Rozprawa doktorska

Biologia i ekologia rozrodu dzierlatki (*Galerida cristata)* w silnie przekształconym krajobrazie rolniczym

Breeding biology and ecology of the Crested Lark (*Galerida cristata)* in highly modified agricultural landscape

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Praca wykonana w Zakładzie Biologii i Ekologii Ptaków

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Poznań 2025

Podziękowania

Mojemu promotorowi prof. dr. hab. Jakubowi Z. Kosickiemu składam serdeczne podziękowania za poświęcony czas, opiekę merytoryczną, ogrom wsparcia i niegasnącą gotowość do pomocy na każdym etapie powstawania niniejszej rozprawy doktorskiej.

Dr Ewie Kosickiej dziękuję za pomoc przy przeprowadzaniu analiz związanych z determinacją płci piskląt.

Moim dzieciom: Dorocie, Ziemowitowi i Michałowi jestem wdzięczny, że zminimalizowali swoje wymagania wobec ojca w okresie jego zmagań z doktoratem.

W szczególności chciałbym podziękować mojej żonie Karolinie za okazane wsparcie, motywację i wiarę w moją osobę bez których przygotowanie tej rozprawy doktorskiej byłoby niemożliwe.

Spis treści

Streszczenie

Antropogeniczne przekształcenia środowiska należą do głównych przyczyn spadku liczebności i zasięgu występowania wielu gatunków ptaków. W zmieniających się warunkach niektóre z nich wykazują jednak dużą zdolność adaptacyjną, zmieniając swoje preferencje siedliskowe i zasiedlając nowe, sztucznie utworzone obszary. Przykładem takiego gatunku jest dzierlatka (*Galerida cristata*) - ptak z rodziny skowronkowatych (Alaudidae), który pierwotnie zasiedlał otwarte tereny stepowe i półpustynne, natomiast w wyniku ekspansji skolonizował szerokie spektrum siedlisk powstałych w wyniku działalności człowieka. Jednym z typów takich siedlisk są przydrożne tereny otwarte, powstałe wraz z budową dróg szybkiego ruchu, takich jak autostrady i drogi ekspresowe. Mimo rosnącego znaczenia tych środowisk, wiedza o funkcjonowaniu populacji dzierlatki w tego rodzaju habitatach pozostaje ograniczona, co uzasadnia potrzebę szczegółowych badań.

Celem rozprawy doktorskiej było scharakteryzowanie biologii i ekologii lęgowej nominatywnego podgatunku dzierlatki (*Galerida cristata cristata*) w siedliskach przydrożnych. Badania terenowe prowadzono w latach 2018–2022 wzdłuż obwodnicy Inowrocławia (centralna Polska), przebiegającej w rolniczym krajobrazie Kujaw. Analizowano lokalizację gniazd, szczegółowe parametry rozrodu (wymiary jaj, wielkość zniesienia i lęgu, sukces klucia i sukces lęgowy, liczba piskląt opuszczających gniazdo), a także stosunkowo słabo poznane aspekty biologii tego gatunku, takie jak przeżywalność lęgów oraz czynniki wpływające na przetrwanie gniazd. Dodatkowo badano wzorzec wzrostu piskląt oraz zmienne wpływające na tempo ich rozwoju.

Wyniki wykazały, że dzierlatki w badanej populacji zakładały gniazda najczęściej w przydrożnych terenach trawiastych, w niewielkiej odległości od krawędzi jezdni. Zaobserwowano wyraźną tendencję do orientowania wejścia do gniazda w kierunku północno-wschodnim. W warunkach centralnej Polski sezon lęgowy trwał od trzeciej dekady marca do drugiej dekady sierpnia. Sukces lęgowy w badanej populacji wyniósł 43,1%. Stwierdzono również, że prawdopodobieństwo przeżycia lęgu było ponad dwukrotnie wyższe na etapie jaj niż na etapie piskląt. Głównymi czynnikami wpływającymi na przeżywalność lęgów były: termin rozpoczęcia lęgu, temperatura powietrza oraz odległość gniazda od drogi. Lęgi rozpoczęte później w sezonie oraz zlokalizowane dalej od krawędzi jezdni miały wyraźnie większe szanse na zakończenie się sukcesem.

Wzorzec wzrostu piskląt wykazał, że podobnie jak u innych skowronków, młode dzierlatki charakteryzowały się szybkim tempem wzrostu. Od momentu wyklucia do dziewiątego dnia życia masa ciała piskląt zwiększała się dziesięciokrotnie, a długość skoku osiągała wartości porównywalne z dorosłymi osobnikami. Płeć nie miała istotnego wpływu na większość analizowanych parametrów wzrostu. Tempo wzrostu piskląt było jednak istotnie zależne od liczebności rodzeństwa - większe zniesienia wiązały się z większą konkurencją wewnątrz lęgową, co mogło wpływać na rozwój poszczególnych osobników.

Podsumowując, tereny przydrożne powstałe w wyniku budowy dróg szybkiego ruchu mogą stanowić ważne siedliska lęgowe dla dzierlatki w silnie przekształconym krajobrazie rolniczym. Uzyskane wyniki poszerzają wiedzę na temat biologii lęgowej tego gatunku i mogą mieć praktyczne zastosowanie w monitoringu liczebności oraz produktywności populacji, badaniach porównawczych na szeroką skalę, a także w planowaniu działań ochronnych tego gatunku, szczególnie w kontekście siedlisk antropogenicznych.

Słowa kluczowe: dzierlatka, *Galerida cristata*, biologia lęgowa, tereny przydrożne, przeżywalność gniazd, tempo wzrostu piskląt

Summary

Anthropogenic environmental changes are among the main causes of decline in the abundance and distribution of many bird species. However, some bird species demonstrate significant adaptability to changing conditions, altering their habitat preferences and inhabiting new, artificially created areas. An example of such a species is the Crested Lark (*Galerida cristata*), a bird of the Alaudidae family that originally inhabited open steppe and semi-desert areas, but has expanded to colonize a wide range of habitats created by human activity. One types of habitat are open roadside areas, created due to construction of motorways and expressways. Despite the growing importance of these environments, knowledge about the functioning of Crested Lark populations in these habitats remains limited, justifying the need for detailed research.

The aim of this doctoral dissertation was to characterize the breeding biology and ecology of the nominate subspecies of the Crested Lark (*Galerida cristata cristata*) in roadside habitats. Fieldwork was conducted between 2018 and 2022 along the Inowrocław bypass road (central Poland), which runs through the agricultural landscape of the Kuyavia region. The study analysed nest location, detailed reproductive parameters (e.g. egg dimensions, clutch and brood size, hatching and breeding success, and number of fledglings), as well as lesser-known aspects of the species' biology such as brood survival and factors affecting nest survival. Additionally, nestling growth patterns and variables influencing their development rate were examined.

The results showed that Crested Lark in studied population most often built nests in grassy roadsides, close to the road edge. Nest entrances orientation showed a clear north-east bias. In central Poland, the breeding season lasted from the third decade of March to the second decade of August. Breeding success in the studied population was 43.1%. It was also found that the nest survival rate in the egg stage was twice as high as in the nestling stage. Time of breeding, air temperature, and the distance from the road were the main factors that affected nest survival. Clutches initiated later in the season and located farther from the road edge had a significantly greater chance of success.

The growth pattern showed that, like other larks, that Crested Lark nestlings were characterized by a rapid growth rate. By day 9, their body weight had increased tenfold, and they had almost reached their final tarsus length. Sex had no significant effect on most of the analysed growth parameters. However, nestlings growth rate was significantly affected by brood size – larger clutches were associated with greater intra-brood competition, which could have influenced individual development.

In summary, roadside habitats created by the construction of expressways, may constitute an important breeding habitat for Crested Larks in heavily transformed agricultural landscapes. These results expand our knowledge of the breeding biology of this species and may have practical applications in monitoring of productivity and population size, conducting large-scale comparative studies, and planning conservation measures for this species, particularly in the context of anthropogenic habitats.

Key words: Crested Lark, *Galerida cristata*, breeding biology, roadsides, nest survival, nestling growth rate

1. Wstęp

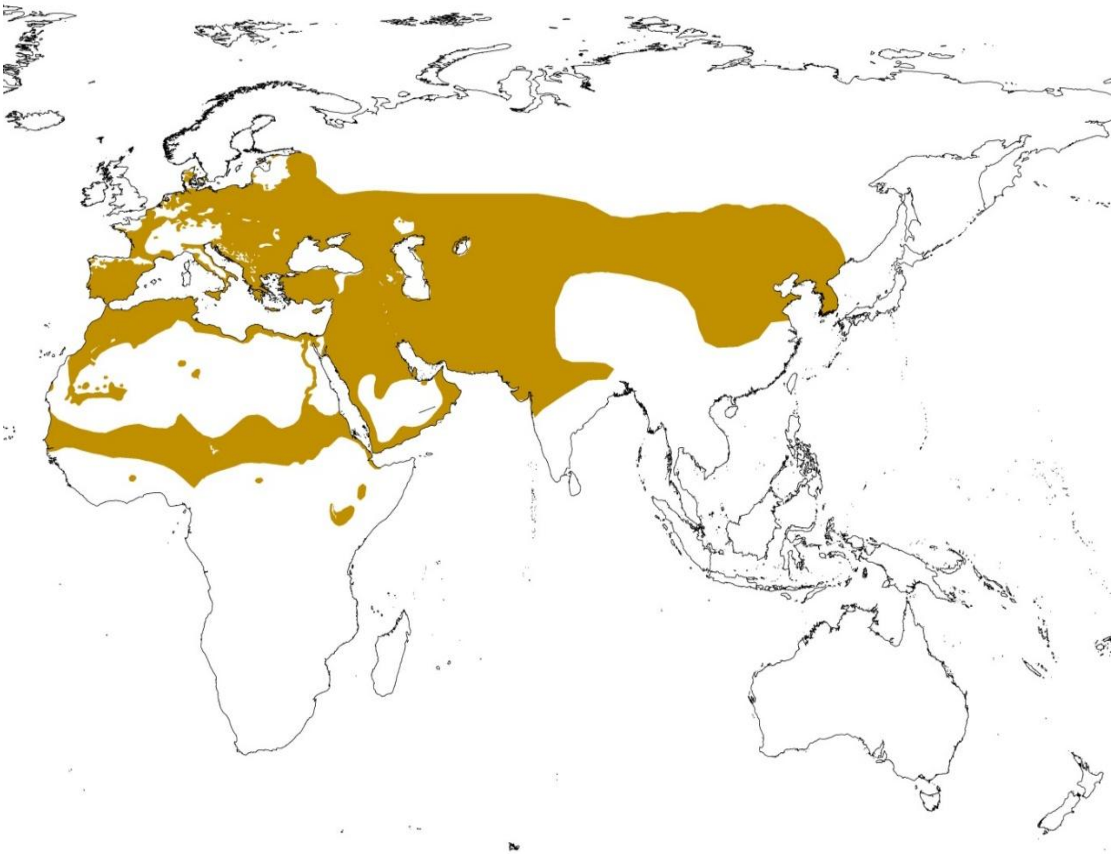
Dzierlatka (zwyczajna) (*Galerida cristata*) to niewielki ptak o długości ciała wynoszącej 17–19 cm i masie 35–50 g (de Juana et al. 2022). Gatunek ten cechuje długi i spiczasty czub na głowie, dość długi dziób oraz stosunkowo krótkie, szerokie i zaokrąglone skrzydła. Upierzenie w odcieniach piaskowo-brązowych pełni funkcję maskującą, ułatwiającą kamuflaż w środowisku naturalnym (Roselaar1988) (ryc. 1). Dymorfizm płciowy dzierlatek jest słabo zaznaczony i przejawia się głównie w nieco większej masie ciała oraz długości skrzydła u samców (Svensson 1992, Demongin 2016). Dzierlatka jest gatunkiem socjalnie monogamicznym (Roselaar 1988).

Ryc. 1 Dzierlatka *Galerida c. cristata* – a) śpiewający samiec, b) gniazdo z jajami, c) pisklęta w wieku ok. 9 dni (fot. R. Sandecki).

Omawiany gatunek należy do rodziny skowronkowatych Alaudidae, która obecnie obejmuje 100 gatunków (Alström et al. 2023). Jest jednym z sześciu przedstawicieli rodzaju Galerida (Alstrom et al. 2023) i obok dzierlatki iberyjskiej *Galerida theklae* — jedynym występującym w Europie. Pozostałe gatunki z tego rodzaju to endemity Afryki: dzierlatka rdzawa *Galerida modesta* i dzierlatka wielkodzioba

Galerida magnirostris, oraz endemity Półwyspu Indyjskiego: dzierlatka dekańska *Galerida deva* i dzierlatka malabarska *Galerida malabarica* (de Juana et al. 2004).

Dzierlatka występuje w niemal całej Europie, z wyjątkiem Islandii, Wielkiej Brytanii, krajów bałtyckich oraz Skandynawii (ryc. 2). W Azji zasięg gatunku rozciąga się od Turcji, poprzez Półwysep Arabski, Iran, północne Indie aż po północno-wschodnie Chiny i Półwysep Koreański. Populacja afrykańska skoncentrowana jest głównie w północnej części kontynentu oraz w rejonie Sahelu (Guillaumet et al. 2006, Shirihai i Svensson 2018, ryc. 2). Gatunek jest osiadły na większości obszaru swojego występowania (de Juana i in. 2004). W obrębie tak szerokiego zasięgu wyróżniono ponad 60 podgatunków, które charakteryzują się dużą zmiennością ubarwienia upierzenia (de Juana et al. 2022). Zróżnicowanie to wynika z przystosowania do lokalnych typów gleby, co zwiększa skuteczność kamuflażu (Guillaumet et al. 2005).

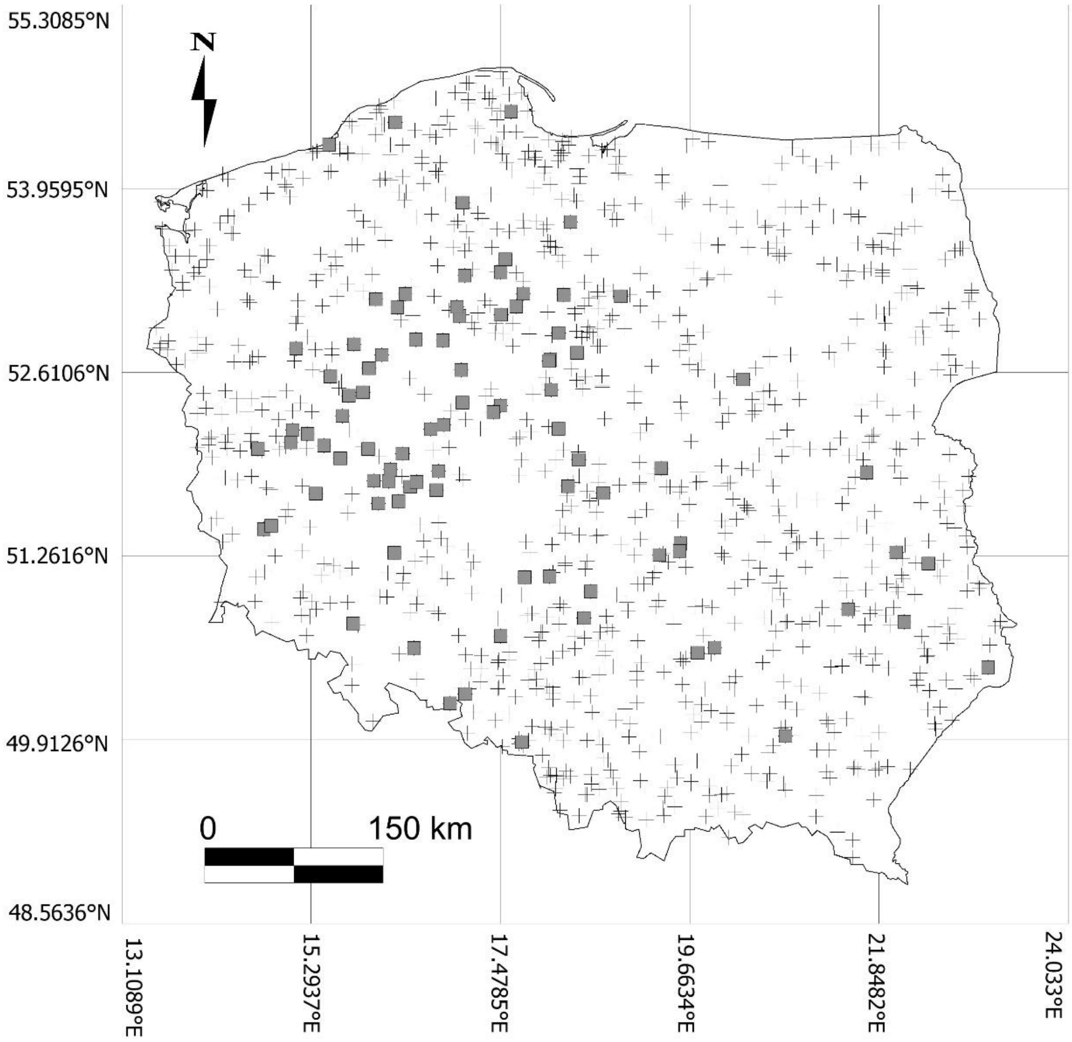


Ryc. 2. Rozmieszczenie dzierlatki na świecie (na podstawie danych z BirdLife International 2020, mapę wykonano w Qgis.3.40.8).

Podobnie jak inni przedstawiciele rodziny skowronkowatych dzierlatka zwyczajna pierwotnie gniazdowała w strefie obszarów półpustynnych i stepowych (Garcia-Navas et al. 2024). Gatunek ten preferuje tereny otwarte, suche, pozbawione drzew, gęstych skupisk krzewów oraz bujnej roślinności zielnej (de Juana et al. 2004). W wyniku rozszerzania zasięgu, dzierlatka zaadaptowała się również do szerokiego spektrum otwartych siedlisk antropogenicznych, charakteryzujących się roślinnością na wczesnym etapie sukcesji. Należą do nich nowo powstające osiedla mieszkaniowe, żwirownie, lotniska, place budów czy tereny przydrożne (Roselaar 1988).

Zgodnie z klasyfikacją IUCN, dzierlatka uznawana jest za gatunek najmniejszej troski (kategoria LC), a całkowitą liczebność populacji w Europie szacuje się na 17 100 000–23 800 000 par lęgowych (BirdLife International 2023). Od końca XX w. w niemal całym europejskim zasięgu gatunku odnotowano spadkowy trend liczebności (PECBMS 2018, Birdlife International 2023). Spadki te, najprawdopodobniej związane z utratą i degradacją siedlisk, były szczególnie silne w Europie Środkowej i Północnej. Doprowadziło to do całkowitego wycofania się gatunku z Holandii, Danii, Szwecji oraz krajów nadbałtyckich (Keller et al. 2020).

W Polsce dzierlatka występuje nierównomiernie (ryc. 3). Najliczniejsze lokalne populacje stwierdzono w centralnej i zachodniej części kraju, przede wszystkim w Wielkopolsce i na Kujawach, podczas gdy w pozostałych regionach Polski gatunek ten jest bardzo rzadki lub nieobecny (Chylarecki et al. 2018).



Ryc 3. Rozmieszczenie dzierlatki w Polsce na podstawie danych MPPL z lat 2000 – 2022. Miejsca stwierdzeń dzierlatki (szare kwadraty, n = 88) na tle wszystkich kontrolowanych powierzchni (plusy, n=1078, mapę wykonano w Qgis.3.40.8).

Dotychczasowe próby oszacowania wielkości populacji dzierlatki w Polsce klasyfikowały ten gatunek jako nieliczny lub bardzo nieliczny ptak lęgowy (Tucker & Heath 1994, Kuźniak & Tryjanowski 2007, Chodkiewicz et al. 2015). Najnowsze dane dotyczące oceny liczebności dzierlatki w samej tylko Wielkopolsce (32 800 par, Wylęgała et al. 2022) są dziesięciokrotnie wyższe dla tego regionu niż ostatnia ocena dla całego kraju (2 500–3 500 par, Chodkiewicz et al. 2015), co jednoznacznie wskazuje na wcześniejsze znaczne niedoszacowanie oraz konieczność rewizji statusu gatunku w Polsce – z nielicznego na średnio liczny. Zgodnie z wynikami Monitoringu Pospolitych Ptaków Lęgowych (2000–2024) po wcześniejszym okresie spadków liczebności (2000-2004, λ^{1}=0.8315, Chylarecki i in. 2006), populacja dzierlatki wykazuje silny wzrost (2013-2024, λ =1.1238, Chodkiewicz i Wardecki 2024). Zjawisko to może być związane zarówno z postępującymi zmianami klimatycznymi, takimi jak wzrost średnich temperatur i okresowe susze (IMGW-PIB 2023), które sprzyjają gatunkom preferującym suche, otwarte siedliska, jak i z kolonizacją nowych typów siedlisk antropogenicznych – np. terenów przydrożnych nowo budowanych dróg szybkiego ruchu (Wylęgała et al. 2009; Sandecki, dane niepublikowane) czy też obszarów w pobliżu dużych ferm drobiu (Rzępała & Szczypiński 2020). Intensywny rozwój sieci autostrad i dróg ekspresowych w Polsce w ostatnich latach (Koziarski 2018), w połączeniu ze zdolnością dzierlatki do adaptacji do siedlisk antropogenicznych, może sprawić, że tereny przydrożne staną się ważnym siedliskiem lęgowym tego gatunku w kraju. W związku z tym zasadne jest podjęcie badań mających na celu szczegółowe scharakteryzowanie parametrów biologii lęgowej dzierlatki oraz identyfikację mechanizmów i strategii rozrodczych, które warunkują sukces lęgowy populacji funkcjonującej w tym nowym typie siedliska.

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[1] λ (lambda) to wskaźnik przyrostu liczebności populacji, wyrażający stosunek liczby osobników w danym roku do liczby osobników w roku poprzednim; wartości $\lambda > 1$ wskazują na wzrost populacji, $\lambda < 1$ – na spadek (Sutherland, W.J. (1996). Ecological Census Techniques: A Handbook. Cambridge University Press).

2. Cele badawcze

Celem niniejszej rozprawy doktorskiej jest opisanie biologii i ekologii lęgowej nominatywnego podgatunku dzierlatki *Galerida cristata cristata* w siedliskach przydrożnych, powstałych w wyniku budowy drogi szybkiego ruchu w krajobrazie rolniczym Kujaw. Ze względu na wielowątkowy charakter badań, rozprawę podzielono na trzy samodzielne rozdziały oraz ogólny wstęp. Każdy rozdział opracowano niezależnie, tj. zawiera osobny wstęp, materiały i metody, wyniki, dyskusję oraz spis literatury, a także indywidualną numerację rycin i tabel.

W **rozdziale 1**[2] szczegółowo opisano parametry rozrodu oraz scharakteryzowano ekologię lęgową dzierlatki. Choć podstawowe aspekty biologii lęgowej tego gatunku są stosunkowo dobrze udokumentowane, dane te pochodzą głównie z populacji zasiedlających obszary zurbanizowane Europy Środkowej, z których dzierlatka obecnie niemal całkowicie się wycofała (Witsack 1968, Krueger 1977, 2000, Misiuna 2005, Lesiński 2009, Praus 2020, Martin et al. 2025). Brakuje tym samym szczegółowych danych dotyczących rozrodu w innych typach siedlisk oraz w różnych częściach szerokiego zasięgu gatunku. Parametry takie jak termin przystępowania do rozrodu, wielkość zniesienia, liczba piskląt czy przeżywalność potomstwa mogą wykazywać zmienność przestrzenną (Maag et al. 2022), a także różnić się w zależności od cech siedliska (Clark i Shutler 1999). Ich poznanie jest kluczowe dla zrozumienia jak gatunki adaptują się do zróżnicowanych warunków środowiskowych, reakcji na zmiany środowiskowe, a także dla wyjaśnienia dynamiki populacyjnej i regionalnych trendów liczebności. Jak dotąd brak jest badań koncentrujących się na biologii i ekologii rozrodu dzierlatki w nowo utworzonych siedliskach liniowych związanych z infrastrukturą drogową (np. autostrad i dróg ekspresowych), które w ostatnich latach były chętnie

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[2] Numeracja odpowiada kolejności poszczególnych rozdziałów/manuskryptów

kolonizowane przez ten gatunek (Wylęgała et al. 2009; Sandecki, dane niepublikowane). Istnieje więc pilna potrzeba uzupełnienia tej luki badawczej.

W **rozdziale 2** oszacowano prawdopodobieństwo przeżywalności lęgów dzierlatki oraz przeanalizowano czynniki mogące wpływać na przetrwanie gniazda i końcowy sukces lęgowy. Ptaki z rodziny skowronkowatych Alaudidae budują gniazda na ziemi, zazwyczaj na terenach otwartych, wśród skąpej roślinności trawiastej (de Juana et al. 2022), co czyni ich lęgi podatnymi na silną presję drapieżniczą (Yanes i Onate 1996; Praus et al. 2014), niekorzystne warunki atmosferyczne (Wright et al. 2009; Martin et al. 2017), a w siedliskach antropogenicznych także na bezpośrednie oddziaływanie człowieka (Lesiński 2009; Martin et al. 2025). W efekcie, sukces lęgowy często nie przekracza 20–30% (Suarez i Manrique 1992; Praus i Weidinger 2010; Mwangi et al. 2018). Przeżywalność gniazd ma bezpośredni wpływ na sukces rozrodczy i może znacząco różnić się w zależności od fazy lęgu (Mitrus i Soćko 2008; Goławski et al. 2023). Dlatego oszacowanie przeżywalności na poszczególnych etapach (jaja, pisklęta) oraz identyfikacja krytycznego momentu lęgu, w którym ryzyko strat jest największe, może znacząco poszerzyć wiedzę na temat ograniczeń sukcesu lęgowego w danym siedlisku i mieć istotne znaczenie dla projektowania skutecznych strategii ochrony gatunku (Zaremba et al. 2020). Dotychczasowa wiedza na temat przeżywalności lęgów dzierlatki oraz czynników ją determinujących w różnych typach siedlisk jest bardzo ograniczona, a temat ten nie został dotąd dostatecznie zbadany (Skhedy i Safriel 1992; Praus 2020).

W **rozdziale 3** określono wzorzec rozwoju piskląt dzierlatki oraz przeanalizowano czynniki wpływające na tempo ich wzrostu. Dynamika wzrostu może różnić się w zależności od warunków środowiskowych, takich jak dostępność pokarmu, temperatura, opady atmosferyczne czy jakość siedlisk, a także od czynników biologicznych, takich jak wielkość lęgu, konkurencja wewnątrz lęgowa oraz strategie rodzicielskie (Ricklefs 1979; Richner 1991). Gatunki o szerokim zasięgu geograficznym, takie jak dzierlatka, często wykazują wysoką zmienność w zakresie wzrostu piskląt, będącą wynikiem lokalnych adaptacji do odmiennych warunków ekologicznych (Ndithia et al. 2017; Sofaer et al. 2018). Pisklęta skowronkowatych zaliczane są do gniazdowników właściwych (Roselaar 1988). Ich rozwój postnatalny odbywa się w jednym z najszybszych możliwych temp u ptaków (de Juana et al. 2004), co umożliwia opuszczenie gniazda już w wieku 7–8 dni po wykluciu (Donald 2004). Tak krótki czas przebywania piskląt w gnieździe, w połączeniu z wysokimi stratami lęgowymi, znacząco utrudnia prowadzenie badań nad tempem ich wzrostu. Zarówno sam wzorzec rozwoju, jak i czynniki wpływające na wzrost piskląt dzierlatki, pozostają jednym z najsłabiej poznanych aspektów jej biologii lęgowej. Jedyna dotąd opublikowana analiza tego zagadnienia, oparta wyłącznie na pomiarze masy ciała piskląt, została przeprowadzona w siedliskach pustynnych (Skhedy i Safriel 1992), co znacznie ogranicza możliwość szerszych porównań ekologicznych.

Populacja zasiedlająca tereny przydrożne obwodnicy Inowrocławia stanowi zatem dogodny model badawczy pozwalający na uchwycenie funkcjonowania gatunku na wczesnym etapie kolonizacji nowego, antropogenicznego siedliska. Jednocześnie umożliwia porównania z wynikami uzyskanymi dla populacji dzierlatki zasiedlających inne typy środowisk, zwłaszcza zurbanizowane.

