The influence of light on breeding biology and ecology of hole-nesting birds

Wpływ światła na biologię i ekologię lęgową ptaków gniazdujących w dziuplach

Paweł Wojciech Podkowa

Promotor:
prof. UAM dr hab. Adrian Surmacki

UAM

Department of Avian Biology and Ecology
Adam Mickiewicz University

ROZPRAWA DOKTORSKA

Rozprawa doktorska została wykonana w Zakładzie Biologii i Ekologii Ptaków, Instytut Biologii Środowiska, Wydział Biologii Uniwersytetu im. Adama Mickiewicza w Poznaniu

Promotor:
prof. UAM dr hab. Adrian Surmacki
Zakład Biologii i Ekologii Ptaków, Instytut Biologii Środowiska, Wydział Biologii
Uniwersytet im. Adama Mickiewicza w Poznaniu

Recenzenci:
prof. MiIZ PAN dr hab. Tomasz Mazgajski
Muzeum i Instytut Zoologii Polskiej Akademii Nauk

prof. dr hab. Piotr Tryjanowski
Katedra Zoologii, Uniwersytet Przyrodniczy w Poznaniu

Spis treści

Streszczenie

Światło dzienne wpływa na wiele aspektów biologii i ekologii dzikich ptaków. Zróżnicowany stopień ekspozycji na światło, zarówno jeśli chodzi o jego spektrum jak i intensywność, wywołuje szereg reakcji fizjologicznych oraz behawioralnych. Wśród nich można wymienić regulację rytmu dobowego i sezonowego, orientację podczas wędrówek, regulację poziomu hormonów płciowych i wynikające z ich działania zmiany zachowania godowego. Wpływ światła dziennego na aspekty związane ze wzrostem i kondycją ptaków, jak dotąd został przetestowany wyłącznie w oparciu o przykłady pochodzące z hodowli drobiu. Nieliczne badania ukazujące pozytywny wpływ światła na wzrost i rozwój zarodków dzikich ptaków wykonano w warunkach laboratoryjnych. Wnioski z tych badań sugerują, że światło odgrywa istotną rolę w ontogenezie, a co za tym idzie, może mieć znaczenie przy podejmowaniu decyzji dotyczących wyboru miejsca gniazdowania.

Głównym celem projektu doktorskiego było znalezienie odpowiedzi na pytanie czy, a jeśli tak to w jaki sposób, zmiany natężenia światła dziennego w miejscu gniazdowania dziko żyjących bogatek (*Parus major* L.), wpływają na biologię lęgową dorosłych osobników i kondycję ich potomstwa. Sikora bogatka to gatunek wtórnie gniazdujący w dziuplach, co oznacza, że osobniki same ich nie wykuwają, ale zajmują dziuple dzięciołów lub naturalne szczeliny i spękania w drzewach. Dziuplaki wtórne, z powodzeniem gniazdują również w skrzynkach lęgowych oraz w otworach i szczelinach pochodzenia antropogenicznego. W ramach swoich badań zrealizowałem dwa rodzaje eksperymentów uwzględniające zmianę natężenia światła dziennego wewnątrz skrzynek lęgowych. W pierwszym eksperymencie, zmiana natężenia światła miała miejsce w trakcie sezonu lęgowego, tuż po złożeniu pierwszych jaj w gniazdach. Drugi eksperyment polegał na zmianie natężenia światła we wnętrzu skrzynek lęgowych na długo przed rozpoczęciem sezonu lęgowego, przez co ptaki wybierały na miejsce gniazdowania „jasne” lub „ciemne” skrzynki lęgowe.

Wyniki badań zaprezentowałem w formie trzech artykułów opublikowanych w recenzowanych czasopismach naukowych. Każda z prac skupiała się na innym aspekcie ekologii badanego gatunku. Po pierwsze, wykazałem, że sikory bogatki dwukrotnie częściej wybierają na miejsce gniazdowania skrzynki lęgowe z większym natężeniem światła w ich wnętrzu, w porównaniu ze standardowymi skrzynkami lęgowymi. Ponadto, w „jasnych” skrzynkach ptaki budowały istotnie niższe gniazda, co wiązało się z zachowaniem większej,

a zatem bardziej bezpiecznej dla lęgu, odległości od otworu wlotowego do gniazda. Budowa niższego gniazda mogła również skutkować mniejszym wydatkiem energetycznym. Z kolei w skrzynkach „ciemnych" ptaki osiągały pożądany poziom oświetlenia czarki lęgowej poprzez budowę wyższych gniazd, zbliżonych tym samym do otworu wlotowego. W drugim artykule wykazałem, że na etapie opieki rodzicielskiej nad pisklętami, rodzice w „jasnych" skrzynkach lęgowych szybciej podejmują decyzje o tym, które pisklę powinno zostać nakarmione. W ten sposób, przy jednoczesnym zachowaniu podobnej dziennej liczby karmień co w skrzynkach „ciemnych", ptaki gniazdujące w „jasnych" skrzynkach lęgowych „oszczędzały" około 30 minut dziennie, był to czas który mogły przeznaczyć na dodatkowe żerowanie lub odpoczynek. Trzecia praca, wchodząca w skład rozprawy doktorskiej dotyczy efektywności układu odpornościowego, wzrostu, kondycji oraz przeżywalności piskląt w kontekście ich ekspozycji na światło dzienne. Pisklęta w skrzynkach „jasnych" cechowały się silniejszą odpowiedzią immunologiczną oraz opuszczały gniazda wcześniej niż ptaki ze skrzynek „ciemnych".

Wyniki przedstawione w niniejszej rozprawie doktorskiej po raz pierwszy jednoznacznie wskazują na to, że dostępność światła dziennego w miejscu gniazdowania dziko żyjących ptaków, może mieć znaczenie adaptacyjne. Światło dzienne nie tylko pełni istotną rolę wśród czynników wpływających na decyzję o wyborze miejsca gniazdowania przez bogatki, ale również przynosi skutki, które być może wpływają na zwiększenie dostosowania osobników. Wybrany gatunek modelowy, którego naturalne miejsca gniazdowania cechują się wysoką zmiennością w zakresie dostępności światła, z powodzeniem może być wykorzystywany do dalszych badań. Wśród nich, wymienić można: analizę dziedziczenia preferencji do danego typu siedlisk, badania korelacyjne nad spektrum światła docierającym do wybranych miejsc gniazdowania, zbadanie wpływu światła na *fitness* osobników czy też komunikację między rodzicami a potomstwem.

Abstract

Daylight influences many aspects of the biology and ecology of birds. The various exposure to the light, in terms of its spectrum and intensity, causes several physiological and behavioral changes. These include the regulation of the circadian and seasonal rhythm, orientation during migration, regulation of the level of sex hormones, and related changes in mating behavior. On the other hand, the effects of daylight on bird growth and health have so far been tested only on poultry farming models. The few studies showing the positive impact of light on the growth and development of wild bird embryos have been performed under laboratory conditions. The above observations suggest that light may play an important role in choosing the best nesting site and may directly affect the biology of the brood. I expected this effect to be evident among secondary cavity nesters. Due to nesting in a habitat with very low lighting conditions and taking into account the evolutionary history of this ecological group of birds, even small changes in light intensity can significantly impact the adaptation of individuals.

The main goal of the doctoral project was to find an answer to the question of whether, and if so, how changes in the intensity of daylight at the nesting sites of wild Great Tit (Parus major L.) affect the biology and breeding ecology of adult individuals and the condition of their offspring. Great tits are secondary cavity nesters, meaning that individuals do not excavate cavities themselves but occupy the hollows of woodpeckers or natural holes and tree cracks. Secondary cavity nesters also successfully nest in nesting boxes, openings, and crevices of anthropogenic origin. As part of my research, I carried out two kinds of experiments considering the change in daylight intensity inside the nest boxes. In the first experiment, the light intensity was modified during the breeding season, right after females laid the first eggs in the nests. In the second experiment, I set the light intensity inside the nesting boxes long before the breeding season began. Therefore, the birds could have chosen "light" or "dark" nesting boxes for their nesting sites.

I have presented the results of the research in the form of three articles published in peer-reviewed scientific journals. Each of the works focused on a different aspect of the ecology of the studied species. Firstly, I have shown that great tits are twice as likely to choose nest boxes with a greater intensity of light inside them compared to standard “dark” breeding boxes. Moreover, in the "bright" boxes, the birds built significantly lower nests, which was

associated with maintaining a more considerable, and therefore safer for the brood, distance from the entrance to the nest cup. Lower nests could benefit from lower energy expenditure related to the building process. In the second study, I showed that at the stage of parental care, parents in the "bright" nesting boxes make faster decisions about which chick should be fed. In this manner, while maintaining a similar daily number of feedings as in the "dark" boxes, the birds nesting in the "light" nesting boxes "saved" about 30 minutes a day, devoting time for additional feeding or resting. The third work, included in the doctoral dissertation, concerns the effectiveness of the immune system, growth, body condition, and survival of chicks in the context of their exposure to daylight. We found the stronger immune response and 1-day earlier fledgling time in “bright” nest boxes.

The results presented in this doctoral dissertation for the first time indicate that the availability of daylight in the nesting places of wild birds may be of adaptive importance. Ambient light not only affects nesting site selection by great tits but also brings effects that may increase the fitness of individuals. Selected model species whose natural nesting sites may differ in natural ambient light level is suitable for further light-related studies. Further research could consider the following directions of investigation: inheritance of the preferences to a given habitat type, detailed impact on the individuals' fitness, communication between parents and offspring, and correlational studies on the light spectrum reaching different nesting sites.

Wprowadzenie

Światło jest jednym z czynników abiotycznych, bez których życie na Ziemi nie byłoby możliwe. Frakcja promieniowania elektromagnetycznego (EMR), która podlega zasadom optyki i może być odebrana przez ludzkie oko nazywana jest światłem widzialnym. Na obu skrajach jego spektrum, leżą niewidzialne dla człowieka światło ultrafioletowe (UV) oraz tak zwana bliska podczerwień (NIR). Nie oznacza to wcale, że inne grupy zwierząt nie są zdolne do percepcji światła o fali krótszej i dłuższej od światła widzialnego dla ludzkiego oka. Jednak bez względu na to czy dany organizm jest w stanie rejestrować światło widzialne, UV czy też IR, frakcje te niezależnie odgrywają istotną rolę w funkcjonowaniu żywych organizmów. Promieniowanie, którego źródłem jest Słońce, zwane dalej światłem dziennym, zależnie od biotopu i warunków atmosferycznych, w różnym stopniu oddziałuje z receptorami zwierząt i roślin. Choć do najlepiej znanych struktur zawierających fotoreceptory należą znajdujące się na siatkówce oka pręciki i czopki, w świecie ożywionym istnieje cały szereg innych fotoreceptorów. Przykładem mogą być chociażby wczesne ewolucyjnie białka zwane kryptochromami, które są receptorami światła niebieskiego i występują zarówno u eukariontów jak i prokariontów (Wilde & Mullineaux 2017). Jeśli chodzi o systemy widzenia u bezkręgowców i kręgowców można zaobserwować duże zróżnicowanie w liczbie typów posiadanych fotoreceptorów co warunkuje różne typy widzenia barwnego. Ptaki, są jedną z kilku grup zwierząt, u których występuje tak zwane widzenie tetrachromatyczne. W przypadku tej konkretnej grupy kręgowców oznacza to posiadanie czterech typów czopków, które umożliwiają percepcję zarówno światła widzialnego jak i UV.

Światło dzienne istotnie wpływa na wiele aspektów biologii i ekologii ptaków. Wśród najbardziej oczywistych zależności należy wymienić postrzeganie otoczenia, zdobywaniem pokarmu czy właśnie percepcję kolorów, pełniących funkcję sygnalizacyjną (Toomey & Ronald 2021). Ponadto, poprzez zmiany fotoperiodu, światło reguluje rytm dobowy i sezonowy (Oishi i in. 2001) oraz wpływa na poziom hormonów płciowych modyfikując zachowania godowe (Kempenaers i in. 2010, Dominoni i in. 2013). Wykorzystywany podczas migracji „zmysł magnetyczny" ptaków bazuje na oddziaływaniu światła ze wspomnianymi wcześniej fotoreceptorami - kryptochromami (Stapput i in. 2010). Zależna od dostępności światła jest także synteza melatoniny, która reguluje rytm okołodobowy i pełni istotną rolę w funkcjonowaniu układu odpornościowego, reakcjach antyoksydacyjnych czy metabolizmie węglowodanów (Carrillo-Vico i in. 2005; Navara & Nelson 2007). Skrajnie długotrwałe oświetlenie zaburza syntezę melatoniny, pośrednio osłabiając funkcjonowanie układu odpornościowego co wykazały badania na przepiórce japońskiej (*Coturnix coturnix japonica*, Navara & Nelson 2007).

Niespełna dekadę temu badacze zaproponowali szereg hipotez dotyczących wpływu światła na rozwój ptasich zarodków (Maurer et al. 2011). Ekspozycja jaj na światło może mieć pozytywne konsekwencje związane między innymi z termoregulacją, rozwojem lateralizacji funkcjonalnej, regulacją rytmu dobowego, indukcją foto-reaktywacji DNA, ochroną przed drobnoustrojami oraz tempem rozwoju embrionów (tzw. foto-akceleracja, Maurer et al. 2011). Dokładny mechanizm foto-akceleracji pozostaje nieznany, ale prawdopodobnie ma podłoże molekularne związane z transdukcją białek. Co ważne, siła i kierunek efektu są związane zarówno z natężeniem światła, jak i jego spektrum. Autorzy wśród korzyści płynących z fotoakceleracji wymieniają m.in. krótszy czas inkubacji jaj, który zmniejsza ryzyko drapieżnictwa gniazd czy infekcji ektopasożytami. Wśród zmiennych mogących wpływać na skalę tego efektu, oprócz pigmentacji jaj i przepuszczalnych właściwości skorupki, autorzy uwzględnili też zróżnicowanie geograficzne oraz sposób gniazdowania wybranych gatunków. Jak dotąd, jedyne badania testujące hipotezę foto-akceleracji, które przeprowadzono na dzikich ptakach wykorzystywały inkubatory ze zmodyfikowanym fotoperiodem (Cooper i in. 2011, Austin i in. 2014). Przy wydłużonej fazie dnia, okres inkubacji ulegał skróceniu o około 10 godzin u kapturki (*Sylvia atricapilla*) i o około 24 godziny u wróbla domowego (*Passer domesticus*). Wyraźniejszy efekt wpływu dłuższej fazy dnia u wróbla, może wynikać z jego większej wrażliwości na światło co wynika ze sposobu gniazdowania (gniazda zamknięte) innego niż w przypadku kapturki (gniazda otwarte). Wspomniane eksperymenty jednoznacznie wskazują, że gatunki budujące gniazda zamknięte mogą być dobrym modelem do badań nad wpływem światła dziennego na rozwój piskląt. Możliwość uzyskania korzyści z oddziaływania światła na pisklęta okazuje się być sporym wyzwaniem dla gatunków gniazdujących w dziuplach. Wesołowski i Maziarz (2012) wykazali, że natężenie światła w niektórych naturalnych otworach gniazdowych wynosi zaledwie 0,01 lx, co jest porównywalne do natężenia światła w bezchmurną księżycową noc. Ekstremalnie niskie natężenie światła w miejscu gniazdowania może zatem wpływać na wybór miejsca gniazdowania w zależności od dostępności światła (Wesołowski i Maziarz 2012, Podkowa i Surmacki 2017), bądź wpływać na grubości skorupki i ilości pigmentu w jajach (Maurer i in. 2015). Ponadto dziuplaki wtórne mogą regulować ilość światła, która dociera do jaj modyfikując czas inkubacji i stopień przykrycia jaj materiałem gniazdowym podczas przerw w wysiadywaniu.

W przypadku rozwoju osobniczego ptaków, niemal cała wiedza na temat znaczenia światła zarówno podczas embriogenezy jak i wzrostu po wykluciu pochodzi z badań prowadzonych na drobiu (Fairchild 2000, Olanrewaju et al. 2006, 2012, Lewis 2010). Specyfika wykorzystania światła w takiej hodowli polega na wykorzystaniu systemów oświetlenia zmieniających takie właściwości światła jak natężenie, barwa oraz czas ekspozycji. Modyfikacja natężenia światła mieści się zazwyczaj pomiędzy wartościami 5 a 500 lx (Hofmann et al. 2020), zaś wyrażony w godzinach stosunek długości dnia (D) do nocy (N) może modyfikowany dowolnie, i wynosić np. 12D:12N lub nawet 23D:1N (Olanrewaju et al. 2006). Nie bez znaczenia pozostaje długość fali wykorzystywanego światła, a więc jego barwa. W hodowli, pozytywny wpływ na przyrost masy ciała i rozwój narządów wewnętrznych odnotowano zarówno przy wykorzystaniu światła niebieskiego jak i zielonego (Soliman & El-Sabrout 2019), a u niektórych odmian także czerwonego (Çapar Akyüz & Onbaşilar 2018). Światło czerwone niejednokrotnie wiązało się także z silnymi zmianami behawioru, zwiększając m.in. agresję u drobiu ras mięsnych (Soliman i El-Sabrout 2019). Ponadto, w hodowli drobiu wykorzystuje się antyrachityczne właściwości światła ultrafioletowego (dokładniej: UVB o długości fali 280 – 315 nm), które katalizując syntezę witaminy D3 w nieopierzonych częściach ciała zmniejsza ryzyko dyschondroplazji piszczelowej i zapobiega krzywicy (Lewis i in. 2009). Istotny z hodowlanego punktu widzenia może być także rodzaj stosowanego źródła światła np. żarowe, jarzeniowe lub LED.

