatarola* and Redshanks *Tringa totanus* in a southern European estuary. — *Ardeola* 43(2): 145–156.
- Muhammed, F. & Sultana, R. 2008: New record of edible jellyfish, *Rhizostoma pulmo* (Cnidaria: Scyphozoa: Rhizostomitidae) from Pakistani waters. — *Marine Biodiversity Records* 1: e67. <https://doi.org/10.1017/S1755267207007294>
- Nankinov, D. 1989: The status of waders in Bulgaria. — *Wader Study Group Bulletin* 56: 16–25.
- Nankinov, D., Ivanov, S. K., Dimitrov, N. & Popov, K. 2016: The Grey Plover *Pluvialis squatarola* in Bulgaria. — *Russian Journal of Ornithology* 25(1353): 4006–4013.
- Natura 2000 protected areas 2022: Natura 2000 protected areas. — Natura 2000, Information system for protected areas from the ecological network. Available at: <https://natura2000.egov.bg/EsriBg.Natura.Public.Web.App/Home/Natura2000ProtectedSites>. Accessed 11 November 2023.
- Ouwerkerk, A. 2008: High key first-winter with Jellyfish — Buiten-Beeld, Alamy Stock Photo. Available at: <https://www.alamy.com/stock-photo-high-key-first-winter-with-jellyfish-high-key-eerste-winter-met-kwal-29375178.html>. Accessed 23 October 2021.
- Palomares, M.L.D. & D. Pauly 2022: *Rhizostoma pulmo*, Barrel jellyfish (Macri, 1778) — SeaLifeBase, World Wide Web electronic publication, www.sealifebase.org, version (11/2023). Available at: <https://www.sealifebase.se/summary/Rhizostoma-pulmo.html>. Accessed 25 April 2022.
- Perez-Hurtado, A., Goss-Custard, J. D. & Garcia, F. 1997: The diet of wintering waders in Cádiz Bay, southwest Spain. — *Bird Study* 44(1): 45–52. <https://doi.org/10.1080/0006359709461037>
- Pienkowski, M. W. 1982: Diet and energy intake of Grey and Ringed Plovers, *Pluvialis squatarola* and *Charadrius hiaticula*, in the non-breeding season. — *Journal of*

- Zoology 197(4): 511–549. <https://doi.org/10.1111/jzo.1982.197.4.511>
- Poole, A. F., Pyle, P., Patten, M. A. & Paulson, D. 2020: Black-bellied Plover (*Pluvialis squatarola*), version 1.0. — In Birds of the World (ed. Billerman, S. M.). Cornell Lab of Ornithology, Ithaca, NY.
- Prostov, A. 1964: Study of the avifauna in Burgas region. — Proceedings of the Zoological Institute with Museum at BAS 15: 5–67. (In Bulgarian)
- Robinson, B. W. 2016: Black-bellied Plover (*Pluvialis squatarola*) Feeding on a Jellyfish — Ornithologi, A studio for bird study. Available at: <https://ornithologi.com/2016/10/01/black-bellied-plover-pluvialis-squatarola-feeding-on-a-jellyfish/>. Accessed 23 October 2021.
- Sato, N. N., Kokubun, N., Yamamoto, T., Watanuki, Y., Kitaysky, A. S., & Takahashi A. 2015: The jellyfish buffet: jellyfish enhance seabird foraging opportunities by concentrating prey. — Biology Letters 11(8): 20150358. <https://doi.org/10.1098/rsbl.2015.0358>
- Valkanov, A. & Rozhdestvenski, A. 1978: Hydrology and Hydrochemistry. — In The Black Sea: 66–68. Gueorgui Bakalov, Varna. (In Bulgarian with English summary)
- Valkanov, A. & Marinov, T. 1978: Invertebrata. — In The Black Sea: 108–124. Gueorgui Bakalov, Varna. (In Bulgarian with English summary)
- Vassileva, L. V. 2023: Supplemental material to the article 'Are Grey Plovers true Jelly Bon lovers? First record of Grey Plovers (*Pluvialis squatarola*) deliberately feeding on Barrel Jellyfish (*Rhizostoma pulmo*) in the Western Palearctic'. — Zenodo. <https://zenodo.org/doi/10.5281/zenodo.10363478>
- Verkuil, Y., Koolhaas, A. & Van Der Winden, J. 1993: Wind effects on prey availability: how northward migrating waders use brackish and hypersaline lagoons in the Sivash, Ukraine. — Netherlands Journal of Sea Research 31(4): 359–374. [https://doi.org/10.1016/0077-7579\(93\)90053-U](https://doi.org/10.1016/0077-7579(93)90053-U)
- WoRMS Editorial Board 2022: WoRMS taxon details: Cnidaria. — World Register of Marine Species, www.marinespecies.org at VLIZ. Available at: <https://www.marinespecies.org/aphia.php?p=taxdetails&id=1267>. Accessed 26 April 2022.
- Zaitsev, Y. 2008: An introduction to the Black Sea ecology. — Smil Editing and Publishing Agency Ltd., Odessa.

Online supplementary material

Supplementary material for this manuscript is deposited to Zenodo (<https://zenodo.org/doi/10.5281/zenodo.10363478>) and can be accessed through the online version of the article. The material includes eleven video clips demonstrating Grey Plovers feeding on barrel jellyfish.

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