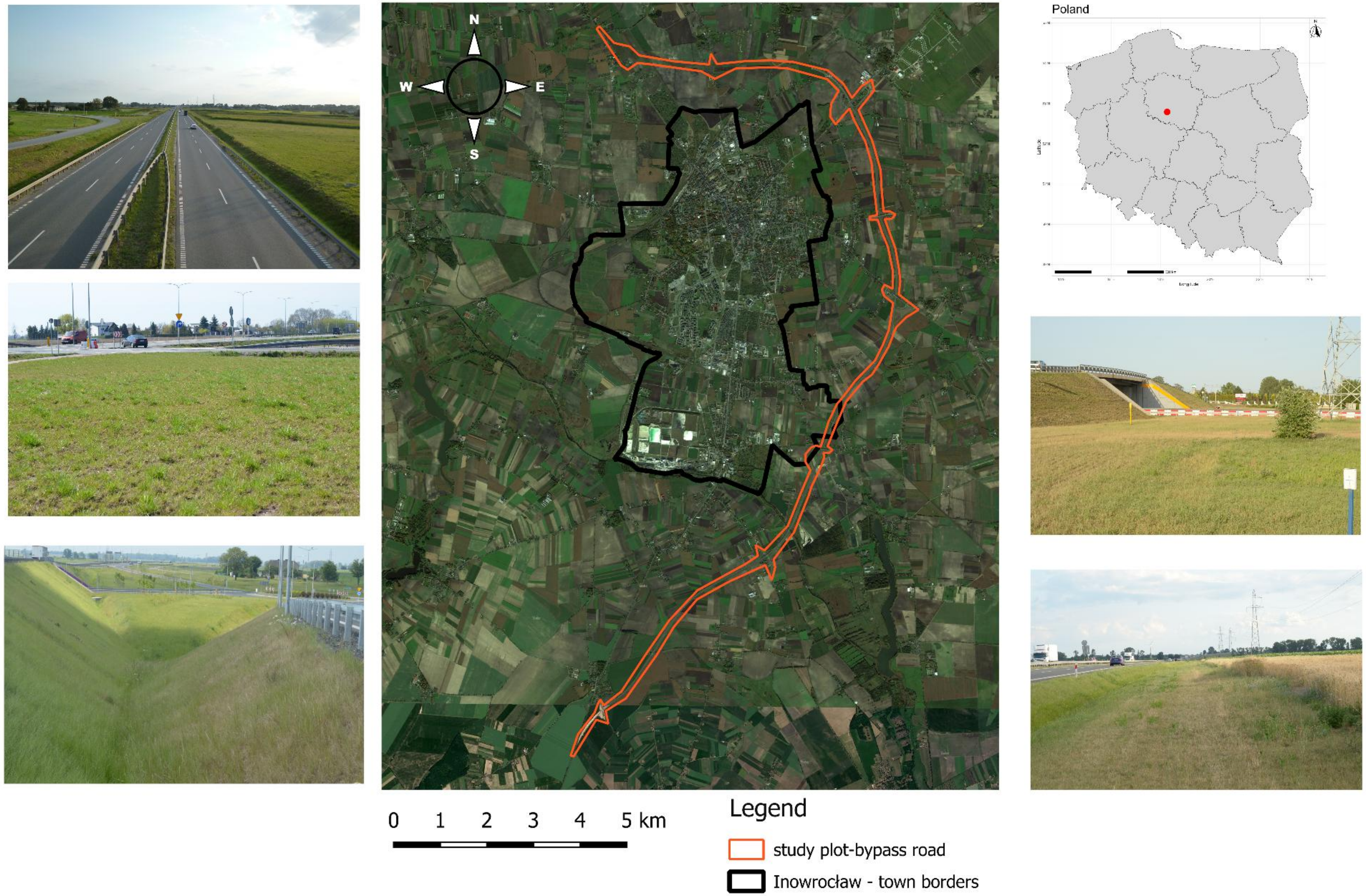
3. Teren badań

Badania prowadzono w sezonie lęgowym (marzec-sierpień) w latach 2018-2022 na terenach powstałych wraz z budową obwodnicy Inowrocławia, stanowiącej odcinek drogi krajowej nr 25 (52°46’55N, 18°18’36E, ryc. 4). Siedlisko to kształtowało się w latach 2014-2019, a ekspansja dzierlatki na te tereny rozpoczęła się już na etapie budowy infrastruktury drogowej. Osobniki kolonizujące nowo powstały habitat, pochodziły prawdopodobnie z pobliskich populacji zasiedlających okoliczny krajobraz rolniczy (Sandecki, dane niepublikowane).

Dominującym elementem przestrzennym nowo utworzonego siedliska antropogenicznego jest dwujezdniowa, dwupasmowa droga szybkiego ruchu wraz z towarzyszącą jej infrastrukturą tj. drogami dojazdowymi, wiaduktami, mostami, węzłami drogowymi, rondami, rowami odwadniającymi oraz niewielkimi zbiornikami retencyjnymi. Bezpośrednie otoczenie drogi tworzy pas drogowy obejmujący głównie obszary porośnięte trawami z rodzaju *Poace* sp., z domieszką roślinności segetalnej i ruderalnej, a także z pasowymi nasadzeniami krzewów i drzew o zróżnicowanym składzie gatunkowym. Pas ten ma szerokość od kilku do kilkudziesięciu metrów i ciągnie się wzdłuż drogi głównej oraz dróg serwisowych na odcinku około 25 km. Podobny charakter ma roślinność porastająca struktury towarzyszące, takie jak nasypy i zbocza wiaduktów, zjazdy, ronda czy rowy odwadniające. Powierzchnie trawiaste są koszone corocznie, z różną częstotliwością w okresie wegetacyjnym. Cała infrastruktura drogowa otoczona jest agrocenozami o zróżnicowanej strukturze upraw, wśród której dominują: pszenica *Triticum aestivum*, rzepak *Brassica napus*, kukurydza *Zea mays* oraz buraki cukrowe *Beta vulgaris*. Całkowity obszar powierzchni na której prowadzono badania liczy 4.6 km^2.

W ujęciu fizycznogeograficznym według Kondrackiego (2009) teren badań położony jest w obrębie makroregionu Pojezierza Wielkopolsko-Kujawskiego (315.5), na granicy dwóch regionów: Równiny Inowrocławskiej (315.55) oraz Pojezierza Gnieźnieńskiego (315.54). Obszar ten ma charakter równinny a wysokości nad poziom morza mieszczą się w granicach 80-100 n.p.m. Małe nachylenie terenu oraz słaby drenaż naturalny sprzyjały nadmiernemu uwilgoceniu gleb, co doprowadziło do wykształcenia się w okolicach Inowrocławia czarnych ziem bagiennych o właściwościach zbliżonych do czarnoziemów stepowych (Olszewski et al. 1962). Wysoka żyzność gleb sprawiła, że region ten ma charakter wybitnie rolniczy, z niskim wskaźnikiem lesistości wynoszącym zaledwie 10% w powiecie inowrocławskim (Helińska i Witkowska 2021).

Obszar Kujaw na którym zlokalizowany jest teren badań, charakteryzuje się przeciętnie cieplejszym i suchszym klimatem w porównaniu do innych regionów Polski. Średnia roczna temperatura powietrza w okresie 1851–2000 wynosiła +8,1°C (Bąk 2003). Ze względu na fakt położenia w tzw. cieniu opadowym wzniesień pojeziernych, roczne sumy opadów należą tu do najniższych w Polsce i często nie przekraczają 500 mm (Kondracki 2009).



Ryc. 4 Teren badań – tereny przydrożne obwodnicy Inowrocławia

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4. Breeding biology and ecology of the Crested Lark (*Galerida cristata)* along expressway road in a homogenized agricultural landscape

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Abstract

The study investigates breeding biology and ecology of the Crested Lark *Galerida cristata* population along verges of a newly built bypass expressway in central Poland. During five consecutive breeding seasons we monitored nests, recorded their placement, time of breeding, analysed egg traits and reproductive output using standard nest checks, circular statistics and mixed-effects models. We found that breeding season lasted from the end of March to the mid-August. Crested Larks placed most of their nests on flat, grassy ground close to the road edge, but also on slopes and ditch banks. Nest entrances orientation showed a clear north-east bias. About 43% of the studied broods turned out to be successful. Egg dimensions were similar to values known for nominate subspecies, with a modest intra-annual variation between years and a high variation within-nest consistency. Environmental predictors explained little variation in clutch size or brood size. Models of fledglings per attempt suggested habitat effects near road edges. Our results indicate that open habitats created by expressway infrastructure can support Crested Larks that breed on homogenised farmland. Targeted road verge management, e.g. adjusted mowing regimes, retention of low, open swards, and safer drainage design may contribute to maintaining structural conditions that meet the species' preferences.

Key words: Crested Lark, *Galerida cristata*, breeding biology, nest location, anthropogenic habitat, roadsides

1. Introduction

Long-term declines in the distributions and abundances of many bird species are linked to habitat loss and degradation (Newton 2013). Road development is among major drivers of such changes, typically exerting negative effects via habitat conversion and fragmentation (Kociolek et al. 2011), disturbance (Forman & Alexander 1998), noise (Kaseloo & Tyson 2004), collision mortality (Erritzoe et al. 2003), and barrier effects (van der Ree et al. 2007). Conversely, roads and associated structures, e.g. bridges, marginal vegetation, lighting, powerlines, windbreaks can also create opportunities for some species (Morelli et al. 2014), including foraging habitats (Kmetová et al. 2012), dispersal corridors (Deckers et al. 2005; Coffin 2007), thermal benefits (Whitford 1985), reduced predation in specific contexts (Yamaç & Kirazlı 2012), and increased habitat heterogeneity (Helldin & Seiler 2003). Several avian guilds, including raptors, farmland birds, and ground-nesters, use components of road infrastructure such as bridges (Bell et al. 1996; Temple 1988), electricity poles (Meyburg et al. 1996; Vepsäläinen et al. 2005; Tryjanowski et al. 2013), and road verge vegetation (Laursen 1981; Li et al. 2010; Morelli et al. 2013) for their nesting sites, sometimes with equal or greater reproductive output than in wilder sites (Chace & Walsh 2006).

The Crested Lark *Galerida cristata* is a ground-nesting, multi-brooded Alauddiae with a vast range across Eurasia and North Africa (>60 subspecies; de Juana et al. 2022). Originally associated with warm sparsely vegetated steppe and semi-desert, it now exploits early-successional human-altered habitats, including railway yards, airfields, road verges, harbours, gravel pits, refuse dumps, urban/industrial wastelands, and open farmland (Roselaar 1988; BirdLife International 2023).

In Europe, the breeding population of the Crested Lark is large as it is estimated to be from at 17.1 to 23.8 million pairs (BirdLife International 2023), however, continent-wide monitoring indicates an overall decline since early 1980s (PECBMS 2018; BirdLife

International 2023). The decline in numbers has been most pronounced in central and northern Europe, culminating in national extirpations from the Netherlands, Denmark, Sweden, Estonia and Lithuania (Keller et al. 2020). In Poland, the species is unevenly distributed, with strongholds in central and western lowlands (Greater Poland, Kuyavia), but rare or absent elsewhere (Chylarecki et al. 2018). Notably, national Common Breeding Bird Survey data indicate a moderate increase over 2000–2024, plausibly linked to recent colonisation of novel linear anthropogenic habitats, particularly verges of newly constructed motorways and expressways (Wylęgała et al. 2009; Sandecki unpubl.). These contrasting patterns, i.e. regional declines versus local increases in transport-infrastructure landscapes, underscore the need to understand how Crested Larks use, and perform within, expressway verges of homogenised agricultural regions.

Despite species broad range, detailed reproductive data remain patchy. Studies on breeding biology of the Crested Lark have focused on urbanised or rural settings in central Europe (Germany: Witsack 1968; Krüger 1977; Martin et al. 2025; Czechia: Praus 2020; Poland: Lesiński 2009). Some aspects of reproduction were also reported from France (Labitte 1957), Hungary (Orbán 2004), North Africa (Heim de Balsac & Mayaud 1962) and south-western Asia (Hartley 1946; Belskaya 1974; Shkedy & Safriel 1992). However, key breeding parameters i.e. timing of breeding, clutch size, brood size and offspring survival can vary substantially across the species' range (Maag et al. 2022) and along habitat gradients (Clark & Shutler 1999). Identifying these variations is crucial for comprehending how the species adapts to diverse environments and responds to environmental changes, ultimately may help explain population dynamics and regional trends. In fact, no study has examined the breeding biology of the Crested Lark in newly created linear transport habitats, such as motorways and expressways, although in Poland these habitats have been rapidly colonised by Crested Lark in recent years. We therefore present a five-year dataset from central Poland quantifying nest-site characteristics, time of breeding, clutch and egg traits, brood size, fledging output, causes of failure and overall breeding success for a population colonising expressway verges embedded in a homogenised agricultural landscape. This data allows us to evaluate whether reproductive performance in transport-infrastructure verges aligns with or departs from patterns known from urban and rural settings.

The study aims to: (i) describe breeding phenology and reproductive output of the Crested Lark (clutch size, hatching success, brood size, fledglings per nest); (ii) characterise nest-site selection and spatial structure; (iii) describe egg morphology and its variation; (iv) identify major nest failures; and finally (v) test how breeding output is effected by breeding timing, nest location, surrounding structure, nest-entrance orientation, and distance to the nearest road.

2. Material and methods

Study Area

The study area of 4.6 km^2 is located near Inowrocław (52°46’55N, 18°18’36E), a town in Kujawsko-Pomorskie Province, located in central Poland. This is a lowland region with elevation between 80 and 100 m a.s.l. and mean annual temperature of about 8.2°C. It is situated in the so called “rain shadow” characterised by the lowest sum of annual precipitation in Poland below 500 mm. (Kondracki 2009, Bąk 2003). The studied population occupies newly established habitats that were created due to a road built between 2014 and 2019. The core of the study plot comprises the main two-lane carriageway and its adjacent structures i.e. access roads, viaducts, bridges, roundabouts, road junctions, draining ditches and retention basins. The immediate surroundings include roadsides covered by grasses with an admixture of segetal and ruderal vegetation and sparsely planted shrubs and trees with a diverse species structure. This type of habitat runs along the main road for a distance of 25.1 km. Along its entire length, the road infrastructure is surrounded by agrocenoses with a diverse crop structure dominated by wheat *Triticum aestivum*, rapeseed *Brassica napus*, maize *Zea mays* and sugar beet *Beta vulgaris*. The boundaries of the study area were established at a distance of 50 meters from the road infrastructure on each side. The entire study area is characterised by constant anthropogenic disturbance, such as the passage of vehicles, runners, walkers with unleashed dogs, and cultivation field works. Additionally, the grassy areas are mown annually with varying frequency during the vegetation period.

Bird data

The study was conducted over five breeding seasons (2018–2022). Nest searches began in mid-March with the onset of the breeding season and continued until mid-August, when last chicks left the nests. Nests were located mainly by a systematic search of the study plot and observations of birds' behaviour which indicated the presence of a brood i.e. when carrying nest material or food for nestlings. After locating a nest, we recorded its position with a handheld GPS receiver. Nest location was classified by (i) terrain/landform type: (1) flat, (2) slope/road embankment, (3) ditch bank, (4) other; and (ii) surrounding vegetation/structure: (A) grass-covered roundabout islands/road junctions, (B) grassy roadsides between the main road and fields or access roads, (C) wheat, (D) rapeseed, (E) maize, (F) oat, (G) green bean, and (H) other. Furthermore we also measured the shortest distance from the nest to the nearest road edge with a tape measure with precision 0.1 m.

Nests were monitored every 2 to 4 days. During each visit we recorded clutch size, brood size, and nest fate (fledged, depredated, abandoned). From 2020 onwards, we measured the orientation of the nest entrance relative to the magnetic north. Nest orientation was defined as the angle bisecting the entrance to the nest and we used a handheld compass. A nest entrance is a section of the nest bowl without typical protective vegetation structure through which incubating birds leave and return (Hartman & Oring 2003) (Fig. 1).

Fig. 1 Determining nest entrance

Clutch size was defined as the number of eggs in a nest that did not change during two consecutive visits. If a nest was found during the chick stage, clutch size was determined by adding the number of unhatched eggs to the number of chicks.

A breeding attempt was defined as a nest with at least one laid egg. For each such nest, we calculated hatching success, i.e. percentage of eggs hatched out of the laid eggs, and breeding success which was expressed as the percentage of nests that fledged at least one fledgling (Bougaham 2021).

First-egg dates were determined either directly for nests found before or during laying, or - when nests were found later-by back-calculation from the hatching date or chick developmental stage, assuming a 12-day incubation period (Roselaar 1998; own data). If hatching or fledging occurred between two visits, we used the midpoint date between the visit immediately before and after that event. The length (l) and breadth (w) of eggs were measured with callipers to 0.1 mm.

Broods were considered successful if at least one fledgling left the nest or if the oldest chick reached 9 days – an age at which chicks are large enough to leave the nest under predator attack or observer disturbance (Roselaar 1988; de Juana 2004; Sandecki unpublished data). Next, failures were assigned to one of the following categories: Predation (torn nest material or remnants of eggs/chicks/adults, or a monitored nest found empty before the expected hatching or fledging date), desertion (all eggs failed to hatch or chicks found dead), human activity (nest trampled/destroyed by mowing or field works), weather events (nest contents flooded or chicks found dead following long-term/heavy rainfall), and other, e.g. infertile eggs. Additionally, we monitored 17 nests using camera traps to identify nest predators. Nestlings were ringed with metal and coloured alphanumeric rings. We did not identify the sequence of breeding attempts of particular pairs during a season i.e. first, replacement, or later broods. During the five-year study we obtained data from 162 nests.

Statistical analysis

All analyses were carried out in R (version 4.3.3; R Core Team 2023). Firstly, we tested distributions of all variables using the Shapiro-Wilk test. Because many variables were not distributed normally, we used non-parametric tests where appropriate. Descriptive statistics are given as mean ± SD for approximately symmetric variables, and as median ± median absolute deviation (MAD) for not normal distributed variables.

To compare nest placement between years, we used χ^2 tests for categorical data (terrain/landform type and surrounding vegetation/structure). We compared distances (e.g. nest-road distance, distance to the nearest-neighbour) and timing variables (first egg dates, fledging dates) between years using Kruskal–Wallis tests. Annual differences in nest density were also assessed with χ^2 tests. To describe spatial patterns of nests, we calculated the Clark-Evans aggregation index (R; values <1 indicate clustering, >1 regularity, Clark and Evans 1954, Donnelly 1978) and summarised it by year to evaluate whether the overall pattern changed through time.

Nest-entrance orientation is an angular variable, so we analysed it with circular statistics (circular package for R, Agostinelli & Lund, 2017). We report the mean direction, circular standard deviation and concentration (ρ), and used Rayleigh's test of uniformity to assess whether nest-entrance orientations were uniformly distributed or showed a preferred (non-random) direction. A significant Rayleigh result indicates that orientations are clustered around a mean bearing (unimodal), rather than randomly distributed from 0 to 359°.

To test whether egg dimensions differed between years, we fitted separate linear mixed models (LMMs) for egg length, breadth and volume, with the year as a fixed effect and nest ID as a random effect (random intercept) using lme4::lmer (Bates et al., 2015). The random effect controls for consistent differences between nests (e.g. parental quality or microhabitat), ensuring that any among-year effects are not masked by nest-level variation. We fitted models with the REML and obtained p-values for fixed effects via Satterthwaite's method (lmerTest, Kuznetsova et al., 2017).

In reporting, we provided an overall F-test for the effect of year in the format F with df_1, df_2, where df1 is the numerator degrees of freedom (number of year levels − 1) and df_2 is the Satterthwaite-approximated denominator degrees of freedom, reflecting the effective sample size after accounting for random effects. When presenting specific between-year differences e.g. 2021 vs 2018, we used one-hot coding with 2018 as the reference level; coefficients are reported as the estimated mean difference (estimate ± SE), with the corresponding t-value and p-value from the lmerTest (a negative estimate indicates a smaller mean in given year than in 2018). To quantify the magnitude of among-nest variation captured by the random effect, we reported the standard deviation (SD) of the nest-ID random intercept. This SD is the square root of the estimated variance component and expresses how much egg measurements vary between nests after accounting for fixed effects. For completeness, we also report marginal and conditional R^2 (MuMIn, Bartoń, 2023), describing variance explained by fixed effects alone and by the full model (fixed + random effects), respectively.

To check whether egg dimensions varied with clutch size, we fitted additional LMMs with clutch size as a fixed predictor, keeping nest ID as a random intercept and reporting effects as described above.

Within-clutch variation was quantified as the coefficient of variation ($CV = SD/mean \times 100$) for each trait; differences in CV among traits were tested with a Friedman ANOVA with nest ID as the repeated-measures factor.

Repeatability (the proportion of variance between nests relative to total variance) of each egg trait was estimated with the rptR (rptGaussian, Stoffel et al., 2017), using nest ID as a random effect and 1000 bootstrap replicates to obtain 95% confidence intervals, following Lessells & Boag (1987) and Falconer & Mackay (1996).

Differences between years in proportions, i.e. hatching success and breeding success were tested with χ^2 tests. Differences between years in brood size (number of nestlings) and in fledglings per nest were tested with Kruskal–Wallis tests.

Finally, to identify which ecological factors were linked to reproductive output, we fitted generalised linear mixed-effects models (GLMMs) with the Poisson error distribution and the log link (lme4::glmer) for three count responses: (1) clutch size (eggs per nest), (2) number of hatchlings, and (3) number of fledglings. We chose Poisson GLMMs because our dependents' variables are counts and because the log link ensures non-negative predictions. Each model used the same fixed effects, i.e. timing of breeding (Julian day of first egg), nest location type (four terrain/landform levels: flat, slope/embankment, ditch bank, other), surrounding vegetation/structure (up to eight classes: roundabout/junction grass, verge grass, wheat, rapeseed, maize, oat, green bean, other), nest-entrance orientation (degrees), and distance to the nearest road (metres). The year was used as a random intercept to account for unmeasured annual differences. We assessed model dispersion using the Pearson-based dispersion parameter φ (ratio of residual variance to that expected under Poisson): Values close to 1 indicate an adequate Poisson, fit $\varphi > 1$ indicates over-dispersion (more variability than expected), whereas $\varphi < 1$ indicates under-dispersion (less variability than expected). The significance of fixed effects was evaluated with Type III Wald χ^2 tests (car::Anova, Fox & Weisberg, 2019). Full model outputs (estimates, standard errors, z-values and p-values) are provided in the Appendix (A).

3. Results

Nest location

Most nests were located on flat terrain (type 1, 119 out of 160 nests), followed by road embankments or slopes (type 2, 25 nests), and ditch banks (type 3, 15 nests), with only one nest found in another landform type (type 4), (Fig. 2). As to the surrounding vegetation structure, nests were predominantly situated in grassy areas between the main road and adjacent fields or access roads (type B, 67 nests) and on grass covered roundabout islands/road junctions (type A, 65 nests). Farmland habitats of wheat (type C), rapeseed (type D), maize (type E), oats (type F), green bean (type G) and retention-basin bottoms (type H) were used less frequently (Fig. 3). The distribution of nests among terrain/landform types did not differ between years ($\chi^2 = 7.33$, df = 12, $p = 0.834$). By contrast, the distribution amid surrounding vegetation/structure categories did vary between years ($\chi^2 = 44.69$, df = 28, $p = 0.023$), suggesting temporal changes of habitat use.

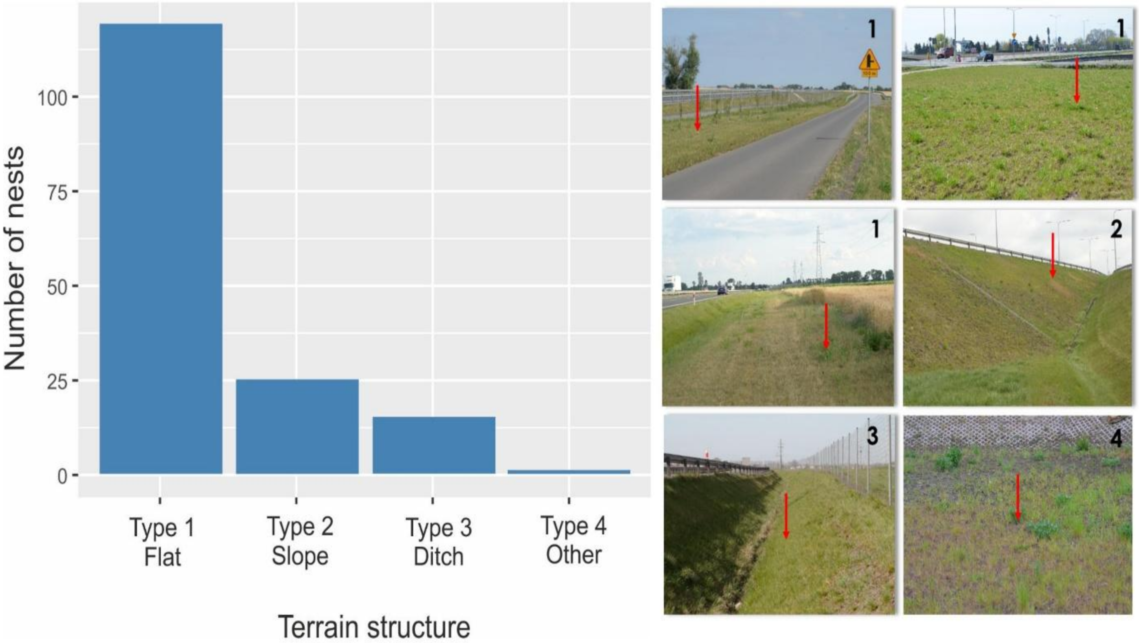

Fig. 2 Main types of terrain/landform used by Crested Lark as a nest location. Top left to bottom right as indicated: 1- flat, 2- slope, 3-ditch, 4 – other (bottom of retention basin). Nest positions arrowed.

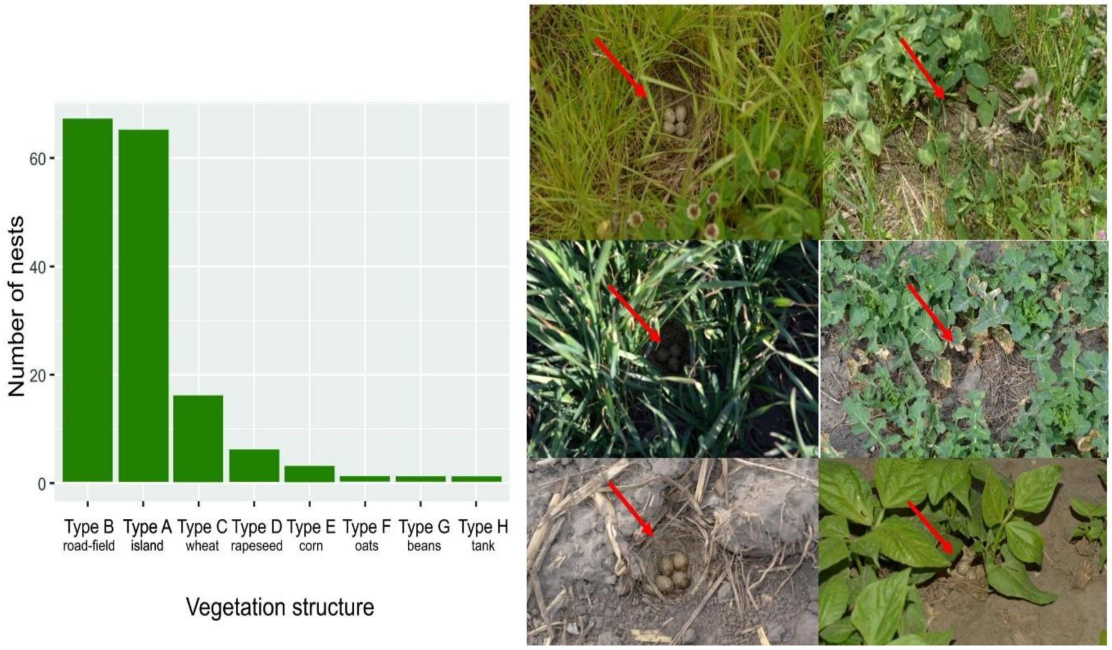

Fig. 3 Vegetation structure used as nesting locations by Crested Lark in the Inowrocław by-pass road. Top left to bottom right as indicated: grasses *Poaceae* sp., clover *Trifolium* sp., Common wheat *Triticum aestivum*, Rapeseed *Brassica napus*, Corn *Zea mays*, Common bean *Phaseolus vulgaris*. Nest positions arrowed.

The mean (± SD) distance from nests to the nearest road edge was 13.5 ± 12.48 m (range 0.50–56.0 m; n = 160; Fig. 4), with almost 60% of nests located within 15 m from the road edge. There were no significant between-year differences in the nest–road distance (Kruskal–Wallis $\chi^2 = 3.27$, df = 4, $p = 0.513$).

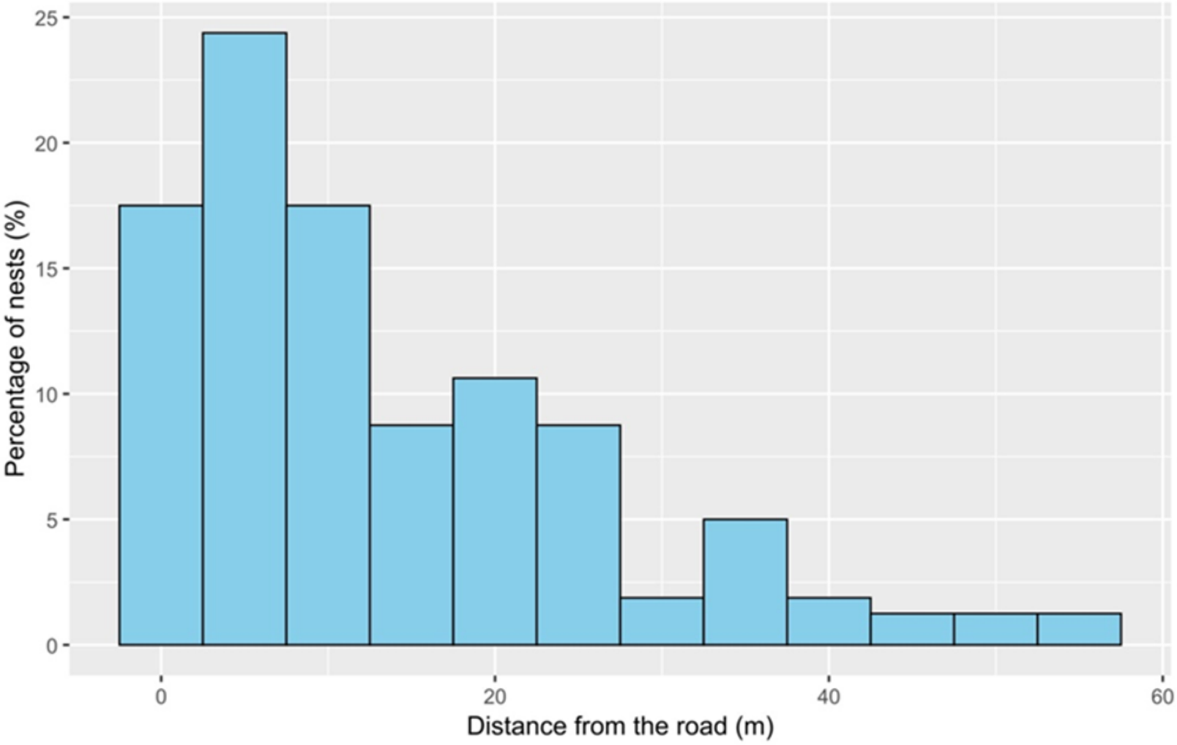

Fig. 4 Distribution of the Crested Lark nests in relation to the nearest road edge

Nest density, clustering, distance among nests and nest entrance orientation

The mean density of nests was 7.01 (95% CI: 4.58 – 9.53) per 1 km^2 and varied from 4.38 in 2018 to 9.42 in 2020 (Table 1), with no significant differences between years ($\chi^2 = 2.17$, df = 4, $p = 0.703$). The shortest distance between two simultaneously active nests was 7.8 m, but it was one polygynous case during our study where two females were paired with one male. So, the minimum distance between active nests of two different pairs was 16.7 m. To characterise nest spacing over the entire study period, for each nest we computed the Euclidean distance to the another geographically nearest nest recorded at any time in given breeding season. The mean distance was 246.0 m (95% CI: 142.9 – 349.1) and the median 65.1 m (MAD = 10.0), with no significant between-year differences (Kruskal–Wallis $\chi^2 = 5.14$, df = 4, p = 0.272; Table 1).