W ostatnich latach, badania ekologiczne nad wpływem światła na różne grupy kręgowców, zdominował aspekt zanieczyszczenia sztucznym światłem w nocy (ALAN; Falcón et al. 2020, Kosicki 2020, Bassi et al. 2022). Zmiany w krajobrazie wywołane obecnością sztucznego światła wpływają, w większości, negatywnie także na ptaki skutkując zaburzeniami snu, migracji, żerowania i reprodukcji (Svechkina 2020). W ostatnim przypadku, obserwuje się pozornie pozytywny efekt jakim jest szybsze osiągnięcie gotowości do reprodukcji i wcześniejsze przystąpienie do składania jaj. W bogatki (*Parus major*) sztuczne światło hamowało jednak wzrost piskląt między 13 a 15 dniem po wykluciu (Raap i in. 2016). Współcześnie brakuje terenowych badań eksperymentalnych uwzględniających zmienność dostępności światła dziennego jako czynnika mogącego wpływać na rozwój, kondycję i sukces lęgowy dzikich ptaków. Należy spodziewać się, że efekt ten będzie szczególnie widoczny w wśród gatunków wtórnie gniazdujących w dziuplach. Z uwagi na gniazdowanie w miejscu, w którym warunki oświetlania są mocno ograniczone oraz biorąc pod uwagę historię ewolucyjną tej grupy ekologicznej ptaków, nawet niewielkie zmiany w natężeniu światła mogą mieć istotny wpływ na biologię lęgu. Podsumowując, dotychczasowe badania prowadzone na fermach drobiu, w warunkach laboratoryjnych lub z uwzględnieniem sztucznego światła, wykraczały poza naturalny zakres zmienności a także nie uwzględniały naturalnych interakcji między behawiorem rodziców a ekspozycją gniazda na światło. Ta interakcja może być szczególnie ważna u gatunków gniazdujących w dziuplach, ale jak dotąd pozostała nie zbadana w tej grupie.

Zrealizowany przeze mnie projekt stanowił pierwsze podejście eksperymentalne mające na celu zbadanie wpływu światła w gnieździe na rozwój piskląt dzikich ptaków i zachowanie osobników dorosłych, wtórnie gniazdujących w dziuplach. Wykonane eksperymenty polegały na dokonaniu manipulacji ilością dostępnego światła dziennego we wnętrzu skrzynek lęgowych, rozmieszczonych na terenie lasów mieszanych w Wielkopolskim Parku Narodowym. Skrzynki lęgowe zostały zaprojektowane na bazie skrzynki typu A Sokołowskiego, z modyfikacją polegającą na umieszczeniu dodatkowych okienek w ścianach bocznych oraz zwiększeniu przestrzeni w górnej części skrzynki w celu zainstalowania fotopułapki rejestrującej przebieg lęgu. Okienka w ścianach bocznych były wykonane z matowego półprzezroczystego materiału pleksi oraz dodatkowo posiadały czarne plastikowe kurtyny, które umożliwiały ich całkowite zasłonięcie. Skrzynki lęgowe, które były wykorzystywane jako „jasne’, po odsłonięciu kurtyn charakteryzowały się 50-krotnie wyższym natężeniem światła we wnętrzu, w porównaniu do skrzynek z zasłoniętymi okienkami (skrzynki „ciemne”). W efekcie tych zabiegów, część par wyprowadzała lęgi w skrzynkach o podwyższonej jasności (skrzynki „jasne”) a część w skrzynkach doświetlonych wyłącznie przez otwór wejściowy (skrzynki „ciemne”). Pozostałe właściwości skrzynek lęgowych takie jak ekspozycja, wysokość nad ziemią, sposób i data montażu były jednakowe dla wszystkich skrzynek lęgowych. W trakcie badań mierzono także wilgotność i temperaturę panującą w dwóch typach skrzynek lęgowych, jednak nie zaobserwowano różnic w obrębie tych charakterystyk. W projekcie wykrozystano autorską metodę zbierania materiału zdjęciowego i filmowego z gniazd sikory bogatki, przy wykorzystaniu fotopułapek umieszczanych w górnej części skrzynek lęgowych (Surmacki & Podkowa 2022a). Metodyka ta była kluczowa dla wykonania analiz zawierających precyzyjnie ustalone daty zniesienia jaj, daty klucia oraz opuszczenia gniazda. Szczegóły dotyczące tej metody oraz przykłady jej zastosowania zostały opublikowane w odrębnych artykułach (Surmacki & Podkowa 2022a, 2022b), które nie wchodzą w skład dysertacji.

W ramach badań wykazałem, że bogatka (*Parus major*) niemal dwukrotnie częściej zasiedlała skrzynki lęgowe, w których zwiększono ilość światła dziennego. Wynik ten sugeruje, że z jakiejś przyczyny miejsce gniazdowania imitujące dziuplę, lecz o wyższym natężeniu światła jest dla ptaków atrakcyjniejsze. Oprócz wpływu na wybór miejsca gniazdowania, doświetlenie skrzynek lęgowych skutkowało budowaniem niemal dwukrotnie niższych gniazd przez samice bogatki. W ciemnych skrzynkach lęgowych, ptaki kompensowały niedobory światła poprzez budowanie wyższych gniazd. Wyjaśnienie tego fenomenu oraz towarzyszących mu mechanizmów uzasadnia podjęcie dalszej problematyki związanej z wpływem światła dziennego na biologię i ekologię lęgową ptaków wtórnie gniazdujących w dziuplach. Wynik ten wskazuje na potencjalne znaczenie światła jako ważnego czynnika środowiskowego dla dziuplaków, którego adaptacyjne znaczenie było jak dotąd marginalizowane. Wyniki tych badań zostały opublikowane w artykule Podkowa, P., & Surmacki, A. (2017). The importance of illumination in nest site choice and nest characteristics of cavity nesting birds. Scientific Reports, 7(1), 1–9.

Zwiększone oświetlenie we wnętrzu skrzynki lęgowej może ułatwiać rodzicom opiekę rodzicielską, między innymi poprzez skracanie czasu potrzebnego na podjęcie decyzji o wyborze pisklęcia do nakarmienia. W celu przetestowania tej hipotezy przeanalizowałem nagrania prezentujące moment wlotu, karmienie oraz wylot rodziców ze gniazda. Nagrania pochodziły z fotopułapek umieszczonych w górnej części skrzynek lęgowych dwóch typów: ciemnych i jasnych. Wyniki analizy jednoznacznie potwierdziły, że czas potrzebny na wybór pisklęcia, któremu ma być przekazany pokarm jest statystycznie istotnie krótszy w skrzynkach jasnych niż w skrzynkach ciemnych, bez jednoczesnego wpływu na całkowitą liczbę karmień w ciągu dnia. Wyniki te zostały opublikowane w artykule Podkowa, P., Malinowska, K., & Surmacki, A. (2019). Light affects parental provisioning behaviour in a cavity-nesting Passerine. *Journal of Avian Biology 50(11).*

Trzecią, a zarazem najbardziej złożoną część rozprawy doktorskiej stanowiła analiza kondycji piskląt i sukcesu lęgowego w zależności od natężenia światła w zajmowanym gnieździe. Przeprowadzony eksperyment nie potwierdził założenia, jakoby światło bezpośrednio przyspieszało wzrost piskląt po wykluciu. Niemniej jednak, w pracy wykazano istotnie silniejszą odpowiedź immunologiczną piskląt w skrzynkach jasnych w porównaniu ze skrzynkami ciemnymi. Ponadto, całkowity czas od wyklucia do opuszczenia gniazda, był krótszy w skrzynkach jasnych. W interpretacji prezentowanych wyników należy uwzględnić wiek oraz kondycję samic wybierających miejsce gniazdowania spośród dwóch typów skrzynek lęgowych. Wśród zmierzonych wskaźników kondycji samic, jedyną różnicę zaobserwowano w masie ciała, która była większa w skrzynkach jasnych. Jednocześnie, wykazaliśmy, że młodsze samice chętniej zasiedlały skrzynki jasne. Z uwagi na charakterystykę zebranych danych, nie było możliwe wykonanie modeli statystycznych, które pozwoliły by na jednoczesne przetestowanie wpływu jakości rodziców na kondycję piskląt, przy uwzględnieniu interakcji ze światłem. Niemniej, wyniki opublikowane w artykule Podkowa P., Surmacki A., (2022) The effect of daylight exposure on the immune response and body condition of Great Tit nestlings. *Journal of Ornithology,* stanowią podstawę do formułowania dalszych pytań i hipotez dotyczących wpływu światła dziennego na biologię lęgową ptaków.

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The importance of illumination in nest site choice and nest characteristics of cavity nesting birds

Paweł Podkowa & Adrian Surmacki

Light has a significant impact on many aspects of avian biology, physiology and behaviour. An increasing number of studies show that illumination may positively influences birds' offspring fitness by e.g. acceleration of embryo development, stimulation of skeleton growth or regulation of circadian rhythm. Because nest cavities have especially low illumination, suitable light levels may be especially important for species which nest there. We may therefore expect that birds breeding in relatively dim conditions should prefer brighter nest sites and/or evolve behavioral mechanisms to secure sufficient light levels in the nest. Using nest boxes with modified internal illumination, we experimentally tested whether light regime is a cue for nest site selection of secondary cavity-nesting species. Additionally, we investigated whether nest building strategies are tuned to internal illumination. Our results demonstrate that, nest boxes with elevated illumination were chosen twice as often as dark nest boxes. Moreover, birds built higher nests in dark nest boxes than birds in boxes with elevated illumination, which suggests a mechanism of compensating for low light conditions. Our results provide the first experimental support for the idea that nest site choice and nest building behaviour in cavity-nesting birds are influenced by ambient illumination.

The majority of bird species are diurnal and thus experience changes in light intensities associated with daily, lunar or seasonal cycles. Not surprisingly, light has an immense impact on many aspects of avian physiology, biology and ecology. In birds, three organs (eyes, pineal organ and hypothalamus) regulate photoperiodism and circadian rhythms[1,2]. The orientation of the avian magnetic compass depends on interactions between blue light and photoactive molecules in the retina[3]. Illumination timing affects duration of singing, development of the reproductive system, testosterone levels and moult in male birds[4,5]. Similarly, illumination timing and light spectrum regulates the hormonal control of fecundity in females; a mechanism used by man for decades to maximize egg production in domestic hen (e.g. *Gallus domesticus*[6–9]), but also observed in wild birds[10].

A recent study[11] has shown that in many bird species eggshells are transparent enough for light to reach the photoreceptors of developing embryos. Moreover, for the majority of species, illumination levels at the nest and incubation behavior of adults (so called off-bouts) do not eliminate light completely[12]. According to a recent review[13], an exposure to light during incubation may positively affect various aspects of bird physiology including: thermo-regulation, photo-acceleration of embryos development, lateralization, circadian rhythm, DNA repair through photo-reactivation and antimicrobial defense. Thus far, most of the above hypotheses have not been rigorously tested, especially in wild birds. However, there is experimental evidence of photo-acceleration of embryo development for both wild species[14,15] and the domestic hen[16–20]. Light may also be beneficial for nestling growth and health. For example, domestic chicks exposed to constant light gain significantly more weight compared with controls reared on a 12L:12D light cycle[21]. Light of the shortest wavelengths (UV) may also play a crucial role in normalizing bone growth in chicks by stimulating the synthesis of vitamin D_3[22]. Finally, light conditions at the nest site may also affect brood rearing behaviour of adult birds. For example, in cavity nesting species, the minimum required amount of light seems to be necessary for birds to see and feed their young

Department of Avian Biology and Ecology, Faculty of Biology, Adam Mickiewicz University, Umultowska 89, 61-614, Poznań, Poland. Correspondence and requests for materials should be addressed to P.P. (email: podkowa@amu.edu.pl)

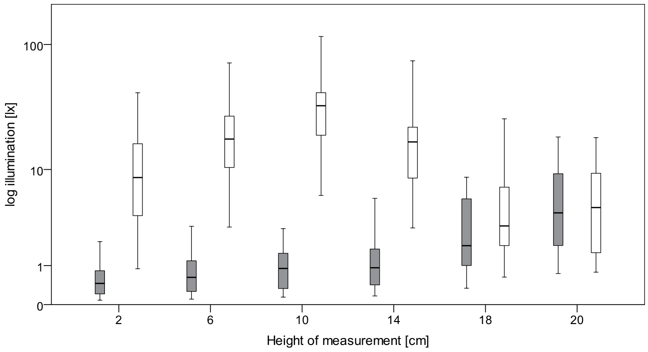

Figure 1. Illumination at different distances from the base of the nest box. Explanations: grey - dark nest boxes; white - bright nest boxes.

efficiently[23, 24]. Although recent studies have shown positive influence of light on birds breeding biology, its negative effect (e.g. in sleep disruption by artificial light) has been also reported[25, 26].

Considering the potentially beneficial effects of light on avian embryo development, nestling condition and adults' behaviour, a variety of mechanisms that could improve nest light environment could evolve. It has been demonstrated that eggshell pigmentation modifies its transparency depending on ambient light spectrum and intensity. Eggshells of species living in darker environments tend to be less pigmented compared to eggshells of species that nest in open habitats to compensate for the light deficiency[11]. Another mechanism that can enhance egg illumination is incubation off-bouts when clutches usually remain uncovered for short periods of time[27]. The main function of this behavior is to forage[27] however, another non-exclusive explanation is that off-bouts provide light for developing embryos[12]. In cavity nesting species, where light intensity is very low, the height of the nest layer may improve illumination, as it can be negatively correlated with a cavity depth[23, 24, 28]. Finally, parents may choose among available nest sites those sites that provide the most favorable light conditions for developing offspring[24].

Despite a growing body of evidence of the importance of light for the condition of avian embryos and nestlings, there are virtually no studies testing the role of light on nest site selection in birds. The only exception is an experimental study performed on domestic hens in artificial laboratory conditions[29]. In wild living species, there are only a few observational studies of nest box breeding birds, from which no solid conclusions can be drawn[30–32] (see details in Discussion). Marked preferences for light nest sites should be especially pronounced in cavity-nesting species, which experience very low intensity of light, especially in a deep cavities[23, 24].

This study has twofold goals. The first is to test experimentally whether light intensity has an effect on nest site selection. We used a secondary cavity-nesting species, the great tit (*Parus major*) breeding in nest boxes with modified interior illumination. Considering a general positive effect of light on nestling condition and adults' behaviour, we predicted that nest boxes with elevated brightness would be occupied more often and earlier in the season, comparing to control, dark analogues. The second goal of the study was to test how light conditions affects nest building behaviour of adult birds. We predicted that in standard, dark nest boxes birds will build higher nest comparing to bright nest boxes, which is a mechanism that regulates the amount of interior light.

Results

Illumination inside nest boxes. During the nest box occupation period (between 5 and 15 April), both the light transfer and the illumination were lower in dark nest boxes ($Me = 0.02\%$, $Q_{25-75\%} = 0.01-0.03$; $Me = 1.41$ lx, $Q_{25-75\%} = 1.04-2.19$, respectively), compared to bright nest boxes ($Me = 0.88\%$, $Q_{25-75\%} = 0.42-1.11$; $Me = 52.67$ lx, $Q_{25-75\%} = 42.83-62.28$, respectively). The differences were strongly statistically significant, both for light transfer (Mann-Whitney *U* test; $Z = -8.393$, $n = 95$, $p < 0.001$) and illumination (Mann-Whitney *U* test; $Z = -8.393$, $n = 95$, $p < 0.001$).

The height above the nest box floor had a significant effect on internal illumination in both bright (Friedman test, $Q = 67.267$, $df = 5$, $p < 0.001$) and dark nest boxes (Friedman test, $Q = 69.590$, $df = 5$, $p < 0.001$; Fig. 1). The detailed results of multiple pairwise comparisons using Nemenyi's procedure are shown in Table 1. In dark nest boxes, there was a gradual increase of illumination (Fig. 1) and light transfer between 2 and 20 cm above the nest box floor. In bright nest boxes, there was an increase in illumination reaching the highest value at 10 cm followed by a decline to 18 cm and a small increase at 20 cm (Fig. 1).

Nest site choice. The results of the logistic regression showed a significant effect of nest box internal illumination (nest box type), previous-year occupation, and study site on nest box choice (results shown in Table 2). However, the most important effect was the nest box type, which was indicated by the highest odds ratio (OR, Table 2). The proportion of bright and dark nest boxes occupied by great tit was 1.9:1 (Fig. 2). Both study sites II and III were more attractive for individuals than study site I. Moreover the interaction between study site and nest box type was not significant, which means that nest box choice was not linked to study site. The effect of previous-year occupation was also statistically significant but its' odds ratio was lower than the other significant factors. We performed two goodness of fit tests supporting our logistic regression model: Omnibus Tests of Model Coefficients: $\chi^2_{(6)} = 28.73$; $p < 0.001$ and Hosmer & Lemeshow $\chi^2_{(7)} = 2.23$; $p = 0.946$.