The mean (± SD) Clark and Evans aggregation index across the study area was 0.037 ± 0.018 (n = 160), indicating a clustered distribution of nests (Fig. 5) There were no significant differences in nest distribution between years ($\chi^2 = 0.038$, df = 4, p = 0.999, Table 1).

Fig. 5 Examples of nests distribution on selected road junctions.

The mean (±SD) nest-entrance orientations was 23.69°±0.79° (northeast direction, n = 107 (years: 2020 - 2022) and the highest number of nests, i.e. 65, was concentrated between 0° and 90°, i.e. from north to east (Fig. 6). The concentration parameter ($\rho = 0.72$) indicated a moderate clustering around the mean direction and Rayleigh's test rejected hypothesis on the random distribution of nest-entrance ($Z = 0.726$, $p < 0.0001$).

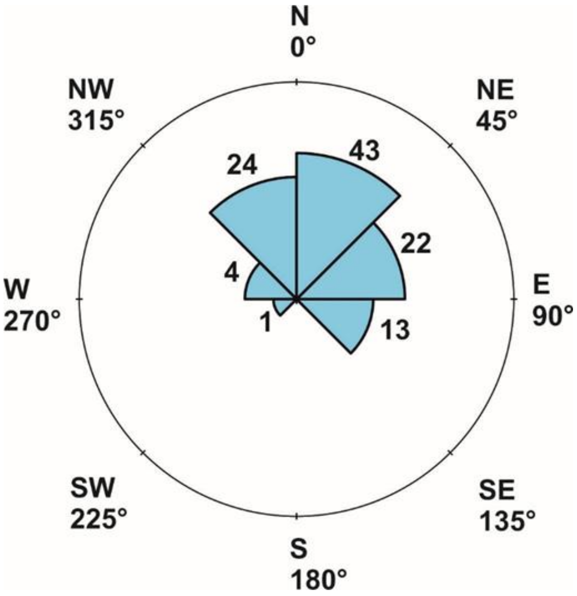

Fig. 6 Distribution of the orientation of nest entrances.

Time of breeding

In the studied population, Crested Larks started to breed, i.e. laid eggs in their first brood attempt, in the 3rd decade of March. The earliest clutch was initiated on March 22 and the latest on July 16 (median±MAD = 126±40.0, 6 May, n = 139, Table 1), and they did not differ significantly between years (Kruskal-Wallis test: $\chi^2 = 0.445$, p = 0.976, n = 139). In turn, fledging dates ranged from April 17 to August 11 (median±MAD = 149±38.5, 29 May, n = 71, Table 1) and also did not show significant differences between years (Kruskal-Wallis test: $\chi^2 = 2.07$, df = 4, p = 0.722, n = 71). The breeding phenology had two distinctive peaks: The first one at the beginning of April and the second one at the beginning of May (Fig. 7). The total length of the breeding season i.e. the time between laying of the first egg in the earliest nest and the latest inspection of the nest with chicks, was 143 days.

On the basis of observations of an individually marked female, we established that during a long breeding season, birds are capable of raising 3 successful broods.

In 2021 individual broods of this female started on March 28, May 8 and June 13, of which 3, 5 and 4 chicks left the nest successfully, respectively.

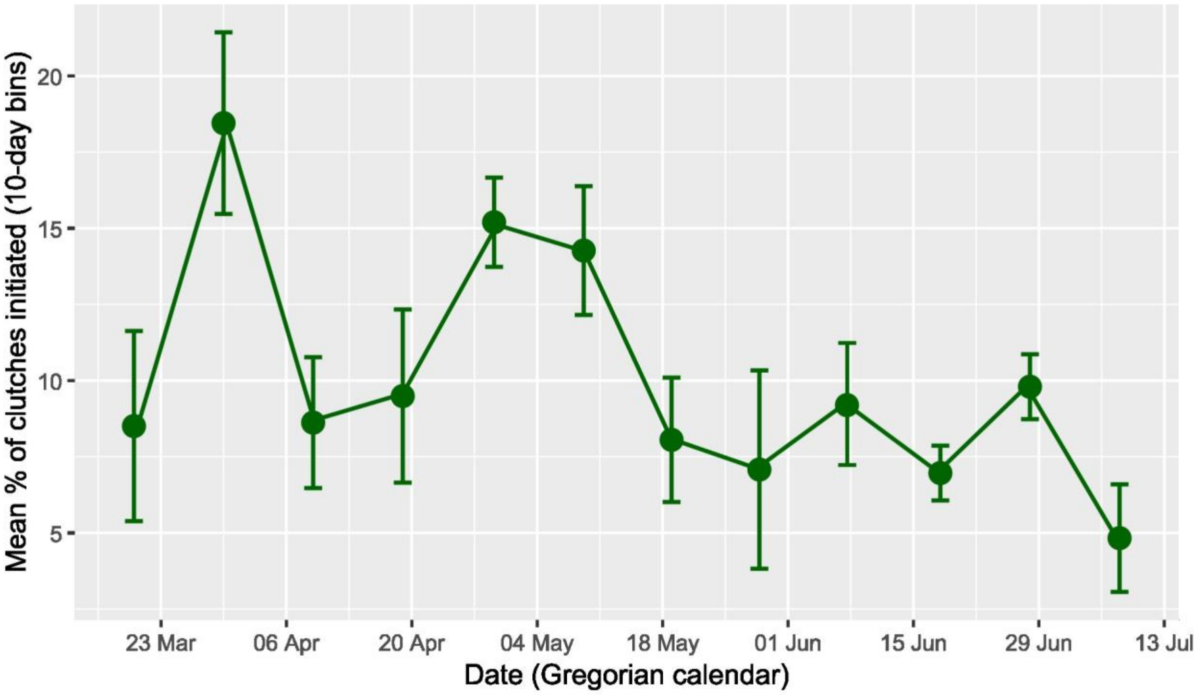

Fig. 7 Breeding phenology of Crested Lark *Galerida cristata*

Clutch size and eggs characteristics

Clutch size in the studied population (n of nest = 160) ranged from 2 to 5 eggs (Fig. 8). The clutches with four and five eggs predominated. The mean clutch size was 4.20 (95% CI: 4.08–4.32), and the most frequent clutch size (mode) was four eggs (mode number = 78). Clutch size did not vary significantly throughout the study years (Kruskal-Wallis test, H = 2.93, df = 4, p = 0.56), suggesting temporal stability in the reproductive output.

Mean egg dimensions were as follows: Length 22.63 mm (95% CI: 22.55–22.71), breadth 16.68 mm (95% CI: 16.64–16.72), and volume 3282.85 mm^3 (95% CI: 3260.08–3305.62) (n = 532 eggs). Egg length, breadth, and volume were all significantly and positively correlated (in all cases p-value for Spearman correlation was < 0.01; Appendix Fig. S1).

Linear mixed-effects models assessing differences in egg characteristics between years ($n = 455$ eggs, 108 nests) showed that egg length did not vary significantly between years ($F_{3,\,102.7} = 2.52$, $p = 0.093$), and the random effect of nest ID accounted for only modest variation ($SD = 0.77$).

In contrast, both egg breadth and volume differed significantly across years (breadth: $F_{3,\,102.0} = 2.10$, $p = 0.038$; volume: $F_{3,\,102.3} = 2.67$, $p = 0.0089$). Eggs laid in 2021 were significantly narrower and had smaller volume compared to those laid in 2018 (breadth: estimate = -0.33 ± 0.16, $t = -2.10$, $p = 0.038$; volume: estimate = -231.2 ± 86.7, $t = -2.67$, $p = 0.009$). The variation explained by the random effect (nest ID) remained relatively low in both cases (breadth: $SD = 0.42$; volume: $SD = 235.5$).

According to another LMM egg length, breadth and volume were not significantly affected by clutch size ($n = 455$ eggs from 108 nests). For egg length, $F_{1,\,110.1} = 0.13$, $p = 0.718$; SD for nest ID = 0.78. For egg breadth, $F_{1,\,110.1} = 2.09$, $p = 0.152$; $SD = 0.42$. For egg volume, $F_{1,\,109.2} = 0.61$, $p = 0.436$; $SD = 240.5$.

The highest within-clutch variation was observed in egg volume (3.75 ± 1.71), followed by egg length (1.95 ± 0.89), and breadth (1.48 ± 0.65). The Friedman ANOVA revealed that differences in within-clutch variation between these egg traits were statistically significant ($\chi^2 = 139.24$, $df = 2$, $p < 0.001$, $n = 108$).

The highest repeatability (ρ) was found for egg volume ($\rho = 0.76$, 95% CI: 0.68–0.81), followed by egg breadth ($\rho = 0.72$, 95% CI: 0.65–0.78), and length ($\rho = 0.70$, 95% CI: 0.62–0.77).

A generalised linear mixed-effects model (GLMM) with a Poisson distribution was used to assess the effects of environmental and temporal variables on clutch size ($n = 92$).

The model included the year as a random intercept and showed no signs of overdispersion ($\varphi = 0.144$). None of the tested predictors were statistically significant (Type III ANOVA, all $p > 0.96$), including timing of breeding (Julian day), nest site characteristics (position and structure), nest entrance orientation, or distance to the nearest road (Table 2). The random effect of the year had a variance estimate of close to zero (0.001), indicating no detectable variation in clutch size between years. In consequences the model explained very low variance ($R^2 = 0.013$).

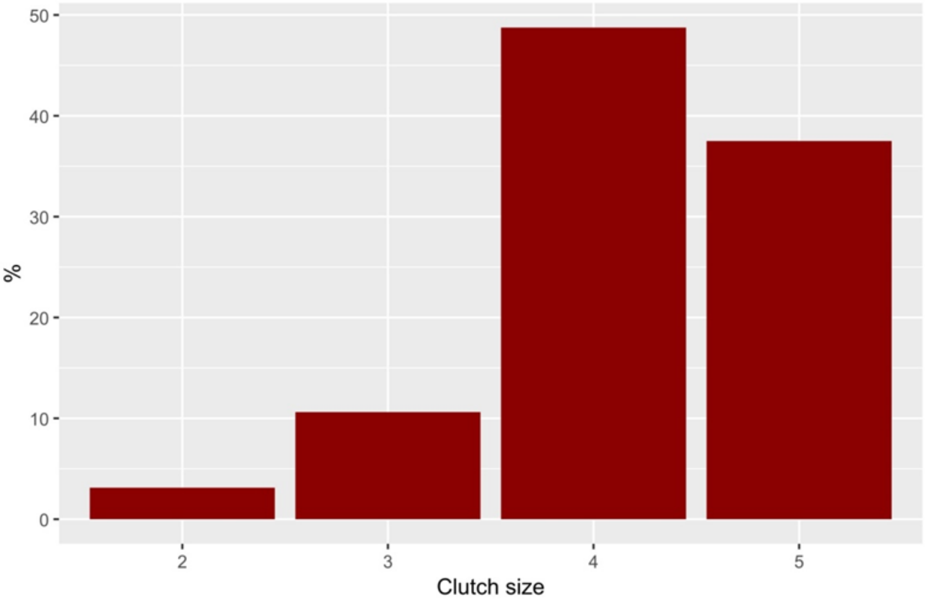

Fig. 8 Frequency distribution of clutch size

Fig. 9 Examples of Crested Lark eggs, showing the variation in pattern and colour

Reproductive parameters

In 160 visited nests, 449 eggs hatched and mean hatching success expressed as the percentage of eggs that hatched out of the number of eggs laid was 65.1% (95% CI: 50.5 – 79.6, Table 1) and the value did not vary between years ($\chi^2 = 8.46$, $p = 0.07$). The breeding success, expressed as the percentage of successful nests out of all nests was 43.1% (95% CI: 31.2– 54.7, Table 1) and there were no differences between years ($\chi^2 = 8.33$, df = 4, $p = 0.182$). The mean number of nestlings per nest was 2.81 (95% CI: 2.52 – 3.08), and it also did not differ significantly between years (Kruskal-Wallis test: $\chi^2 = 5.25$, df = 4, $p = 0.261$, Table 1). Similarly the mean number of fledglings per nest was 1.46 (95% CI: 1.18– 1.74), and it also did not differ between years (Kruskal-Wallis test: $\chi^2 = 4.19$, df = 4, $p = 0.380$). The number of nestling and number of fledglings were correlated ($rs = 0.474$, $p < 0.0001$)(Fig. 10).

The number of nestlings per nest was not associated with any of the tested predictors (GLMM–Poisson, $n = 92$; $\varphi = 0.87$; marginal $R^2 = 0.09$; all $p > 0.10$; Table 2). In contrast, the model for fledglings showed negative association with distance to the road ($\beta \pm SE = -0.019 \pm 0.004$; $z = -4.115$; $p <0.001$; $\varphi = 1.74$; $n = 92$), while the timing of breeding, surrounding vegetation and nest-entrance orientation were non-significant (Table 2).

Table 1. Number of nests, nests densities, mean (with 95% CI) distance to the nearest neighbour and nest aggregation index (R) in the studied population. Time of breeding (TB), clutch size, number of nestlings and number of fledglings are expressed as mean value per year with standard deviation (SD).

Year	No. of nests	Density [1km^2]	Distance [m]	R	TB±MAD	Fledging day±MAD	Clutch size±SD	Hatching success [%]	Breeding success [%]	No. of. Nestlings ±SD	No. of. Fledglings ±SD
2018	20	4.38	439.0 (39.5 – 939.0)	0.064	117±25.2	136.5±17.05	4.25±0.55	75.0	40.0	3.00±1.89	1.25±1.74
2019	31	6.79	313.0 (21.3 – 606.0)	0.045	131±45.9	174±35.58	4.26±0.73	74.1	48.3	3.23±1.61	1.61±1.87
2020	43	9.42	273.0 (57.4 – 488.0)	0.036	129±44.4	154±41.51	4.37±0.58	62.7	53.4	2.84±1.85	1.77±1.89
2021	38	8.33	97.8 (53.2 – 142.0)	0.013	119±37.0	153±40.03	4.11±0.86	65.7	44.7	2.82±1.67	1.47±1.75
2022	28	6.14	193.0 (16.7 – 370.0)	0.028	121±44.4	141.5±25.2	4.00±0.94	46.2	28.5	2.14±1.96	0.96±1.69

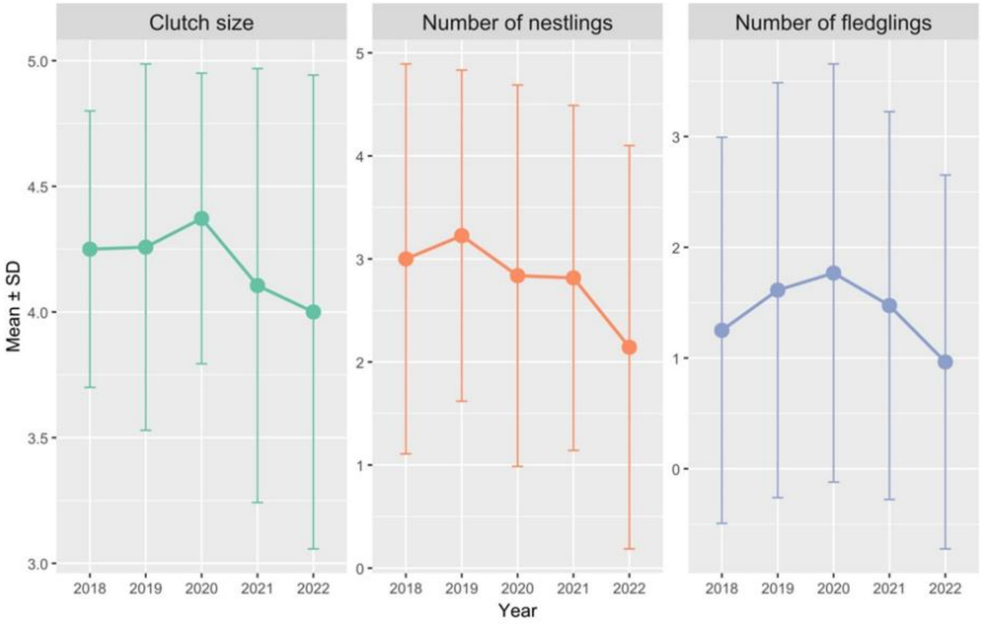

Fig. 10 Mean clutch size, number of nestlings and fledglings of the Crested Lark in 2018-2022 period

Table 2. Results of Type III Wald chi-square tests for fixed effects from the GLMM predicting the number of eggs, nestlings and fledglings per nest (details See Appendix for full model summary)

For eggs

Predictor	χ^2	df	p
Julian day of first egg	0.011	1	0.915
Terrain type	0.510	3	0.916
Vegetation structure	0.473	5	0.993
Nest entrance orientation (°)	0.251	1	0.616
Distance to road (m)	0.002	1	0.964

For nestlings

Predictor	χ^2	df	p
Julian day of first egg	0.002	1	0.960
Terrain type	0.345	3	0.951
Vegetation structure	2.403	5	0.790
Nest entrance orientation (°)	0.088	1	0.765
Distance to road (m)	1.384	1	0.239

For fledglings

Predictor	χ^2	df	p
Julian day of first egg	1.790	1	0.180
Terrain type	1.009	3	0.798
Vegetation structure	6.518	5	0.259
Nest entrance orientation (°)	0.196	1	0.657
Distance to road (m)	**18.369**	**1**	**<0.001**

Nest failures

Out of the 160 nests with known fate, 91 (56.9%) failed to produce fledglings. In most cases, any direct evidence was limited, for example nests were found empty before the expected hatch/fledge date or with egg/chick remains. Only two predation events were directly confirmed by camera traps, both by corvids such as the Eurasian Magpie *Pica pica* and the Rook *Corvus frugilegus* (Fig. 11). Other observed causes of nest failure included human activity such as lawn mowing and fieldwork, nest desertion and weather events such as flooding due to heavy/long term rainfall.

Fig. 11 Screen shots of video-recorded predators at Crested Lark nests. Rook *Corvus frugilegus* and Eurasian Magpie *Pica pica*.

4. Discussion

Our study shows that verges of express roads embedded in intensive farmland can provide a functional breeding habitat for the Crested Lark. Several of our patterns are consistent with findings from urban and rural sites, but we also showed other patterns which are specific to linear transport infrastructure.

Most nests were placed on flat grassy ground close to the road edge, with additional use of slopes and ditch banks. This preference may reflect a balance between concealment and visibility in short swards. Nesting near road edges and paved surfaces has often been interpreted as an anti-predator strategy in human-dominated settings (da Silva et al. 2019), and similar behaviour of this species has been reported in towns and cities (Baumann 1987; Lesiński 2009; Praus 2020; Martin et al. 2025). At the same time, placing nests close to roads and drainage features can impose risks that are rare or absent in more natural grasslands. Flightless fledglings may be exposed to vehicle collisions and be trapped in water-filled open ditches, a situation that was observed in the studied population.

Arable fields adjacent to the road were used less often for nest sites. In fact, this is an expected outcome for Crested Lark, an early-successional specialist. Field observations in central Europe show that Crested Larks tend to build their nests in open areas with low and sparse vegetation not higher than 20 cm (Praus 2020). Indeed, crops provide suitable nest surroundings only for a short window due to fast growth of plants, their height and density. Low vegetation cover offers good visibility in the vicinity of the nest, thus allowing adults to detect approaching predators early and maximize the likelihood of escaping or perform distraction displays more effectively (de Juana 2004). Similar preferences are well documented for other lark species (Yanes et al. 1996; Pearson & Hopey 2005; Erdös et al. 2009).

The distribution of nests was uneven in the study area. Instead, they formed clusters, especially on larger continuous grassy patches such as roundabouts and junction islands. Very short distances between some simultaneously active nests suggest weak territoriality at a finer scale. We found that the shortest distance between active nests of two different pairs was 16.7 m. This record is compliant with other reports on small territories and close neighbours, even though these distances were slightly larger, i.e. 30 m and 100 m, respectively (Praus 2020; Pätzold 1986). Although the Crested Lark is considered a socially monogamous species (Roselaar 1988), such spacing patterns along with territory aggregation on grassy patches may favour extra-pair copulations. Although this possibility has been raised for larks, it has not been studied sufficiently, so far (Sanchez et al. 2004; Hutchinson & Griffith 2008). We also recorded a case consistent with polygyny, a fact which suggests that more complex mating systems can also occur among Crested Lark.

Nest-entrance orientation showed a clear bias towards the north-east. Circular statistics rejected a uniform distribution of bearings, which means there was a preferred direction. A non-random entrance can help control microclimate in the nest cup. A northerly component reduces direct solar radiation during the hottest part of the day and may improve concealment from visually hunting predators (Högstedt 1978; Hartman & Oring 2003). An easterly component provides morning warming and reduces exposure to prevailing westerly winds (Nelson & Martin 1999). These effects are likely to be most important early in the season when nights are cold and frosts possible. North or north-east orientations have been reported in Crested Lark population in the Middle East and in roof-nesting in central Europe i.e. Hungary (Chappell 1946; Simms 1992; Orbán 2004). Similar biases also occur among temperate ground-nesters (Yanes et al. 1996; Burton 2006; Mallord et al. 2007).

The breeding season started in late March and extended into August. Similar first egg-laying dates were recorded in other parts of Europe, i.e. in France (March 27 – Labitte 1957), Germany (March 26 – Krüger 1977, March 30 – Abs 1963, March 31 – Martin et al. 2025) and Czechia (March 24 – Praus 2020). It should be also noted that in favourable conditions, earlier clutches are also possible. For instance, Pätzold (1986) recorded construction of a nest in Germany as early as on March 9. So in this context, it is surprising that in another Polish population studied within administrative boundaries of Warsaw

(1980-2006), the first egg was reported on April 12 (Lesiński 2009). There were also slight differences in the latest fledging date between the two Polish Crested Lark populations. The latest active nest in roadsides habitat was observed on August 11, while in the Warsaw settlements habitat, it was July 31. In other European populations, reproductive seasons ended in the first ten-day period of August in Czechia (Praus 2020) or even as late as August 24 in Germany (Martin et al. 2025). Thus, the breeding season of the studied population lasted almost 5 months and was 32 days longer when compared with another Polish population studied in Warsaw by the end of 20th century (Lesiński 2009). This extension of the breeding season may be the species' response to the ongoing climate change. More favourable weather conditions, e.g. higher temperatures, lack of snow cover in early spring, create suitable conditions for ground-nesting birds which are able to start breeding earlier. A longer breeding season creates opportunities to raise more broods (Ricklefs & Bloom 1977), and produce more offspring, a strategy which may compensate high rates of nest failures, especially due to predation (Slagsvold 1984; Newton 1999; Di Giacomo et al. 2011). This conclusion may be further confirmed by the fact that in the studied population one colour-ringed female raised three successful brood attempts, a number which had not been described before with regard to Polish Crested Lark populations (Lesiński 2009).

In the studied population, clutches of 4 or 5 eggs predominated. The mean clutch size was 4.20 and the number corresponds with other clutch sizes in Poland (4.36, Lesiński 2009) and Czechia (4.19, Praus 2020) slightly exceeding German clutches (3.76 - Witsack 1968, 3.92 - Krüger 1977, 2000 and 3.96 - Martin et al. 2025). Larger clutches have been noted in parts of Asia (4.60, Skhedy and Sufriel 1992, 4.75, Belskaya 1974). Complete clutches found in the present study ranged from 2 to 5 eggs. Interestingly, clutches of 6 eggs were not observed, although single cases of them were reported in a nearby German population (Krüger 1977; Martin et al. 2025). Small clutches were more frequent at the beginning and at the end of the breeding season, which is a common seasonal pattern among passerines (Rodrigues et al. 1995; Mallord et al. 2008). Egg dimensions were similar to values reported for nominate *cristata* (22.9 x 16.6, Roselaar 1988). Our models indicate that egg dimensions did not vary regardless of the clutch size. These patterns suggest that the egg form is tightly constrained within attempts and that inter-annual differences, when present, are small relative to among-nest consistency.

Reproductive output showed some inter-annual variation but no clear differences between years. This likely reflects fluctuations in a new early-successional habitat that is maintained by mowing and exposed to disturbance. However, direct comparisons with other studies are not straightforward because different methods were used to quantify success. Breeding success in studied population (43.1%) was slightly higher than obtained in German town - Güstrow (36%, Martin et al. 2025). In Czechia, Praus (2020) using the Mayfield method estimated breeding success to be approximately 40%, but recalculating using the traditional method would have reached almost 63%. Nevertheless, the traditional method may overestimate breeding success (Jehle et al. 2004). In turn, Lesiński (2009) reported 38% fledged juveniles out of laid eggs (n=156 eggs) which was much lower than 62.5% noted in Turkmenia (n=48 eggs, Belskaya 1974). In the population that we studied, nest productivity expressed as the number of fledglings per nest (1.46) was similar to the one reported from Warsaw settlements (1.55, Lesiński 2009).

Our models showed no link between the number of nestlings per nest and the tested ecological predictors. However model for fledglings per nest showed statistically significant negative association with distance to the road. The estimated coefficient (β) for this predictor was small, implying only a modest change in the expected fledglings number across the observed range. Therefore, despite strong statistical support, the biological relevance is likely limited. We interpret this pattern cautiously because it may reflect local conditions near road verges (e.g., vegetation or predator behavior), but unmeasured heterogeneity could also contribute.

Inference on predation pressure was based mainly on field signs, such as intact but empty nests before the expected hatch/fledge date or remains of eggs and chicks. Only two events were directly confirmed by cameras, and those involved corvids. This, together with previous reports from towns and cities in central Europe (Praus 2020; Martin et al. 2025), suggests that avian predators may play an important role in human-transformed landscapes. Corvid birds, such as the Eurasian Magpie *Pica pica*, Hooded Crow *Corvus cornix* and Jackdaw *Corvus monedula,* were also mentioned as predators of Crested Lark nests occupying urban habitats of Warsaw and Güstrow (Lesiński 2009; Martin et al. 2025). Human activity can also be a significant factor. Mowing and field operations did not always destroy nests outright but often removed plant cover, exposing eggs and nestlings to predators and unfavourable weather conditions, such as excessive sunlight or heavy rain. At the same time, mowing is necessary to keep verges open and to prevent succession to tall, dense vegetation that the species avoids. The observed nest abandonment was presumably related to predation risk and unrecognised predation on females (Wołoszkiewicz et al. 2024) or anthropogenic disturbance. Weather events, i.e. cold, rainy periods were relatively irrelevant due to stable weather conditions (dry and warm springs and summer) during study.

It is important to note some methodological limitations of our analyses and potential inconsistencies with other studies (see Sandecki & Kosicki 2024). In our case, the count model suggested fewer fledglings farther from the road, while the survival models showed higher daily survival farther from the road (Sandecki & Kosicki 2024).

This can happen for simple biological and statistical reasons. Counts per attempt are very sensitive to the share of complete failures and to changes in clutch size. By contrast, the survival models pointed to a short, high-risk window (late incubation and the first days after hatching), which does not always translate linearly into total fledglings per attempt, especially if clutch size and hatching rate vary within microhabitat. For these reasons, we interpret the distance effect from the number of fledglings model with caution and place more weight on the survival results when discussing environmental drivers of risk.

Our assignment of failure causes should also be seen as indicative rather than definitive. Many failed nests were found intact or simply empty, so cryptic predation can be labelled as desertion. Mowing may reduce success indirectly by removing cover, not only by destroying the nests themselves. A survival analysis helps to offset these limits by providing formal estimates of temporal risk and by testing environmental correlates across the nesting cycle (Sandecki & Kosicki 2024).

In conclusion, our results shed light on the breeding biology and ecology of the Crested Lark in linear transportation habitats. Our findings highlight the importance of expressway verges embedded in intensive farmland as breeding habitat for this species. We speculate that simple management in the form of adjusted mowing and refuge strips, could be advantageous for studied species. Additionally, due to the low ability of the Crested Lark to disperse (Martin et al. 2025), linear structures may be also beneficial for the species by providing corridors that let them colonise new areas. Further research should be focus on long-term monitoring as well as post-fledging survival and recruitment in order to assess whether roadside habitats are demographic sources or sinks.

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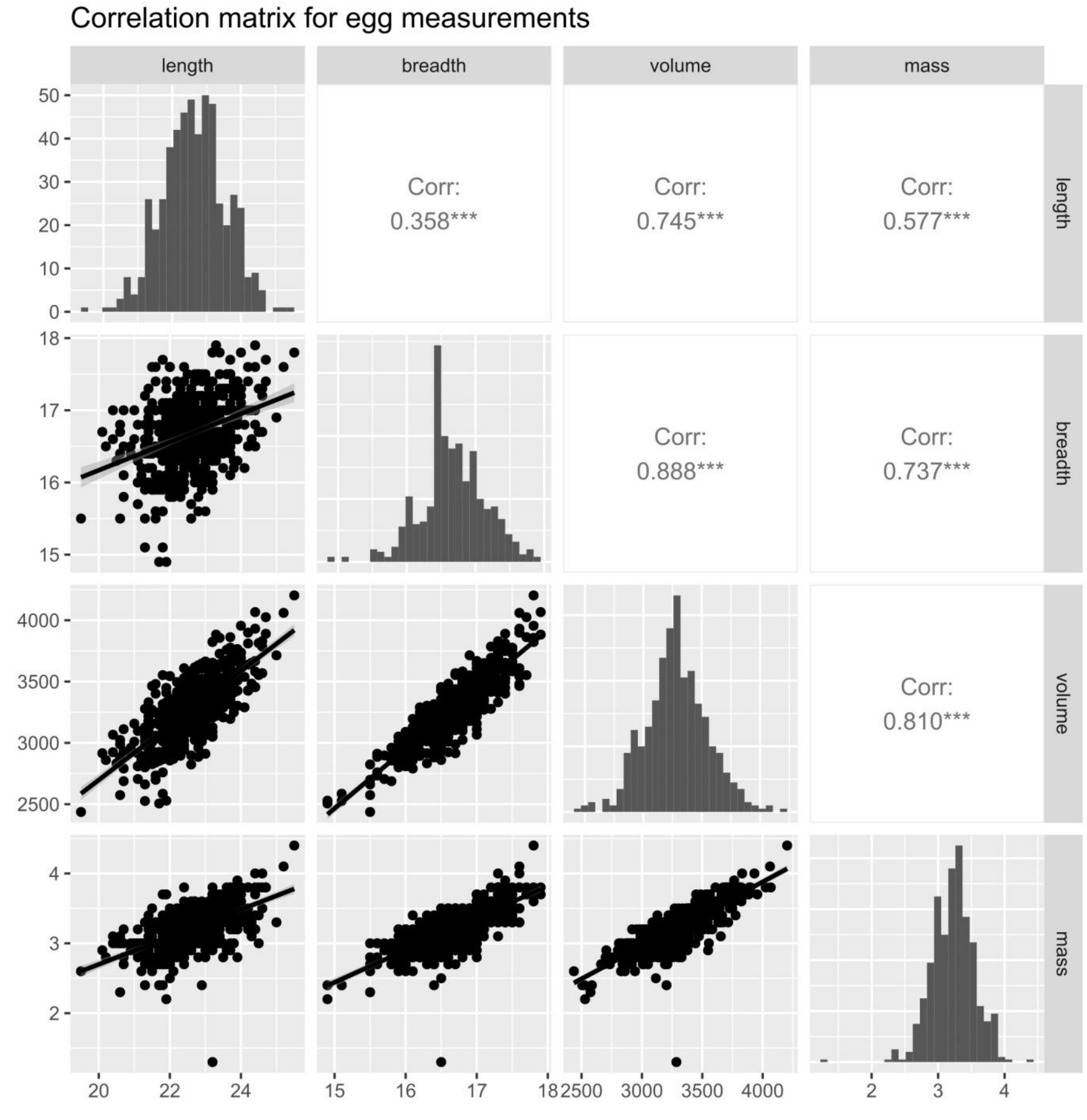
Appendix

Fig S1. Correlation matric between eggs measurements



GLMM for clutch size

```
Generalized linear mixed model fit by maximum likelihood (Laplace Appr
oximation) ['glmerMod']
 Family: poisson  ( log )
Formula: Liczba.jaj ~ Julian.day.1.jajo + factor(Posadowienie.gniazda)
+
    factor(Struktura.terenu) + as.numeric(orientacja) + Odleglosc.od.d
rogi +      (1 | Rok)
   Data: dane2

      AIC       BIC    logLik -2*log(L)  df.resid
    342.2     374.9    -158.1     316.2        79

Scaled residuals:
     Min       1Q   Median       3Q      Max
-1.06552 -0.15119 -0.03008  0.27116  0.67193

Random effects:
 Groups Name        Variance Std.Dev.
 Rok    (Intercept) 0        0
Number of obs: 92, groups:  Rok, 3

Fixed effects:
                                Estimate Std. Error z value Pr(>|z|)
(Intercept)                    1.4110821  0.2835960   4.976  6.5e-07 *
**
Julian.day.1.jajo             -0.0001869  0.0017598  -0.106    0.915
factor(Posadowienie.gniazda)2  0.0483828  0.1724730   0.281    0.779
factor(Posadowienie.gniazda)3 -0.0861727  0.2179699  -0.395    0.693
factor(Posadowienie.gniazda)4  0.2151192  0.4659020   0.462    0.644
factor(Struktura.terenu)2      0.0354885  0.1489094   0.238    0.812
factor(Struktura.terenu)3      0.0927515  0.1927292   0.481    0.630
factor(Struktura.terenu)4     -0.0922592  0.3125820  -0.295    0.768
factor(Struktura.terenu)6     -0.0091046  0.5161096  -0.018    0.986
factor(Struktura.terenu)7      0.0393769  0.3022692   0.130    0.896
as.numeric(orientacja)         0.0001930  0.0003853   0.501    0.616
Odleglosc.od.drogi             0.0002627  0.0058958   0.045    0.964
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) Jl..1. f(P.)2 f(P.)3 f(P.)4 f(S.)2 f(S.)3 f(S.)4 f(
S.)6 f(S.)7 as.n()
Jln.dy.1.jj -0.803
fctr(Psd.)2 -0.364 -0.051
fctr(Psd.)3 -0.393  0.235  0.244
fctr(Psd.)4 -0.189  0.083  0.149  0.088
fctr(Str.)2 -0.556  0.123  0.555  0.197  0.184
fctr(Str.)3 -0.443  0.302  0.298  0.196  0.171  0.416
fctr(Str.)4 -0.252  0.272  0.080  0.083  0.118  0.147  0.335
fctr(Str.)6 -0.121  0.045  0.112  0.058  0.067  0.136  0.151  0.117
fctr(Str.)7 -0.202  0.078  0.216  0.108  0.094  0.280  0.255  0.160  0
.083
as.nmrc(rn)  0.050 -0.230  0.009 -0.033  0.077 -0.117 -0.081  0.028  0
.073 -0.091
```

```
Odlglsc.d.d -0.288 -0.140  0.400  0.204  0.000  0.426 -0.142 -0.354 -0
.055 -0.020 -0.029
fit warnings:
fixed-effect model matrix is rank deficient so dropping 1 column / coe
fficient
optimizer (Nelder_Mead) convergence code: 0 (OK)
```

GLMM for number of nestlings

```
Generalized linear mixed model fit by maximum likelihood (Laplace Appr
oximation) ['glmerMod']
 Family: poisson  ( log )
Formula: Liczba.pis.wyklutych ~ Julian.day.1.jajo + factor(Posadowieni
e.gniazda) +
    factor(Struktura.terenu) + as.numeric(orientacja) + Odleglosc.od.d
rogi +      (1 | Rok)
   Data: dane2

      AIC       BIC    logLik -2*log(L)  df.resid
    368.9     401.7    -171.4     342.9        79

Scaled residuals:
    Min      1Q  Median      3Q     Max
-1.9075 -0.4478  0.1783  0.5954  1.2498

Random effects:
 Groups Name        Variance Std.Dev.
 Rok    (Intercept) 0        0
Number of obs: 92, groups:  Rok, 3

Fixed effects:
                                Estimate Std. Error z value Pr(>|z|)
(Intercept)                    1.212e+00  3.297e-01   3.677 0.000236 *
**
Julian.day.1.jajo             -1.014e-04  2.034e-03  -0.050 0.960248
factor(Posadowienie.gniazda)2 -6.548e-02  2.027e-01  -0.323 0.746603
factor(Posadowienie.gniazda)3 -6.548e-02  2.429e-01  -0.270 0.787508
factor(Posadowienie.gniazda)4 -3.555e-01  7.239e-01  -0.491 0.623372
factor(Struktura.terenu)2      5.107e-02  1.728e-01   0.296 0.767560
factor(Struktura.terenu)3      3.069e-01  2.185e-01   1.404 0.160226
factor(Struktura.terenu)4     -9.896e-05  3.776e-01   0.000 0.999791
factor(Struktura.terenu)6     -2.589e+01  2.538e+05   0.000 0.999919
factor(Struktura.terenu)7      4.275e-02  3.634e-01   0.118 0.906343
as.numeric(orientacja)         1.316e-04  4.421e-04   0.298 0.765951
Odleglosc.od.drogi            -8.114e-03  6.897e-03  -1.177 0.239373
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) Jl..1. f(P.)2 f(P.)3 f(P.)4 f(S.)2 f(S.)3 f(S.)4 f(
S.)6 f(S.)7 as.n()
Jln.dy.1.jj -0.809
fctr(Psd.)2 -0.356 -0.042
fctr(Psd.)3 -0.400  0.243  0.243
fctr(Psd.)4 -0.142  0.065  0.111  0.067
fctr(Str.)2 -0.559  0.128  0.551  0.205  0.141
fctr(Str.)3 -0.466  0.301  0.329  0.215  0.138  0.460
```

```
fctr(Str.)4 -0.258  0.261  0.099  0.091  0.092  0.167  0.339
fctr(Str.)6  0.000  0.000  0.000  0.000  0.000  0.000  0.000  0.000
fctr(Str.)7 -0.204  0.080  0.216  0.112  0.072  0.285  0.269  0.161  0
.000
as.nmrc(rn)  0.035 -0.200 -0.002 -0.032  0.057 -0.121 -0.082  0.027  0
.000 -0.097
Odlglsc.d.d -0.277 -0.125  0.362  0.199 -0.011  0.402 -0.136 -0.335  0
.000 -0.029 -0.043
fit warnings:
fixed-effect model matrix is rank deficient so dropping 1 column / coe
fficient
optimizer (Nelder_Mead) convergence code: 0 (OK)
```

GLMM for number of fledglings

```
Generalized linear mixed model fit by maximum likelihood (Laplace Appr
oximation) ['glmerMod']
 Family: poisson  ( log )
Formula: Liczba.pis.opuszczajacych.gniazdo ~ Julian.day.1.jajo + as.fa
ctor(Posadowienie.gniazda) +
    as.factor(Struktura.terenu) + as.numeric(orientacja) + Odleglosc.o
d.drogi +      (1 | Rok)
   Data: dane2

      AIC       BIC    logLik -2*log(L)  df.resid
    350.4     383.2    -162.2     324.4        79

Scaled residuals:
    Min      1Q  Median      3Q     Max
-1.7931 -1.2488  0.0000  0.8528  2.4788

Random effects:
 Groups Name        Variance Std.Dev.
 Rok    (Intercept) 0        0
Number of obs: 92, groups:  Rok, 3

Fixed effects:
                                  Estimate Std. Error z value Pr(>|z|)
(Intercept)                    1.5332680  0.3084632   4.971 6.67e-07 *
**
Julian.day.1.jajo             -0.0026527  0.0019823  -1.338   0.1808
factor(Posadowienie.gniazda)2 -0.0734011  0.0985018  -0.745   0.4562
factor(Posadowienie.gniazda)3 -0.1069152  0.1087643  -0.983   0.3256
factor(Posadowienie.gniazda)4 -0.0556921  0.1285776  -0.433   0.6649
factor(Struktura.terenu)2      0.0501228  0.1186278   0.423   0.6726
factor(Struktura.terenu)3     -0.0318885  0.1180767  -0.270   0.7871
factor(Struktura.terenu)4     -0.2089902  0.1264457  -1.653   0.0984 .
factor(Struktura.terenu)6      0.0734637  0.1464833   0.502   0.6160
factor(Struktura.terenu)7     -0.0669598  0.1585952  -0.422   0.6729
as.numeric(orientacja)         0.0001555  0.0003507   0.443   0.6575
Odleglosc.od.drogi            -0.0191525  0.0046542  -4.115 3.87e-05 *
**
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

```
(Dispersion parameter for poisson family taken to be 1)