Type of nest box	Distance from the nest box floor	6	10	14	18	20
Bright	2	n/s	**<0.01**	n/s	n/s	n/s
Dark		n/s	n/s	**<0.01**	**<0.01**	**<0.01**
Bright	6		n/s	n/s	**<0.01**	**<0.01**
Dark			n/s	n/s	**<0.01**	**<0.01**
Bright	10			n/s	**<0.01**	**<0.01**
Dark				n/s	**<0.05**	**<0.01**
Bright	14				**<0.01**	**<0.05**
Dark					n/s	**<0.05**
Bright	18					n/s
Dark						n/s

Table 1. Pairwise differences in illumination at different distance from the nest box floor in brightened and dark nest boxes. Results shown are significance levels (*p*) of Nemenyi's post hoc tests.

Predictor	β	SEβ	Wald's	df	p	OR (95% CI)
Nest box type	1.864	0.61	9.348	1	**0.002**	6.45 (1.95–21.3)
Occupied in 2015	1.087	0.425	6.533	1	**0.011**	2.97 (1.29–6.82)
Study site	0	0	7.696	2	**0.021**	
Study site (1)	1.756	0.704	6.221	1	**0.013**	5.79 (1.46–23)
Study site (2)	1.733	0.796	4.743	1	**0.029**	5.66 (1.19–26.94)
Study site* Nest box type			2.322	2	0.313	
Study site (1)* Nest box type	−1.347	0.972	1.923	1	0.165	0.26 (0.04–1.75)
Study site (2)* Nest box type	−1.155	1.065	1.177	1	0.278	0.32 (0.04–2.54)
Intercept	−2.341	0.561	17.397	1	**0.000**	0.10

Table 2. Logistic regression model assessing predictors of nest box occupation by great tits in 2016. Study site (1) and (2) refers to dummy variables (see Methods).

The second measure of nest site preference was the sequence of nest boxes occupancy expressed by the first egg laying date (Table 3). We did not find any effect of the nest box internal illumination (Table 3). However, the result of the GLM showed a significant effect of study site on the nest box occupation sequence pattern (Table 3). There was a weakly significant trend towards nest boxes at site II being occupied significantly earlier comparing to the site I (Tukey's *post hoc* test, $p = 0.049$).

Nest height. The mean (±SD) height of the nest bottom was significantly greater in dark (10.23 cm ± 2.44) than in bright boxes (4.78 cm ± 2.66; Table 3, Fig. 3). Among the tested factors, only nest box type significantly influenced nest height, while the effect of egg laying date, study site and clutch size remained not significant (Table 3).

Discussion

The results presented in this study provide the first known experimental evidence for the importance of light in the nest environment of a wild-living avian species. Great tits chose nest boxes with artificially elevated illumination almost twice as often compared to standard dark nest boxes. Beside of nest site choice, light inside nest boxes affected also the nest building strategy. Great tits tuned the nest height to gain the greatest illumination for the nest-cup contents in a given nest box type.

Existing data on avian preferences to occupy well illuminated nests sites are sparse and based mainly on observational studies. The only experimental survey was performed on domestic hens[29]. Birds could choose between

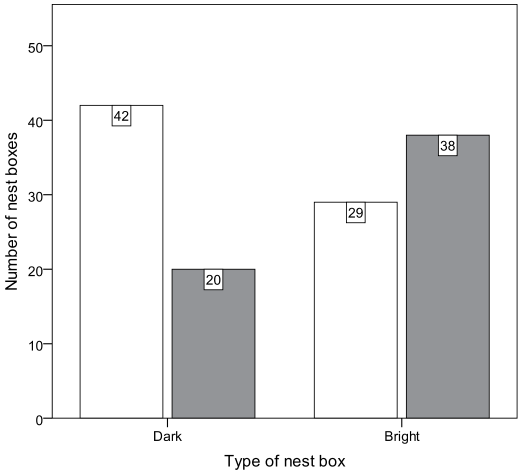

Figure 2. Nest box occupation by great tits in relation to light conditions. Grey bars – occupied, white bars – unoccupied.

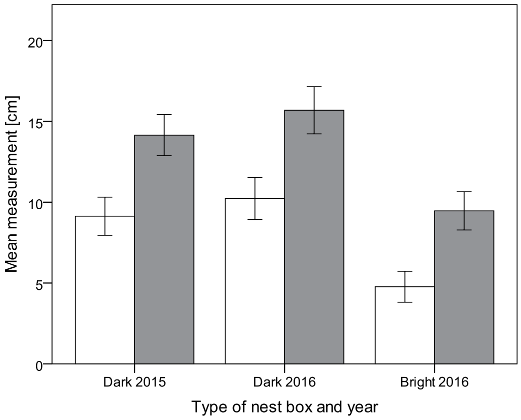

Figure 3. The mean nest height (white bars) and nest depth (grey bars) in dark and bright nest boxes, data collected in 2015 and 2016. Error bars shows 95% confidence intervals.

	Explanatory variables	Mean Square	F	df	p
Occupation sequence	Nest box type	25.48	1.59	1	0.216
	Study site	81.82	5.09	2	**0.011**
	Occupied in 2015	3.07	0.19	1	0.664
Nest height	Nest box type	247.07	34.79	1	**<0.001**
	Study site	6.58	0.93	2	0.406
	Clutch size	15.28	2.15	1	0.151
	Egg laying date	11.48	1.62	1	0.212

Table 3. Results of GLMs explaining variation in nest box occupation sequence and nest height.

dark and artificially illuminated nest boxes to lay eggs. The main assumption of that study was that hens prefer dark sites because lower illumination is evolutionary associated with more concealed and thus safer nest sites. However, only one of four experimental groups of hens followed this pattern. Moreover, preferences for nest sites with lower illumination depended also on the maturity and earlier experience of birds. In another study[32], nest box use by American kestrels (*Falco sparverius*) depended on internal illumination during the nestling period but not during the nest site selection period. This result suggested some importance of light in nest-site choice, but due to the observational nature of the study, they could also be a product of a correlation between illumination and other habitat variables, e.g. the degree of nest box concealment by vegetation[32]. In a number of studies, bird preferences for interior coloration of nest boxes have been observed. Nest boxes painted white are favored compared to those painted black or unpainted in the following species: common goldeneye (*Bucephala clangula)*[31], pied flycatcher (*Ficedula hypoleuca)*[33], eastern bluebird (*Sialia sialis*) and house sparrow (*Passer domesticus)*[34]. In contrast, starlings (*Sturnus vulgaris*) show high preference for black interiors[30], whereas for tree swallows (*Tachycineta bicolor*) and house wrens (*Troglodytes aedon*), no evident pattern has been reported[35]. Those findings could be interpreted as a preference for brighter nesting conditions because light reflected from white walls increases overall internal illumination[33]. On the other hand, those experimental designs do not allow the separation of the effect of light from the effect of walls' coloration or presence of paint. The importance of light conditions on nest site choice in secondary cavity-nesters breeding in natural conditions was investigated in Białowieża primeval forest (E Poland)[23, 24]. These findings demonstrate that mesopic-scotopic range of illumination that occurs in nest-holes is close or below a threshold enabling color vision[36]. Thus, many tree cavities may be too dark to be usable by birds, which might explain their underutilization by birds[24]. This assumption is indirectly supported by the fact that nests of collared flycatchers (*Ficedula albicollis*) in cavities with entrances oriented upward (and potentially entering more light), were located deeper compared to cavities with entrance oriented sideward[24].

Nest-site selection in birds is a complex decision-making process, which involves many factors of varying importance (e.g. food availability, nest site availability and social environment[37]). In the studied population, beside the nest box illumination, these were previous year nest box occupancy and habitat type. These findings are consistent with previous studies suggesting, that birds assess nest site attractiveness using evidence of successful breeding left by former residents or themselves the previous year[38]. Habitat preferences for sites dominated by oak (*Quercus petrea Liebl.*) have previously been observed in other great tit populations[39] and are most likely to be an effect of better foraging conditions. Oak is the most important host-plant for caterpillars[40], which are a crucial component of great tit nestling diet[41]. Habitat preferences were mirrored by the sequence of nest box occupancy found in our population. We observed the earliest egg laying in oak-dominated sites. In many bird species, including great tits[39], the sequence of occupancy of breeding areas depends on quality of habitat patches. The best habitats are occupied first, followed by suboptimal and marginal ones[37]. Contrary to our expectations, brightened nest boxes were not occupied earlier than dark ones. The most plausible explanation of this pattern is that brightened nest boxes were not limited in the study area. Great tits occupied less than a half of the available nest boxes and 29 brightened nest boxes were left unoccupied by any bird species. This suggests that preferred nest sites were not limited in the study area, so they were not likely be an object of severe competition. Another explanation is that nest box (territory) occupation took place long before nest building and is not correlated with the timing of reproduction. On the other hand, the date of egg laying may be determined by food availability which was equal for bright and dark nest boxes.

Great tits that chose dark nest boxes built significantly deeper nests compared to birds breeding in brightened nest boxes. Several lines of evidence suggest that this relationship was shaped by preferences for light. First, illumination inside dark nest boxes showed an increasing trend from the nest box bottom to the entrance hole. This correlation is intuitive, as the entrance hole is the only source of light in cavities (compare[23, 24]). Thus, selection for building higher nests appears to be the only mechanism that enables improvement of light conditions in the dark, unmodified cavities. On the contrary, in brightened nest boxes, light remained at very high level (>10 lux) across the entire depth of the nest box. In such conditions birds do not need to build high nests to obtain the desired illumination. Because nest building is a condition-dependent behavior[42–44], we may therefore expect, that in the absence of other selective pressures, birds build shallower nest to save time and energy for other activities. Another advantage of building shallower nests is to decrease predation risk by increasing the distance between nest contents and the entrance hole[45]. Our results provide the first experimental evidence that cavity-nesting species actively manipulate nest height to achieve the desirable amount of light in the nest cup. Great tits, and many other cavity-nesting passerines, built nests of a greater height when compared to other similar sized open-nesters. Moreover, many studies report great variability of their nest dimensions, even in nest boxes[46]. To date, no explicit explanation for selective pressures for building deeper nests in cavities have been found. It has been suggested that deeper nests provide protection from soaking[47] or plays a role in sanitation[48]. However, unlike horizontal dimensions[49, 50], nest height is not related to various parameters of breeding success[46, 49, 51, 52] (but see ref. 53 for a positive relationship between the nest depth and breeding success in blue tits). On the other hand, building big nests is a costly and condition-dependent process, which has been demonstrated for tits[42–44] and other bird species (reviewed[54]). The costs of building larger nests encompass not only greater time and energy expenditures[54], but also longer exposure of adults for predators[55]. Our results show that illumination may be one of the most important, and generally overlooked factors, causing selection for higher nests of cavity-nesting species.

Most of the previous studies focused on the role of nest predation as the main force reducing nest height in cavity nesting passerines. Studies in natural conditions demonstrate that there is a minimal distance between the entrance hole and the nest-cup which prevents terrestrial predators like pine martens (*Martens martens*) from reaching the nest content with their paws (so called "danger distance"[45]). To obtain the desired greater entrance-nest-cup distance, birds may choose deeper cavities, build shallower nests or both. Experimental and observational studies seem to confirm this mechanism. Great tits that bred in taller nest boxes (with longer entrance-floor distance) built deeper nests compared to shallower nest boxes[56]. The same pattern was reported from a great tit population breeding in natural nest holes[28]. Similarly, the nests of great and blue tits breeding in nest boxes fitted with anti-predator entrance tubes were higher compared to a control nest boxes with standard entrances[57]. However, it is important to notice that cavity (or nest box) depth affects both light conditions and predation risk, so the effect of both factors on the nest depth might be difficult to untangle. We therefore cannot rule out the possibility that greater nest height in predator-safe nest boxes at least partially an effect of compensating for low light in deep cavities.

Although illumination had an overwhelming effect on nest depth in our population, in most cases it is a result of a trade-off between different conflicting selection pressures, e.g. predation and light. For example, nesting further from the entrance would give collared flycatchers a selective advantage due to predation avoidance[24]. Despite that, many flycatchers build nests relatively close to the entrance which makes them accessible to pine martens, but on the other hand, probably also provides the minimal amount of light for the brood[24]. In our study, the mean nest height in dark nest boxes (ca. 10 cm) was below the greatest illumination level (ca. 20 cm). This result suggests that both illumination and predation avoidance may influence the height the bottom of nests of great tits.

Our results imply an important question: why have preferences for light in the nest environment evolved? Although there are a number of hypotheses pointing at possible advantages of exposing the clutch and/or nestlings to the light[13], experimental studies testing these in wild birds are rare. Laboratory experiments on house sparrows[14] and blackcaps (*Sylvia atricapilla*)[15] showed that longer exposure of eggs to light increase the rate of embryonic development and confirms the photo-acceleration hypothesis previously tested on poultry. It is important to notice that the response to light in blackcaps was weaker than in house sparrows, which could result from higher light-sensitivity of the cavity-nesting species[15]. There are some premises that better illumination at the nest site may be beneficial for parents by improving their ability to assess nestling visual begging signals (i.e. mouth coloration)[58], discrimination between their own and parasitic eggs[59, 60] or to aid in general orientation in dim cavities[23, 24]. Future surveys are needed to investigate the possible fitness consequences of light within nest sites of birds. Such studies should embrace both physiological effects of light on early stages of nestling development (e.g. growth rate, condition, functional lateralization) and light-dependent effects on adults' behavior (e.g. incubation, feeding strategies).

Our study opens new avenues for further research on light-dependent nest site selection in birds. Further studies are needed to investigate whether light preferences are consistent within different ecological groups of birds. We may expect that light might be less important in open-nesting species due to higher overall illumination and selection may even favor behaviors that limit access of light to eggs and nestlings (see ref. 13). On the other hand, even some cavity-nesting species may avoid bright sites[30, 34] if they are perceived as less secure (compare[29]). The separation of effects of illumination and nest concealment will be one of the most challenging methodological problems in future studies on the importance of light on nest-site selection.

Methods

Study area and nest boxes. The study was conducted on a population of great tits breeding in nest boxes in Wielkopolski National Park, Western Poland, in 2016. In 2014, nest boxes (n = 159) were placed at regular 50 meter intervals on 3 study sites (I–III), in a total area 48,35 ha. The number of boxes differed between study sites: I – 89, II – 42, III – 28. Every box was hung at a height of three meters with the entrance hole oriented South-East to standardize light conditions during the day. All the nest boxes had the same size, with internal dimensions of 12.0 × 16.0 × 36.0 cm and the entrance with diameter of 3.3 cm located 24 cm from the floor. To facilitate access to the nest, every nest box was equipped with a "drawer" (12.0 × 16.0 × 12.0 cm), where nests were built. All nest boxes were fitted with two 5.0 cm diameter resin windows (www.Handykam.com®) located in side-walls (one on each side), 14 cm from the bottom. The windows were opaque at the degree that prevents seeing interior of the nest box and transparent enough to let the light in. Each window was equipped with an adjustable shutters made of black plastic sheets.

General procedures. From the middle of March 2016 onwards, nest boxes were checked regularly to determine the date on which the first egg was laid and to quantify clutch size. We quantified nest size by using two variables: the depth of nest[61], which was an average of the maximum height of the nest material measured in four corners of the nest box and the height of nest, which was a distance from the nest box floor to the deepest point of the nest-cup bottom. Measurements were performed using a ruler (to an accuracy of 5 mm) and caliper (to an accuracy of 1 mm), respectively. We measured in total 48 nests at the end of the egg laying stage. Both measurements were highly and positively correlated (Pearson: $r = 0.97$, $p < 0.01$, $n = 48$), so in a further analysis we used only nest height. The same nest box monitoring and nest measurements were performed in 2015 when no internal nest box illuminance was modified (i.e. all nest boxes were naturally dark). This data set was used as additional control group (beside dark nest boxes in 2016) to analyze the effect of nest box internal illumination on nest dimensions. Moreover, nest box occupation data collected in 2015 was used as explanatory factor in nest site choice analysis in 2016, because of its potential influence on nest box attractiveness (see ref. 38).

Experiment design. To test the effect of nest box illumination on nest site choice and nest building behavior, we manipulated illumination inside nest boxes. Between September 2015 and early March 2016, shutters in all nest boxes remained closed. At the beginning of nest site choice period (16–17 March 2016), windows were opened in every second box creating two types of nest boxes: "bright" – with opened shutters (n = 79) and "dark" – with closed shutters (n = 80). In addition to great tits, three other species bred in the nest boxes: pied flycatchers (n = 2), blue tits (n = 16) and European nuthatches (*Sitta europaea*, n = 12). These nest boxes were excluded from further analysis; therefore the final number of bright and dark nest boxes was 67 and 62, respectively. Opening shutters significantly increased both absolute illuminance and light transfer in bright nest boxes comparing to dark nest boxes (see Results). The old nest material was removed from all nest boxes in the autumn preceding the experiment.