Correlation of Fixed Effects:
            (Intr) Jl..1. a.(P.)2 a.(P.)3 a.(P.)4 a.(S.)2 a.(S.)3 a.(S
.)4 a.(S.)6 a.(S.)7 as.n()
Jln.dy.1.jj -0.803
as.fct(P.)2 -0.418 -0.009
as.fct(P.)3  0.000  0.000  0.000
as.fct(P.)4  0.000  0.000  0.000   0.000
as.fct(S.)2 -0.576  0.148  0.596   0.000   0.000
as.fct(S.)3 -0.493  0.305  0.399   0.000   0.000   0.497
as.fct(S.)4 -0.221  0.218  0.109   0.000   0.000   0.154   0.292
as.fct(S.)6  0.000  0.000  0.000   0.000   0.000   0.000   0.000   0.0
00
as.fct(S.)7 -0.244  0.110  0.257   0.000   0.000   0.311   0.307   0.1
50   0.000
as.nmrc(rn)  0.049 -0.208 -0.021   0.000   0.000  -0.138  -0.128   0.0
06   0.000  -0.124
Odlglsc.d.d -0.304 -0.106  0.388   0.000   0.000   0.410  -0.091  -0.2
67   0.000  -0.011  -0.043
fit warnings:
fixed-effect model matrix is rank deficient so dropping 1 column / coe
fficient
optimizer (Nelder_Mead) convergence code: 0 (OK)
```

5. Nest survival of Crested Lark (*Galerida cristata)* in intensively used habitats in Central Poland

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Published in: *Journal of Ornithology*. Published online: 15 May 2024, Volume 165, pages 947–958 DOI:10.1007/s10336-024-02183-y

Abstract

Breeding success of birds depends on survival during two critical stages of the reproductive period: First, egg laying and incubation, and then nestling and fledgling. This essential element of avian life history mirrors an evolutionary adaptation of parents to existing environmental conditions. The main factors that determine nest survival involve weather, predation and sibling competition. Despite numerous studies documenting their impact on breeding success, only a few have analysed the issue with regard to ground-nesting birds and estimated their survival functions. Therefore, we decided to examine nest survival probability of the Crested Lark *Galerida cristata* in a population that occupies newly established roadside habitats in Central Poland. The analysis is based on 141 nests monitored between 2018–2022.

We found that the mean survival probability of the whole nesting period was 0.376, and it was higher during the egg stage (0.836) than during the nestling period (0.392). The Cox proportional hazards model shows that nest survival in the nestling stage is mainly affected by the time of breeding and the distance from the road edge, and also by mean temperature of the whole nesting period. In other words, the probability of a brood failure in the nestling stage decreases as the breeding season advances, whereas it increases among nests located closer to the road edge. Furthermore, during the whole nesting period nest failure decreases as the temperature rises. Our study suggests that the Crested Lark, being a multi-brood and thermophilic species inhabiting temperate regions, may benefit more if its nesting attempts begin later during the season when breeding conditions become more favourable. However, we also take into consideration a hypothesis that nesting in grassy habitats near road edges may prove to be an ecological trap, attracting high densities of nesting birds but leading to their low nest success.

Key words: *Galerida cristata*, linear habitats, nest survival, roadside

1. Introduction

Nest survival is a parameter of the adaptation of birds, reflecting their reproductive success, which subsequently regulates the dynamics of the population size (Newton 1998; Cresswell 2010). It can be governed by predation and weather as keys factors affecting nest failure, especially among ground nesting species (Newton 1993, Wright et al. 2009, Martin et al. 2017, Reif et al. 2023). Since parents' adaptation to ensure nest survival is under strong pressure from natural selection (Lack 1968, Martin 1995), it is not surprising that birds have developed many behavioural adaptations that ensure their reproductive success. Anti-predatory strategies of ground nesting birds include a selection of a nesting place with sufficient concealment from predators (Mallord et al. 2007, MacDonald et al. 2016), active defence, attack and distraction of potential predators (Gomez-Serrano et al. 2017), repetition of broods in the case of loss (Lesiński 2009, Gates et al. 2013), and shorter time spent by chicks in the nest (Martin et al. 2011, Remes et al. 2020). Nest survival is also influenced by weather (Chmura et al. 2018, Grudinskaya et al. 2022), because until nestlings develop their thermoregulatory ability (Starck & Ricklefs 1998), episodes of cold weather, such as a sharp temperature and/or precipitation drop, can significantly reduce the number of nestlings in the nest and consequently shape breeding success. Therefore, parental fitness is enhanced by well-hidden nests that attenuate the sounds of chicks begging for food, their smell and movement, and by their ability to balance the time spent on searching for food and warming chicks, especially during unfavourable weather (Auer & Martin 2017, Lejeune et al. 2019).

Although there are numerous studies documenting relationships between predation, weather and nest survival, there are no unambiguous patterns of these relationships with regard to ground nesting birds living in open habitats. A good example is the family of larks (*Alaudidae* spp.), which may be an important indicator value of avian diversity not only in grassland, steppe or traditional habitats, but also in many previously degraded open spaces (Han et al. 2023). Lark broods are subject to strong predation and weather pressure (Donald et al. 2002, Praus et al. 2014, de Zwaan et al. 2018), as a result of which only 20 to 30% turn out to be successful (Suarez & Marique 1992, de Juana 2004, Praus & Weidinger 2010, Mwangi et al. 2018). Thus, despite these achievements in understanding nest survival of larks, all earlier studies quantified reproductive success exclusively as a binary success vs. failure variable and thus did not take gradual changes in egg or nestling number into account. This classic approach focuses only on nest success and nest failure, but it entirely disregards gradual declines in brood size that may result from predation and (even more likely) adverse weather. Nest survival may vary significantly during different nesting stages. Many studies on nesting passerines, including larks, suggest that during the eggs stage nests tends to have a higher survival rate than in the nestling period (Skhedy&Sufriel 1992, Praus 2020, Golawski et al. 2023), but others have found the opposite (Mitrus&Soćko 2008), also showing differences occurred even within the same species (Mallord 2008, Praus et al.2014). It is likely that multiple factors influence age-specific patterns of nest survival. Thus, estimating phase-specific (egg and nestling phases) survival and pinpointing the critical moment of survival during a nesting attempt may increase our understanding of breeding success limitations in a particular habitat and be essential for developing adequate conservation strategies (Zaremba et al. 2020). So far, no detailed research has been conducted on the Crested Lark *Galerida cristata* with regard to this aspect, and studies on this species focused mainly on breeding biology (Lesiński 2009, Praus 2020) and habitat selection (Šímová et al. 2015, Lisiecki et al. 2020, Chiatante 2022).

The Crested Lark is a small, mainly sedentary bird species belonging to larks *Alaudidae* family. This species, which features many subspecies, has a wide distribution ranging from north-central Africa throughout Asia Minor to Central Asia and Europe (Guillamet et al. 2006). Originally, it inhabited dry warm open areas with very low and sparse vegetation, for example semi-deserts and steppes, but it has also adapted to various human-modified landscapes, such as open farmland, urban settlements and outskirts, railway yards, airfields and roadsides. (BirdLife International 2023, Roselaar 1988). At present, its population is decreasing across many parts of Europe (Birdlife International 2023) and a widespread decline was recorded during the second half of 20th and at the beginning of the 21st century (de Juana et. al 2004), a trend whose exact reasons are unknown and require urgent in-depth studies.

The Crested Lark is a ground-breeding open-cup nester. At our study site in central Poland, the species breeds from the end of March to mid-August, having 2-3 broods per season. In this paper, we show the results of our analysis of the Crested Lark's nest survival on the basis of regular nest inspections over a five-year period. We examine relationships between nest survival (eggs/chicks), weather conditions, and predatory pressure during a breeding season.

Our study aims to: (1) describe nest survival of the Crested Lark in intensively used habitats during the egg incubation and nestling stages; (2) establish the critical period of the reproductive cycle that influences reproductive success; (3) analyse how weather and predation pressure affect reproductive success during the incubation and nestling stages. In this analysis, we expect predation pressure to be relatively constant over years in monotonous landscapes (e.g., Kosicki et al. 2016). Moreover, since Crested Larks are evolutionarily adapted to relatively predictable weather on the continental steppe in spring and summer, they may be particularly sensitive to more fluctuating weather conditions in their recently occupied ranges in Central Europe, which are further exacerbated by increasing weather fluctuations resulting from climate change (Perez-

Granados et al. 2023, Tscharntke and Batáry 2023). Therefore, we hypothesise that the reproductive success of the Crested Lark is more dependent on weather conditions than on predation pressure.

2. Material and methods

Study Area

The study was conducted in central Poland, a region which is dominated by flat landscape with the average elevation of 80–100 m a.s.l. It is characterised by temperate continental climate with the average annual temperature of 8.2°C and the so-called "rain shadow", i.e. annual precipitation of about 500 mm, which is lower than in other regions (Kondracki 2009).

The surveyed population of the Crested Lark lives in roadside habitats along a bypass road round the town of Inowrocław (52°46'55N, 18°18'36E). The study area of 4.6 km^2 is parallel to a dual carriageway. Since the road was built between 2014 – 2019, it is a relatively new element of the landscape, which has changed from arable land to regularly mown grassland. Along its entire length (25.1 km), the immediate surroundings of the bypass include service roads, lanes of grassy vegetation interspersed with planted shrubs and small trees as well as adjacent arable fields with a varied crop structure, mainly winter wheat, rapeseed, maize and sugar beets.

Bird data

The data were collected from mid-March to mid-August in five consecutive breeding seasons between 2018 and 2022. Nests were spotted through a systematic search of the area along the road and associated structures by means of flushing incubating females, and observing adults carrying nesting material or food for the chicks. Once a nest was found, it was regularly inspected at intervals of 2-4 days to observe its content and status. During the five-year period, each nest was inspected on average (±SD) 5.96±3.08 times. During the last inspection nestlings were ringed with metal and coloured alphanumerical rings.

When a nest was found during the egg-laying stage, we calculated the time of the clutch initiation on the basis of the number of eggs, assuming that one egg per day was laid (de Juana et al. 2004, Roselaar 1988). When a nest was discovered during incubation, the date of the first egg laying was determined by back-dating (since hatching) using a 12-day incubation period. If a nest was found during the advancement brood, we weighed and measured the nestlings and estimated their age according to the age–body weight relationship (Skhedy & Sufriel 1992). We assumed that the maximal brood duration was 30 days, including the egg-laying and incubation period (17 days) and the nestling stage (13 days) (Roselaar 1988, de Juana 2004).

By nesting success, we meant a nest that produced at least one fledgling aged at least 9 days, which is a minimum age for leaving the nest (de Juana et al. 2004). Also, when the last inspection revealed adult birds feeding the chicks outside the nest or showing anxiety if an observer appeared in the nest's vicinity, we considered it as a nesting success. In our analysis, we included successful nests, nests that were totally lost, i.e. all eggs had failed or all nestlings had died, as well as those whose number of nestlings decreased between inspections. We excluded from the analysis nests with a brood destroyed by a predator as documented by trail cameras (2 cases) and also nests that were destroyed (9) or abandoned (10) at the incubation stage without the possibility of determining the approximate date of clutch initiation. Thus, our dataset consisted of 141 broods out of the total of 162 recorded ones. However, excluding nests from the analysis may overestimate survival at the egg stage. Therefore, we conducted an alternative survival analysis (see Appendix), assuming that the day the nest was found was the first day of incubation. The average breeding density in this population was 5.4 pairs per 1 km^2.

During each nest control, a 5-minute-point counting of potential nest predators was made within 50 meters of the nest. The mean (±SD) number of predatory birds per control was 2.84±2.72 individuals (range: 0 – 14), and it differed between the years (except 2018 vs. 2019; Appendix), while the mean (±SD) number of predatory mammals was 0.18±0.44 individuals (range: 0 – 2), and in that case we found no differences between the years (Appendix). The shortest distance from the nest to the edge of the nearest road was measured with a tape measure (to the nearest 0.1 m).

To assess the effect of weather conditions on nest survival, climatic data were obtained from meteorological stations of the Institute of Meteorology and Water Management – National Research Institute, located in the vicinity of the bypass road. Temperature data were obtained from a station in Kołuda Wielka, located 12 km away from the center of the study plot, whereas precipitation was provided by stations in Pakość, Jaksice and Więcławice, located 15.1 km NW, 11.3 km N and 7.1 km NE, respectively, from the center of the study plot, so accurate rainfall values were provided for the entire study area. The mean (±SD) temperature during the study period (from 22nd March to 15th August) was 13.35±6.17 °C (range: -0.63 – 28.60) and it differ between the years (except 2018 *vs.* 2019, see Appendix), while the average (±SD) daily precipitation was 1.54±4.15 mm (range: 0 – 40.4), and was different between years (except 2018 *vs.* 2020 and 2018 *vs.*2021, see Appendix).

Data processing and analysis

Nest survival was calculated as a change in the number of active nests or their contents during each breeding season (Kleinbaum 1996). We analysed the data according to life tables, which are the most universal method for estimating survival functions, where the life history of each brood, i.e. from brood initiation to the offspring leaving the nest/destruction of the nest during a particular breeding season is known. When analysing life tables, survival is considered to be a function of time (Kleinbaum 1996; Kosicki 2012, Langowska and Zduniak 2020), contrary to the most frequently analysed cases when breeding success is expressed as a simple proportion of surviving broods. Thus, in our approach, we were able to calculate critical time points during the breeding season of the studied population (Zduniak 2010; Zduniak et al. 2011, Kosicki 2012, Goławski et al. 2023). We estimated the survival time of each nest during the whole nesting period, i.e. from first egg laying in the nest to the date of the last visit, but also separately for the egg stage (egg laying and incubation) and the nestling stage (form hatching to fledging). The day when eggs or nestlings failed was considered as a halfway point between two consecutive nest controls.

To analyse the impact of weather conditions, predatory pressure and breeding parameters on nest survival, we used the Cox proportional hazards model (Cox 1972, Muenchow 1986; Moya-Larano and Wise 2000; Reino et al. 2009), where time of life and status (survival/mortality) were used as input parameters of the response variable. In this approach, the hazard ratio, i.e. the probability that an individual that survived till the beginning of a given interval will die before the end of that interval is a function of independent variables. Accordingly, it is possible to estimate the regression of coefficients (and test them to see if they are significantly different from 0) for independent variables. When a regression coefficient for a given independent variable is positive and statistically significant, it shows decreased survival (higher risk of failure), and – vice versa – a statistically significant but negative coefficient is associated with increased survival (lower risk of death).

This approach let us test several environmental components that might influence nest survival, such as temperature, precipitation, distance between the nest and the road, the number of bird and mammal predators, as well as the date of the brood onset, i.e. the date of the first egg laying. This variable is expressed as the number of days after 1st January (first day) and it was median-centred for the particular breeding season. The number of bird and mammal predators was also mean-centred for a particular breeding season. Weather conditions were expressed as mean daily values of air temperature and mean sum of precipitation (from three nearest meteorological stations) calculated for duration time of each nest stage, separately for eggs, nestlings and whole nesting period (Kosicki 2012). Due to the fact that the survival rate of the egg stage was relatively high (see results), we developed the Cox proportional hazards model for: 1) the nestling period, and 2) the whole nesting period (from egg laying to the fledglings' departure from the nest).

In order to verify whether full models (with all predictors) could be simplified, the Akaike Information Criterion (Burnham & Anderson, 2002) was employed. By adding or removing predictors, it generated all possible combinations of candidate models. The model with the lowest AIC value and thus the highest Akaike weight was considered to be the best and the most parsimonious (Burnham & Anderson, 2002).

3. Results

We found 162 nests located mainly in roadside areas covered with grassy vegetation (83%) and in adjacent arable fields (17%) (Fig. 1) The mean distance from the nest to the road was 13.48±12.45 m.

The mean survival ratio for the whole nesting period (30 days from egg laying to fledgling) was 0.376 (95% CL: 0.244 – 0.581, n = 141, Fig. 2A) and did not differ over the five-year study period ($\chi^2 = 2.8$, df = 4, $p = 0.6$). The mean survival during the eggs stage (egg laying+incubation = 17 days) was 0.836 (95% CL: 0.746 – 0.937), and it also did not differ significantly between years ($\chi^2 = 1.2$, df = 4, $p = 0.9$), but the result was statistically higher than during the whole nesting period (Gehan–Wilcoxon test, test value = 2.31, $p < 0.01$). Finally, the mean survival ratio for the nestling period was 0.392 (95% CL: 0.212 – 0.727), and it also did not differ in particular study years ($\chi^2 = 2.1$, df = 4, $p = 0.7$). Besides, there was no difference between this period and the whole nesting period (Gehan–Wilcoxon test, test value = 0.73, $p < 0.54$).

According to the hazard ratio, the most critical moment for the survival of eggs/chicks occurs at the end of the incubation period and during the first days of the nestlings' life. The highest hazard ratio was observed from the 15th day of egg stage, i.e. just before hatching, to the 9th day of nestlings' life (Fig. 2B). Therefore, the analysis of the impact of environmental factors on survival was performed separately for the whole nesting period (from egg laying to nest leaving) and for the nestling period (from hatching to nest leaving).

Out of all analysed Cox proportional hazards models (Table 1) for the nestling period, the most parsimonious model included only two predictors, i.e. the hatching day and the distance between the nest and the road (Table 1, model 1A). This model turned out to be slightly better than the second model in our candidate set (evidence ration = 2.69), which additionally contained temperature as a predictor (Table 1, model 2A).

The best supported model was statistically significant (likelihood ratio test = 50.09, $p<0.0001$, $R^2 = 0.335$) and it showed that the risk of chicks' death, expressed as a hazard ratio, decreased during the breeding season (β for Hazard ratio (±SE) = -0.639 (±0.09), Wald statistic = -6.64, $P < 0.001$, Fig.3A). In other words, the later in the season birds started to breed, the lower the risk of their chicks' death. What is more, we showed that the risk of chicks' death decreased with the increase in the distance from the nest to the road (β for Hazard ratio (±SE) = -0.342 (±0.07), Wald statistic = -5.64, $P < 0.02$, Fig.3B). According to the second model, our candidate set could also suspect that the temperature will be high statistically significant impact on probability of nestlings death, but this factor was not significant (β for Hazard ratio (±SE) = -0.04 (±1.00), Wald statistic = 0.140, $P < 0.88$, Fig. 3C).

The most parsimonious Cox proportional hazards model for the whole nesting period (from first egg laying to fledge) (Table 1) was also significant (Likelihood ratio test= 41.78, $p<0.0001$, $R^2 = 0.253$). It included three predictors, i.e. the time of breeding, temperature and the distance from the nest to the road. This model was slightly better than the second model, which also included the number of bird predators and may be considered a valid alternative in our candidate set (evidence ratio = 1.80).

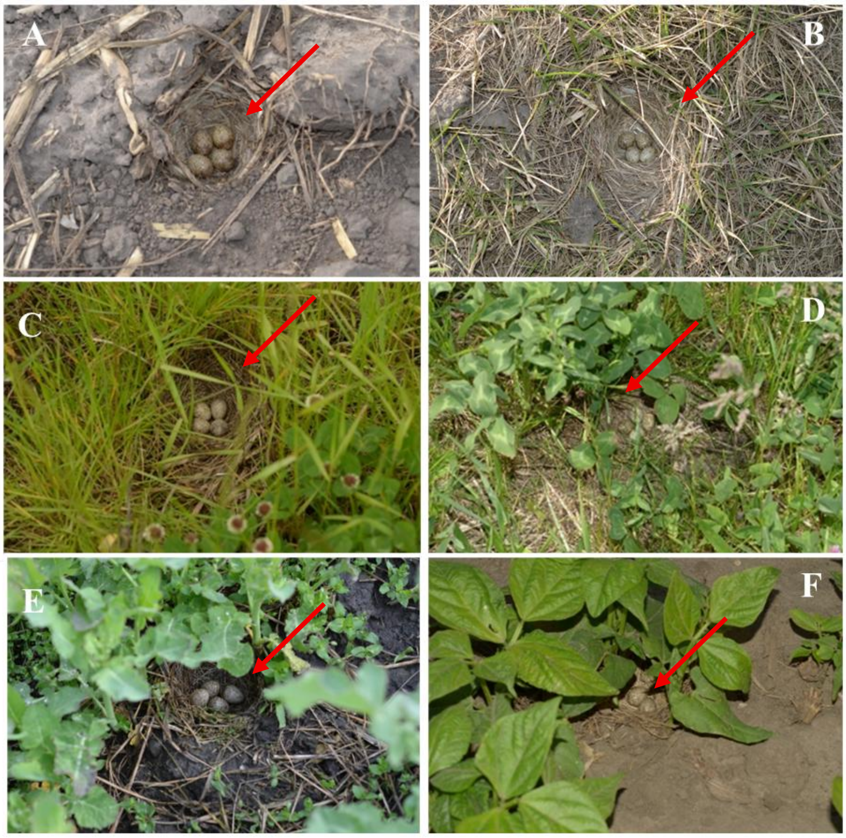

Fig. 1. Nests of the Crested Lark *Galerida cristata* located in different micro-habitat patches with plant cover at various stages of development. A – arable field at the beginning of growing season; B – grassy area at the beginning of growing season; C - grassy area at the peak of growing season; D – red clover *Trifolium pratense*; E – rapeseed *Brassica napus*; F – common bean *Phaseolus vulgaris*.

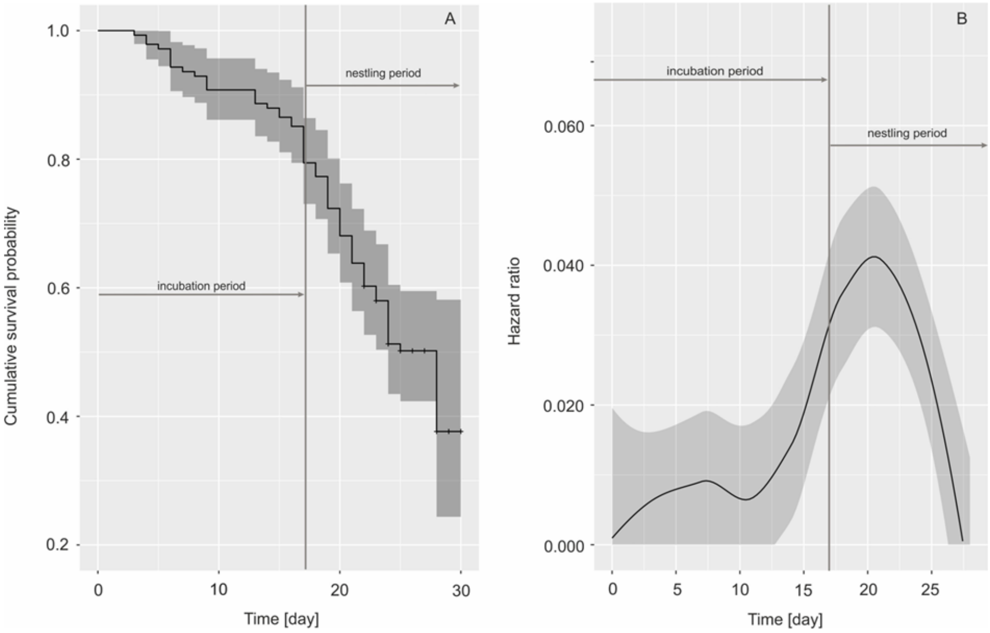

Fig. 2. Survival probability and hazard ratio for the Crested Lark's nests in different brood stages in roadside habitats of the bypass road in Central Poland.

According to the best supported model, we found that the death risk of the content of the nest (eggs or chicks) decreased during the breeding season. In other words, the later the breeding attempt was undertaken, the better survival of the offspring (β for Hazard ratio = - 0.134, Wald statistic = -1.382, P = 0.045, Fig. 3D). A similar tendency was established with regard to temperature: The risk of death decreased with the increase of air temperature (β for Hazard ratio = - 0.179, Wald statistic = -3.038, P = 0.002, Fig. 3E). Finally, the highest survival rate, i.e. the lowest hazard rate, was found for nests located the furthest from the road (β for Hazard ratio = - 0.013, Wald statistic = -2.323, P = 0.02, Fig. 3F). In the second model in our candidate set, we also found that probability of nestlings death increase proportionally to the number of bird predators, but it should be noted that this relationship is on the border of statistical significance (β for Hazard ratio = 0.010, Wald statistic = 1.03, P = 0.05, Fig. 3G). So the time of breeding, distance from the edge of the road and temperature explain most cases of nest success, even though bird predators may also play a role in the process.

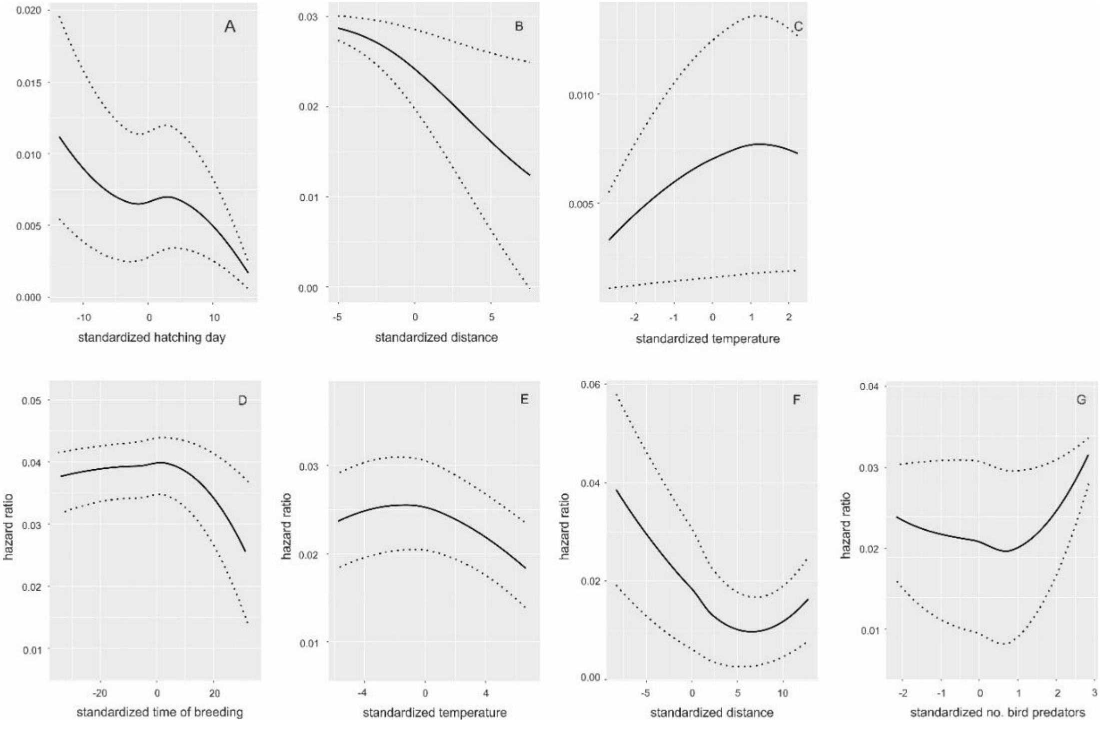

Fig. 3. Relationship between the hatching day, distance to the road, temperature and the hazard rate.

Table 1. Models with variables influencing nest survival probability of the Crested Lark in the nestling and full breeding periods.

model	predictor	logLik	AIC	delta	weight
Nestlings period					
1	**HD+DISTANCE**	**-205.97**	**415.9**	**0**	**0.585**
2	HD+DISTANCE+TEMPERATURE	-205.96	417.9	1.98	0.217
3	HD	-205.709	419.4	3.48	0.103
4	HD+DISTANCE+TEMPERATURE+PRECIPITATION	-205.552	421.1	5.17	0.044
5	HD+DISTANCE+TEMPERATURE+PRECIPITATION+PRED.BIRD	-205.165	422.3	6.39	0.024
6	HD+DISTANCE+TEMPERATURE+PRECIPITATION+PRED.BIRD+PRED.MAM	-205.074	424.1	8.21	0.01
7	HD+DISTANCE+TEMPERATURE+PRECIPITATION+PRED.BIRD+PRED.MAM+SIBLING	-205.074	424.1	8.21	0.01
8	HD+DISTANCE+TEMPERATURE+PRECIPITATION+PRED.BIRD+PRED.MAM+SIBLING+INSPECTIONS	-204.28	424.6	8.62	0.008
9	HD+DISTANCE+TEMPERATURE+PRECIPITATION+PRED.BIRD+PRED.MAM+SIBLING+INSPECTIONS+PRED.ALL	-230.873	461.7	45.81	0
10	NULL	-230.797	463.6	47.66	0
Whole nesting period					
1	**TB+TEMPERATURE+DISTANCE**	**-298.213**	**604.4**	**0**	**0.344**
2	TB+TEMPERATURE+DISTANCE+PRED.BIRD	-297.8	605.6	1.17	0.191
3	TB+TEMPERATURE+DISTANCE+PRED.BIRD+PRED.MAM	-296.854	605.7	1.28	0.181
4	TB+INSPECTIONS+TEMPERATURE	-300.621	607.2	2.81	0.084
5	TB+TEMPERATURE+DISTANCE+PRED.BIRD+PRED.MAM+DISTANCE	-296.657	607.3	2.89	0.081
6	TB+TEMPERATURE+DISTANCE+PRED.BIRD+PRED.MAM+SIBLING	-296.657	607.3	2.89	0.081
7	INSPECTIONS	-296.656	609.3	4.89	0.03
8	TB+INSPECTIONS	-303.972	611.9	7.52	0.008
9	NULL	-318.802	637.6	33.18	0
10	TB	-318.66	639.3	34.89	0

4. Discussion

Our study is the first of this kind to have estimated nest survival of the Crested Lark during different brood stages. It also tested the impact of a variety of factors that potentially affected survival. We found that the survival rate in the egg stage was twice as high as in the nestlings stage, a result which is consistent with earlier studies on birds nesting on the ground (Mallord 2007, Perez-Granados 2017). We also found similar tendency in the our extended analysis (see Appendix), which also included broods for which there was uncertainty about the start date of laying. Thus, the nest survival pattern of the Crested Lark is generally consistent with that of ground-nesting birds, showing overall low survival in comparison with species using other nesting niches (Shochat et al. 2004).

The overall nest survival during the whole nesting period (0.376) of the Crested Lark is similar to the value (0.367) obtained for a population of this species studied in Czechia (Praus 2020), but higher than among birds breeding in the Negev Desert (0.238) (Skhedy and Sufriel 1993). The differences may result from different conditions in Central Europe and the Near East. As regards other lark species from habitats in temperate regions, the results we obtained for whole nesting period were comparable or slightly higher. In Kazakhstan, the mean probability of the Black Lark's *Melanocorypha yeltoniensis* nest to survive the entire nesting period in the steppe and among abandoned crops was 0.207 (Lameris et al. 2016), whereas in the case of the Woodlark *Lullula arborea* nesting in heathlands in southern England the probability was 0.470 (Mallord et al. 2007), while for the Skylark *Alauda arvensis* in farmlands of southern England it was 0.242 (Donald et al. 2002), and 0.322 for the Horned Lark *Eremophila alpestris* in the alpine environment of Canada (McDonald et al. 2016).

Our results show that two factors, such as the time of breeding and the distance from the road, affect the probability of nestlings' survival. Besides, the whole nesting cycle (from egg laying to nest leaving) is also affected by temperature. Thus, the probability of nestling failure decreases as the breeding season advances, and increases when nests are closer to the road. What is more, during the whole nesting period, nest failure decreases as the temperature increases. The survival probability is higher during the egg stage than in the nestling period. It can be explained by increased parental feeding activity and nestlings' begging calls for food. These two types of visual and acoustic cues may disclose the location of the nest and attract potential predators (Martin et al. 2000, MacDonald 2009, Ibáñez-Álamo et al. 2012).

Our findings on the time of brood initiation are surprising, because opposite results have been described many times. Generally, pairs that breed earlier grant lower nest mortality than pairs beginning to breed later (Siikamaki 1998, Currie et al. 2000, Morrison et al. 2019). Additionally, this relationship has a strong theoretical basis, as studies show that birds that start breeding earlier are more experienced and they are the first to occupy better territories (Weggler 2000; Kokko et al. 2006). However, this assumption may not be applied to sedentary and multi-brood species that originally inhabited steppe and semi-desert landscapes with much warmer and arid climate than the climate in temperate regions. We speculate that our contrasting results may reflect a reproductive strategy of the studied species in the face of changing weather conditions, which occur regularly during the whole breeding season (from late March to mid-August). As a multi-brood species, the Crested Lark may potentially compensate for the loss of earlier nests by several nesting attempts throughout an extended breeding season. The Crested Lark nests on the ground, building nests lined mainly by grass in a shallow depression under the shelter of tussock or – less frequently – shrub. At the beginning of the breeding season in the third decade of March (23/03/2018), when the first egg was laid in the studied population, vegetation on the ground was relatively low and sparse, thus making the nest more visible to the predator. This hypothesis may be supported by a study conducted on the Negev Desert (Skhedy and Sufriel 1993), where survival in the eggs stage was 0.368 as compared to 0.836 obtained in our study. The differences may result both from the structure of the desert vegetation cover providing poorer nest concealment as well as the character and activity of nest predators (Skhedy and Sufriel 1993). During the whole nesting period, the second model selected by the AIC showed that bird predators may also play a role in determining breeding output. There may be several potential explanations for why predation pressure was not included in the most parsimonious model, despite the fact that this factor was also marginally statistically significant. Firstly, it is plausible that the five-minute-point counting of potential predators is not long enough and may not reflect their real impact on nest survival. Secondly, the obtained field data could be biased as only diurnal predators were observed, whereas nocturnal animals, e.g. like Red Foxes *Vulpes vulpes*, Feral Cats *Felis catus*, hedgehogs *Erinaceus sp.*, Stone Martens *Martes foina*, rodents *Rodentia sp.*, could be potentially more responsible for nest losses. This explanation can be supported by results obtained from studies on the Eurasian Skylark and the Woodlark in the Netherlands, where nest predation occurred in the dark in 55% cases (Praus et. al 2014). Alternatively, due to the fact that the area we study is a linear habitat running along the motorway, it is also likely that potential predators, which are opportunists, benefit from the carcass on the road and thus scavenge their food, while bird nests remain an alternative source of food (Pescador & Peris 2007). Still, due to specific features of the study area and methodological limitations, the actual impact of predators on nest survival may have been masked in favour of weather conditions, especially temperature, which may have influenced the breeding success of the Crested Lark. Moreover, local frosts that occur at the beginning of the breeding season can pose a problem for this typically steppe species.

During the incubation period, this factor is less important, because the brood is predominantly incubated by the female (with short feeding breaks), which maintains a constant temperature of the nest (Hartley 1946, own data). Still, low air temperature right after hatching may impact nestling survival in two ways. First, it happens directly, because days with low temperatures are dangerous for small nestlings whose homeothermic regulation has not developed. In the period just before hatching, embryos and nestlings soon after hatching have reduced thermoregulation so they suffer from cooling (Rodriguez & Barba 2016). Second, which is a more probable explanation, air temperature in spring and summer indirectly affects potential food resources, such as beetles *Coleoptera*, grasshoppers *Acrididae*, ants *Formicidae*, caterpillars, snails *Gastropoda* and spiders *Araneae* (de Juana 2004) that adults feed on, whereas the offspring are fed mainly with insects, especially caterpillars and small *Orthoptera* (Roselaar, 1988). These organisms, which are the main element of the Crested Lark's diet, are poikilothermic, so they cannot regulate their body temperature and their activity largely depends on thermal conditions of the surrounding environment (Lehmann 2009, Zhang et al. 2020, Hannigan et al. 2023). Thus, when it is cold, invertebrates are scarce, which may lead to nestling starvation, their reduced growth rate and general poor condition. Additionally, adverse weather forces adult birds to increase their energy expenditure and foraging activity to provide the same amount of food for nestlings. Consequently, when parents need more time for foraging, their chicks are exposed to hypothermia, especially in the first few days after hatching. Also, reduced food availability and severe weather constitute a stress factor, which is often connected with parasite infections (Newton 1998), additionally increasing the mortality of nestlings. Finally, we found that the further from the road, the higher survivability of the brood. Higher survival rates of nests located further from the road can stem from the fact that they are located mostly on agricultural fields, where denser vegetation provides more stable temperature and better nest concealment. Our findings are consistent with results from studies on the Eurasian Skylark, whose nests in cereal crops had a significantly higher survival rate than those located in other field types (Donald et al. 2002). Meanwhile, the lower survival rate of nests located closer to the road edge may result from increased human disturbance in this zone, including agricultural machines movements to adjacent fields and mowing grass works.

5. Conclusion

The breeding success of the Crested Lark nesting in road margins depends mainly on the microhabitat and climatic conditions. Our study suggests that in temperate regions the Crested Lark, which is a multi-brood and thermophilic species, may benefit more from later nesting attempts when breeding conditions, such as higher temperature and peak of food abundance, have improved. Therefore, the ongoing climate changes may contribute to better survival of broods and a recovery of its populations in Northern and Central Europe.

Our findings also demonstrate the importance of nest location, because it is a factor that might seriously reduce or increase the number of fledglings. Nesting in grassy habitats near road edges may prove to be “ecological traps”, attracting high densities of nesting birds, but leading to low nest success due to increased nest failure. That is why colonisation of new man-made linear habitats, such as roadsides, may be detrimental for the Crested Lark. However, we are aware that our assessment method of nest predators is limited and the data regard mainly diurnal predators, so our conclusions may not reflect the real impact of predators on nest survival. Hence, future studies using trail cameras should be initiated to identify nest predators, predator abundance, and predators’ activity patterns throughout the breeding season in different types of habitats occupied by the Crested Lark. Last but not least, further research is necessary to widen our knowledge on how factors related to human activity, e.g. field work, lawn moving, affect nest survival of this ground-nesting species.

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Appendix

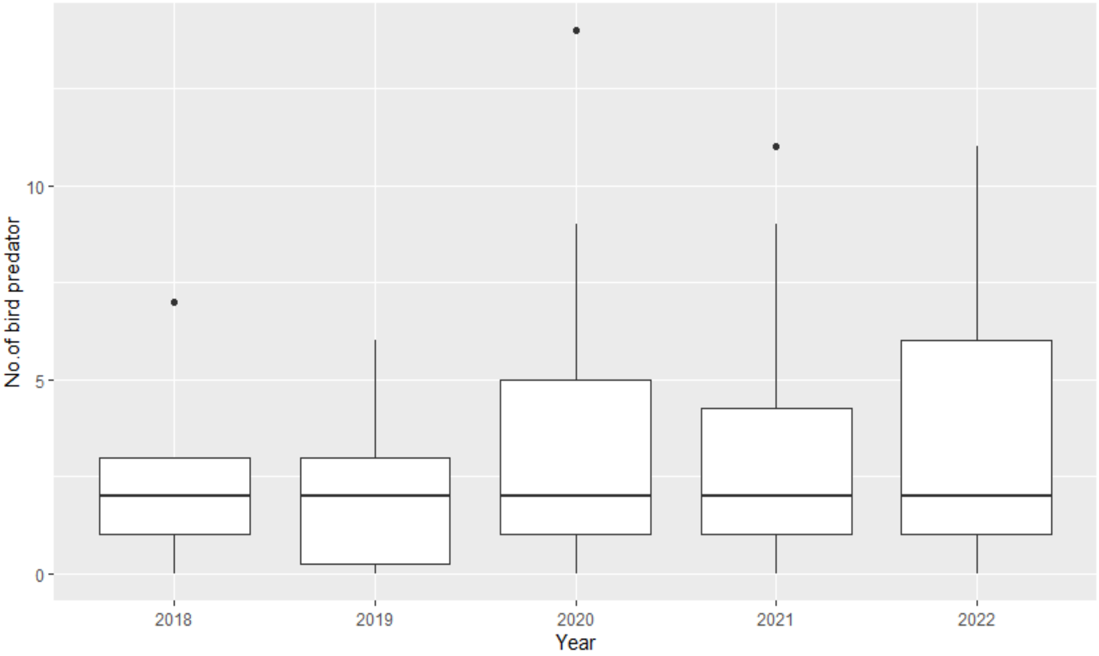
Material and methods

Differences in number of birds predator between years

```
Call:
glm(formula = Bird.pred ~ as.factor(year), family = "poisson",
    data = data)

Coefficients:
                   Estimate Std. Error z value Pr(>|z|)
(Intercept)          0.69315    0.17150   4.042 5.31e-05 ***
as.factor(year)2019  0.01653    0.21402   0.077  0.93844
as.factor(year)2020  0.44953    0.19502   2.305  0.02116 *
as.factor(year)2021  0.46827    0.19521   2.399  0.01645 *
as.factor(year)2022  0.56640    0.20718   2.734  0.00626 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for poisson family taken to be 1)
```

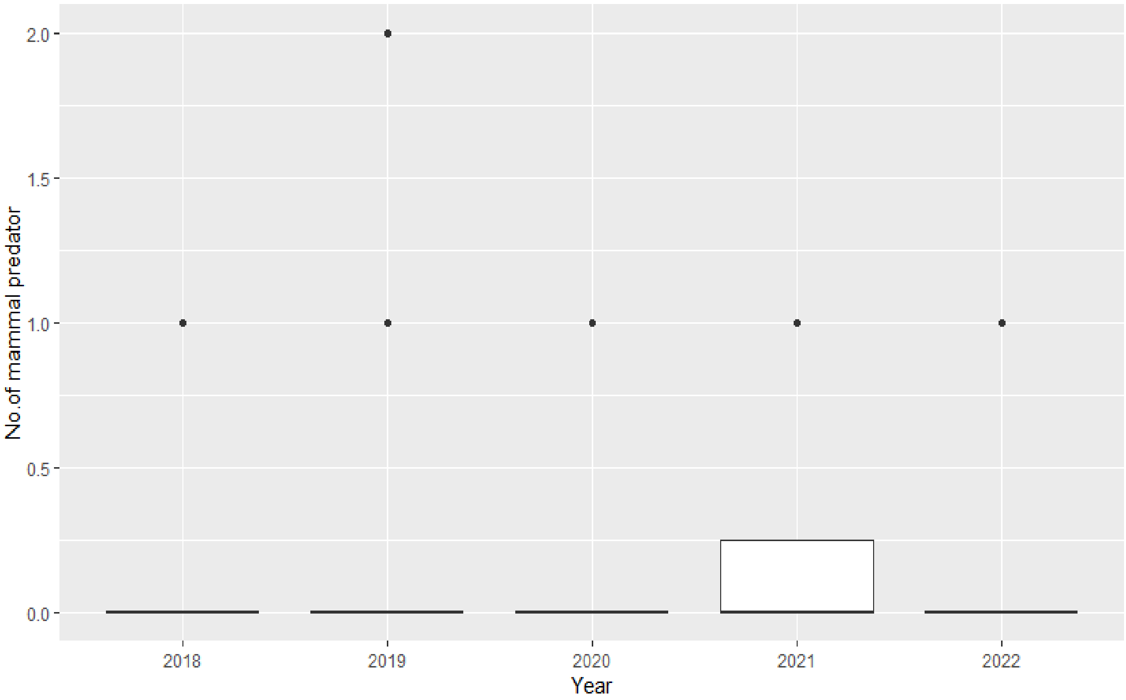


Differences in number of mammals predator between years

```
Call:
glm(formula = mamal.pred ~ as.factor(year), family = "poisson", 
    data = data)

Coefficients:
                    Estimate Std. Error z value Pr(>|z|)   
(Intercept)          -1.7346     0.5774  -3.004  0.00266 **
as.factor(year)2019   0.4128     0.6770   0.610  0.54199   
as.factor(year)2020  -0.7777     0.8165  -0.952  0.34085   
as.factor(year)2021   0.3483     0.6667   0.522  0.60135   
as.factor(year)2022  -0.2113     0.8165  -0.259  0.79579   
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for poisson family taken to be 1)
```

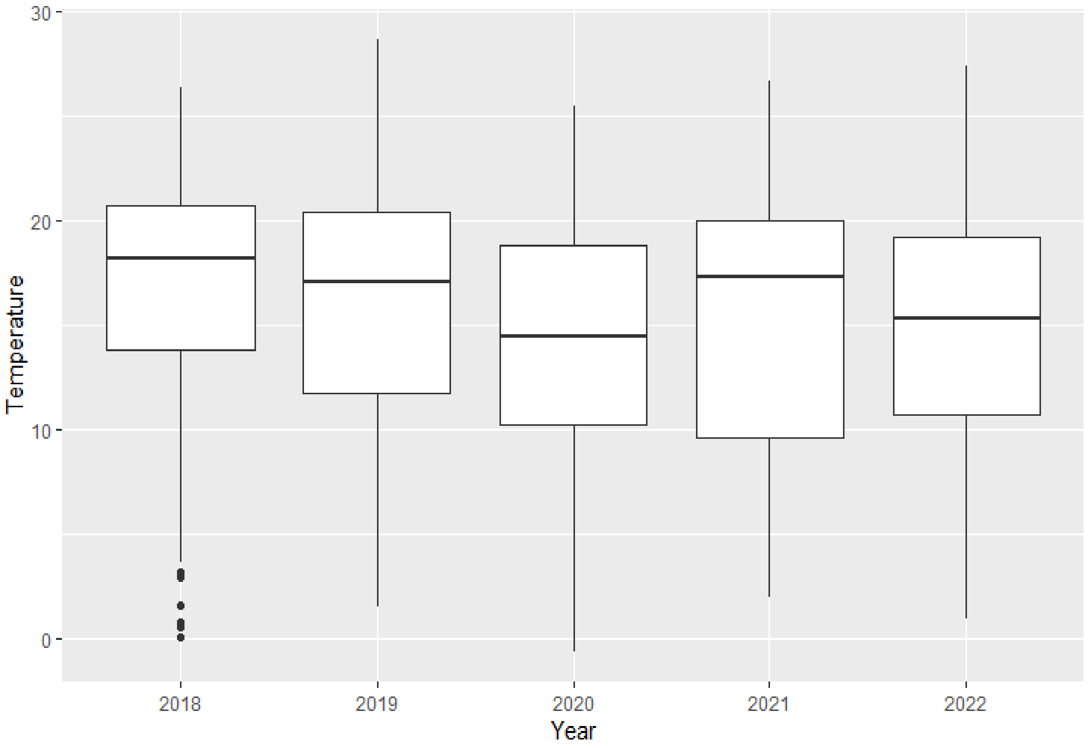


Differences in temperature between years

```
Call:
glm(formula = temp ~ as.factor(Rok), data = pogoda)

Coefficients:
                   Estimate Std. Error t value Pr(>|t|)    
(Intercept)         16.7823     0.5051  33.225  < 2e-16 ***
as.factor(Rok)2019  -0.9097     0.7143  -1.274 0.203235    
as.factor(Rok)2020  -2.5740     0.7143  -3.603 0.000335 ***
as.factor(Rok)2021  -1.8738     0.7143  -2.623 0.008894 ** 
as.factor(Rok)2022  -1.7946     0.7143  -2.512 0.012212 *  
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for gaussian family taken to be 37.5052)
```

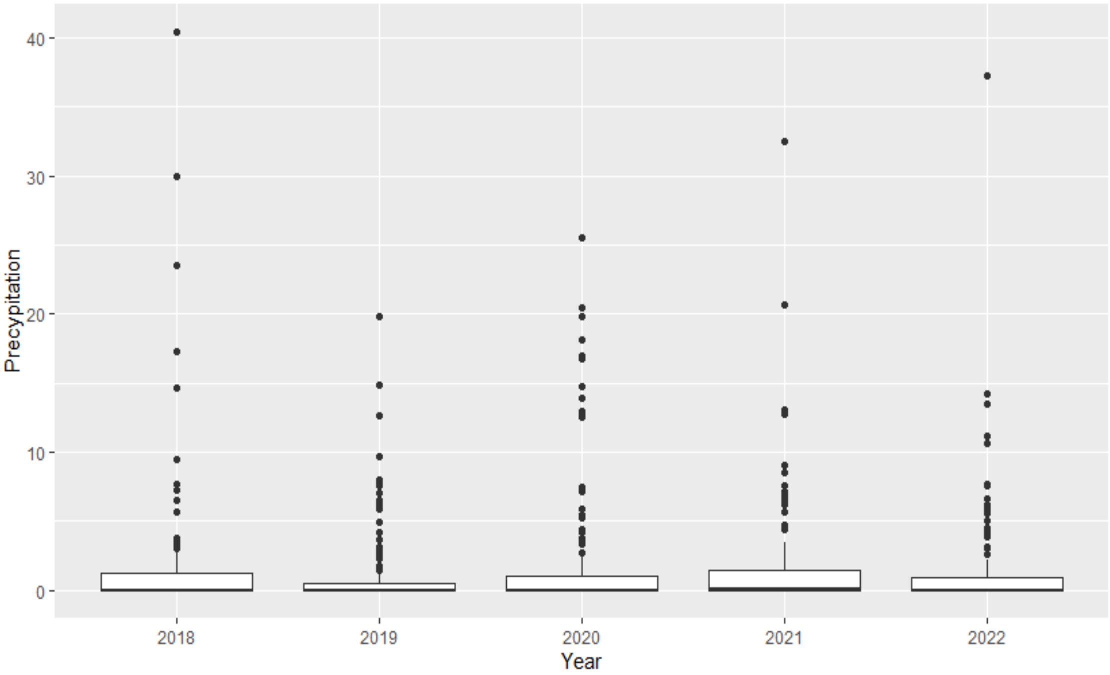


Differences in precipitation between years

```
Call:
glm(formula = opady ~ as.factor(Rok), family = "poisson", data = pogod
a)

Coefficients:
                   Estimate Std. Error z value Pr(>|z|)    
(Intercept)         0.53227    0.06321   8.421  < 2e-16 ***
as.factor(Rok)2019 -0.41476    0.10022  -4.139 3.49e-05 ***
as.factor(Rok)2020  0.11487    0.08693   1.321   0.1864    
as.factor(Rok)2021 -0.07192    0.09104  -0.790   0.4295    
as.factor(Rok)2022 -0.21206    0.09452  -2.244   0.0249 *  
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for poisson family taken to be 1)
```



Results

Alternative characterization of the nest survival for whole nesting period and eggs stage, taking into account nests with an unknown time of breeding and nests with recorded predation events. The estimation of this time for the purposes of this analysis was performed individually for each "nest". We assumed that the day when nest was found is 1st day of incubation. Two nests used in these analyzes were under recorded predator pressure.

The mean survival ratio for the whole nesting period (30 days from egg laying to fledgling) was 0.290 (95% CL: 0.186 – 0.451, n = 162) and did not differ over the five-year study period ($\chi^2 = 6.5$, df = 4, p = 0.2). The mean survival during the eggs stage (egg laying+incubation = 17 days) was 0.727 (95% CL: 0.640 – 0.827), and it also did not differ significantly between years ($\chi^2 = 5.2$, df = 4, p = 0.3), but the result was statistically higher than during the whole nesting period (Gehan–Wilcoxon test, test value = 2.43, $p < 0.01$).

6. Patterns and drivers of nestling growth in Crested Lark (*Galerida cristata*) in anthropogenically altered habitat of Central Poland

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Abstract

This study investigates factors influencing development of Crested Lark nestlings in a breeding population in central Poland on the basis of monitoring that spanned over five consecutive breeding seasons (2018–2022). Using a logistic growth function, we modelled the growth of body mass, wing chord, tarsus and head lengths, estimating such key parameters as the asymptote (A), integration constant (B), and growth rate constant (k). Additionally, the maximum growth rate was calculated to capture growth at its inflection point, thus offering insights into nestlings' developmental speed. We analysed how sex, nestling sex ratio, brood and clutch size, time of breeding, and local weather conditions influenced growth rate parameters (A, B, and k) for each measured morphological trait. We established that – despite individual variations in nestling size and growth – sex did not impact significantly most of analysed growth parameters (A, B, or k) of the measured biometrics. Both males and females reached similar asymptotic sizes and growth rates, thus demonstrating consistent developmental patterns. However, brood size turned out to affect growth negatively as larger broods were characterised by a reduced growth rate, possibly due to intensified sibling competition. Our results indicate that the development of Crested Lark nestlings is primarily driven by brood size and sibling competition, whereas other factors, i.e. sex, timing of breeding, nestling sex ratio and local weather conditions, have minor influence. Given the limited knowledge of this species' developmental patterns, our findings advance understanding of the growth rate and ecological factors that influence nestling development in anthropogenic environments of temperate climate.

Keywords: nestling growth rate, anthropogenic habitats, sex, weather, biometric modelling

1. Introduction

Nestling growth rates and developmental trajectories are critical determinants of early survival and long-term fitness, shaping competitive abilities in later life stages through territory acquisition, mate selection, and reproductive success (Lindström 1999; Metcalfe and Monaghan 2001; Bakaloudis et al. 2005). While many bird species exhibit similar developmental patterns (Verbeek 1988; Björklund 1996), their growth trajectories can vary within populations according to environmental factors, such as food availability, temperature fluctuations and habitat quality, as well as biological aspects, including brood size, sibling competition and parental provisioning strategies (Ricklefs 1979; Richner 1991). Such differences in growth trajectories provide insights as to how developmental strategies respond to environmental and biological pressures. Species with broad geographical distributions tend to exhibit particularly high variability, as local populations adapt to diverse ecological conditions that shape growth dynamics (Ndithia et al. 2017; Sofaer et al. 2018).

Nestling growth dynamics is typically described by means of three key components, i.e. the initial growth rate, growth asymptote and duration of the rapid growth phase. Each of them reflects different developmental processes and may respond uniquely to the same environmental factor (Barba et al. 1993). For instance, food availability, being a primary environmental variable, can influence all three elements simultaneously but with differing intensities. While an abundant food supply can accelerate the initial growth rate and extend the growth phase, it may also lead to higher asymptotic values by supporting a more substantial energy investment in nestling mass and structural development (Becker and Specht 1991; Klaassen et al. 1992). Conversely, limited food availability may force nestlings to achieve their asymptotic size earlier and result in reduced mass or structural size because energy allocation prioritises immediate survival (Benharzallah et al. 2015; Perez et al. 2016). Likewise, factors, such as the timing of breeding and the number of siblings can exert distinct influence on each component of the growth function. For example, differences in the timing of clutch initiation may expose nestlings to changing environmental conditions as the season progresses. Nestlings from earlier broods often benefit from favourable environmental conditions, which can enhance initial growth rates and potentially extend duration of the rapid growth phase as observed for the Common Starling *Sturnus vulgaris* (Ricklefs and Peters 1979). In contrast, later-hatched broods exposed to different resource dynamics or parental investment levels may reach lower asymptotic values as resources dwindle across the season, e.g. the Guillemot *Uria aalge,* Snow Goose *Anser caerulescens* or Cassin's Auklet *Ptychoramphus aleuticus* (Hedgren and Linnman 1979; Lepage et al. 1999; Morbey and Ydenberg 2000). The number of siblings also introduces competition for resources, which may slow the initial growth rate and reduce final asymptotic size due to limited food intake shared among nest-mates (Rickfles 2002; Kasprzykowski et al. 2015). Finally, the same factors can have sex-specific effects on growth function parameters, especially for species where environmental conditions interact differently with male and female developmental trajectories. For example, differences in parental investment or competitive dynamics within mixed-sex broods may result in distinct growth asymptotes or rates for each sex, even within a single species as demonstrated by studies on the Black-tailed Godwit *Limosa limosa*, Common Tern *Sterna Hirundo* or Whiskered Tern *Chlidonias hybrida* (Becker and Wink 2003; Loonstra et al. 2018; Banach et al. 2021). Therefore, understanding how each growth component responds to environmental conditions and biological factors provides a nuanced perspective on how external pressures shape developmental trajectories within and between species.

Among mechanisms that have been studied most frequently, there are such environmental factors as food availability (Becker and Specht 1991) and parental provisioning, which is determined by parental condition and experience (Velando 2002; Minias et al. 2012). Furthermore, among biological, i.e. intra-brood factors, studies have most often focused on the influence of variables that include brood size (Gililliand et al. 2016; Hadad et al. 2024), egg volume (Diaz-Real et al. 2016), hatching date and order (Bosman et al. 2016; Loonstra et al. 2018), and sibling sex (Becker and Wink 2003). Interestingly, while differences between sexes in growth patterns are predominantly associated with species displaying sexual size dimorphism, even species without pronounced sexual dimorphism may show sex-specific growth dynamics during the nestling period (Loonstra et al. 2018). Building on these concepts, we focused on the Crested Lark *Galerida cristata* of the family Alaudidae, which is a passerine bird with non-pronounced sexual size dimorphism. This ground nesting species is distributed widely across Eurasia and North Africa, inhabiting both natural and anthropogenic open habitats and exhibiting a high degree of ecological plasticity (Roselaar 1998; Guillaumet et al. 2008). In Poland, the Crested Lark is sedentary and typically raises multiple broods between late March and mid-August, exposing each brood to varying environmental conditions throughout the breeding season. While previous studies on the breeding biology of the Crested Lark have primarily focused on basic reproductive metrics (Labitte 1957; Lesiński 2009; Praus 2020), factors influencing nestling growth remain largely unexplored, particularly in anthropogenic habitats of temperate regions. Notably, the only prior investigation of the Crested Lark's nestling growth (Skhedy and Safriel 1992) was conducted in desert conditions, limiting broader ecological comparisons. In this study, we aim to examine growth dynamics of Crested Lark nestlings in a highly modified environment, evaluating the influence of biological and environmental factors on three key growth parameters, namely the initial growth rate, asymptotic size, and duration of the rapid growth phase. Specifically, we investigate how brood size, nestling sex, timing of breeding, and weather conditions, including temperature and humidity, impact these growth metrics. We hypothesise that growth rates may vary in response to environmental and biological pressures, with potential differences between sexes reflecting subtle developmental adaptations. To the best of our knowledge, this is the first comprehensive study to address these aspects of the Crested Lark's nestling growth, contributing to a better understanding of growth dynamics of species with minimal sexual dimorphism.

2. **Material and methods**

Study Area

The study site is located near the town of Inowrocław (52°46'55N, 18°18'36E) in central Poland. The study area of 4.6 km^2 is a human-modified rural landscape that has been recently cut through by a two-lane bypass road with adjacent grassy roadsides surrounded by intensively cultivated fields that feature wheat, rapeseed, maize and sugar beet as the main crops.

The terrain is predominantly flat with an average elevation of 80–100 m a.s.l. The region has a temperate continental climate, characterised by the average annual temperature of 8.2°C and the total yearly precipitation of about 450–500 mm. These values rank among the lowest in Poland (Bąk 2002; Kondracki 2009).

Bird data

The data were collected over five consecutive breeding seasons from 2018 to 2022. Nests were located through a systematic search of the study area and observations of bird behaviour, such as nest building or chick feeding. Nests were typically found while they were being built, during the incubation or nestling phase, and they were monitored every 2 to 4 days to record clutch initiation date, clutch size, brood size, and nest fate (fledged, depredated, abandoned). The onset of breeding (TB) was considered to be the date of the first egg laid in the nest, expressed as the number of days after 1 January. Laying dates were recorded directly for nests found before laying had begun or estimated by counting back and assuming that one egg was laid daily in clutches found during the laying period (Roselaar 1988; this study). For nests found during incubation, the laying date was calculated back from the hatching date according to a 12-day incubation period (Roselaar 1998; own data). For nests discovered during the nestling stage, laying dates were estimated according to the age of the nestlings. A nestling's age was determined either on the basis of the observed hatching date, body weight (Skhedy and Sufriel 1992) or by comparing the development of feathers with broods whose age was known, the error margin being ±1 day. The age of nestlings is expressed in days and day 1 is the hatching day. Each nestling was marked individually with a non-toxic marker pen on its bare part so as to enable its identification during consecutive controls and measurements taken every 2–4 days until it left the nest. On average (±SD), 3.2±1.43 measurements per chick were performed. Body mass (to 0.1 g) was measured with a digital scales (Ohaus CS200). The right wing chord (to 0.5 mm) was measured with a steel ruler, the tarsus length (to 0.1 mm) with callipers, and the total head length (to 0.1 mm) was also measured with callipers from the bill tip to the occipital bone. Besides, nestlings were ringed with metal and coloured alphanumerical rings. Over the five-year study, 430 chicks from 117 nests were measured overall, but only 284 chicks (from 86 nests) had at least three measurements and thus were included in the main analysis. Occasionally, when it was not feasible to measure body components with acceptable precision, these specific measurements were not included in the analysis. Consequently, the final sample size varied accordingly.

To assess the effect of weather conditions on nestling growth, daily climatic data were obtained from the Institute of Meteorology and Water Management – National Research Institute and extracted from a climate stations situated nearest to the study site. Temperature and humidity data were obtained from a station located 12 kilometres away from the centre of the study plot. Mean daily values were calculated for periods between consecutive nest inspections.

Molecular determination of the nestling's sex

In order to establish the sex of nestlings, molecular sex determination was conducted. Since 2019, blood samples have been collected from the brachial vein of nestlings older than six days and stored on FTA Whatman® Cards. DNA was extracted with the Tissue DNA Purification Kit (Eurx). The CHD gene (chromodomain helicase DNA binding), which differs in structure between Z and W sex chromosomes, was amplified using the PCR (Griffiths and Tiwari 1995). Fluorescently labelled primers P2bs-6FAM (5'-TCTGCATCGCTAAATCCTTT–3') and P8bs (5'-CTCCCAAGGATGAGRAAYTG–3') were used. The PCR reactions were conducted in 5 µL volumes with Type-it polymerase (Qiagen) and a thermo-cycling profile of 95°C for 5 min, followed by 30 cycles (95°C for 30 s, 50°C for 90 s, 72°C for 30 s) and a final elongation at 65°C for 45 min. Amplified products were diluted with 30 µL water and analysed with capillary electrophoresis in the Molecular Biology Techniques Laboratory. The obtained results were visualised with the Peak Scanner Software v1.0.

Statistical analysis

To model nestling growth, we employed a logistic growth function and described changes over time. The logistic model was:

$$y(t) = \frac{A}{1 + B \times e^{-k \times t}}$$

where y(t) represents the biometric measurement of a given individual on day *t*. Parameter A denotes the asymptote, i.e. the expected final size, B is a constant that places individuals on a common time scale and indicates the onset of rapid growth, and k is the growth rate constant (day^{-1}), which is inversely proportional to the duration of the rapid growth phase (Paillisson et al. 2008; Minias et al. 2012; Ricklefs 1979). Importantly, B does not literally represent the day on which rapid growth begins, but it is a constant in the logistic equation that, together with k, determines when the growth rate reaches its maximum (the inflection point). To find the actual day of the most rapid growth, we calculated:

$$\frac{ln\ (B)}{k}$$

To obtain growth estimates, we fitted the logistic model to the data of 284 individuals using non-linear least squares (NLS) with the nlsLM function in the minpack.lm package in R (Elzhov et al. 2016). The initial parameters were set as follows: A was initialised to the maximum observed value for each biometric measurement, B was set to 1, and k was set to 0.01.

We also calculated the maximum growth rate (g_{max}) at the inflection point of the growth curve with the following formula (Richner 1989, 1991; Banach et al. 2021):

$$g_{max} = \frac{k \times A}{4}$$

The maximum growth rate represents the highest rate at which a nestling's size or mass increases during the growth period. It occurs at the inflection point of the growth curve, where the growth rate shifts from acceleration to deceleration. This point provides a measure of how quickly a nestling reaches a substantial portion of its final size, offering an insight into its developmental speed. Higher values of g_max indicate a rapid growth, which can be advantageous for early fledging or preparing for independent survival. This metric helps to compare growth dynamics among individuals or conditions and it is sensitive to both intrinsic and extrinsic factors affecting developmental rates (Richner 1989, 1991; Banach et al. 2021). To evaluate differences between growth parameters (A, B and k) of both sexes, we used a t-test to compare growth constants between males and females.

The effects of sex and other factors on growth parameters were examined using a Linear Mixed-Effects Model. The model structure was as follows:

Y=as.factor(sex) + as.factor(clutch.size) + (mean.no.nestling) + sex.ratio + TB + humidity + temperature + (1|ID.nest)

where sex and clutch size were fixed categorical factors, and the time of breeding, sex ratio, humidity and temperature were continuous variables. The nest ID served as a random factor to account for nest-specific effects. The sex ratio was defined as the proportion of males in the brood, the clutch size as the number of eggs after laying was completed, and the mean number of nestlings equaled the number of live chicks from hatching till fledging.

Collinearity was not taken into account as all pairwise correlations between predictors remained below 0.3. Model selection relied on the Akaike's Information Criterion, which was corrected for small sample sizes (AICc), performed with the MuMIn package (Bartoń 2015). Coefficients from models with ΔAICc < 2 were averaged to finalise inference (Zuur et al. 2009).

3. **Results**

Growth patterns of mass, head, wing and tarsus lengths follow a typical S-shaped growth curve, characterised by a slow initial growth, a period of a rapid growth, and a subsequent deceleration (Fig. 1). Main growth parameters of Crested Larks are presented in Table 1. At hatching, the tarsus length was approximately one-third of the adult size, and by day 9 chicks acquired almost final size of tarsus (Fig. 1, 2). Their body weight increased tenfold during that period, enabling most nestlings to leave the nest by day 9.

Table 1 Averaged parameters (mean ± SD) of logistic models (A – asymptote, B – constant of integration, k – growth rate constant) fitted to biometrics of individual nestlings of both sexes and undetermined ones (all), and separately for males (M) and females (F); gmax – maximum growth rate calculated from B and k, N – number of measured individuals used to estimate parameters; t-test/p-value represents sex differences of particular parameters.

Biometric variable	Sex	A±SD	B±SD	k±SD	g_{max}±SD	N
Head	All	30.869±3.361	1.768±0.831	0.306±0.095	2.306±0.551	254
	M (1)	30.990±3.300	1.747±0.815	0.299±0.084	2.273±0.500	101
	F (2)	30.992±3.308	1.746±0.805	0.298±0.084	2.266±0.503	107
	t-test/p-value	-0.279 / 0.780	0.003 / 0.997	1.683/0.093		
Tarsus	All	28.123±4.688	6.050±2.885	0.423±0.102	2.909±0.526	252
	M (1)	28.279±4.601	5.868±2.618	0.415±0.089	2.883±0.491	102
	F (2)	28.359±4.609	5.853±2.588	0.413±0.091	2.871±0.495	108
	t-test/p-value	-0.138/0.889	0.247/0.804	0.215/0.829		
Wing	All	85.972±47.543	24.255±12.260	0.402±0.086	8.169±3.001	224
	M (1)	87.166±47.622	24.073±11.967	0.397±0.074	8.219±3.002	94
	F (2)	86.436±47.596	24.142±12.061	0.402±0.078	8.223±2.984	103
	t-test/p-value	-1.761/0.080	-1.739/0.084	0.192/0.847		
Mass	All	30.336±8.383	34.752±254.667	0.566±0.188	4.083±1.003	278
	M (1)	30.286±8.386	37.601±273.485	0.568±0.192	4.105±4.949	102
	F (2)	30.404±8.328	37.146±270.145	0.565±0.190	4.100±1.027	107
	t-test/p-value	-0.200/0.840	1.024/0.308	1.246/0.214		

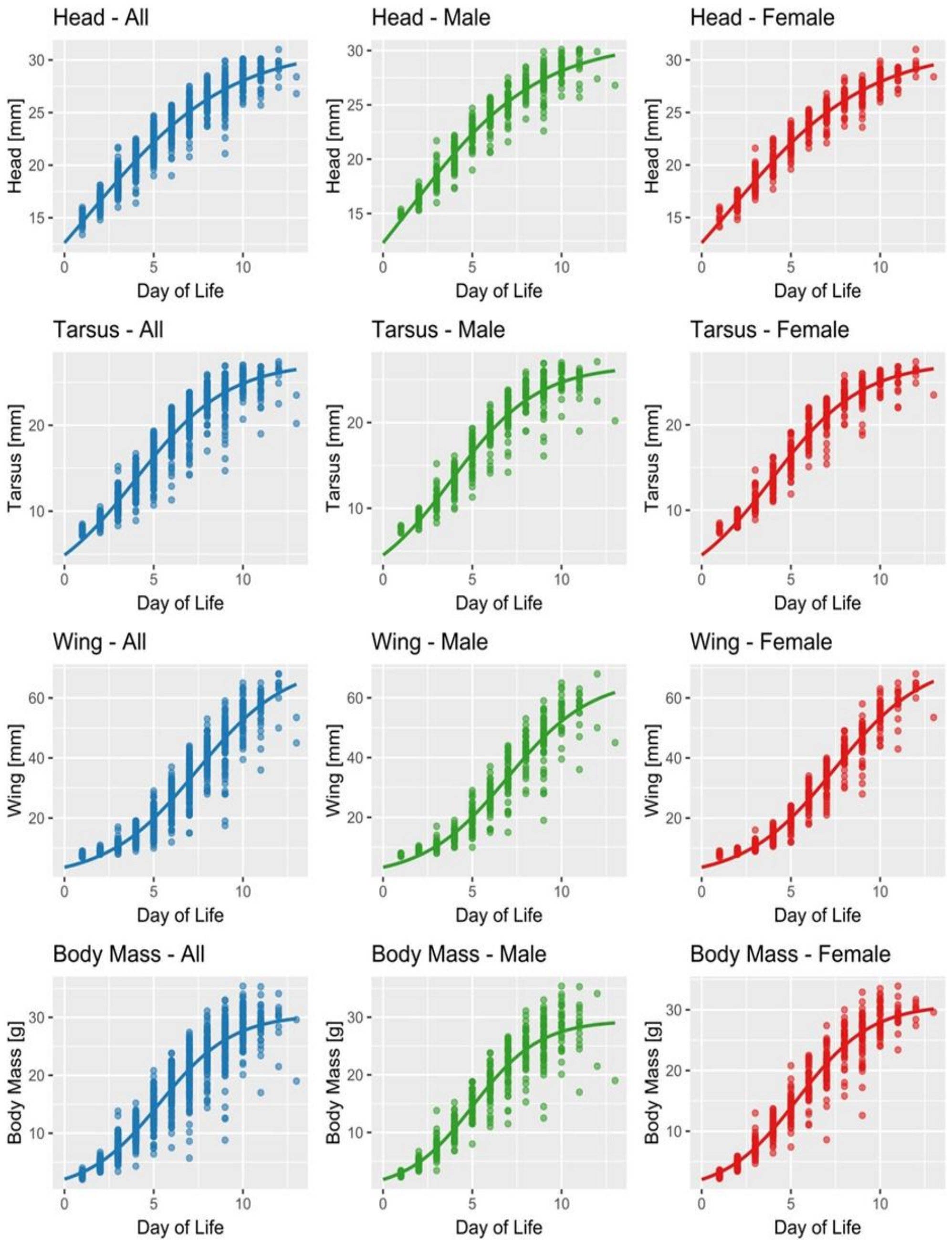

Fig. 1 Growth of Crested Lark nestlings. Points represent original measurements; lines are fitted logistic growth curves.

Parameter estimates indicated higher growth rates (larger k) for body mass compared to wing, tarsus, and head lengths (Table 1). Males and females achieved similar asymptotic sizes and displayed no notable differences within body mass or head, tarsus and wing lengths (Tables 1, 2; Fig. 1). Similarly, the maximum growth rate (gmax) did not differ significantly between sexes, indicating comparable growth dynamics in structural development. Integration constants (B) and growth rate constants (k) of all biometric variables also showed no significant differences between sexes, suggesting similar timing and duration of the rapid growth phase for males and females (Table 1).

Following our LMM approach, we also found that certain environmental and biological factors influenced specific growth parameters (Table 2). Brood size affected growth patterns of bones, as nestlings in smaller broods achieved larger final sizes, particularly with respect to head dimensions. Also, brood size negatively impacted the integration constant (B) implying that nestlings in smaller broods grew faster and more efficiently due to reduced competition for resources. Notably, humidity and temperature also influenced growth rates, particularly impacting the maximum growth rate (gmax) of tarsus and wing (Table 2). This result suggests that environmental conditions may play a role in modulating skeletal growth trajectories of nestlings.

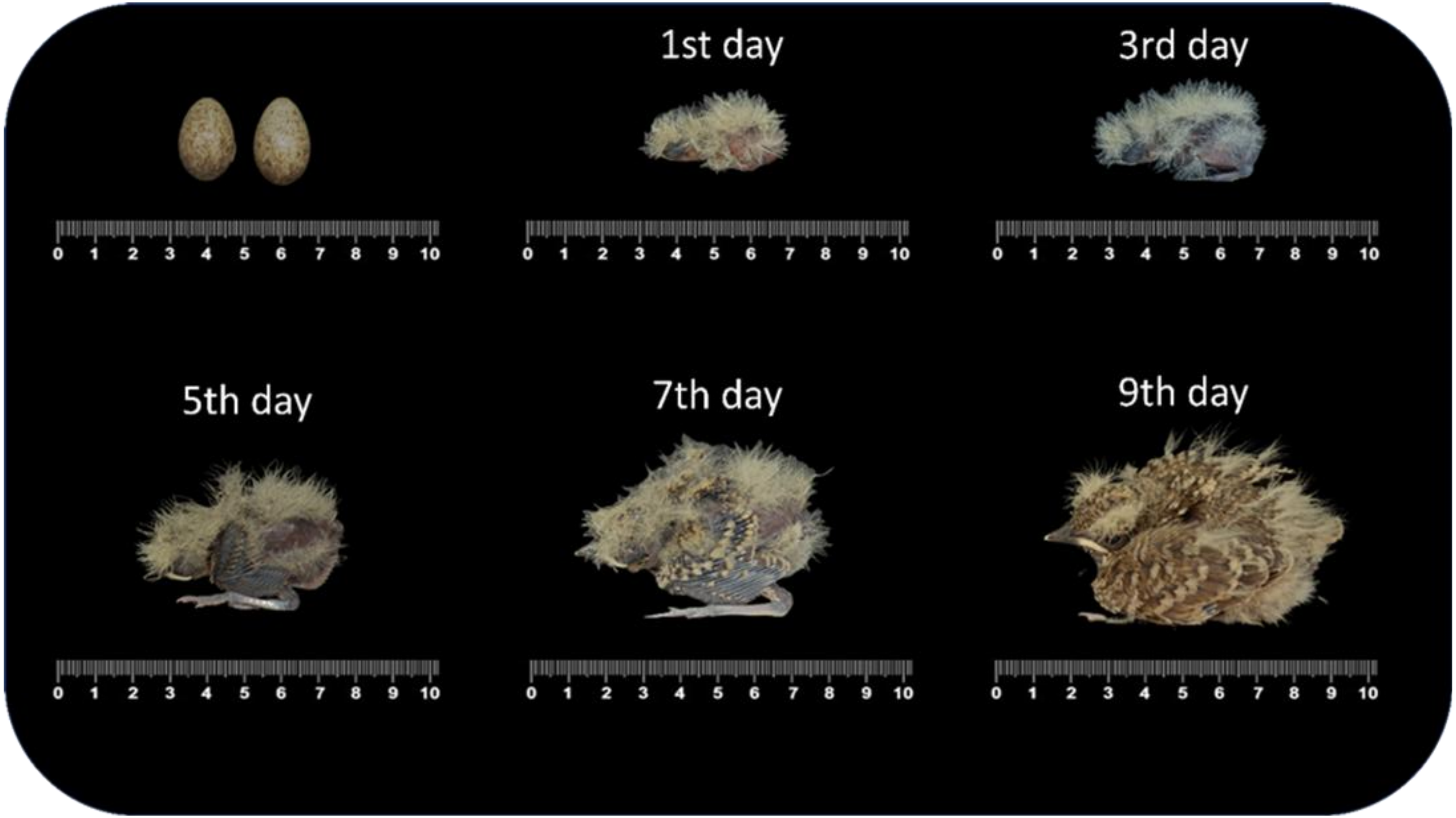

Fig. 2 Development of Crested Lark nestlings with 2-day intervals till day 9 after hatching

Table 2 Model-averaged coefficients from generalised linear mixed models used to explain variation in growth parameters of biometric variables (models with $\Delta\mathrm{AICc} < 2$ after model selection were used for averaging).

Biometric variable	Growth parameter	Fixed effects	Coefficient	SE	z	p
Head	A	Intercept	33.535	1.733	19.354	<0.001***
		Sex: female	-0.454	0.336	1.352	0.176
		Clutch size: 4	0.188	1.205	0.156	0.876
		Clutch size: 5	1.269	1.331	0.953	0.341
		Mean.no.nestlings	**-0.913**	**0.373**	**2.448**	**0.014***
		Sex ratio	-0.643	1.244	0.517	0.605
		TB	0.006	0.011	0.512	0.608
		humidity	0.016	0.482	0.323	0.746
		temperature	0.177	0.143	1.235	0.217
	B	Intercept	1.752	0.079	22.154	<0.001***
		Sex: female	-0.004	0.098	0.045	0.964
		Clutch size: 4	0.005	0.272	0.019	0.985
		Clutch size: 5	0.058	0.285	0.204	0.839
		Mean.no.nestlings	0.108	0.088	1.227	0.220
		Sex ratio	-0.138	0.294	0.471	0.638
		TB	0.001	0.002	0.425	0.671
		humidity	0.0002	0.011	0.026	0.979
		temperature	0.027	0.033	0.809	0.418
	k	Intercept	0.295	0.009	33.771	<0.001***
		Sex: female	-0.010	0.009	1.203	0.229
		Clutch size: 4	0.021	0.030	0.693	0.488
		Clutch size: 5	0.016	0.032	0.496	0.620
		Mean.no.nestlings	**0.021**	**0.009**	**2.185**	**0.029***
		Sex ratio	0.018	0.032	0.564	0.573
		TB	0.0001	0.0002	0.614	0.539
		humidity	-0.0008	0.001	0.731	0.465
		temperature	0.002	0.004	0.537	0.591
	g_{max}	Intercept	2.265	0.064	35.303	<0.001***
		Sex: female	**-0.107**	**0.052**	**2.048**	**0.041***
		Clutch size: 4	0.074	0.183	0.405	0.686
		Clutch size: 5	0.044	0.206	0.215	0.830
		Mean.no.nestlings	**0.120**	**0.056**	**2.122**	**0.034***
		Sex ratio	0.045	0.190	0.239	0.811
		TB	0.002	0.002	1.233	0.217
		humidity	-0.007	0.007	0.981	0.327
		temperature	0.019	0.022	0.866	0.387
Tarsus	A	Intercept	30.853	1.423	21.684	<0.001***
		Sex: female	-0.257	0.504	0.511	0.609
		Clutch size: 4	**-2.976**	**1.182**	**2.518**	**0.012***
		Clutch size: 5	**-3.637**	**1.257**	**2.892**	**0.004****
		Mean.no.nestlings	0.245	0.393	0.624	0.532

		Sex ratio	-0.581	0.570	1.019	0.308
		TB	0.004	0.011	0.364	0.716
		humidity	0.021	0.049	0.429	0.668
		temperature	-0.202	0.144	1.404	0.160
	B	Intercept	5.635	0.724	7.776	<0.001***
		Sex: female	-0.082	0.295	0.279	0.780
		Clutch size: 4	-0.334	0.909	0.368	0.713
		Clutch size: 5	-0.502	1.038	0.483	0.629
		Mean.no.nestlings	**0.567**	**0.287**	**1.977**	**0.048***
		Sex ratio	-0.212	0.345	0.615	0.539
		TB	0.007	0.008	0.853	0.394
		humidity	-0.022	0.037	0.588	0.556
		temperature	0.112	0.108	1.034	0.301
	k	Intercept	4.127	9.601	42.983	<0.001***
		Sex: female	-5.364	7.934	0.007	0.995
		Clutch size: 4	2.635	3.277	0.804	0.421
		Clutch size: 5	4.590	3.348	1.371	0.170
		Mean.no.nestlings	6.284	1.034	0.608	0.543
		Sex ratio	-5.011	9.613	0.005	0.996
		TB	3.526	2.920	1.208	0.227
		humidity	-2.483	1.303	1.906	0.057
		temperature	6.293	3.808	1.652	0.098
	g_{max}	Intercept	2.865	0.055	52.024	<0.001***
		Sex: female	-0.025	0.042	0.608	0.543
		Clutch size: 4	-0.013	0.189	0.068	0.946
		Clutch size: 5	0.062	0.199	0.309	0.757
		Mean.no.nestlings	0.090	0.058	1.548	0.122
		Sex ratio	-0.030	0.051	0.588	0.557
		TB	0.003	0.002	1.871	0.061
		humidity	**-0.015**	**0.007**	**2.131**	**0.033***
		temperature	0.026	0.021	1.217	0.224
Wing	A	Intercept	97.581	35.654	2.737	0.006***
		Sex: female	3.284	6.452	0.509	0.611
		Clutch size: 4	-5.621	18.169	0.309	0.757
		Clutch size: 5	-5.975	20.232	0.295	0.768
		Mean.no.nestlings	-4.186	5.890	0.711	0.477
		Sex ratio	-20.371	17.604	1.157	0.247
		TB	0.193	0.166	1.164	0.244
		humidity	0.524	0.457	1.147	0.252
		temperature	-1.467	1.262	1.162	0.245
	B	Intercept	36.431	5.536	6.580	<0.001***
		Sex: female	0.181	1.773	0.102	0.919
		Clutch size: 4	-2.429	3.911	0.621	0.535
		Clutch size: 5	-2.114	4.387	0.482	0.630

		Mean.no.nestlings	-2.156	1.280	1.685	0.092
		Sex ratio	-6.167	3.889	1.585	0.113
		TB	0.031	0.026	1.55	0.248
		humidity	0.122	0.117	1.042	0.298
		temperature	0.012	0.328	0.037	0.971
	k	Intercept	4.003	9.859	40.605	<0.001***
		Sex: female	7.209	8.152	0.884	0.377
		Clutch size: 4	1.525	3.380	0.045	0.964
		Clutch size: 5	-9.092	3.460	0.263	0.793
		Mean.no.nestlings	-6.904	4.665	1.480	0.139
		Sex ratio	1.786	3.110	0.574	0.566
		TB	1.956	1.234	1.584	0.113
		humidity	-1.508	6.337	0.238	0.812
		temperature	6.674	1.748	0.382	0.703
	g_{max}	Intercept	8.697	0.841	10.342	<0.001***
		Sex: female	-0.204	0.419	0.487	0.627
		Clutch size: 4	-0.013	1.041	0.012	0.990
		Clutch size: 5	-0.927	1.102	0.841	0.400
		Mean.no.nestlings	-0.090	0.346	0.262	0.794
		Sex ratio	-0.271	1.054	0.257	0.797
		TB	0.0004	0.009	0.039	0.969
		humidity	-0.017	0.032	0.535	0.593
		temperature	**0.224**	**0.085**	**2.628**	**0.009****
Mass	A	Intercept	37.765	2.759	13.688	<0.001***
		Sex: female	-0.402	0.733	0.548	0.583
		Clutch size: 4	-4.199	2.222	1.890	0.059
		Clutch size: 5	**-5.790**	**2.406**	**2.407**	**0.016***
		Mean.no.nestlings	-0.599	0.718	0.834	0.404
		Sex ratio	-0.333	2.505	0.133	0.894
		TB	-0.020	0.020	1.018	0.309
		humidity	0.035	0.090	0.384	0.701
		temperature	-0.071	0.271	0.263	0.793
	B	Intercept	-18.334	226.192	0.081	0.935
		Sex: female	-25.792	45.921	0.562	0.574
		Clutch size: 4	-41.661	89.617	0.465	0.642
		Clutch size: 5	-12.671	103.131	0.123	0.902
		Mean.no.nestlings	15.936	29.228	0.545	0.586
		Sex ratio	57.214	101.438	0.564	0.573
		TB	-0.496	1.461	0.340	0.734
		humidity	-0.312	3.396	0.094	0.925
		temperature	7.424	10.068	0.737	0.461
	k	Intercept	0.547	0.020	27.204	<0.001***
		Sex: female	-0.013	0.015	0.890	0.374
		Clutch size: 4	0.034	0.069	0.497	0.619
		Clutch size: 5	0.055	0.071	0.778	0.436

	Mean.no.nestlings	0.017	0.022	0.788	0.431
	Sex ratio	0.024	0.078	0.306	0.760
	TB	0.0005	0.0006	0.866	0.386
	humidity	-0.002	0.003	0.787	0.432
	temperature	0.008	0.008	0.926	0.354
g_{max}	Intercept	4.223	0.147	28.788	<0.001***
	Sex: female	-0.177	0.093	1.915	0.055
	Clutch size: 4	-0.297	0.351	0.847	0.397
	Clutch size: 5	-0.381	0.361	1.054	0.292
	Mean.no.nestlings	-0.014	0.113	0.123	0.902
	Sex ratio	-0.062	0.404	0.152	0.879
	TB	0.002	0.003	0.496	0.620
	humidity	-0.012	0.015	0.788	0.431
	temperature	0.040	0.044	0.917	0.359

4. **Discussion**

While sex had no major effect on growth dynamics, brood size and environmental factors, e.g. humidity and temperature significantly influenced growth rates and asymptotic sizes. These findings highlight the interplay between biological and environmental pressures shaping developmental trajectories of Crested Lark nestlings.