Although all nest boxes used in the study were identical with respect to the material used, dimensions and all construction details, opening windows could potentially increase internal temperature, what in turn could influence nest box choice. Therefore, we set temperature loggers (i-Button, Maxim Integrated®) in 91 randomly selected nest boxes (47 dark and 44 bright). They were located on the internal side of the front wall, about 5 cm below entrance hole. Temperature measurements were taken every 30 minutes, from 18 March to 10 April 2016. The time of measurements falls into the limits of nest choice period in great tits in the studied population, which spans between mid-March and mid-April. There were no significant differences in the mean (±SD) day temperature between both groups (dark nest box: 8.39 °C ± 0.28; bright nest box: 8.38 °C ± 0.33; $t = 0.096$, $df = 89$, $p = 0.924$), therefore we did not include temperature in the nest site choice analysis.

Light measurements. Two measurements of illumination inside nest boxes were performed. The first one took place within the time of nest site choice, between 5 and 15 April 2016. We measured randomly chosen 46 dark and 49 bright nest boxes with no visible evidence of nest material. The purpose of this measurement was to assess the efficiency of opening windows in bright nest boxes comparing to dark nest boxes. The illumination was measured about 2 cm above the nest box floor. The second measurement was performed between 6 May and 8 June, which corresponds to the time of incubation in the studied population. In order to prevent disturbance to broods, we used only nest boxes unoccupied by great tits. We measured 16 randomly chosen nest boxes. The purpose of this measurement was to assess how illumination inside nest box depends on the distance from the nest box floor. We measured illumination 2, 6, 10, 14, 18, 20 cm above the floor. The first measurement was done by putting the lux meter head (of 2 cm height) on the nest box floor. To obtain other heights, we put lux meter head on 4, 8, 12, 16 and 18 cm high cartoon boxes. In the case of two last measurements (18 and 20 cm), windows were partially and completely covered by cartoon boxes, respectively. In each nest box, all measurements were performed twice: with open and shut windows.

Measurements inside nest boxes were performed with a lux meter pointed toward the nest box ceiling. All the measurements per given nest box/distance from nest box floor were taken three times and then averaged. To assess precision of the light measurements, we calculated repeatability[62] within three measurements taken at the nest box floor in dark and bright nest boxes during the nest site choice period. Analyses show that our measurements were highly and significantly repeatable in both bright and dark nest boxes ($r > 0.99$, ANOVA, $F_{48, 98} = 217$, $p < 0.01$; $r > 0.99$; ANOVA; $F_{45, 98} = 94.72$, $p < 0.01$, respectively). Repeatability of measurements performed during the egg incubation period at six heights in bright and dark nest boxes was also significantly high ($r > 0.99$ in all cases). Measurements were performed during constant weather conditions (sunny, clear sky), between 08:00 AM and 02:00 PM. Time of measurement may affect brightness level inside nest boxes due to changes of the sun's position. To cope with this problem, we measured bright and dark nest boxes alternately. There was no significant difference in the time of light measurement between dark and bright nest boxes measured during the time of nest site choice (Student's *t*-test, $t = 0.47$, $p = 0.64$) and during the time of egg incubation (Mann - Whitney *U* test, $Z = -1.597$, $p = 0.11$).

All measurements of illumination were taken by using lux meter LS-100 (Sonopan®, Poland) with accuracy 0.001 lux. Each internal light measurement was preceded by the measurement of the ambient light entering the nest box through the entrance hole. These measurements were performed at the nest box entrance hole with a head of the lux meter was pointed perpendicularly to the nest box front wall. There was no difference in the illumination at the entrance between dark and bright nest boxes (Mann – Whitney *U* test, $Z = -0.015$, $n = 95$, $p = 0.988$).

We analyzed two measures of light intensity inside the boxes: the absolute illumination, hereafter illumination and the percentage of ambient light that reaches the interior of the nest box, hereafter light transfer.

Data analysis. We examined the normality of data distribution using Shapiro-Wilk tests. When data was not normally distributed, non-parametric tests were applied. In the nest site choice experiment, the binomial dependent variable was 'nest box occupation' (1 – occupied, 0 – not occupied) and was tested by using logistic regression model (LOGISTIC). In this model we used two binomial explanatory variables 'type of nest box' (1 – bright, 0 – dark) and 'occupation in 2015' (1 – occupied in 2015, 0 – not occupied in 2015). We also used one categorical independent variable, which was 'study site' (0 – site I, 1 – site II, 2 – site III). In the logistic regression model, categorical variables with more than two levels were recoded into binominal dummy variables[63]. In this procedure "study site I" was used as baseline, which means that each other study site (II and III) was compared in the model with "study site I". Model fit was tested with Omnibus Tests of Model Coefficients ($p < 0.05$ indicates good fit) and Hosmer and Lemenshow Tests ($p > 0.05$ indicates good fit)[64].

To analyze the variation in nest height and the sequence of nest box occupation, we used type III General Linear Model (GLM) with type of nest box (bright or dark) and study site (I, II or III) as the grouping factors. In the nest height model, we used clutch size and the date of first egg lay as covariates. Both factors are often related to an individuals' quality in birds, i.e. superior individuals breeds earlier and lay bigger clutches[65–67]. On the other hand, nest size may reflect individual quality[49]. Therefore, we controlled the potential effect of clutch size and the date of first egg lay on the nest height variation. In the sequence of the nest box occupation model, we used the date of first egg lay (converted to Julian date) as a dependent variable. In both models the interaction terms were removed when non-significant. All tests were two-tailed and the alpha level for significant differences was set to 0.05. All statistical analyses were conducted in SPSS Statistics (v.23, IBM). Descriptive statistics were presented as a mean ± standard deviation or as a median (Me) with the first and the third quartile ($Q_{25-75\%}$).

All methods were approved by the Local Ethical Committee and State Office for Environment Protection and performed in accordance with Polish law.

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Author Contributions

Both authors, P.P. and A.S. equally contributed to this work. P.P. analyzed and interpreted data, prepared the figures and tables. A.S. designed and coordinated the study. P.P. and A.S. wrote the manuscript. Both authors reviewed the manuscript.

Additional Information

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Article

Light affects parental provisioning behaviour in a cavity-nesting Passerine

Paweł Podkowa, Katarzyna Malinowska and Adrian Surmacki

P. Podkowa (https://orcid.org/0000-0001-8148-9968) ✉ (podkowa@amu.edu.pl), K. Malinowska and A. Surmacki (https://orcid.org/0000-0001-9875-6479), Dept of Avian Biology and Ecology, Faculty of Biology, Adam Mickiewicz Univ., Poznań, Poland.

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Nocturnal bird species possess special adaptations to maximise visual efficiency under low light levels. However, some typically diurnal species also experience low-light environments. For example, cavity-nesting Passerines raise broods in dark cavities and search for food in light-abundant surroundings. It is not clear whether they possess special adaptations for low light vision or breed in cavities at the expense of impaired parental care. In this study, we tested whether light conditions affect the provisioning efficiency of great tits. We experimentally tested how the level of natural and artificially increased illumination inside nest boxes affects parental feeding duration, frequency and timing. We monitored 15-h of provisioning activity of great tit parents when nestlings were day seven post hatch. We used traditional 'dark' nest boxes and 'bright' nest boxes with increased illumination obtained by using semi-transparent plastic windows. The duration of single feedings were, on average, shorter in brightened nest boxes compared to dark ones. This difference tended to be higher early in the morning and in the evening, when the illumination in dark nest boxes was the lowest. Nest box type, however, did not influence feeding frequency or times of the onset and the end of feeding. Our findings provide new evidence for impaired efficiency of parental care due to lowered light conditions. Further research is needed to test whether prolonged feeding duration has negative effects on adult time budgets and nestling energy expenditures.

Keywords: cavity nesters, feeding rate, *Parus major*, light, nest luminosity, trail cameras

Introduction

Most bird species are diurnal and rely mainly on vision (Birkhead 2012). Nocturnal or cavity-nesting birds often use other senses (Snow 1961, Konishi and Knudsen 1979), but still have well-developed eyes adapted to seeing in the dark. The most pronounced examples are tapeta lucida (Nicol and Arnott 1974), high rod to cone ratios in the retina or colorless oil droplets in cones (Bowmaker and Martin 1978, Cuthill 2006). On the other hand, typically diurnal species, like Passerines, have proportionally more cones, which are covered with pigmented oil droplets enhancing color discriminability, but simultaneously limiting overall cone sensitivity to light (Vorobyev et al. 1998, Vorobyev 2003). As a consequence, diurnal species have excellent color vision

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but only under sufficient light conditions. On the contrary, night vision of nocturnal species has evolved at the expense of efficient color vision. Despite adaptations to specific light conditions, some bird species are active in both darkness and abundant light. Perhaps the most intriguing example of such a phenomenon occurs in cavity-nesting Passerines (Wesołowski and Maziarz 2012). In cavities, the illuminance level during mid-day could be classified as mesopic, and at dawn, even as scotopic (0.1 lx and 0.001 lx respectively, Wesołowski and Maziarz 2012, Maziarz and Wesołowski 2014). In such 'nocturnal' conditions, birds have to undertake visually demanding activities crucial for their efficient reproduction like nest building and offspring feeding. The problem is not only the low illuminance inside the cavity, but also the quick transitions between darkness of cavity and bright surroundings, and vice versa (Cassey 2009, Wesołowski and Maziarz 2012).

An unsolved issue is how diurnal cavity nesters visually cope with the dim light conditions inside the cavity. One possibility is that they possess some anatomical or physiological adaptations enabling them low-light vision. To date, however, studies suggest that the ratio of rods to cones in the retinas of cavity nesting passerines do not differ from those of other diurnal species (Hart et al. 2000), although other adaptations are possible. For example, some dawn or dusk active species have elongated outer rods segment (Rojas et al. 1999) or higher number synaptic connections between ganglion cells (McNeil et al. 2005), which maximize their sensitivity to low-light conditions.

The other possibility is that cavity nesters have no special adaptations for vision in dim light. This suggests the existence of a trade-off between advantages of breeding in cavities and costs related to light deficiency. Cavities provide good protection from predators (Fontaine et al. 2007) and stable microclimate conditions (Maziarz et al. 2017), which result in higher breeding success of cavity nesters compared to open nest species (Wesołowski 2007). On the other hand, birds breeding in cavities may experience significant costs associated with low-light conditions. A recent study indicates that access to appropriate light might be a crucial factor regulating physiological processes important for the normal development of birds at early stages of life (reviewed in Maurer et al. 2011).

The dark-cavity environment may limit efficiency of parental care (Wesołowski and Maziarz 2012, Maziarz and Wesołowski 2014). Aside from localizing nestlings (or their mouths) in a dark cavity, parents need to make decisions regarding which nestling to feed. Research demonstrates that nestlings within a brood vary in mouth coloration (Kilner 1997, Kilner and Davis 1998, Thorogood et al. 2008) and that parental feeding activity depends on this characteristic (Saino et al. 2000, De Ayala et al. 2007, Ewen et al. 2008, Dugas 2009). Natural light levels in cavities limit color perception (Reynolds et al. 2009, Avilés et al. 2011), which may hinder the feeding process. Aside from assessing the visual signals of their offspring, parents perform other activities like removing feaces or nest cleaning. It might be assumed that, under dim light, all these activities require more time to undertake which should lead to less effective nestling provisioning.

To date, several experimental studies investigated potential relationships between cavity lighting and parental care (Götmark and Ahlstrom 1997, Heeb et al. 2003, Wiebe and Slagsvold 2009). In all these cases, the change of nestling mass was used as a measure of parental feeding behaviour. This method is useful to measure parent preferences for feed particular nestlings (e.g. due to modified gape color), but does not necessary reflect visual problems during feeding. A more precise way of dealing with this issue is to measure the time required to transfer food from parent to offspring (Dugas 2015).

This study provides a new approach into studies of avian parental care with regard to light limitation. For the first time, we investigate how light availability affects both feeding duration and feeding frequency during entire day activity. The aim of our study was to investigate whether the efficiency of parental care in cavity nesting diurnal Passerine, the great tit *Parus major*, is affected by the deficiency of light. To test this hypothesis, we created artificial cavities with a dark and brightened interiors and performed daylong observations of parental care. We assumed that birds breeding in brighter nest boxes would: 1) spend less time on a single nestling feeding visit, 2) start feeding earlier and cease feeding later in a day due to earlier onset of dawn and later onset of dusk detected inside nest boxes. Moreover, we predicted that feeding duration in dark nest boxes would be more related to ambient light intensity compared to bright nest boxes.

Material and methods

Study area and general procedures

We studied a nest box breeding population of great tits in deciduous and mixed forest of Wielkopolski National Park, Western Poland (total area 48.35 ha) in 2016. We hung nest boxes (n = 159) oriented SE at height of 3 m. We equipped all nest boxes with two semitransparent, round windows (5 cm, 15 cm above the floor) and opaque shutters allowing the regulation of internal light intensity. A previous study demonstrated that the presence of windows increases internal nest box illumination (1.41 lx with shut versus 52.67 lx with open windows, Podkowa and Surmacki 2017). Internal dimensions of the nest boxes were 12 × 14 × 40 cm and the diameter of entrance was 3.3 cm. For more details on study area and nest box construction, see Kudelska et al. (2017) and Podkowa and Surmacki (2017). We used 34 broods randomly divided into two groups: 'dark' (n = 15) with closed shutters, and 'bright' (n = 19) with opened shutters. We performed the nest box illumination manipulation prior to a breeding season. From the middle of March onwards, we regularly monitored nest boxes to determine clutch size and to follow brood fate. At the beginning of incubation, we measured nest height (0.1

cm) as a distance between nest-cup bottom and nest box floor (Podkowa and Surmacki 2017). Additionally, after ca 7 days of incubation, we mounted trail cameras in the ceiling of the each nest box to determine the exact day of hatching.

The median Julian date (min–max) of hatching was 133 (125–145) in dark nest boxes and 130 (125–135) in bright and this difference was not statistically significant (t-test; t = 1.366, df = 32, p = 0.182). Similarly, there was no significant difference in a median (min–max) clutch size between dark 10 (7–12) and bright 11 (8–13) nest boxes (t-test; −1.053, df = 32, p = 0.300). At the day of the experiment, median (min–max) brood size in dark nest boxes was 6 (3–10), while in bright nest boxes it was 9 (4–11) and this difference was statistically significant (Mann–Whitney test; Z = −2.019, p = 0.047).

Luminosity in a nest box

A previous study, based on luxometer measurements in 95 nest boxes, indicated that side windows increase luminosity approximately 50 times compared to traditional dark boxes (Podkowa and Surmacki 2017). To investigate hourly changes in light conditions of nest boxes, we measured day-long luminosity in a single nest box during two consecutive days, with open and closed shutters, respectively. The measurement was performed in a random, unoccupied nest box under constant sunny weather conditions. We used lux meter LS-100 (Sonopan®, Poland), recording luminosity continuously at 10 min intervals, with precision to 0.001 lx. For more details see Podkowa and Surmacki (2017). The first measurement was performed about 0.5 h before the sunrise and the last one about 0.5 h after the sunset. Changes in luminosity inside dark and bright nest boxes throughout the day are presented in Fig. 1. It clearly shows that internal light level is lower in the morning and evening compared to the daytime, but overall light intensity was always higher in bright nest boxes (Fig. 1).