The growth pattern of Crested Lark nestlings is a classic sigmoidal curve found in other passerines (Verbeek 1988; Nidithia et al. 2017). The development is rapid (9-10 days) and nestlings leave the nest before they are capable of flight, a behaviour typical for ground-nesting species facing high predation risks (Bosque and Bosque 1995; Remeš and Martin 2002). The ability to leave the nest at an early nestling stage depends on rapid development of bipedal locomotion, which is closely tied to the growth of the tarsometatarsus bone. In our study, Crested Lark nestlings demonstrated a fast tarsal growth, fledging at an adult tarsus length (adult tarsus nominate *Cristata* – 24.3-26.5mm, Roselaar 1988, nestlings *Cristata* in this study – 24.7 mm±1.84). This pattern aligns with findings from other lark species (Donald 2004; Engelbrecht and Dikagale 2014). However, asymptotic values for head and wing lengths as well as body mass at fledging did not achieve adult dimensions (nominate adult *Cristata* – HL:37-41 mm (unpublished data), WL: 97-114 mm, BM:37-55 g, Roselaar 1988; Shirihai and Svenssson 2018), suggesting that these traits continue to grow after leaving the nest (Table 1; Fig. 2). In our study conducted in temperate conditions of Central Europe, the growth rate (k) of body mass of Crested Lark nestlings amounted to 0.566 and it was higher than 0.473 achieved by a population studied in the Negev Desert (Skhedy and Sufriel 1992; Tieleman et al. 2004), a difference that may be linked to more favourable conditions in our study area. The k-value observed in our population was also relatively high compared to lark species in other regions. Studies of primarily African lark species revealed k values ranging from 0.34 to 0.57, including the Barlow's Lark *Calendulauda erythrochlamys* barlowi (0.37; Engelbrecht and Lonzer 2009), Pink-billed Lark *Spizocorys conirostris* (0.45; Engelbrecht and Mathonsi 2012), Red-capped Lark *Calandrella cinerea* (0.34–0.54; Nidithia et al. 2017), Dupont's Lark *Chersophilus duponti* (0.508–0.531; Perez-Granados et al. 2017) and Chestnut-backed Sparrow-Lark *Eremopterix leucotis* (0.57; Engelbrecht and Dikgale 2014). A broader analysis by Tieleman et al. (2014) comparing growth constants (k) of nine lark species revealed a variation between 0.307 and 0.622 along a gradient from desert to temperate environments. This pattern suggests that increasing aridity is associated with a slower growth of nestlings. We speculate that a relatively high k value for body mass in our study may be attributable to the availability of water bodies, retention-infiltration ponds and irrigation canals being part of road infrastructure in the study area. These features are likely to promote development of diverse arthropod communities (Thornhill et al. 2017; Straka et al. 2020), providing protein-rich prey, such as herbivorous insects and their larvae (Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, and Orthoptera), which fosters faster nestling growth.

Our findings reveal that sex does not have significant influence on growth parameters (A, B, and k) of the measured biometric variables, including body mass, head, tarsus and wing lengths. Both male and female nestlings achieved similar asymptotic size, with no notable differences within these traits, suggesting comparable growth trajectories of structural dimensions for both sexes. Additionally, the maximum growth rate (gmax) showed no significant variation between males and females, indicating that both sexes gained body mass and reached structural benchmarks at similar rates. The constants of integration (B) and growth rate (k) also did not differ significantly between sexes with regard to all measurements, indicating that the timing and duration of the rapid growth phase are consistent, regardless of sex. This uniformity in growth dynamics implies that both male and female nestlings follow parallel developmental patterns, reflecting similar physiological growth strategies under stable environmental conditions. This conclusion is further supported by our model-based approach. Sexual dimorphism in growth patterns appears to be less pronounced in the studied species than among other species, particularly as regards primary biometric measurements observed among nestlings (Vedder et al. 2005). While both male and female nestlings exhibited rapid development, pressures shaping their growth may not strongly favour size differences between sexes, unlike patterns observed in more dimorphic species.

Our study also found that nestlings from smaller broods reached larger final sizes compared to those from larger broods, a pattern also documented in other avian studies (e.g. Sicurella et al. 2014; Vedder et al. 2017). Smaller broods, facing less intense competition for parental provisioning, have an advantage in achieving larger body sizes, particularly with respect to body mass and skeletal traits. This relationship is often attributed to decreased energy expenditure on competitive interactions among siblings, allowing for higher nutrient assimilation in smaller broods (Stenning 1996; Yosef et al. 2013).

These findings are parallel to previous studies suggesting that a reduced brood size can positively affect the overall chick growth rate by alleviating competitive pressures for limited parental resources (Gombobaatar et al. 2009). However, our results contrast with those reported for a population in the Negev Desert, where brood size did not influence the linear growth rate of Crested Lark nestlings (Skhedy and Sufriel 1992). This discrepancy may reflect differences in resource availability and parental strategies in different habitats. In arid environments where food resources are more constrained, growth rates may be uniformly limited across broods, regardless of size. In contrast, temperate conditions in our study area are likely to provide higher food availability, enabling smaller broods to benefit from reduced sibling competition and thus achieve faster growth.

Interestingly, our findings also differ from studies of other larks from temperate regions, such as the Skylark, where chick growth rates were higher in larger broods (Donald et al. 2001). This divergence may be attributed to differences in life history strategies and provisioning patterns between species. Crested Larks, for example, may adopt a strategy that prioritises growth uniformity within broods, ensuring that all offspring reach adequate fledging size under variable environmental conditions. Such strategies could buffer against fluctuations in food availability or environmental stressors, which may disproportionately impact larger broods. However, our study revealed a pattern in which the timing of breeding had no significant impact on the majority of growth parameters. Contrary to our predictions and prior research findings (Segura and Palacio 2017), nestlings that hatched later in the breeding season in more favourable weather conditions did not exhibit accelerated growth compared to nestlings from earlier broods. Additionally, unlike previous studies suggesting a decline in growth rates of later breeding (Penteriani et al. 2005; Dalbeck and Heg 2006), our results also did not show such relations. This lack of significant intra-seasonal changes in nestling growth may have several possible explanations. Firstly, it could be ascribed to consistent food resources available to breeding pairs throughout the season or better utilisation of temporal availability of particular invertebrate resources. When specific prey availability declines, adults may switch diets, ensuring consistent provisioning rates for both early and late broods (Naef-Daenzer et al. 2000). In regions with fluctuating food availability, for example those impacted by seasonal changes in prey abundance, pairs that breed later may struggle to meet energy demands of rapidly growing nestlings (Newton 1976; Bogdanova and Nager 2008). In contrast, our findings suggest that stable food resources can buffer against such seasonal effects, allowing nestlings to maintain steady growth rates regardless of hatch timing. Secondly, adult birds may mitigate the impact of deteriorating conditions during the course of the breeding season by increasing food delivery rates to compensate for spatial and temporal variations in habitat quality (Kadin et al. 2016; Auer and Martin 2017; Senécal et al. 2021). This compensation strategy enables parents to maintain the number and the quality of nestlings throughout the season (Leugger-Eggimann 1997; Forbes and Mock 2000). Thirdly, in the early and late season, brood sizes of the Crested Lark are smaller than during the peak of the nesting period (May, June) (Lesiński 2009; own data). Smaller broods may mitigate negative effects of food availability, poor nutrition, or suboptimal temperatures by reducing competition for resources. Thus, the lack of intra-seasonal changes in the chick growth rate may provide a breeding strategy that ensures high-quality nestlings throughout the breeding season, regardless of whether nest failure rates (especially predation) are constant or variable during the nesting period. In our study, a predicted growth of body mass may reflect species-specific developmental strategies where sexual dimorphism of the mass may develop post-fledging, rather than during the nestling period (Gwiazda and Ledwoń 2015). A slower growth of body mass when compared to skeletal structures in other studies of similar avian species supports this idea, as wing and tarsus lengths are often fully developed by fledging, while body mass may continue to fluctuate (Penteriani et al. 2005; Becker and Ludwigs 2004). This developmental strategy may allow fledglings to prioritise structural development, ensuring mobility and predator avoidance, while continuing to accumulate body reserves after leaving the nest.

Interestingly, environmental factors, such as humidity and temperature, influenced only the maximum growth rate of the tarsus and wing contrary to studies on owlets and other raptors where climate variability impacts food availability, potentially slowing growth (Bettega et al. 2011; Yosef et al. 2013). Our results might suggest that in our study site, either these environmental factors do not reach extremes that would affect growth or ample food resources mitigate any potential impacts. Previous research has shown that regions with abundant food, can buffer nestlings against detrimental effects of fluctuating weather conditions on the growth rate (Ledwoń and Neubauer 2017).

In conclusion, our findings indicate that while some degree of sexual dimorphism may be present among Crested Larks, it does not manifest strongly in growth parameters measured during the nestling stage. Contrary to our predictions, the Crested Lark does not show variation in nestling growth rates throughout the breeding season in temperate climate conditions of Central Europe. Factors such as clutch size and brood composition influence growth more significantly than sex alone, with environmental stability likely to enable both sexes to reach similar developmental milestones. Overall, our study highlights how environmental conditions and sibling competition may allow for equal growth opportunities for both sexes. These results lay a foundation for future research on how local adaptations influence growth dynamics of passerine species. Given the limited knowledge of detailed nestling developmental patterns and geographic variations of growth parameters of the Crested Lark, this study provides valuable results suitable for further large-scale intra-specific comparisons.

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7. Podsumowanie

Zebrane dane i przeprowadzone na ich postawie analizy pozwoliły na potwierdzenie, że tereny powstałe wraz z budową dróg szybkiego ruchu mogą być ważnym siedliskiem lęgowym dzierlatki, zwłaszcza w jednorodnym krajobrazie rolniczym. Uzyskane wyniki przyczyniły się także do scharakteryzowania parametrów rozrodu oraz do poszerzenia wiedzy na temat mało poznanych aspektów biologii lęgowej tego gatunku.

W obrębie analizowanego siedliska dzierlatka zakładała gniazda głównie w przydrożnych terenach trawiastych, w niewielkiej odległości od drogi. Zaobserwowano wyraźną tendencję do orientowania wejścia do gniazda w kierunku północno-wschodnim. W warunkach centralnej Polski sezon lęgowy trwał od trzeciej dekady marca do drugiej dekady sierpnia. Stanowiska lęgowe dzierlatek były rozmieszczone skupiskowo w obrębie większych powierzchni trawiastych, porastających wyspy rond i węzłów drogowych. Parametry rozrodu tj. sukces lęgowy, wielkość zniesienia, liczba piskląt opuszczających gniazdo były zbliżone do wartości notowanych w populacjach zasiedlających tereny zurbanizowane Europy Środkowej.

Analizy przeżywalności wykazały, że najbardziej krytyczny moment dla przeżycia zawartości gniazda występował pod koniec okresu inkubacji i w pierwszych dniach po wykluciu piskląt. Prawdopodobieństwo przeżycia lęgu było ponad dwukrotnie wyższe na etapie jaj niż na etapie piskląt. Głównymi czynnikami wpływającymi na przeżywalność lęgów były: termin rozpoczęcia lęgu, temperatura powietrza oraz odległość gniazda od drogi. Lęgi rozpoczynane później w sezonie oraz zlokalizowane dalej od krawędzi jezdni miały wyraźnie większe szanse na zakończenie się sukcesem.

Pisklęta dzierlatek, podobnie jak u innych gatunków skowronków, charakteryzowały się szybkim tempem wzrostu. Od momentu wyklucia do dziewiątego dnia życia masa ciała piskląt zwiększała się dziesięciokrotnie, a długość skoku osiągała wartości porównywalne z dorosłymi osobnikami. Płeć piskląt nie miała istotnego wpływu na większość analizowanych parametrów wzrostu. Tempo wzrostu piskląt było jednak istotnie zależne od liczebności rodzeństwa - większe zniesienia wiązały się z większą konkurencją wewnątrz lęgową, co mogło wpływać na rozwój poszczególnych osobników.

Uzyskane wyniki mogą mieć praktyczne zastosowanie w monitoringu liczebności oraz produktywności populacji a także badaniach porównawczych na szeroką skalę. Ponadto mogą być wykorzystane w planowaniu działań ochronnych tego gatunku, szczególnie w kontekście siedlisk antropogenicznych. Ochrona dzierlatki gniazdującej w siedliskach przydrożnych powstałych wraz z budową autostrad i dróg ekspresowych powinna być realizowana przede wszystkim przez zachowanie otwartych terenów porośniętych niską i słabo zwartą roślinnością trawiastą oraz poprzez ograniczenie częstotliwości koszenia i dostosowanie terminu tego zabiegu do okresu lęgowego. Pozwoli to na ograniczenie strat lęgowych nie tylko badanego gatunku ale innych gatunków ptaków krajobrazu otwartego (tj. skowronek *Alauda arvensis*, potrzeszcz *Miliaria calandra*, pliszka siwa *Motacilla alba*, pliszka żółta *Motacilla flava*) wykorzystujących przydrożne tereny jako siedliska lęgowe.

Załączniki

Załączone publikacje oraz oświadczenia doktoranta i współautorów

Poznań dnia 26.09.2025

Dr Ewa Kosicka
Zakład Bioenergetyki,
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Oświadczenie o współautorstwie i wkładzie w publikację naukową

Mój wkład w powstanie manuskryptu:
Sandecki R., Kosicka E., Kosicki J.Z. Patterns and drivers of nestling growth in Crested Larks (Galerida cristata) in anthropogenically altered habitat of Central Poland, polegał na:

- przeprowadzaniu analiz związanych z determinacją płci piskląt,
- nauczaniu doktoranta wykonywania tych analiz oraz nadzorowaniu jego pracy laboratoryjnej.

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Oświadczenie o współautorstwie i wkładzie w publikację naukową

Mój wkład w powstanie publikacji:
Sandecki R., Kosicki J.Z. 2024. Nest survival of Crested Lark Galerida cristata in intensively used habitats in Central Poland. Journal of Ornithology 165: 947–958, polegał na:

- dostosowaniu koncepcji badawczej doktoranta do dostępnych możliwości metodycznych,
- wykonaniu części analiz statystycznych oraz weryfikacji analiz przeprowadzonych przez doktoranta,
- merytorycznej i technicznej korekcie rozdziałów: „Wstęp", „Materiały i metody", „Wyniki" oraz „Dyskusja" przygotowanych przez doktoranta.

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- dostosowaniu koncepcji badawczej doktoranta do dostępnych możliwości metodycznych,
- wykonaniu nieliniowych modeli wzrostu piskląt oraz weryfikacji analiz przeprowadzonych przez doktoranta,
- merytorycznej i technicznej korekcie rozdziałów: „Wstęp", „Materiały i metody", „Wyniki" oraz „Dyskusja" przygotowanych przez doktoranta.

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Oświadczenie o współautorstwie i wkładzie w publikację naukową

Mój wkład w powstanie manuskryptu:
Sandecki R., Kosicki J.Z. Breeding Biology and Ecology of the Crested Lark Galerida cristata along Expressway road in a Homogenized Agricultural Landscape, polegał na:

- dostosowaniu koncepcji badawczej doktoranta do możliwości metodycznych,
- weryfikacji analiz przeprowadzonych przez doktoranta,
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Mój wkład w powstanie publikacji:
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- koncepcja powstania artykułu
- zebraniu całości materiału w terenie
- wstępnej analizie statystycznej i zestawieniu wyników
- czynnym udziale w pisaniu wszystkich części pracy.

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Poznań dnia 26.09.2025

Oświadczenie o współautorstwie i wkładzie w publikację naukową

Mój wkład w powstanie manuskryptu:
Sandecki R., Kosicka E., Kosicki J.Z. Patterns and drivers of nestling growth in Crested Larks (Galerida cristata) in anthropogenically altered habitat of Central Poland, polegał na:

- koncepcja powstania artykułu
- zebraniu całości materiału w terenie
- udział w pracach laboratoryjnych związanych z analizami dotyczącymi determinacji płci piskląt
- wstępnej analizie statystycznej i zestawieniu wyników
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Poznań dnia 26.09.2025

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Journal of Ornithology
https://doi.org/10.1007/s10336-024-02183-y

ORIGINAL ARTICLE

Nest survival of Crested Lark (*Galerida cristata*) in intensively used habitats in Central Poland

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Received: 7 November 2023 / Revised: 18 March 2024 / Accepted: 23 April 2024

Abstract

Breeding success of birds depends on survival during two critical stages of the reproductive period: First, egg laying and incubation, and then nestling and fledgling. This essential element of avian life history mirrors an evolutionary adaptation of parents to existing environmental conditions. The main factors that determine nest survival involve weather, predation and sibling competition. Despite numerous studies documenting their impact on breeding success, only a few have analysed the issue with regard to ground-nesting birds and estimated their survival functions. Therefore, we decided to examine nest survival probability of the Crested Lark (*Galerida cristata*) in a population that occupies newly established roadside habitats in Central Poland. The analysis is based on 141 nests monitored between 2018 and 2022. We found that the mean survival probability of the whole nesting period was 0.376, and it was higher during the egg stage (0.836) than during the nestling period (0.392). The Cox proportional hazards model shows that nest survival in the nestling stage is mainly affected by the time of breeding and the distance from the road edge, and also by mean temperature of the whole nesting period. In other words, the probability of a brood failure in the nestling stage decreases as the breeding season advances, whereas it increases among nests located closer to the road edge. Furthermore, during the whole nesting period, nest failure decreases as the temperature rises. Our study suggests that the Crested Lark, being a multi-brood and thermophilic species inhabiting temperate regions, may benefit more if its nesting attempts begin later during the season when breeding conditions become more favourable. However, we also take into consideration a hypothesis that nesting in grassy habitats near road edges may prove to be an ecological trap, attracting high densities of nesting birds but leading to their low nest success.

Keywords *Galerida cristata* · Linear habitats · Nest survival · Roadside

Zusammenfassung

Überleben im Nest: Haubenlerchen (*Galerida cristata*) in intensiv genutzten Habitaten in Zentralpolen

Der Bruterfolg von Vögeln hängt vom Überleben in zwei kritischen Phasen während der Fortpflanzung ab: die erste ist die Eiablage und das Ausbrüten der Eier, die zweite die Aufzucht der geschlüpften Vögel bis zum Ausfliegen. Diese wesentlichen Merkmale im Leben eines Vogels spiegeln eine evolutionäre Anpassung der Eltern an bestehende Umweltbedingungen wider. Die wichtigsten, für das Überleben im Nest ausschlaggebenden Faktoren sind dabei das Wetter, Nesträuber und die Konkurrenz unter den Geschwistern. Trotz zahlreicher Studien über deren Auswirkungen auf den Bruterfolg haben sich nur wenige mit dieser Thematik bei bodenbrütenden Vögeln befasst und deren Überlebenschancen eingeschätzt. Deshalb wollten wir die Überlebenswahrscheinlichkeit im Nest bei einer Haubenlerchen-Population (*Galerida cristata)* in einem von neu angelegten Straßen durchzogenen Habitat in Zentralpolen untersuchen. Grundlage der Studie waren 141 Nester, die zwischen 2018 und 2022 überwacht wurden. Wir ermittelten über die gesamte Nistperiode hinweg eine durchschnittliche

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Communicated by F. Bairlein.

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Überlebenswahrscheinlichkeit von 0,376, die mit 0,836 während des Eistadiums höher war als während der Nestlingszeit (0,392). Das Cox-Proportional-Hazards-Modell zeigt, dass das Überleben der Jungvögel im Nestlingsstadium hauptsächlich von der Dauer des Brütens, der Entfernung von den Straßenrändern sowie von der Durchschnittstemperatur während der gesamten Brutphase abhängt. Mit anderen Worten: die Wahrscheinlichkeit eines Brutausfalls im Nestlingsstadium nimmt mit fortschreitender Brutsaison ab, während sie bei Nestern näher am Straßenrand steigt. Außerdem nimmt die Zahl der Nestausfälle während der gesamten Brutzeit mit steigender Temperatur ab. Unsere Studie weist darauf hin, dass die Haubenlerche als mehrbrütige, wärmeliebende und in gemäßigten Regionen lebende Art eventuell eher davon profitiert, mit ihren Brutversuchen später in der Saison zu beginnen, wenn die Bedingungen dafür günstiger werden. Wir halten es aber auch für möglich, dass sich das Nisten in grasbewachsenen Lebensräumen in Straßennähe als ökologische Falle erweisen könnte, die zwar zu einer hohen Dichte nistender Vögel anlockt, ihnen aber nur einen geringen Nesterfolg beschert.

Introduction

Nest survival is a parameter of the adaptation of birds, reflecting their reproductive success, which subsequently regulates the dynamics of the population size (Newton 1998; Cresswell 2010). It can be governed by predation and weather as keys factors affecting nest failure, especially among ground-nesting species (Newton 1993; Wright et al. 2009; Martin et al. 2017; Reif et al. 2023). Since parents' adaptation to ensure nest survival is under strong pressure from natural selection (Lack 1968; Martin 1995), it is not surprising that birds have developed many behavioural adaptations that ensure their reproductive success. Anti-predatory strategies of ground-nesting birds include a selection of a nesting place with sufficient concealment from predators (Mallord et al. 2007; MacDonald et al. 2016), active defence, attack and distraction of potential predators (Gómez-Serrano et al. 2017), repetition of broods in the case of loss (Lesiński 2009; Gates et al. 2013), and shorter time spent by chicks in the nest (Martin et al. 2011; Remeš et al. 2020). Nest survival is also influenced by weather (Chmura et al. 2018; Grudinskaya et al. 2022), because until nestlings develop their thermoregulatory ability (Starck and Ricklefs 1998), episodes of cold weather, such as a sharp temperature and/or precipitation drop, can significantly reduce the number of nestlings in the nest and consequently shape breeding success. Therefore, parental fitness is enhanced by well-hidden nests that attenuate the sounds of chicks begging for food, their smell and movement, and by their ability to balance the time spent on searching for food and warming chicks, especially during unfavourable weather (Auer and Martin 2017; Lejeune et al. 2019).

Although there are numerous studies documenting relationships between predation, weather and nest survival, there are no unambiguous patterns of these relationships with regard to ground-nesting birds living in open habitats. A good example is the family of larks (*Alaudidae* spp.), which may be an important indicator value of avian diversity not only in grassland, steppe or traditional habitats, but also in many previously degraded open spaces (Han et al. 2023). Lark broods are subject to strong predation and weather pressure (Donald et al. 2002; Praus et al. 2014; de Zwaan et al. 2019), as a result of which only 20% to 30% turn out to be successful (Suarez and Manrique 1992; de Juana et al. 2004; Praus and Weidinger 2010; Mwangi et al. 2018). Thus, despite these achievements in understanding nest survival of larks, all earlier studies quantified reproductive success exclusively as a binary success vs. failure variable and thus did not take gradual changes in egg or nestling number into account. This classic approach focuses only on nest success and nest failure, but it entirely disregards gradual declines in brood size that may result from predation and (even more likely) adverse weather. Nest survival may vary significantly during different nesting stages. Many studies on nesting passerines, including larks, suggest that during the eggs stage nests tend to have a higher survival rate than in the nestling period (Shkedy and Safriel 1992; Praus 2020; Golawski et al. 2023), but others have found the opposite (Mitrus and Soćko 2008), also showing differences occurred even within the same species (Mallord et al. 2008; Praus et al.2014). It is likely that multiple factors influence age-specific patterns of nest survival. Thus, estimating phase-specific (egg and nestling phases) survival and pinpointing the critical moment of survival during a nesting attempt may increase our understanding of breeding success limitations in a particular habitat and be essential for developing adequate conservation strategies (Zaremba et al. 2020). So far, no detailed research has been conducted on the Crested Lark (*Galerida cristata*) with regard to this aspect, and studies on this species focused mainly on breeding biology (Lesiński 2009; Praus 2020) and habitat selection (Šímová et al. 2015; Lisiecki et al. 2020; Chiatante 2022).

The Crested Lark is a small, mainly sedentary bird species belonging to larks *Alaudidae* family. This species, which features many subspecies, has a wide distribution ranging from north central Africa throughout Asia Minor to Central Asia and Europe (Guillaumet et al. 2006). Originally, it inhabited dry warm open areas with very low and sparse vegetation, for example semi-deserts and steppes, but it has also adapted to various human-modified landscapes, such as open farmland, urban settlements and outskirts, railway yards, airfields and roadsides (Roselaar 1988; BirdLife

International 2023). At present, its population is decreasing across many parts of Europe (Birdlife International 2023) and a widespread decline was recorded during the second half of 20th and at the beginning of the twenty-first century (de Juana et al. 2004), a trend whose exact reasons are unknown and require urgent in-depth studies.

The Crested Lark is a ground-breeding open-cup nester. At our study site in Central Poland, the species breeds from the end of March to mid-August, having two to three broods per season. In this paper, we show the results of our analysis of the Crested Lark's nest survival on the basis of regular nest inspections over a five-year period. We examine relationships between nest survival (eggs/chicks), weather conditions, and predatory pressure during a breeding season.

Our study aims to: (1) describe nest survival of the Crested Lark in intensively used habitats during the egg incubation and nestling stages; (2) establish the critical period of the reproductive cycle that influences reproductive success; (3) analyse how weather and predation pressure affect reproductive success during the incubation and nestling stages. In this analysis, we expect predation pressure to be relatively constant over years in monotonous landscapes (e.g., Kosicki et al. 2016). Moreover, since Crested Larks are evolutionarily adapted to relatively predictable weather on the continental steppe in spring and summer, they may be particularly sensitive to more fluctuating weather conditions in their recently occupied ranges in Central Europe, which are further exacerbated by increasing weather fluctuations resulting from climate change (Pérez-Granados et al. 2023; Tscharntke and Batáry 2023). Therefore, we hypothesise that the reproductive success of the Crested Lark is more dependent on weather conditions than on predation pressure.