Recordings of parents' behaviour

To investigate how nest box luminosity and time of the day affected feeding duration, frequency and timing, we recorded parental care behaviour in each brood for 24 h when nestlings were seven days old. We chose this age because after the 6th day post hatching, prey size did not vary significantly between feedings which could affect results (Royama 1966). All recordings were taken by using trail cameras mounted in the chamber of ceiling of the nest box. We used NatureView HD cameras, (Bushnell, Overland Park, KS, USA) equipped with a 250 mm lenses and invisible infrared light source. Recordings were triggered by passive infrared sensor (PIR). We recorded continuously 10–20 s videos with the interval set to one second. In practice, the gap between continuous videos ranged from 5 to 6 s. Total time of each activity captured in two subsequent recordings was summarized according to time stamp available on each film frame. In this way, we gained all motion-triggered behaviours of parents and nestlings (e.g. begging, feeding, preening, nest cleaning, etc.). The timing of feeding analysis ranged from 05:00 to 20:00 h. Feedings before 05:00 and after 20:00 h were rare and did not occur in all nests (on average 4.8 and 2.9 feedings per nest, n = 16 and n = 22, respectively). Therefore, we excluded 04:00–05:00 and 20:00–21:00 intervals from analysis on feeding duration and frequency. We defined feeding duration as the total time between entering and leaving nest box by a parent that provided food during a single visit. We did not take into account visits when parent undertook other activities after or before feeding (e.g. nest grooming, feces removing, preening). We also excluded videos in which two adults were present during one feeding visit because it could interfere with the time spent in a nest box. We defined the number of feedings as the total number of provisioning visits performed by both parents. In further analyses, we used total number of feedings and mean feeding duration calculated separately for

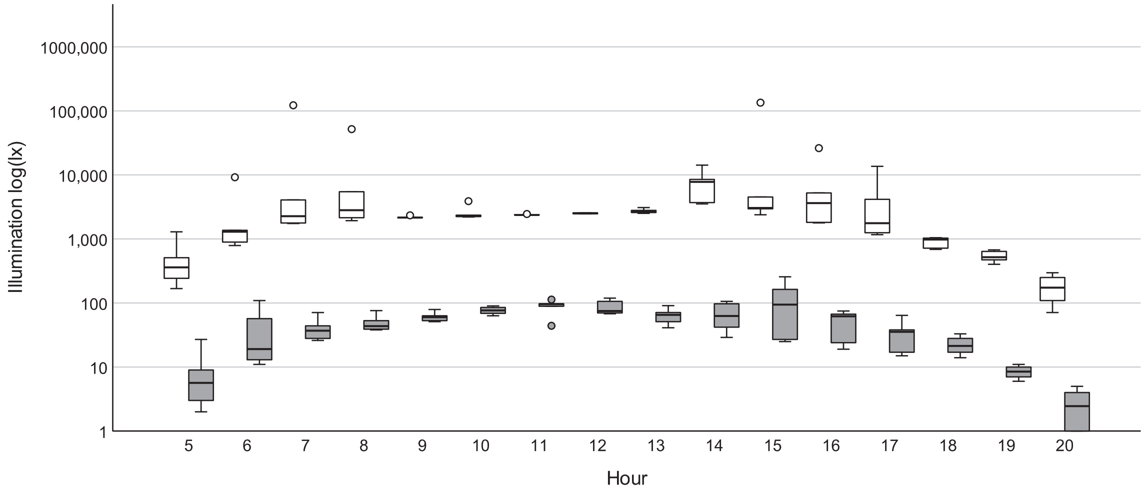

Figure 1. Daily changes (medians) in illuminance in a one nest box taken in two consecutive days with closed (grey boxplot) and open (white boxplot) windows. Lines across boxes represents medians, length of the box shows interquartile range, whiskers shows min-max value, circles are considered as an outliers.

each hour and nest box between 05:00 and 20:00 h. The hour of the first and the last feeding in a day was calculated as the minutes that elapsed between the feeding visit and sunrise or sunset, respectively. The above information were gathered from all recordings obtained between 04:00 and 21:00 h.

Statistical analyses

We used generalized linear mixed models (GLMM) to estimate the effect of nest box type (dark versus bright) on total number of feedings and duration of single feeding attempts. The predicted variables were 'number of feedings' and 'feeding duration' (Poisson and Gamma distributed, respectively, both with LOG link function). We tested the effect of the 'nest box type', timing across the season ('hatching date'), number of nestlings ('brood size'), nest cup height ('nest height') and hour (both linear and quadratic term) as a fixed factors, as well as for interactions between those factors and box type. We also performed two separate models for each nest box type to test both linear and quadratic effect of the hour on feeding duration and number of feedings. Because analyzed variables were gathered for the same broods during 16 consecutive hours, we considered 'hour' also as a repeated term label. Nest ID was included as random factor to take into account the non-independence of feeding behaviour measured in the same brood. Selection of the best-fitted model was done by using ΔAIC with the lowest value as an indicator of the best model (Burnham and Anderson 2002). We analyzed the difference between two nest boxes types (i.e. dark and bright) using Mann–Whitney U test for variables with non-normal distribution and t-test for normally distributed data. All statistical analyses were done using SPSS Software (IBM SPSS Statistics for Windows ver. 24.0.).

Results

The results of the GLMM revealed that feeding duration was significantly longer in dark nest boxes (Table 1, Fig. 2A). This difference was especially pronounced in the morning and evening, revealed by the marginally significant interaction between nest box type and quadratic term of hour (Table 1, Fig. 2A). The nest height, clutch size, hatching date and the brood size had no significant effect on feeding duration (Table 1). When dark and bright nest boxes were analyzed separately, feeding duration was significantly related to linear hour (in both bright and dark nest boxes), while in dark nest boxes, a quadratic effect of hour was also observed (Table 1, Fig. 2A).

There was no significant effect of nest box luminosity on the number of feedings (Table 1, Fig. 2B). The time of the day significantly affected number of feedings (Table 1). This effect was different depending on nest box type, which, was indicated by the interaction between nest box type and the hour (Table 1, Fig. 2B). In bright nest boxes, the highest feeding intensity occurred at about 05:00 h then showed a smooth decline toward the evening (Table 1, Fig. 2B). The feeding peak in the dark nest boxes was shifted to 08:00 h, followed by steep decline (Table 1, Fig. 2B). We also found a significant relationship between the number of feedings, brood size and hatching date. Larger broods received more food from parents and later breeders brought less food to their offspring (Table 1).

Table 1. The results of GLMMs showing the relationship between feeding duration and number of feedings and hour, nest box type, nest height, brood size, hatching date and their interactions. Models were created for both nest box types together and for each nest box type separately.

	Feeding duration				Number of feedings			
	Estimate	SE	t	p	Estimate	SE	t	p
Dark and bright nest boxes								
Intercept	2.421	0.163	14.88	**0.000**	8.876	1.576	5.63	**< 0.001**
Nestbox type	0.490	0.196	2.50	**0.013**	0.244	0.383	0.64	0.526
Hour (linear)	−0.035	0.021	−1.69	0.092	−0.036	0.017	−2.07	**0.039**
Hour (quadratic)	0.002	0.001	1.30	0.193	0.001	0.001	0.78	0.438
Hour (linear) × nestbox type	−0.055	0.035	−1.58	0.116	0.106	0.030	3.49	**< 0.001**
Hour (quadratic) × nestbox type	0.004	0.002	1.92	**0.056**	−0.007	0.002	−3.56	**< 0.001**
Nest height	−0.006	0.025	−0.23	0.821	0.008	0.018	0.44	0.660
Clutch size	–	–	–	ns	0.026	0.035	0.74	0.457
Hatching date	–	–	–	ns	−0.051	0.011	−4.46	**< 0.001**
Brood size	–	–	–	ns	0.131	0.028	4.73	**< 0.001**
Brood size × nestbox type	–	–	–	ns	−0.083	0.047	−1.75	0.081
Dark nest boxes								
Intercept	−1.806	4.370	−0.41	0.680	8.328	2.758	3.02	**0.003**
Hour (linear)	−0.096	0.038	−2.52	**0.013**	0.071	0.026	2.78	**0.006**
Hour (quadratic)	0.006	0.002	2.62	**0.010**	−0.006	0.002	−3.74	**< 0.001**
Bright nest boxes								
Intercept	4.196	2.314	1.81	0.071	9.457	2.277	4.15	**< 0.001**
Hour (linear)	−0.036	0.015	−2.42	**0.016**	−0.037	0.017	−2.12	**0.035**
Hour (quadratic)	0.002	0.001	1.89	0.061	0.001	0.001	0.82	0.416

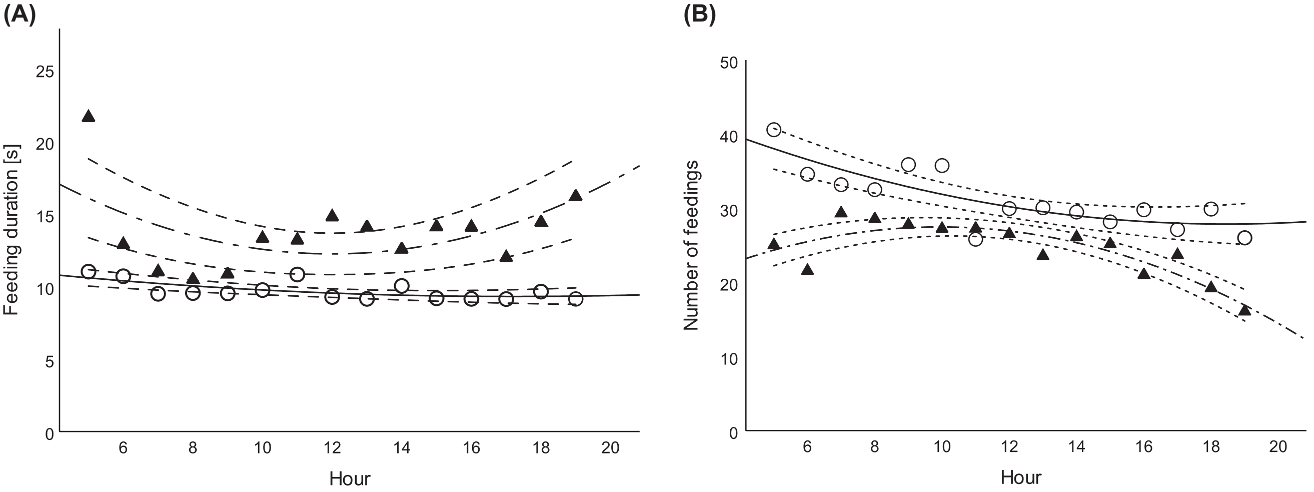

Figure 2. Duration of single feeding attempt per hour (A) and number of feedings (B) collected in dark (triangles, dash-dotted line) and bright (open circles, solid line) nest boxes. Each point represents mean score for a given hour. Dash-dotted and solid fit lines are presented with 95% confidence intervals (dashed lines).

The models performed separately for both types of nest boxes revealed high statistical significance of linear and quadratic term of hour in dark nest boxes and a significant effect of linear hour in bright nest boxes. In both types of nests, we found a significant effect of hatching date, while brood size was observed as an important term only in bright nest boxes.

Birds breeding in bright nest boxes started feeding slightly earlier (9.8 ± 3.32 min before sunrise) compared to birds breeding in dark nest boxes (2.4 ± 1.98 min before sunrise), but this difference was just above the statistical significance limit (t test; $t = 2.010$, $df = 30$, $p = 0.054$). The observed time of the last feeding in dark nest boxes (42.9 ± 4.56 min after sunset) did not differ significantly from the time of the last feeding in bright nest boxes (42.8 ± 3.10 after sunset; t test; $t = 0.018$, $df = 30$, $p = 0.986$).

Discussion

Our experiment confirmed the hypothesis that breeding in dark cavities might lead to reduced parental feeding efficiency. Feeding event duration was significantly shorter in experimentally brightened nest boxes, and this effect was the most pronounced at dawn and evening, when illumination in nest boxes may be the lowest. We did not observe a concordant reduction in feeding frequency in dark compared to bright nest boxes, however the daily feeding schedule differed between both nest box types. Parents from bright nest boxes provisioned nestlings most intensively soon after dawn compared to parents at dark nest boxes wherein feeding peak was shifted approximately three hours later. The total daytime devoted for food delivery was comparable in both types of nest boxes.

In addition to light conditions, other factors, not controlled in our study, could potentially affect feeding behaviour. Some earlier studies suggest that parent condition could influence feeding behaviour (Pagani-Núñez and Senar 2014, Grzędzicka 2018). The nest box luminosity modification in our study was performed prior to the onset of the breeding season and birds preferably occupied bright nest boxes (Podkowa and Surmacki 2017). This pattern raises the possibility that brightened nest boxes are occupied by higher-quality individuals, that may cope better with offspring feeding. Although we did not assess parental condition, we think this explanation is less probable. First, there was no difference between dark and bright nest box breeders in either the time of hatching or in clutch size. Moreover, despite clear preferences for bright nest boxes, about 65% of both types of nest boxes were left unoccupied (Podkowa and Surmacki 2017). This suggests that, regardless of individual quality, all birds have unlimited access to preferred nesting sites. Finally, parent condition usually affects feeding frequency (Grzędzicka 2018), which remained constant across nest box types in our study.

The prey type and size may affect the time parents need to transfer food to the offspring. Earlier studies demonstrated that parents need more time to feed nestlings larger prey (Dugas 2015). In blue tit nestlings, the total time needed to swallow food increases according to the following order: caterpillars < spiders < grasshoppers (Bańbura et al. 1999). The type and size of prey could explain the pattern of feeding duration in our study, if parents from dark nest boxes feed their offspring with larger, and more difficult to swallow prey, compared to parents from bright nest boxes. There is, however, no evidence that parents adjust their foraging preferences to the nest luminosity. Both types of nest boxes were located in the same homogeneous habitat, spaced ~50 m apart. It is therefore reasonable to assume that the prey brought to the nest represent a subsample of the available food base in the territory (Bańbura et al. 1999).

To date, the effect of nest site illumination on parents' prey handling time has not been studied. Dugas (2015), show that house sparrows transfer food faster to those nestlings whose flanges were painted white compared to those painted grey. Although light in a nest box was not manipulated in the Dugas (2015) study, we may assume that the results are in concordance with our findings. Painting flanges white causes greater light reflectance, which is analogous to increasing ambient illumination. Previous studies (Maziarz and Wesołowski 2014), as well as our study, show that in cavities of passerines, the illuminance at midday is higher than at dawn when parents commence feeding. Therefore, we may expect that, in standard dark nest boxes, parents should face the greatest feeding problems at dawn and dusk, when the amount of light entering the nest box is the lowest. The daily pattern of feeding duration confirmed this prediction. Food transfer in dark nest boxes took the longest time during the first and the last hours of a day, while in bright nest boxes it remained almost uniformly short. It is important to notice, however, that the long feeding duration in the morning in dark nest boxes was observed only between 05:00 and 06:00 h. About 08:00 h, it reached the lowest values followed by linear increase until 20:00 h. This pattern suggests that, beside changes in illumination, other factors shape feeding duration in naturally dark cavities.

The shorter feeding durations observed in bright nest boxes did not increase the total number of feeding trips. This result is consistent with findings from earlier studies in which internal illumination has been manipulated (Götmark and Ahlström 1997, Heeb et al. 2003, Wiebe and Slagsvold 2009). The most probable explanation for this finding is that parents saved time on shorter feeding and then spent time on activities other than parental care. This result is in line with findings from brood size manipulations that shown that brood reduction decreases the number of parental feedings (Nur 1984, Smith et al. 1988). Despite the similarity in the feeding frequency between the nest box types, we found that their feeding schedules differ significantly. In bright nest boxes, the highest number of feedings occurred early in the morning, then decreased towards the evening. On the contrary, in dark nest boxes, feeding frequency increased from dawn until the midday peak, which was followed by a gradual decrease in frequency. These patterns could be affected by a combination of nestling food demands and parent feeding constraints related to light intensity. In bright nest boxes in which light is abundant throughout the day, parents provision most intensively at the dawn, when nestling hunger is the highest due to nighttime fasting and low temperature. In dark nest boxes, the feeding peak is shifted toward midday, when light is the most abundant. On the other hand, feeding at dawn and in the evening was reduced due to less favorable light conditions. Such an explanation is supported by the negative relationship between feeding duration and the number of feedings in dark nest boxes.

Our results clearly indicate that low illumination of cavities significantly increases the time needed to feed nestlings. However, based on these data, we cannot be sure of the mechanism causing this pattern. The first possibility is that parents have difficulty detecting nestling gapes in the dark (compare Avilés et al. 2008, Dugas 2015). Second, prolonged feeding in the dark could be due to a parental decision-making process. In this population, adults bring only one prey item and feed one nestling per visit. Thus, on each occasion, the parent spends some time assessing how to distribute food in a most efficient way. The choice of which nestling to feed is probably based on a number of visual cues like gape and flanges color (De Ayala et al. 2007), gape size capacity in relation to prey size (Stalwick and Wiebe 2019), and/or the intensity of begging movements (Smith et al. 2017). Low light may significantly depress, or even disable, color vision in birds (Lind and Kelber 2009, Gomez et al. 2014). Thus, assessment of nestling signals should be more difficult and time consuming under dim light. The third explanation is that parents entering dark nest boxes need to allow their eyes more time to accommodate to the low light conditions (compare Wesołowski and Maziarz 2012).

The lack of a significant illumination effect on feeding frequency does not preclude its effect on both parent and offspring condition. Assuming that the mean difference in feeding duration between dark and bright nest boxes during a single visit is 4 s, and that parents perform about 450 trips a day, the difference in parental care time between nest box types is about 30 min per day per pair. Parents from bright nest boxes could use this additional time to forage or to rest, which may increase their body condition and therefore improve their opportunity for further reproduction. Differences in feeding duration may also potentially affect nestlings; when parents take longer time to feed nestlings, nestlings must spent more energy on begging, which does not provide any additional payoff (Kilner 2001, Moreno-Rueda 2010).

The feeding timing did not differ markedly between dark and bright nest boxes. This result suggests that the time of the onset and the end of feeding was related to light intensity outside, rather than inside, the nest box. In other words, parents likely provisioned as long as the ambient light enabled them to detect prey. This pattern is confirmed by findings from earlier studies. Captive great tits are less successful in finding prey, spend less time on hunting and handle individual prey items for longer time when dawn luminance is less than ~7 cd m^{-2} (Kacelnik 1979).