Materials and methods

Study area

The study was conducted in Central Poland, a region which is dominated by flat landscape with the average elevation of 80 m to 100 m a.s.l. It is characterised by temperate continental climate with the average annual temperature of 8.2 °C and the so-called "rain shadow", i.e. annual precipitation of about 500 mm, which is lower than in other regions (Kondracki 2009).

The surveyed population of the Crested Lark lives in roadside habitats along a bypass road round the town of Inowrocław (52°46′55N, 18°18′36E, Fig. 1). The study area of 4.6 km^2 is parallel to a dual carriageway. Since the road was built between 2014 and 2019, it is a relatively new element of the landscape, which has changed from arable land to regularly mown grassland. Along its entire length (25.1 km), the immediate surroundings of the bypass include service roads, lanes of grassy vegetation interspersed with planted shrubs and small trees as well as adjacent arable fields with a varied crop structure, mainly winter wheat, rapeseed, maize and sugar beets.

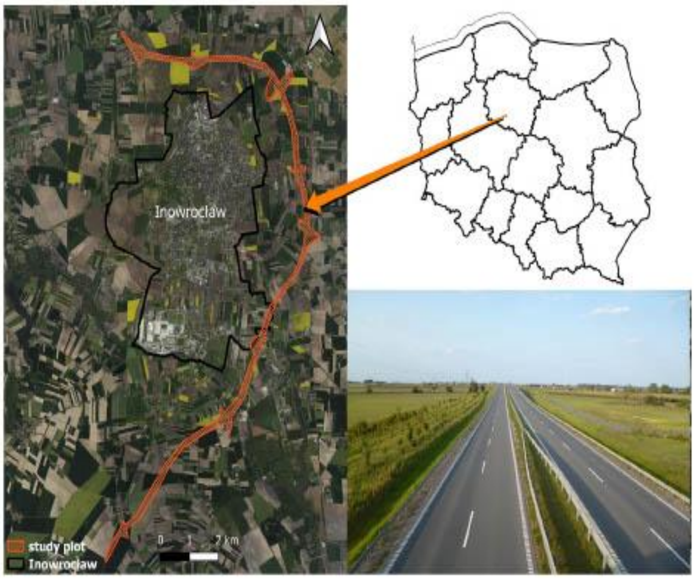

Fig. 1 Location of the study site and a general view of the bypass road located in agricultural landscape in Central Poland

Bird data

The data were collected from mid-March to mid-August in five consecutive breeding seasons between 2018 and 2022. Nests were spotted through a systematic search of the area along the road and associated structures by means of flushing incubating females, and observing adults carrying nesting material or food for the chicks. Once a nest was found, it was regularly inspected at intervals of two to four days to observe its content and status. During the five-year period, each nest was inspected on average (±SD) 5.96±3.08 times. During the last inspection, nestlings were ringed with metal and coloured alphanumerical rings.

When a nest was found during the egg-laying stage, we calculated the time of the clutch initiation on the basis of the number of eggs, assuming that one egg per day was laid (Roselaar 1988; de Juana et al. 2004). When a nest was discovered during incubation, the date of the first egg laying was determined by back-dating (since hatching) using a 12-day incubation period. If a nest was found during the advancement brood, we weighed and measured the nestlings and estimated their age according to the age–body weight relationship (Shkedy and Safriel 1992). We assumed that the maximal brood duration was 30 days, including the egg-laying and incubation period (17 days) and the nestling stage (13 days) (Roselaar 1988; de Juana et al. 2004).

By nesting success, we meant a nest that produced at least one fledgling aged at least nine days, which is a minimum age for leaving the nest (de Juana et al. 2004). Also, when the last inspection revealed adult birds feeding the chicks outside the nest or showing anxiety if an observer appeared in the nest's vicinity, we considered it as a nesting success. In our analysis, we included successful nests, nests that were totally lost, i.e. all eggs had failed or all nestlings had died, as well as those whose number of nestlings decreased between inspections. We excluded from the analysis nests with a brood destroyed by a predator as documented by trail cameras (two cases) and also nests that were destroyed (nine) or abandoned (ten) at the incubation stage without the possibility of determining the approximate date of clutch initiation. Thus, our dataset consisted of 141 broods out of the total of 162 recorded ones. However, excluding nests from the analysis may overestimate survival at the egg stage. Therefore, we conducted an alternative survival analysis (see Electronic Supplementary Material), assuming that the day the nest was found was the first day of incubation. The average breeding density in this population was 5.4 pairs per 1 km^2.

During each nest control, a five-minute-point counting of potential nest predators was made within 50 m of the nest. The mean (±SD) number of predatory birds per control was 2.84±2.72 individuals (range: 0–14), and it differed between the years (except 2018 vs. 2019; Electronic Supplementary Material), while the mean (±SD) number of predatory mammals was 0.18±0.44 individuals (range: 0–2), and in that case we found no differences between the years (Electronic Supplementary Material)).

The shortest distance from the nest to the edge of the nearest road was measured with a tape measure (to the nearest 0.1 m).

To assess the effect of weather conditions on nest survival, climatic data were obtained from meteorological stations of the Institute of Meteorology and Water Management—National Research Institute, located in the vicinity of the bypass road. Temperature data were obtained from a station in Kołuda Wielka, located 12 km away from the center of the study plot, whereas precipitation was provided by stations in Pakość, Jaksice and Więcławice, located 15.1 km NW, 11.3 km N and 7.1 km NE, respectively, from the center of the study plot, so accurate rainfall values were provided for the entire study area. The mean (±SD) temperature during the study period (from 22nd March to 15th August) was 13.35±6.17 °C (range: −0.63 to 28.60) and it differ between the years (except 2018 vs. 2019, see Electronic Supplementary Material), while the average (±SD) daily precipitation was 1.54±4.15 mm (range: 0–40.4), and was different between years (except 2018 vs. 2020 and 2018 vs. 2021, see Electronic Supplementary Material).

Data processing and analysis

Nest survival was calculated as a change in the number of active nests or their contents during each breeding season (Kleinbaum 1996). We analysed the data according to life tables, which are the most universal method for estimating survival functions, where the life history of each brood, i.e. from brood initiation to the offspring leaving the nest/destruction of the nest during a particular breeding season is known. When analysing life tables, survival is considered to be a function of time (Kleinbaum 1996; Kosicki 2012; Langowska and Zduniak 2020), contrary to the most frequently analysed cases when breeding success is expressed as a simple proportion of surviving broods. Thus, in our approach, we were able to calculate critical time points during the breeding season of the studied population (Zduniak 2010; Zduniak et al. 2011; Kosicki 2012; Golawski et al. 2023). We estimated the survival time of each nest during the whole nesting period, i.e. from first egg laying in the nest to the date of the last visit, but also separately for the egg stage (egg laying and incubation) and the nestling stage (form hatching to fledging). The day when eggs or nestlings failed was considered as a halfway point between two consecutive nest controls.

To analyse the impact of weather conditions, predatory pressure and breeding parameters on nest survival, we used the Cox proportional hazards model (Cox 1972;

Muenchow 1986; Moya-Larano and Wise 2000; Reino et al. 2009), where time of life and status (survival/mortality) were used as input parameters of the response variable. In this approach, the hazard ratio, i.e. the probability that an individual that survived till the beginning of a given interval will die before the end of that interval is a function of independent variables. Accordingly, it is possible to estimate the regression of coefficients (and test them to see if they are significantly different from zero) for independent variables. When a regression coefficient for a given independent variable is positive and statistically significant, it shows decreased survival (higher risk of failure), and—vice versa—a statistically significant but negative coefficient is associated with increased survival (lower risk of death).

This approach let us test several environmental components that might influence nest survival, such as temperature, precipitation, distance between the nest and the road, the number of bird and mammal predators, as well as the date of the brood onset, i.e. the date of the first egg laying. This variable is expressed as the number of days after 1st January (first day) and it was median-centred for the particular breeding season. The number of bird and mammal predators was also mean-centred for a particular breeding season. Weather conditions were expressed as mean daily values of air temperature and mean sum of precipitation (from three nearest meteorological stations) calculated for duration time of each nest stage, separately for eggs, nestlings and whole nesting period (Kosicki 2012).

Due to the fact that the survival rate of the egg stage was relatively high (see results), we developed the Cox proportional hazards model for: (1) the nestling period, and (2) the whole nesting period (from egg laying to the fledglings' departure from the nest).

In order to verify whether full models (with all predictors) could be simplified, the Akaike information criterion (AIC; Burnham and Anderson 2002) was employed. By adding or removing predictors, it generated all possible combinations of candidate models. The model with the lowest AIC value and thus the highest Akaike weight was considered to be the best and the most parsimonious (Burnham and Anderson 2002).

Results

We found 162 nests located mainly in roadside areas covered with grassy vegetation (83%) and in adjacent arable fields (17%) (Fig. 2). The mean distance from the nest to the road was 13.48 ± 12.45 m.

The mean survival ratio for the whole nesting period (30 days from egg laying to fledgling) was 0.376 (95% CL: 0.244–0.581, n = 141, Fig. 3a) and did not differ over the five-year study period (Chi^2 = 2.8, df = 4, p = 0.6). The mean survival during the eggs stage (egg laying + incubation = 17 days) was 0.836 (95% CL: 0.746–0.937), and it also did not differ significantly between years (Chi^2 = 1.2, df = 4, p = 0.9), but the result was statistically higher than during the whole nesting period (Gehan–Wilcoxon test, test value = 2.31, $p < 0.01$). Finally, the mean survival ratio for the nestling period was 0.392 (95% CL: 0.212–0.727), and it also did not differ in particular study years (Chi^2 = 2.1, df = 4, p = 0.7). Besides, there was no difference between this period and the whole nesting period (Gehan–Wilcoxon test, test value = 0.73, $p < 0.54$).

According to the hazard ratio, the most critical moment for the survival of eggs/chicks occurs at the end of the incubation period and during the first days of the nestlings' life. The highest hazard ratio was observed from the 15th day of egg stage, i.e. just before hatching, to the ninth day of nestlings' life (Fig. 3b). Therefore, the analysis of the impact of environmental factors on survival was performed separately for the whole nesting period (from egg laying to nest leaving) and for the nestling period (from hatching to nest leaving).

Out of all analysed Cox proportional hazards models (Table 1) for the nestling period, the most parsimonious model included only two predictors, i.e. the hatching day and the distance between the nest and the road (Table 1, model 1A). This model turned out to be slightly better than the second model in our candidate set (evidence ration = 2.69), which additionally contained temperature as a predictor (Table 1, model 2A).

The best supported model was statistically significant (likelihood ratio test = 50.09, $p < 0.0001$, $r^2 = 0.335$) and it showed that the risk of chicks' death, expressed as a hazard ratio, decreased during the breeding season (β for Hazard ratio (± SE) = -0.639 (± 0.09), Wald statistic = −6.64, $p < 0.001$, Fig. 4a). In other words, the later in the season birds started to breed, the lower the risk of their chicks' death. What's more, we showed that the risk of chicks' death decreased with the increase in the distance from the nest to the road (β for hazard ratio (± SE) = −0.342 (± 0.07), Wald statistic = −5.64, $p < 0.02$, Fig. 4b). According to the second model, our candidate set could also suspect that the temperature will be high statistically significant impact on probability of nestling death, but this factor was not significant (β for hazard ratio (± SE) = −0.04 (± 1.00), Wald statistic = 0.140, $p < 0.88$, Fig. 4c).

The most parsimonious Cox proportional hazards model for the whole nesting period (from first egg laying to fledge) (Table 1) was also significant (Likelihood ratio test = 41.78, $p < 0.0001$, $r^2 = 0.253$). It included three predictors, i.e. the time of breeding, temperature and the distance from the nest to the road. This model was slightly better than the second model, which also included the

Fig. 2 Nests of the Crested Lark (*Galerida cristata*) located in different micro-habitat patches with plant cover at various stages of development. **A** arable field at the beginning of growing season; **B** grassy area at the beginning of growing season; **C** grassy area at the peak of growing season; **D** Red Clover (*Trifolium pratense*); **E** Rapeseed (*Brassica napus*); **F** Common Bean (*Phaseolus vulgaris*)

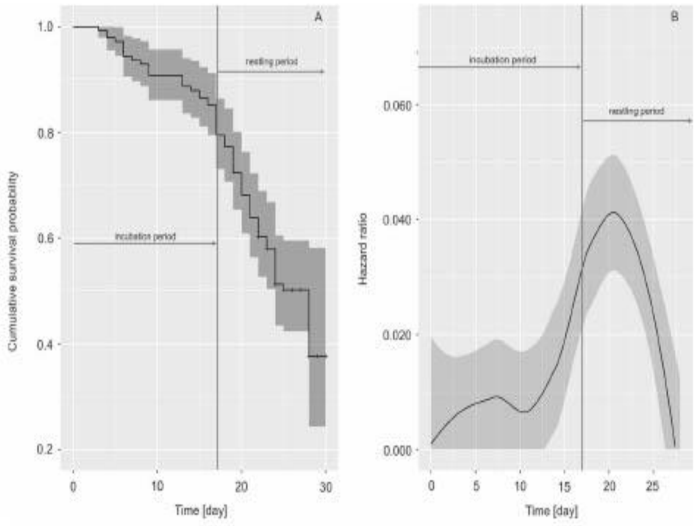

Fig. 3 Survival probability and hazard ratio for the Crested Lark's nests in different brood stages in roadside habitats of the bypass road in Central Poland

Table 1 Models with variables influencing nest survival probability of the Crested Lark in the nestling and full breeding periods

Model	Predictor	LogLik	AIC	Delta	Weight
Nestlings period					
1	**HD + Distance**	**−205.97**	**415.9**	**0**	**0.585**
2	HD + Distance + Temperature	−205.96	417.9	1.98	0.217
3	HD	−205.709	419.4	3.48	0.103
4	HD + Distance + Temperature + Precipitation	−205.552	421.1	5.17	0.044
5	HD + Distance + Temperature + Precipitation + Pred.Bird	−205.165	422.3	6.39	0.024
6	HD + Distance + Temperature + Precipitation + Pred.Bird + Pred.Mam	−205.074	424.1	8.21	0.01
7	HD + Distance + Temperature + Precipitation + Pred.Bird + Pred.Mam + Sibling	−205.074	424.1	8.21	0.01
8	HD + Distance + Temperature + Precipitation + Pred.Bird + Pred.Mam + Sibling + Inspections	−204.28	424.6	8.62	0.008
9	HD + Distance + Temperature + Precipitation + Pred.Bird + Pred.Mam + Sibling + Inspections + Pred.All	−230.873	461.7	45.81	0
10	Null	−230.797	463.6	47.66	0
Whole nesting period					
1	**TB + Temperature + Distance**	**−298.213**	**604.4**	**0**	**0.344**
2	TB + Temperature + Distance + Pred.Bird	−297.8	605.6	1.17	0.191
3	TB + Temperature + Distance + Pred.Bird + Pred.Mam	−296.854	605.7	1.28	0.181
4	TB + Inspections + Temperature	−300.621	607.2	2.81	0.084
5	TB + Temperature + Distance + Pred.Bird + Pred.Mam + Distance	−296.657	607.3	2.89	0.081
6	TB + Temperature + Distance + Pred.Bird + Pred.Mam + Sibling	−296.657	607.3	2.89	0.081
7	Inspections	−296.656	609.3	4.89	0.03
8	TB + Inspections	−303.972	611.9	7.52	0.008
9	Null	−318.802	637.6	33.18	0
10	TB	−318.66	639.3	34.89	0

The most parsimonious model is given in bold

number of bird predators and may be considered a valid alternative in our candidate set (evidence ratio = 1.80).

According to the best supported model, we found that the death risk of the content of the nest (eggs or chicks) decreased during the breeding season. In other words, the later the breeding attempt was undertaken, the better survival of the offspring (β for hazard ratio = −0.134, Wald statistic = −1.382, $p = 0.045$, Fig. 4d). A similar tendency was established with regard to temperature: The risk of death decreased with the increase of air temperature (β for hazard ratio = −0.179, Wald statistic = −3.038, $p = 0.002$, Fig. 4e). Finally, the highest survival rate, i.e. the lowest hazard rate, was found for nests located the furthest from the road (β for hazard ratio = −0.013, Wald statistic = −2.323, $p = 0.02$, Fig. 4f). In the second model in our candidate set, we also found that probability of nestlings death increase proportionally to the number of bird predators, but it should be noted that this relationship is on the border of statistical significance (β for Hazard ratio = 0.010, Wald statistic = 1.03, $p = 0.05$, Fig. 4g). So the time of breeding, distance from the edge of the road and temperature explain most cases of nest success, even though bird predators may also play a role in the process.

Discussion

Our study is the first of this kind to have estimated nest survival of the Crested Lark during different brood stages. It also tested the impact of a variety of factors that potentially affected survival. We found that the survival rate in the egg stage was twice as high as in the nestling stage, a result which is consistent with earlier studies on birds nesting on the ground (Mallord et al. 2007; Pérez-Granados 2017). We also found similar tendency in our extended analysis (see Electronic Supplementary Material), which also included broods for which there was uncertainty about the start date of laying. Thus, the nest survival pattern of the Crested Lark is generally consistent with that of ground-nesting birds, showing overall low survival in comparison with species using other nesting niches (Shochat et al. 2005).

The overall nest survival during the whole nesting period (0.376) of the Crested Lark is similar to the value (0.367) obtained for a population of this species studied in Czechia (Praus 2020), but higher than among birds breeding in the Negev Desert (0.238) (Shkedy and Safriel 1992). The differences may result from different conditions

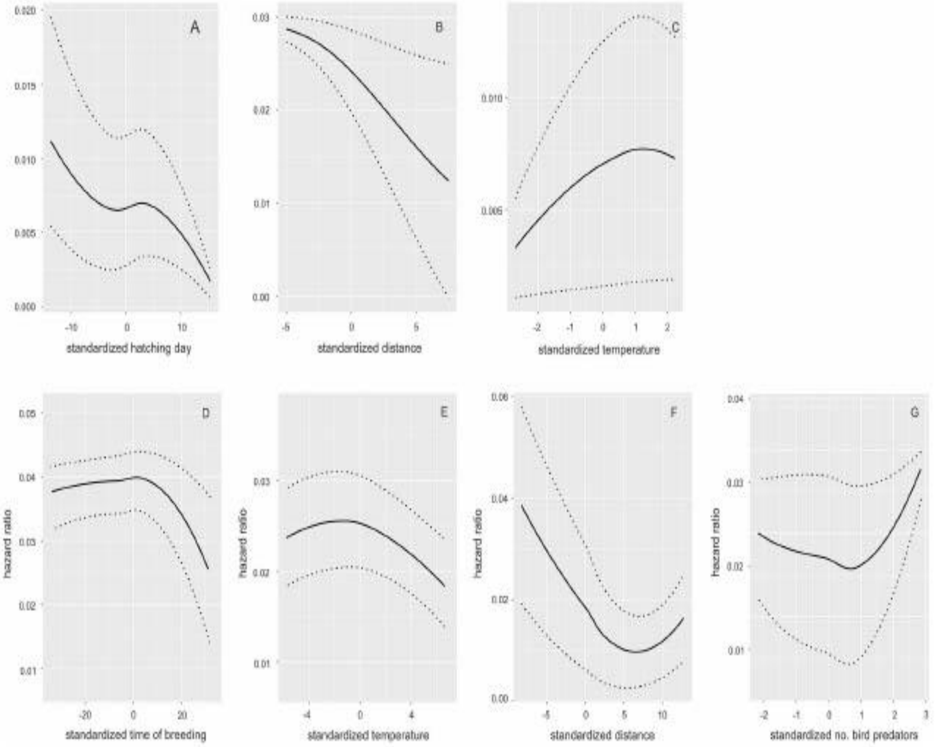

Fig. 4 Relationship between the hatching day, distance to the road, temperature and the hazard rate

in Central Europe and the Near East. As regards other lark species from habitats in temperate regions, the results we obtained for whole nesting period were comparable or slightly higher. In Kazakhstan, the mean probability of the Calandra Lark's (***Melanocorypha calandra***) nest to survive the entire nesting period in the steppe and among abandoned crops was 0.207 (Lameris et al. 2016), whereas in the case of the Woodlark (***Lullula arborea***) nesting in heathlands in southern England the probability was 0.470 (Mallord et al. 2007), while for the Eurasian Skylark (***Alauda arvensis***) in farmlands of southern England, it was 0.242 (Donald et al. 2002), and 0.322 for the Horned Lark (***Eremophila alpestris***) in the alpine environment of Canada (MacDonald et al. 2016).

Our results show that two factors, such as the time of breeding and the distance from the road, affect the probability of nestlings' survival. Besides, the whole nesting cycle (from egg laying to nest leaving) is also affected by temperature. Thus, the probability of nestling failure decreases as the breeding season advances, and increases when nests are closer to the road. What is more, during the whole nesting period, nest failure decreases as the temperature increases. The survival probability is higher during the egg stage than in the nestling period. It can be explained by increased parental feeding activity and nestlings' begging calls for food. These two types of visual and acoustic cues may disclose the location of the nest and attract potential predators (Martin et al. 2000; MacDonald et al. 2009; Ibáñez-Álamo et al. 2012).

Our findings on the time of brood initiation are surprising, because opposite results have been described many times. Generally, pairs that breed earlier grant lower nest mortality than pairs beginning to breed later (Siikamaki 1998; Currie et al. 2000; Morrison et al. 2019). Additionally, this relationship has a strong theoretical basis, as studies show that birds that start breeding earlier are more experienced and they are the first to occupy better territories (Weggler 2000; Kokko et al. 2006). However, this assumption may not be applied to sedentary and multi-brood species that originally inhabited steppe and semi-desert landscapes with much warmer and arid climate than the climate in temperate regions. We speculate that our contrasting results may reflect a reproductive strategy of the studied species in the face of changing weather conditions, which occur regularly during the whole breeding season (from late March to mid-August). As a multi-brood species, the Crested Lark may potentially compensate for the loss of earlier nests by several nesting attempts throughout an extended breeding season. The Crested Lark nests on the ground, building nests lined mainly by grass in a shallow depression under the shelter of tussock or—less frequently—shrub. At the beginning of the breeding season in the third decade of March (23/03/2018), when the first egg was laid in the studied population, vegetation on the ground was relatively low and sparse, thus making the nest more visible to the predator. This hypothesis may be supported by a study conducted on the Negev Desert (Shkedy and Safriel 1992), where survival in the eggs stage was 0.368 as compared to 0.836 obtained in our study. The differences may result both from the structure of the desert vegetation cover providing poorer nest concealment as well as the character and activity of nest predators (Shkedy and Safriel 1992). During the whole nesting period, the second model selected by the AIC showed that bird predators may also play a role in determining breeding output. There may be several potential explanations for why predation pressure was not included in the most parsimonious model, despite the fact that this factor was also marginally statistically significant. First, it is plausible that the five-minute-point counting of potential predators is not long enough and may not reflect their real impact on nest survival. Secondly, the obtained field data could be biased as only diurnal predators were observed, whereas nocturnal animals, e.g. like Red Foxes (*Vulpes vulpes*), Feral Cats (*Felis catus*), hedgehogs (*Erinaceus sp.*), Stone Martens (*Martes foina*), rodent *Rodentia sp.*, could be potentially more responsible for nest losses. This explanation can be supported by results obtained from studies on the Eurasian Skylark and the Woodlark in the Netherlands, where nest predation occurred in the dark in 55% cases (Praus et al. 2014). Alternatively, due to the fact that the area we study is a linear habitat running along the motorway, it is also likely that potential predators, which are opportunists, benefit from the carcass on the road and thus scavenge their food, while bird nests remain an alternative source of food (Pescador and Peris 2007). Still, due to specific features of the study area and methodological limitations, the actual impact of predators on nest survival may have been masked in favour of weather conditions, especially temperature, which may have influenced the breeding success of the Crested Lark. Moreover, local frosts that occur at the beginning of the breeding season can pose a problem for this typically steppe species. During the incubation period, this factor is less important, because the brood is predominantly incubated by the female (with short feeding breaks), which maintains a constant temperature of the nest (Hartley 1946; own data). Still, low air temperature right after hatching may impact nestling survival in two ways. First, it happens directly, because days with low temperatures are dangerous for small nestlings whose homeothermic regulation has not developed. In the period just before hatching, embryos and nestlings soon after hatching have reduced thermoregulation so they suffer from cooling (Rodriguez and Barba 2016). Second, which is a more probable explanation, air temperature in spring and summer indirectly affects potential food resources, such as beetles *Coleoptera*, grasshoppers *Acrididae*, ants *Formicidae*, caterpillars, snails *Gastropoda* and spiders *Araneae* (de Juana et al. 2004) that adults feed on, whereas the offspring are fed mainly with insects, especially caterpillars and small *Orthoptera* (Roselaar 1988). These organisms, which are the main element of the Crested Lark's diet, are poikilothermic, so they cannot regulate their body temperature and their activity largely depends on thermal conditions of the surrounding environment (Lehmann 1999; Zhang et al. 2020; Hannigan et al. 2023). Thus, when it is cold, invertebrates are scarce, which may lead to nestling starvation, their reduced growth rate and general poor condition. Additionally, adverse weather forces adult birds to increase their energy expenditure and foraging activity to provide the same amount of food for nestlings. Consequently, when parents need more time for foraging, their chicks are exposed to hypothermia, especially in the first few days after hatching. Also, reduced food availability and severe weather constitute a stress factor, which is often connected with parasite infections (Newton 1998), additionally increasing the mortality of nestlings. Finally, we found that the further from the road, the higher survivability of the brood. Higher survival rates of nests located further from the road can stem from the fact that they are located mostly on agricultural fields, where denser vegetation provides more stable temperature and better nest concealment. Our findings are consistent with results from studies on the Eurasian Skylark, whose nests in cereal crops had a significantly higher survival rate than those located in other field types (Donald et al. 2002). Meanwhile, the lower survival rate of nests located closer to the road edge may result from increased human disturbance in this zone, including agricultural machines movements to adjacent fields and mowing grass works.

Conclusion

The breeding success of the Crested Lark nesting in road margins depends mainly on the micro-habitat and climatic conditions. Our study suggests that in temperate regions the Crested Lark, which is a multi-brood and thermophilic species, may benefit more from later nesting attempts when breeding conditions, such as higher temperature and peak of food abundance, have improved. Therefore, the ongoing climate changes may contribute to better survival of broods and a recovery of its populations in Northern and Central Europe.

Our findings also demonstrate the importance of nest location, because it is a factor that might seriously reduce or increase the number of fledglings. Nesting in grassy habitats near road edges may prove to be "ecological traps", attracting high densities of nesting birds, but leading to low nest success due to increased nest failure. That is why colonisation of new man-made linear habitats, such as roadsides, may be detrimental for the Crested Lark. However, we are aware that our assessment method of nest predators is limited and the data regard mainly diurnal predators, so our conclusions may not reflect the real impact of predators on nest survival. Hence, future studies using trail cameras should be initiated to identify nest predators, predator abundance, and predators' activity patterns throughout the breeding season in different types of habitats occupied by the Crested Lark. Last but not least, further research is necessary to expand our knowledge on how factors related to human activity, e.g. field work and lawn moving affect nest survival of this ground-nesting species.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10336-024-02183-y.

Acknowledgements We thank Justyna Grześkowiak for her linguistic assistance. We are also grateful to two anonymous reviewers for their numerous and valuable comments. This study was funded by Adam Mickiewicz University, Poznań, ID-UB Doctoral mini-grants No. 017/02/SNP/0027. The study are comply with the current laws of the Poland. All experiments were conducted with the permission of the Local Ethical Committee for Animal Experiments in Poznań (No. 25/2018) and Bird Ringing Permit of Polish Ornithological Scheme (No.343/2023).

Author contributions Conceptualization: Rafał Sandecki, Jakub Kosicki; Methodology: Jakub Kosicki, Rafał Sandecki; Formal analysis and investigation: Jakub Kosicki, Rafał Sandecki; Writing—original draft preparation: Rafał Sandecki, Jakub Kosicki; Writing—review and editing: Rafał Sandecki, Jakub Kosicki.

Data availability The data is available directly from the author, Rafał Sandecki rafal.sandecki@amu.edu.pl

Declarations

Conflict of interest The authors declare no competing interests.

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