Our study provides evidence that breeding in dark cavities may bear some costs related to low illumination; lower illumination impaired the feeding efficiency of nestlings by bird parents. Despite the lack of a significant effect on feeding frequency, artificially increased illumination led to shorter feeding duration. Beneficial effects of light level on the feeding process probably explains the marked preferences of birds to breed in brighter nest boxes found in the same population (Podkowa and Surmacki 2017). Future studies are needed to investigate whether the pattern that our dataset revealed affects parental time budgets and consequently fitness. Moreover, the results of this study highlight the importance of future studies to investigate how light regime influences offspring energy expenditure and survivorship.

Data availability statement

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.t4b8gthx9> (Podkowa et al. 2019).

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Author contributions – PP and AS wrote an article. PP, KM and AS collected and analyzed data.

Permits – All applicable international, national and institutional guidelines for the care and use of animals were followed.

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ORIGINAL ARTICLE

The effect of daylight exposure on the immune response and body condition of Great Tit nestlings

Paweł Podkowa[1] · **Adrian Surmacki**[1]

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Abstract

Natural light plays an important role in many aspects of birds' biology, ecology and behaviour. Wild birds experience various light conditions, both in terms of its intensity and spectral properties, which vary within the nesting habitat of avian species. Recent study has shown that some bird species prefer to build their nests in bright nest sites. Light is one of the major factors affecting early development and condition of nestlings, but to date, this effect has not been tested in wild conditions. This study aims to answer whether birds could benefit from nesting in brighter light environment. Potential benefits may occur in nestlings' condition, growth rate and breeding output. The research was carried out in the population of Great Tits (*Parus major*) breeding in two types nest boxes which differed with internal illumination. In "dark" boxes, the only source of light was the entrance hole. "Bright" boxes have additional side semi-transparent windows. We conducted two experiments in which light environment in nest box was set after (Experiment I) or before (Experiment II) birds settle in. Our study showed that light environment did not significantly affect nestlings body condition and growth. However, females in their first breeding attempt showed strong preference to the brightened nest boxes. In this group, the offspring were heavier and showed stronger immune responses than nestlings reared in dark nest boxes. Nestlings in bright nest boxes fledged about one day earlier. Nesting in brightened nest boxes may provide potential benefit for adult females in their first breeding attempt. The interaction between maternal effect and light environment is being discussed.

Keywords Daylight · PHA · Immunocompetence · Body condition · Growth · Cavity nesters

Zusammenfassung

Natürliches Licht spielt für viele Aspekte der Biologie, Ökologie und des Verhaltens von Vögeln eine wichtige Rolle. Freilebende Vögel sind verschiedensten Lichtverhältnissen bzgl. Intensität und spektralen Eigenschaften ausgesetzt, die innerhalb des Nistplatzes der Vogelarten variieren. Jüngste Studien haben gezeigt, dass einige Vogelarten ihre Nester bevorzugt an hellen Nistplätzen bauen. Licht ist einer der Hauptfaktoren, welche die Entwicklung und Kondition der Nestlinge beeinflussen. Jedoch wurde dieser Effekt bisher noch nicht in Freiland untersucht. Mit dieser Studie soll geklärt werden, ob Vögel davon profitieren, in einer helleren Umgebung zu brüten. Mögliche Vorteile könnten sich auf die Kondition und Wachstumsrate der Nestlinge sowie dem Bruterfolg auswirken. Die Untersuchung wurde in einer Population von Kohlmeisen (*Parus major)* durchgeführt, die in zwei Arten von Nistkästen mit unterschiedlicher Innenbeleuchtung brüteten. In „dunklen " Nistkästen war die einzige Lichtquelle das Einflugloch. „Hellere " Nistkästen hatten zusätzlich seitliche, halbtransparente Fenster. Wir führten zwei Experimente durch, in welchen die Lichtverhältnisse in den Nistkästen festgesetzt wurden, nachdem (Experiment I) oder bevor (Experiment II) die Vögel die Kästen besetzten. Unsere Studie zeigte, dass die Lichtverhältnisse keinen signifikanten Einfluss auf die Körperkondition und das Wachstum der Nestlinge hatten. Allerdings zeigten die Weibchen bei ihrem ersten Brutversuch eine starke Präferenz für die helleren Nistkästen. In dieser Gruppe waren die

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✉ Paweł Podkowa
podkowa@amu.edu.pl

[1] Department of Avian Biology and Ecology, Adam Mickiewicz University, Poznań, Poland

Nachkommen schwerer und zeigten eine stärkere Immunantwort als Nestlinge, die in dunklen Nistkästen aufgezogen wurden. Nestlinge in hellen Nistkästen wurden etwa einen Tag früher flügge. Das Brüten in hellen Nistkästen könnte für adulte Weibchen bei ihrem ersten Brutversuch von Vorteil sein. Die Interaktion zwischen maternalen Effekten und Lichtverhältnisse wird diskutiert.

Introduction

Natural light plays an important role in many aspects of birds' biology, ecology and behaviour. It affects timing of courtship and breeding (Kempenaers 2010; Dominoni et al. 2013), migratory behaviour (Rowan 1925; Gwinner 1996), magnetic orientation (Stapput et al. 2010; but see Bolte et al. 2021), sleep (Raap et al. 2016; Aulsebrook et al. 2021), nest site selection (Marchetti 1993; Podkowa and Surmacki 2017), activity of endocrine system (Meddle et al. 2002; Gwinner et al. 1997; Sur et al. 2021). Light my also affect birds indirectly, for example, by altering daily energy expenditure (Welbers et al. 2017) and nest survival (Russ et al. 2017). Birds experience various light conditions, both in terms of its intensity and spectral properties (Endler 1993). This variation may result from daily and seasonal changes (Thorne 2009), artificial lighting infrastructure (Senzaki et al. 2020), the latitude (Da Silva & Kempenaers 2017), habitat types and structure (Endler and Théry 1996; Langmore et al. 2005).

The effect of luminance within the nesting habitat of avian species might be critically important. Light is known to influence the development and condition of young birds. Theoretically, this process starts as early as at the embryo stage, due to the fact that eggshells transmit some portion of the light waves to the developing organisms (Maurer et al. 2011, 2015). Exposure of eggs to light during incubation is, in general, beneficial because it accelerates embryo development (Cooper et al. 2011; Austin et al. 2014), increases functional brain asymmetry, helps to establish circadian rhythm, activates antimicrobial defense mechanisms on the surface of the eggshell, and plays the role in repairing DNA in the process of photoreactivation (reviewed by Maurer et al. 2011). The positive effect of light continues after hatching and it promotes body mass growth (Robbins et al. 1984) and synthesis of vitamin D3 (Lewis et al. 2009), and also prevents arrhythmia, tibial dyschondroplasia and rickets (Lewis et al. 2009). Evidence for the impact of light on development and conditions of young birds is rare and come mainly from experiments in poultry farms, where the light intensity and wavelength spectrum is beyond its natural range (Fairchild 2000; Olanrewaju et al. 2006, 2012; Lewis 2010). Rare studies on wild species were also confined to laboratory experiments (Cooper et al. 2011; Austin et al. 2014). In wild free-living bird species, a large majority of studies investigate the effect of Artificial Light at Night (ALAN) on various aspects of biology and physiology (e.g. Kempenaers et al. 2010; de Jong et al. 2015; Russ et al. 2017). Although these studies are valuable sources of knowledge on the effect of disturbance of daily light rhythm, however, they do not provide information about natural light variation on avian biology.

Light conditions in an offspring rearing environment may differ even within the same population of a given species (Muñoz et al. 2007; Honza et al. 2011; Maziarz and Wesołowski 2014). Consequently, birds use light characteristics as a cue when choosing the nest sites. This phenomena in known in both open cup nesters (Hartman and Oring 2003; Burton 2007), as well as in cavity nesting birds (Maziarz and Wesołowski 2014; Podkowa and Surmacki 2017; Monti et al. 2019).

The light may be crucial for development of young birds in diurnal cavity nesters. As was shown in an earlier study, natural cavities are very dark, so birds that breed there face light conditions similar to those during moonless night (Wesołowski and Maziarz 2012). On the other hand, especially in secondary cavity nesters, there is a significant variation in the illuminance within the natural cavities due to their depth, and the shape and orientation of the entrance hole (Wesołowski and Maziarz 2012; Maziarz and Wesołowski 2014). Moreover, birds may adjust the amount of light entering the cavity by modifying the nest construction (Podkowa and Surmacki 2017). It can be assumed that due to the deficiency of light in cavities, diurnal species whose life history is closely related to well-lit environments (Kluijver 1951; Austin et al. 2014) should be particularly sensitive to dim light conditions experienced during reproduction.

In the present paper, we made the first attempt to assess the impact of natural daylight on the condition and development of nestlings of a free-ranging birds' species. Our goal was to extract the effect of natural light on birds' biology without interrupting their circadian rhythm nor photoperiod perception. We performed our surveys on Great Tit (*Parus major*) breeding in standard, dark nest boxes in which the only source of light was the entrance hole (hereafter "dark" nest boxes) and nest boxes in which daylight illuminance was increased by applying semitransparent plastic windows (hereafter "bright" nest boxes). Basing on findings from earlier studies, we expected that birds raised in brighter nest boxes would (i) grow faster, (ii) have better body condition, and (iii) have a greater immune response.

Materials and methods

General procedures

The research was carried out between 2015 and 2017 in the Wielkopolski National Park (Western Poland, 52° 18′ N 16° 49′ E). In 2014, 159 wooden breeding boxes were hung in three study sites: Site I (27, 7 ha), Site II (11,2 ha) and Site III (9,45 ha), for more details see Kudelska et al. (2017). Internal dimensions of nest boxes were 12 × 14 × 40 cm and the entrance hole diameter was 3.2 cm. Each nest box was equipped with two translucent synthetic resin windows with a diameter of 5 cm located on side walls, 15 cm above nest box floor. Daylight intensity inside the breeding box was controlled by opening/closing the windows with external shutters made of black opaque plastic. Over the course of the study, we created two types of boxes: dark with closed shutters, where the only source of light was the entrance hole, and bright, with opened shutters. Because all boxes were equipped with windows, we could freely change the type of nest box type and decide when it happens (Podkowa & Surmacki 2017). Light intensity (lx) in nesting boxes was measured using a Sonopan L-100 luxmeter (Sonopan, Poland). The internal illuminance in bright nest boxes (Me = 52.67 lx, Q25–75% = 42.83–62.28) was about fifty times higher than in dark nest boxes (Me = 1.41 lx, Q25–75% = 1.04–2.19, Podkowa and Surmacki 2017).

At the ceiling of the nest box, we placed a trail camera (Bushnell® HD LiveView), to record the timing of the first egg-laying and hatching. For more details on nest box design and the use of trail cameras see Surmacki and Podkowa (2022). From mid-March to the end of June, the boxes were monitored to determine history of broods.

We performed two experiments, which differed in the time when both experimental groups (dark and bright boxes) were created. In the first approach conducted in 2015 (hereafter Experiment I), at the beginning of the breeding season, shutters in all nest boxes were shut (all boxes were initially dark). Soon after clutch completion, half of nest boxes were randomly assigned to bright group in which we opened the windows. Other boxes in which windows remained shut served as a dark group. In the second approach conducted in 2016–2017 (hereafter Experiment II), we opened windows in a half of the randomly chosen nest boxes before the onset of nest building (the ratio of available bright and dark nest boxes was 1:1). While in Experiment I the effect of light was separated from the effect of nest box choice by the parents, in Experiment II, adult birds could choose between the dark and bright nest boxes. In the studied population, Great Tits showed strong preference to bright nest boxes which were occupied about twice as often comparing to the dark ones (Podkowa and Surmacki 2017). In both experiments, we assessed the effect of light on nestlings' biometrics and breeding success. In Experiment II, we assessed also nestlings' immunocompetence and fledging time. Because more than 50% of nests in year 2017 were abandoned due to weather collapse in mid-April, season 2017 were excluded from further biometric analysis. During seasons 2015–2016 we did not observe any suboptimal weather condition nor between-years differences in daily temperature measured for 19 consecutive days (starting 10 days prior to median egg lying date, $t = 1.588$, $p = 0.130$). We did not find any differences in the date of first egg laying between years 2015 and 2016 ($t = -0.214$, $p = 0.831$). However, we noticed earlier hatching date in year 2015, (Me = 129, Min–Max = 123–137) comparing to year 2016 (Me = 131, Min–Max = 125–143; $t = -2.278$, $p = 0.026$).

Biometric measurements of nestlings

We used a standard protocol for biometric measurement of the nestlings (e.g. Mainwaring et al. 2010). Birds were weighed on an electronic scale (0.1 g) on the 2nd and 12th day after hatching (day of hatching being the "0" day). The chicks were individually marked by painting their claws with a black marker (2nd day), followed by ringing (8th day). We obtained biometrical measurements from nestlings hatched in 78 nests (2015: 21 dark and 16 bright boxes; 2016: 14 dark and 27 bright boxes). When nestlings were 12 days old, we took the following measurements: right wing length (ruler, 0.5 mm), head length with beak and right tarsus length (electronic caliper, 0.1 mm). To assess condition of nestlings, we calculated Scaled Mass Index (SMI) proposed by Peig and Green (2009). SMI is an alternative for traditional body mass index (i.e. residuals from body mass-linear measure regression), which might be biased towards larger individuals (Arnold and Green 2007). We calculated SMI from body mass and a linear body measurement which has the strongest correlation with body mass. In our population the highest correlation was observed between body mass and head–beak length (2015: Pearson's $r^2 = 0.525$, $n = 320$, $P < 0.001$; 2016: Pearson's $r^2 = 0.672$, n = 319, $P < 0.001$). Body mass index was than scaled using coefficient estimated by standardized major axis (SMA) regression of body mass and beak–head length (following Peig and Green 2009).

Breeding success and timing

To assess the relation between nest box illumination and breeding characteristics, we compared clutch size, number of hatchlings, number of fledglings, hatching success, fledging success, breeding success and duration of nestling phase between dark and bright nest boxes. Number of hatchlings were the number of eggs which hatched, while number of fledglings was the number of nestlings which left the nest box. The hatching success was expressed as the hatched eggs/laid eggs ratio, while the fledging success was fledglings/hatchlings ratio. The breeding success was calculated as fledglings/laid eggs ratio.

In 2016 (Experiment II), we investigated also the effect of light on duration of nestling phase. For this purpose, for each brood, we calculated difference (days) between the dates when the first nestling fledged and the first egg hatched. To assess hatching and fledging times we used trail cameras recordings (see Surmacki & Podkowa 2022 for details). To establish egg hatching date, we inserted trail cameras between 10 and 12th day of incubation. In order to record fledging date cameras were installed when nestlings were ~ 15 days old, i.e., about 5 days before fledging. Cameras recorded one 3 MP photo every 5 and 30 min, during the hatching and fledging period, respectively. In total, we used data from 20 bright and 14 dark nest boxes.

Immunocompetence analysis

The immune system is a key defense mechanism against pathogens in birds (Wakelin and Apanius 1997). Studies have confirmed that the test using underskin injection with phytohemagglutinin (PHA) as a pathogenic simulator reliably reflects not only T lymphocytes immunocompetence (Smits et al. 1999) but also assess the potential of multiple immune-cell response (Martin et al. 2006). This test has been successfully used in ecological immunology to evaluate nestlings immunity in response to changing rearing environment, ectoparasite load, hatching order, nutrition condition (Brinkhof et al. 1999; Saino et al. 2001; De Ayala et al. 2007, reviewed in Martin et al. 2006). We performed immunocompetence PHA test in 2016–2017 (Experiment II). When the nestlings were 7 days old, 26 individuals from 13 bright boxes and 22 nestlings from 11 dark nest boxes were tested. We used standard PHA protocol from studies on passerines (e.g. Dubiec et al. 2006). In each brood, two nestlings with a mass closest to the average brood mass were tested. The wing skin (patagium) of each nestling was injected with 0.2 mg of PHA suspended in 0.04 ml of saline. Patagium thickness and body mass were measured just before and 24 h after injection. The patagium thickness was measured with a dial thickness gauge (0.01 mm, Baker Gauges, India). The level of immune response was expressed as a percentage increase in patagium thickness 24 h after injection. No control injection was made following the protocol by Smits et al. (1999). Each tested individual was weighed before and 24 h after injection to measure the daily body mass increase, which was used as a covariate in the analysis to control nestlings' overall body condition.

Molecular sexing

We used standard protocol used in the study of related species (e.g. Dubiec et al. 2006). Blood for analysis was taken from the brachial vein on the 14th day of life of the nestlings. DNA isolation was performed using the DNeasy Blood & Tissue Kit protocol (Qiagen GmbH, Hilden, Germany). Sex was determined based on the amplification of the CHD1W and CHD1Z genes (Griffiths et al. 1998).

Maternal effect

To assess the condition of parent female, and possible contribution of maternal component in development of nestlings, we collected a set of measurements of 37 females caught during late nestling stage in 2016 ($N = 23$) and 2017 ($N = 14$). We used the self-made nest box traps to catch feeding females. Each female entering nest box automatically triggered the trap plate that closes the entrance. Each nest box was observed during the catching trial to shorten the captivity time and reduce the possible stress. Females were aged using wing plumage colors and divided into two groups: second year of life (SY) and after second year of life (ASY). Similarly, to the nestlings' protocol, we measured wing length (0.5 mm), head length with beak, tarsus length (0.1 mm), and body mass (0.1 g). Because of the low correlation between females' body mass and each of linear measures (and all $p > 0.05$) we were not able to calculate reliable SMI index. Such low correlation may be explained by the rapid changes in caught females' body mass (mean ± SD = 18.14 ± 1.56, Min–Max = 16.3–23.40) during period of intensive parental care effort. Instead in 2016, we have taken blood samples from 17 females to assess the condition index based on proportion of heterophils to lymphocytes (*H*/*L* ratio). Such index has been used commonly in passerine birds to assess the magnitude of the stressors, diseases, infections or stress hormones levels (reviewed in Davis et al. 2008; Skwarska 2018). Blood smears were collected in the field and air-dried. Next, we followed the protocol from Hauptmanová et al. (2002) regarding to smear stain and blood cell count procedures. All smears were examined according to the criteria from Campbell (1994).

Statistical analysis

Due to the different experimental approach, we conducted the separate statistical analyses for each experiment. For biometrical analysis, we performed generalized linear mixed models (GLMM) with dependent variables: 'Body mass' (2nd and 12th day after hatch), 'tarsus length' (at 12th day), and 'SMI' (scaled mass index). As independent variables, we used fixed factors: 'Nest box type' (dark/bright), 'Sex' (male/female), Study site (I, II or III), and covariates: 'First hatch day', 'Clutch size' and 'Nest height'. Nest height was the distance between the bottom of the nest cup and the nest box floor. We included nest height to analysis because it is positively correlated with illumination of the nest cup (Podkowa and Surmacki 2017). Moreover, clutch size and nest height may be related to parental performance thus potentially affects the growth rate and condition of the offspring. In PHA analysis, we performed Linear Mixed Model (LMM) using dependent variable 'Patagium thickness increase', and explanatory variables: 'Nest box type' (dark/bright), 'Season' (2016/2017) and 'Body mass increase' as a covariate. In all mixed models, nest box identity was added as random factor. The choice of the best fitted models based on the values of the Akaike Information Criteria (AIC), we present final models with $\Delta\text{AIC} < 2$.

For between groups comparison of breeding success and females' condition we used Student's *t* test for normally distributed data (biometrics) and *U* Mann–Whitney test for other parameters that were non-normally distributed (breeding success and *H*/*L* ratio). To assess breeding success, we compared 'Clutch size', 'Number of hatchlings', 'Number of fledglings', 'Hatching success', 'Fledging success', and 'Breeding success' between experimental groups. To assess the relation between females' age and the occupied type of nest box we used Chi-squared test with Fisher's exact test. All tests were two tailed. Analyses were performed using IBM SPSS Statistics statistical package. Scaled mass index was obtained using R studio software with 'SMATR' package (Warton et al. 2012).

Results

Biometric measurements

Experiment I, in which adult females were not able to choose the nest box type, did not reveal any effect of nest box type on nestlings' biometrics nor SMI. We observed the significant effect of sex on body mass and tarsus length (all $p < 0.05$, Table 1) showing that male nestlings were heavier and bigger than female nestlings but with no effect on body condition (SMI). Nestlings reared in study site I were significantly heavier at day 2 comparing to other sites. We observed statistically significant, but inconsiderable effect of nest height on nestlings' body mass and tarsus length at day 12. We did not find any effect of hatch date on body mass nor tarsus length (Table 1).

In Experiment II, in which light choice was possible, 2 days old nestlings from bright nest boxes were significantly heavier than the nestlings reared in dark nest boxes ($F_{1,31.18} = 9.628$, $p = 0.004$, Fig. 1A). Similarly, 12-day nestlings reared in bright boxes had longer tarsus ($F_{1,34.20} = 4.635$, $p = 0.038$, Fig. 1B). We did not find any significant effect nest box type on body mass at 12th day and SMI (Fig. 1C, D). We also found significant sex dependent variation in body mass at 12th day, tarsus length and SMI being higher in male nestlings. The study site had a significant effect on mass and tarsus measurements in Experiment I and SMI in Experiment II.

Fledging time and breeding success

The duration of nestling phase in bright nest boxes was almost one day shorter when compared to dark nest boxes (Table 2). We observed the non-significant tendency of breeding success to be higher in bright nest boxes (Fig. 2). However, the only difference that was on the border of statistical significance (Table 2) was observed within 'Hatching success' during Experiment II (Fig. 2A). The results of comparison of breeding success between nest box types is presented in Table 2.

Immunocompetence analysis

We observed that the magnitude of the response to PHA injections differed between two types of nest boxes. The swelling reaction was stronger in bright nest boxes ($F_{1,20.05} = 13.851$, $p = 0.001$), what indicates a better response of immune system. During the treatment we did not observe any effect of body mass increase ($F_{1,25.48} = 3.659$, $p = 0.067$) nor a year ($F_{1,20.04} = 1.202$, $p = 0.286$) on daily differences in patagium thickness (Table 3). We also did not observe any significant interaction between type of the nest box and body mass increase ($F_{1,33.27} = 0.024$, $p = 0.878$).

Maternal effect

Comparison of adult females' H/L ratio as well as most of biometrical measurements showed no differences between females breeding in dark and bright nest boxes during Experiment II (Table 4). The only significant difference was observed in female body mass, which was higher in SY females (Table 4). Bright nest boxes were occupied mainly by SY females while the opposite trend was observed in ASY females (Fischer's exact test $p = 0.002$, Fig. 3). We did not observe any differences in the date of the first egg-lying between females' age groups ($t = 1.262$, $df = 22$, $p = 0.226$). The offspring of SY females was heavier at day 12 comparing to the offspring of ASY females ($t = 2.265$, $df = 15$, $p = 0.039$, Fig. 4). We also found that female age correlated with nestlings' body mass at day 12 ($r^2 = -0.505$, n17, $p = 0.039$) and SMI ($r^2 = -0.524$, $n = 17$, $p = 0.031$).

Table 1 General linear mixed models to assess the condition (body mass, tarsus length and SMI) in relation to nest box type, nestlings' sex and brood parameters

	Mass at day 2			Mass at day 12			Tarsus at day 12			SMI		
	Estimate (SE)	*t*	*p*	Estimate (SE)	*t*	*P*	Estimate (SE)	*t*	*p*	Estimate (SE)	*t*	*p*
Experiment I (no choice)												
Nest box type	−0.09 (0.25)	−0.39	0.696	−0.23 (0.13)	−1.75	0.096	−0.02 (0.09)	−0.18	0.859	−0.12 (0.20)	−0.57	0.576
Sex	0.17 (0.07)	2.42	0.016	0.71 (0.10)	7.01	<0.001	0.44 (0.06)	7.13	<0.001	0.19 (0.12)	1.67	0.097
Study site I	1.16 (0.33)	3.55	0.002	−0.16 (0.17)	−0.91	0.376	−0.07 (0.13)	−0.56	0.582	−0.21 (0.26)	−0.80	0.435
Study site II	0.73 (0.40)	1.82	0.083	−0.65 (0.22)	−3.02	0.007	−0.25 (0.15)	−1.60	0.126	−0.49 (0.33)	−1.50	0.150
Study site III	0	–	–	0	–	–	0	–	–	0	–	–
Nest height	−0.01 (0. 45)	−0.14	0.890	−0.05 (0.02)	−2.17	0.043	0.04 (0.02)	2.45	0.025	−0.02 (0.04)	−0.54	0.596
First hatch date							−0.02 (0.02)	−0.85	0.403			
Clutch size							−0.10 (0.05)	−1.85	0.081			
Experiment II (light choice)												
Nest box type	−0.68 (0.22)	−3.10	0.004	−0.45 (0.49)	−0.92	0.364	−0.38 (0.18)	−2.15	0.038	0.29 (0.36)	0.80	0.430
Sex	−0.04 (0.05)	−0.78	0.438	0.79 (0.11)	6.99	<0.001	0.58 (0.06)	9.77	<0.001	0.23 (0.10)	2.27	0.020
Study site I	0.27 (0.18)	1.51	0.141	−0.27 (0.40)	−0.68	0.501				−0.51 (0.30)	−1.72	0.100
Study site II	0.37 (0.21)	1.74	0.092	−0.67 (0.47)	−1.43	0.161				−0.93 (0.35)	−2.70	0.010
Study site III	0	–	–	0	–	–	0	–	–	0	–	–
Nest height	0.08 (0.03)	2.61	0.014	0.04 (0.07)	0.56	0.577	0.02 (0.03)	0.81	0.430	−0.01 (0.05)	−0.19	0.850

Study site III was used as a reference

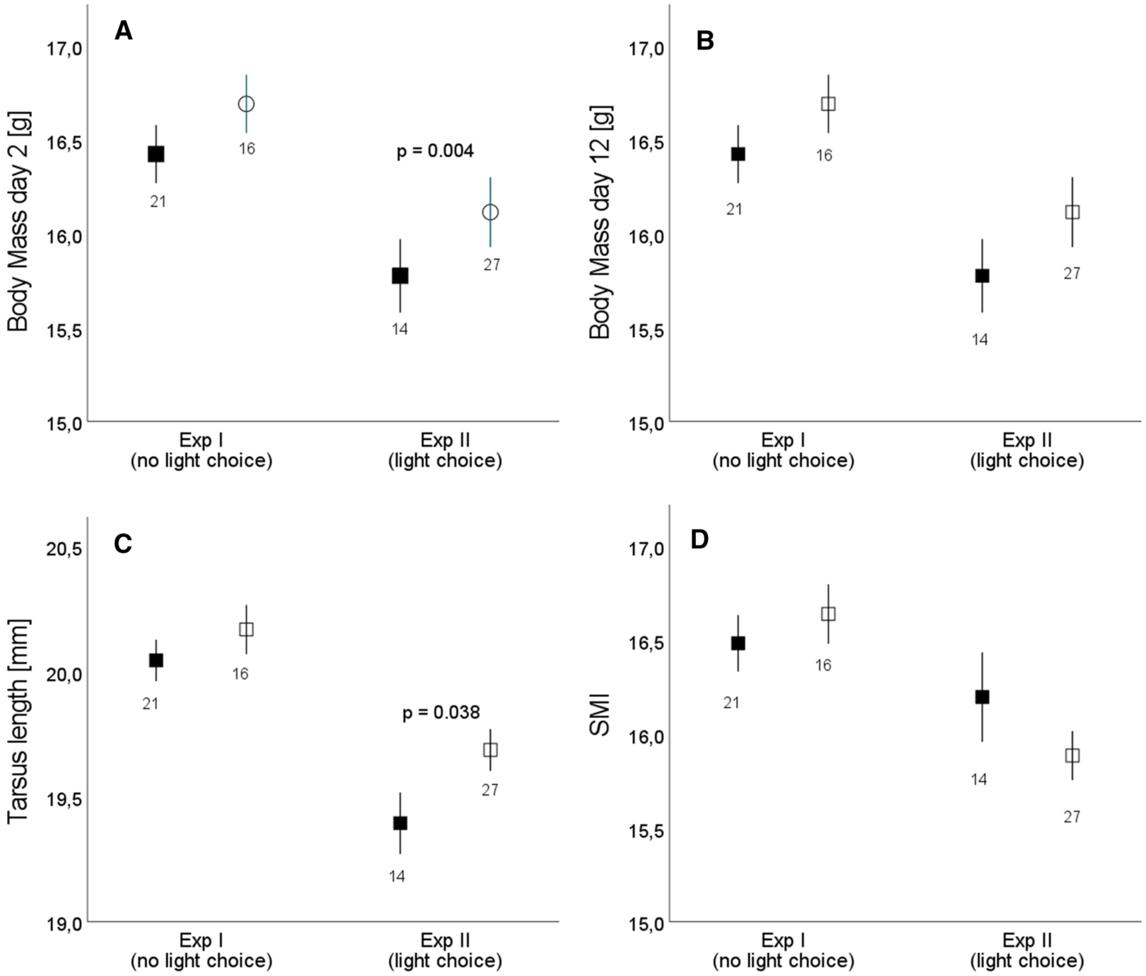

Fig. 1 The effect of nest box type effect on biometric measurements. **a** Body mass at day 2, **b** body mass at day 12, **c** tarsus length, and **d** SMI. Black squares represent dark nest boxes while white circles represents bright nest boxes. Numbers indicate sample size. Error bars shows 95% confidence intervals

Discussion

Biometry, body condition and breeding success

In the light-choice experiment (Experiment II), nestlings reared in bright nest boxes were significantly heavier and had longer tarsus compared to nestlings from dark boxes. On the contrary, in experiment based on random nest box selection (Experiment I), no effect of light regime on biometry was observed. Moreover, in both experiments, offspring from dark and bright nest boxes had similar body condition (SMI). Several lines of evidence suggests that the positive effect of light in Experiment II was related to the maternal effect. First, nest boxes were occupied by females in no random fashion; bright boxes were chosen mainly by second year (SY) females, while the opposite tendency was found for after second year (ASY) females. Second, SY females were significantly heavier than ASY females. Third, there was a positive correlation between females' mass and offspring mass and body condition at day 12. The lack of the effect of light in the Experiment I could be explained by the fact that boxes were occupied randomly with respect to females' age. Although we did not study females' age in 2015, light condition in bright boxes were set after clutch completion; therefore, light could not affect the age females which choose best site.

The age-related difference in a female's mass found between dark and bright nest boxes probably results from fat reservoirs, because both groups were similar with respect to linear body measurements. It is not clear what factor could drive this difference. One possible explanation is the energy expenditures for nest building and chick feeding. Earlier studies in the studied population showed that Great Tit females in dark boxes built over two times higher nest compering to bright box females presumably to compensate for poorer light conditions (Podkowa and

Table 2 The effect of nest box type on variables describing nesting success

	Exp I (No light choice)				Exp II (Light choice)			
	N	Effect size	*Z*	*p*	*N*	Effect size	*Z*	*p*
Clutch size								
Dark	21	− 0.095	− 0.6	0.548	20	− 0.150	− 1.085	0.278
Bright	19				32			
Number of hatchlings								
Dark	21	− 0.065	− 0.414	0.679	20	− 0.216	− 1.561	0.119
Bright	19				32			
Number of fledglings								
Dark	21	− 0.039	− 0.243	0.808	17	− 0.225	− 1.558	0.119
Bright	18				31			
Hatching success								
Dark	21	− 0.029	− 0.182	0.855	20	− 0.252	− 1.814	0.070
Bright	19				32			
Fledgling success								
Dark	21	− 0.063	− 0.396	0.692	17	− 0.112	− 0.774	0.439
Bright	18				31			
Breeding success								
Dark	21	− 0.052	− 0.326	0.744	17	− 0.243	− 1.682	0.093
Bright	18				31			
Duration of the nestling phase								
Dark	–	–	–	–	13	− 0.550	− 3.206	0.002
Bright	–				21			

Surmacki 2017). Moreover, duration of feeding in bright boxes is significantly shorter, probably because a higher illuminance helps females to quickly locate chicks' gapes and decide which one to feed (Podkowa et al. 2019). As a result, young females from bright boxes may have more time for self-maintenance, which in turn may increase their fat reservoirs and body mass. Earlier studies showed that in optimal nutritional conditions, there are significant genetic correlations between mother and nestlings biometric measures in the Great Tit (Gebhardt-Henrich and van Noordwijk 1991). Lower mass of ASY females could be also attributed to senescence processes, which in the Great Tit is especially pronounced after the second year of life (Bouwhuis et al. 2009). Despite some differences in nestlings' characteristics, which could be ascribed to mother's age, the indirect effect of light conditions on breeding output was relatively weak. Although there was some tendency in breeding success to be higher in bright boxes, differences in nestlings' characteristics and breeding success between nest box types were not statistically significant. Further studies are needed to investigate whether nestlings from bright boxes perform better after fledging. For example, our study demonstrated that duration of nestling phase in bright boxes is about one day shorter comparing to dark boxes. This difference could be due to a better tarsus development in bright nest boxes. Results from earlier studies on nest box nesting species suggest that tarsus length determines the time of fledging (Cornell et al. 2017). Shorter duration of nestling phase should be regarded as advantageous, because it is inversely correlated with the exposure to ectoparasites inhabiting nest (Richner et al. 1993). It is possible that tarsus length, as well as other body dimensions, would increase survival chances of young birds. Although we did not find any differences in nestlings' body mass at late stage of nestlings' phase, in other Great Tit populations, it was found that fledgling with a higher body mass had greater survival and recruitment chances (Monrós et al. 2002; Naef-Daenzer et al. 2001). It is also possible that light affected nestlings' behavior displayed just before the fledging and strengthened the interaction between nestlings (Santema et al. 2021). It is not clear why SY females preferred to breed in brightened cavities. Perhaps for young inexperienced females, it is easier to undertake some activities connected with rearing offspring like nest building or food provisioning (see Podkowa et al. 2019), which are generally visually oriented. This result led us to the conclusion that increased internal daylight level may not only affect nestlings' condition by itself, but also may interact with the experience of females in their first breeding attempt.

It is important to remember that, aside from the manner in which "bright" boxes were created, there might be other factors, that could potentially account for differences between different experimental output between years. For example, factor which is strongly related with the accessibility of food and thus affects nestlings body mass is the

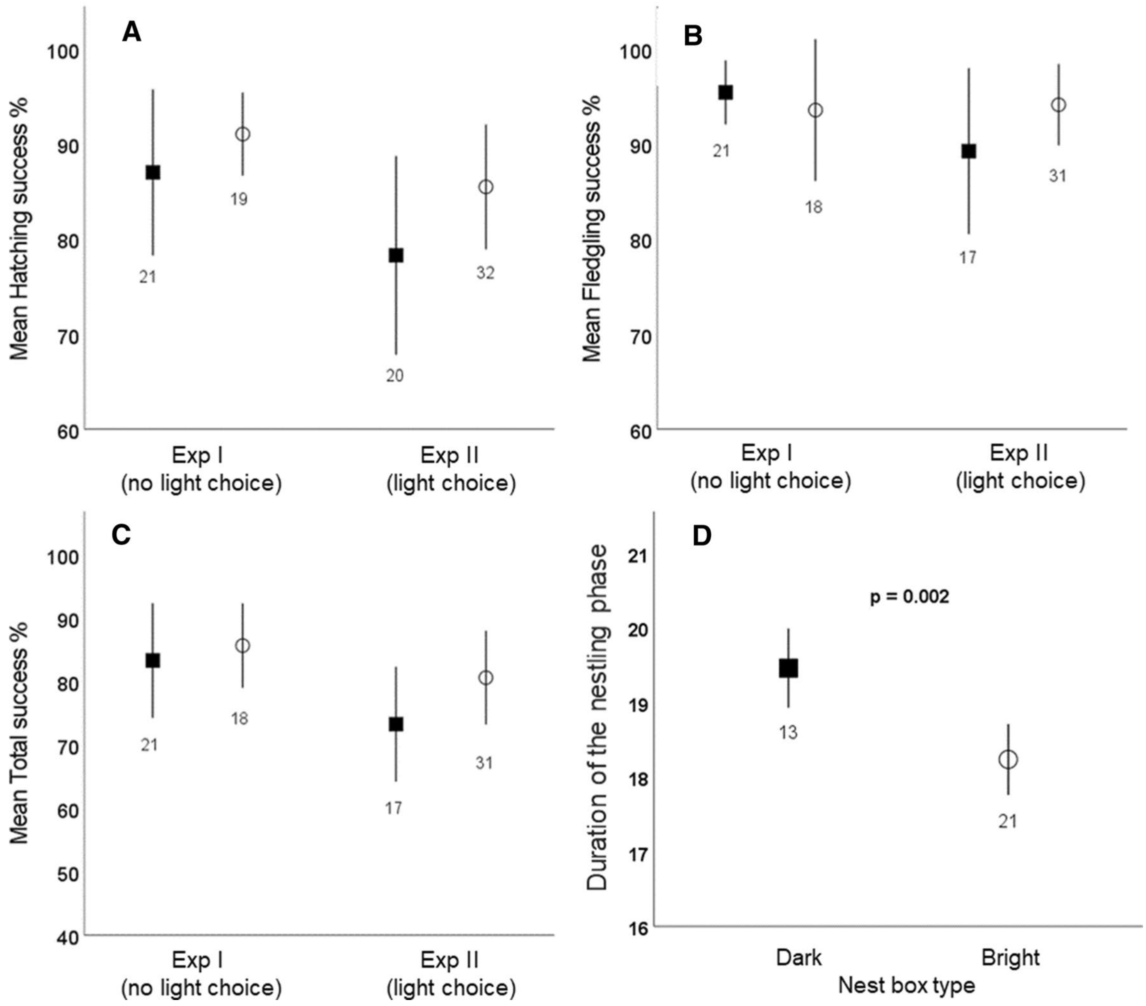

Fig. 2 Effect of nest box type and experimental approach on breeding output. Graphs shows mean values of: **a** hatching, **b** fledging, **c** breeding success and **d** duration of the nestling phase (days). Dark squares represent dark nest boxes, white circles represent bright nest boxes. Numbers indicates sample size. Error bars shows 95% confidence intervals

Table 3 General linear mixed models to assess the immunocompetence of nestlings included the effects of nest box type, season, body mass increase and the interaction nest box type and nestlings' daily body mass increase (Experiment II)

Patagium thickness increase	Estimate (SE)	SE	*df*	*t*	*p*
Nestbox type	–46.48	12.49	20.05	–3.722	0.001
Season	13.68	12.48	20.04	1.096	0.286
Body mass increase	1.89	0.99	26.48	1.913	0.067

time in season (Naef-Daenzer and Keller 1999; Kaliński et al. 2019), however, we did not find any significance of the day of hatch on body mass and tarsus length in studied population. Moreover, there was no difference in the date of the first egg lying. Although, in 2016 eggs hatched statistically earlier, but the difference was only 2 days. Also, the nest temperature that could affect the nestlings' growth (Rodríguez and Barba 2016), did not differ between both types of nest boxes used in this study (Podkowa and Surmacki 2017) nor between Exp I and Exp II. We also did not observe any cold or hot spells in both years.

Studies on poultry repeatedly show positive effects of light on the growth of young birds (Robbins et al. 1984; Fairchild and Christensen 2000; Olanrewaju et al. 2006; Gharahveysi et al. 2020) which contradicts our results. A possible explanation for this discrepancy is the intensity, duration and the spectrum of light used in lab experiments. In most of poultry experiments light intensity ranged between 5 and 500 lx (Olanrewaju et al. 2006; Khalil et al. 2016; Hofmann et al. 2020), what is considerably greater than differences in illumination between in dark and bright nest boxes used

Table 4 Comparison of female characteristic between nest box type during the Experiment II

Nest box type	Mean ± SE	*N*	Test statistic	*p*
Tarsus				
Dark	19.66 ± 0.09	18	− 1.038	0.306
Bright	19.77 ± 0.06	18		
Head				
Dark	30.79 ± 0.11	18	0.785	0.438
Bright	30.67 ± 0.11	18		
Wing				
Dark	73.79 ± 0.68	17	− 0.581	0.566
Bright	74.24 ± 0.34	17		
Body mass				
Dark	17.30 ± 0.20	16	− 2.738	0.010
Bright	18.57 ± 0.41	17		
H/*L* ratio				
Dark	0.41 ± 0.12	6	− 0.727	0.480
Bright	0.55 ± 0.13	11		

Biometrical measurements (tarsus, head, wing length and body mass) were tested using Student t test. *H*/*L* ratio was tested using Mann–Whitney *U* test

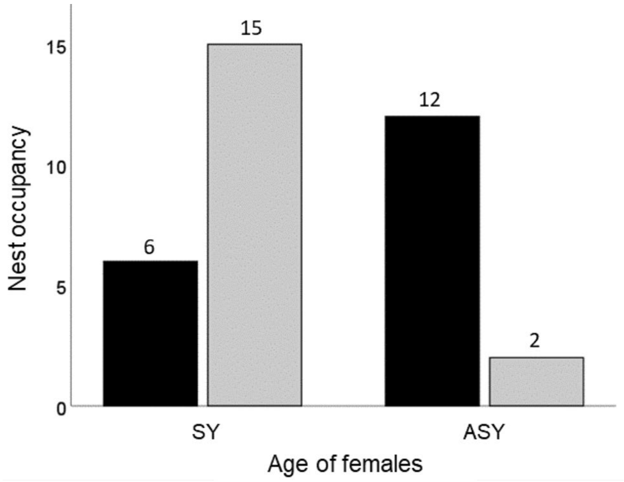

Fig. 3 Nest site preference by adult females' age. Graph shows the preference in nest box occupation during the Experiment II regarding to females' age. Females attempting first breeding season significantly preferred ($p = 0.002$) to settle in bright nest boxes (grey bars) instead of dark nest boxes (black bars). Numbers of females are indicated above the bars

in our study (1.4 and 52.7 lx, respectively). On the other hand, it has been shown that the light intensity which met our study design (50 lx) might have favorable effect on chick growth (Gharahveysi et al. 2020). Another difference between our study and poultry experiments is the spectral property of the light source. In nest boxes, we used natural sunlight slightly filtered by resin windows. On the other hand, in poultry experiments incandescent, fluorescent or LED bulbs were used (Olanrewaju et al. 2006; Khalil et al. 2016; Hofmann et al. 2020). Such a light sources are often characterized by "spikey" spectrum, which is very different from a sunlight (Troscianko and Stevens 2015). Moreover, in some of poultry experiments, birds were exposed only to particular wavelengths, which affected their body weight and general performance (Olanrewaju 2006; Soliman and El-Sabrout 2020). In most of poultry species, the body growth is positively affected by blue and green light, but in turkeys and ducks higher weight gain was observed under red light (Çapar Akyüz and Onbaşilar 2018). Red light increases also the reproduction and possibility of aggressive behavior in hens, while blue light has calming effect (Rozenboim 1999). Only one study used full-spectrum with UV wavelengths to imitate the effect of daylight on hens' behavior, but such effect was rather small (Wichman 2021). Finally, it is important to remember, that the possible effect of light on nestlings' biometry and body condition in our study may have been affected by other factors like presence of ectoparasites (Dufva and Allander 1996) or siblings' competition (Nilsson and Svensson 1996), which were not controlled.

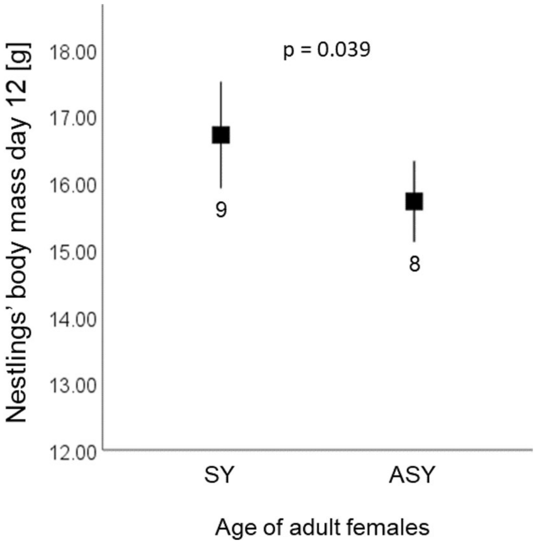

Fig. 4 Comparison of the 12-day old nestlings' body mass between two age groups of adult females during the Experiment II. Numbers indicates sample size. Error bars shows 95% confidence intervals

Immune system

Our study supported the hypothesis that light has a positive effect on efficiency of the immune system. Tissue swelling reaction after PHA injections in nestlings reared in bright nest boxes were significantly greater compared to birds from dark nest boxes. It is commonly assumed that greater PHA swelling indicates a better T cell-mediated response, but it is worth to mention that it is rather related to the presence of the numerous classes of immune cells (e.g. macrophages, basophiles and heterophiles), hormones and acute-phase response (Martin et al. 2006). The difference in such complex immune response, observed under control of the age and body condition of the nestlings, leads to question the environment vs genetic effects. All PHA tests were performed under Experiment II, meaning that nestlings who were tested were reared by females that chose the nest box type and probably differed with respect to age and body mass. Nevertheless, we may assume that any potential differences in females' characteristics have no effect on the obtained results. The majority of earlier studies on wild passerines showed that immune response to pathogens is not heritable and depends mainly on rearing conditions (Tella et al. 2000, Kilpimaa et al. 2005, Pitala et al. 2007, but see Cichoń et al. 2006). In addition, previous research has showed no link between parasite infestation and cell-mediated immune response that may result from yolk-carotenoid content (Berthouly et al. 2007). Finally, we tested nestlings that were at the same age, and we controlled the effect of weight gain, which was not significant.

Our study provides the first information about the effect of light intensity on immune system in wild living birds. Earlier investigations on this subject were mostly focused on poultry kept indoor under artificial light and used various methods to characterize immune response (reviewed in Hofmann et al. 2020). Results of these experiments are not conclusive, but most studies in poultry indicate that low light intensity has no negative effect on birds' immune system (Hofmann et al. 2020). However, another study showed that a continuous light phase affected organization of gene expression and hormones involved in immune system in zebra finches (Mishra et al. 2019), but this result is probably due to disruption of circadian clock, rather than to the intensity of natural light (Mishra et al. 2019).

We did not fully confirm our predictions regarding a direct and positive effect of light on body condition and breeding success. However, we found a strong and positive effect of light within the cavity on immune response of young birds. This result warrants further studies to investigate potential link between the light and T cell-mediated immunocompetence. Our study revealed also indirect positive effects of light on nestlings' size, which could be ascribed to females' age. Bright nest boxes were preferably occupied by younger females, which were on average heavier than older female. Probable consequence of these differences was the nestlings' ability to fledge earlier, what could be regarded as advantageous. Future studies are needed to explain preference of young females to the brighter nest sites and potential benefits resulting from that decision.

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Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Oświadczenia doktoranta o wkładzie w powstanie artykułów

UNIWERSYTET IM. ADAMA MICKIEWICZA W POZNANIU
Wydział Biologii
Zakład Biologii i Ekologii Ptaków

mgr Paweł Podkowa
Uniwersytet im. Adama Mickiewicza
w Poznaniu, Wydział Biologii
Zakład Biologii i Ekologii Ptaków
ul. Uniwersytetu Poznańskiego 6
61-614 Poznań
e-mail: podkowa@amu.edu.pl

Poznań, 12.09.2022

Oświadczenie określające wkład w powstanie artykułu

Niniejszym oświadczam, że mój wkład w powstanie artykułu: **Podkowa, P., & Surmacki, A. (2017). The importance of illumination in nest site choice and nest characteristics of cavity-nesting birds. Scientific Reports, 7(1), 1–9**, polegał na: wykonaniu badań terenowych, przeprowadzeniu analiz statystycznych, interpretacji wyników i przygotowaniu rycin i tabel, przygotowaniu manuskryptu oraz jego poprawie po uwagach recenzentów.

W tym artykule jestem pierwszym i korespondencyjnym autorem.

Mój całkowity wkład w pracę wynosi 50%.

Paweł Podkowa
....

UAM

UNIWERSYTET IM. ADAMA MICKIEWICZA W POZNANIU
Wydział Biologii
Zakład Biologii i Ekologii Ptaków

mgr Paweł Podkowa
Uniwersytet im. Adama Mickiewicza
w Poznaniu, Wydział Biologii
Zakład Biologii i Ekologii Ptaków
ul. Uniwersytetu Poznańskiego 6
61-614 Poznań
e-mail: podkowa@amu.edu.pl

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Paweł Podkowa
....

UNIWERSYTET IM. ADAMA MICKIEWICZA W POZNANIU
Wydział Biologii
Zakład Biologii i Ekologii Ptaków

mgr Paweł Podkowa
Uniwersytet im. Adama Mickiewicza
w Poznaniu, Wydział Biologii
Zakład Biologii i Ekologii Ptaków
ul. Uniwersytetu Poznańskiego 6
61-614 Poznań
e-mail: podkowa@amu.edu.pl

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Oświadczenia współautorów o wkładzie w powstanie artykułów

Oświadczenie współautora o wkładzie w powstanie artykułu

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UNIWERSYTET IM. ADAMA MICKIEWICZA W POZNANIU
Wydział Biologii
Zakład Biologii i Ekologii Ptaków

prof. UAM dr hab. Adrian Surmacki
Uniwersytet im. Adama Mickiewicza
w Poznaniu, Wydział Biologii
Zakład Biologii i Ekologii Ptaków
ul. Uniwersytetu Poznańskiego 6
61-614 Poznań
e-mail: adrian@amu.edu.pl

Poznań, 12.09.2022

Oświadczenie określające wkład w powstanie artykułu

Niniejszym oświadczam, że mój wkład w powstanie artykułu: **Podkowa, P., & Surmacki, A. The importance of illumination in nest site choice and nest characteristics of cavity-nesting birds. Scientific Reports, 7(1), 1–9** polegał na zaprojektowaniu badań, wykonaniu prac terenowych, przygotowaniu manuskryptu oraz jego poprawie po uwagach recenzentów

Mój całkowity wkład w pracę wynosi 50%.

A. Surmacki
....

Oświadczenia współautorów o wkładzie w powstanie artykułu

Podkowa, P., Malinowska, K., & Surmacki, A. (2019). Light affects parental provisioning behaviour in a cavity-nesting Passerine. Journal of Avian Biology 50(11).

UNIWERSYTET IM. ADAMA MICKIEWICZA W POZNANIU
Wydział Biologii
Pracownia Ekologii Populacyjnej

Poznań, 10.09.2022

Katarzyna Malinowska
Uniwersytet im. Adama Mickiewicza w Poznaniu
Wydział Biologii
Pracownia Ekologii Populacyjnej
e-mail: katarzyna.malinowska@amu.edu.pl

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Mój całkowity wkład w pracę wynosi 5%.

Katarzyna Malinowska
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Mój całkowity wkład w pracę wynosi 45%.

A. Surmacki
....

Oświadczenia współautora o wkładzie w powstanie artykułu

Podkowa, P., Surmacki A. (2022). The effect of daylight exposure on the immune response and body condition of Great Tit nestlings. Journal of Ornithology

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Mój całkowity wkład w pracę wynosi 50%.

A. Surmacki
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Podziękowania

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