Reprodukční strategie pěvců během inkubace

Dizertační práce

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Přírodovědecká fakulta Univerzity Palackého v Olomouci
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„Tabon tedy pro inkubaci svých vajec musí jedině vyhrabat přes dva metry krychlové zeminy, nacpat do jámy přes dva metry krychlové materiálu, udělat z toho hromadu, a pak už stačí jen nepřetržitě zkoumat teplotu a přidávat a ubírat z hromady. Tím si tedy ušetří tu neskutečnou otravu občas sedět na vejcích.“

(Douglas Adams)

PODĚKOVÁNÍ

Od okamžiku, kdy jsem nastoupila na doktorát až do chvíle, kdy jsem dopsala tuto práci uplynuly téměř čtyři roky. Je to dlouhá doba, a tak není divu, že jsem během ní potkala mnoho lidí, kteří více či méně přispěli ať už přímo ke vzniku této práce, nebo k tomu, že jsem se v psychické pohodě dostala až sem a nesekla s tím v jedné z mnoha chvil absolutní beznaděje.

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Kromě svého „nejvyššího“ jsem na univerzitě byla obklopena dalšími lidmi, které nemohu ve svém poděkování nezmínit. Maťovi Paclíkovi děkuji za neuvěřitelně milé přijetí do tehdy ještě jeho „kanclu“, a hlavně za to, že po celou dobu našeho „kanclového“ soužití snášel ty moje kecy. Určitě jsem ho stála minimálně jeden „pejpr“. Taky mu děkuji za hektolitry bádacího čaje, které do mne (na vlastní náklady) nalil. Kolegyňa Lucia Turčoková byla vždy po ruce, když už člověk (myšleno já) nevěděl kudy kam a potřeboval si postěžovat. Většinou to stejně vedlo k tomu, že jsem se dozvěděla, že jsem vlastně „nána“. Ale ať už to znamená, co chce, často to stačilo. Peterovi Adamíkovi, Tomáši Grimovi, Miloši Kristovi a Karlu Weidingerovi děkuji, že pomáhali vytvářet podnětné prostředí, ve kterém člověk musí zabrat, i kdyby nechtěl. Tomáši Grimovi pak patří speciální dík za Calibri. „Měl jsi pravdu, je to mnohem lepší“. Beátě, Julii a paní Janě Mlčochové děkuji, že i přesto, že každý student přece ví, jak se zapisuje do STAGu a co s objednávkami či paragony, vždy mi ochotně v tomto směru pomohly, čímž můj život na univerzitě učinily podstatně snazším. Se sběrem dat v komáry zamořeném Grygově mi pomáhaly Kristýna Bártlová a Jana Šuterová.

Během doktorského studia jsem měla příležitost navštívit dvě zahraniční univerzity a podívat se, jak to tam v té cizině vlastně chodí. Umožnilo mi to potkat mnoho zajímavých lidí, kteří mne po odborné stránce hodně obohatili. Jelikož nemůžu děkovat každému zvlášť (určitě bych stejně na někoho zapomněla), ráda bych poděkovala alespoň dvěma z nich, těm nejdůležitějším. Prvním je Piotr Tryjanowski, kterému děkuji nejen za milé přijetí v jeho „labu“, ale i za ochotu věnovat se mým vědeckým problémům a také za odborné debaty během Malých a Velkých Darwinů. A hlavně za tu týkající se čápů. „Piotr, czy ty wogóle pamiętasz, ile było tych bocianów?“ Druhým je pak Andrew Cockburn, díky kterému teď vím mnohem více o modropláštnících, než jsem věděla kdy předtím, znám strategii využívanou lyrochvosty během požárů (samozřejmě, že tomu nevěřím) a taky vím, že i ti největší vědci chodí do terénu a dokáží být neskutečně vtipní a přátelští. Pobyt na „jeho“ univerzitě mi navíc ukázal, že všechno může vypadat úplně jinak a že záleží hlavně na lidech.

Kotěti, Moťkovi, Janě Pavlíčkové a Jíti Mádrové děkuji, že se celá ta léta zajímali o mé studium. I když teď , když tak nad tím přemýšlím, nevím, zda dotaz: „A kdy ty vlastně dostuduješ?“ lze až tak úplně brát jako zájem o studium.... Velký zájem o mé vzdělání vždy překvapivě projevoval i můj milovaný starší bratr Marek, takže: „Díky brácho“. Honza Koutný, kdykoli bylo třeba nějaké té gramatické korektury, vždy ochotně pomohl, případně neváhal zmobilizovat své příbuzenstvo. Jeho bratru Tomovi děkuji, že když jsem před lety prohlašovala, že na ty přijímačky určitě nepůjdu, protože na to nemám, přesvědčil mne, ať to alespoň zkusím.

Pavlu Kantorkovi děkuji za svolení použít jeden z jeho vskutku geniálních obrázků. Kosi černí z první strany jsou dílem Johna Goulda.

Speciální poděkování patří mým rodičům Soni a Januszowi, kteří mne podporovali nejen finančně, ale hlavně psychicky během mého studia i přesto, že dodnes vlastně nechápou, jak může někdo strávit devět let na vysoké škole „hraním si se zvířátky“. A navíc tvrdit, že ho to baví.

Nejen kolegové, přátelé či moje rodina však mají zásluhy na vzniku této práce. Microsoftu děkuji za Windows Media Player (nechápu, jak někdo může „házet“ data do Excelu a neposlouchat u toho muziku) a Austrálii za Cabernet Sauvignon. Bez něj by těch článků bylo jistě více, ale určitě ne tak kvalitních:-). Všem sýkorám děkuji, že to s námi vydržely, ochotně nastavovaly běháky a poskytovaly peří a neváhaly se zase za rok vrátit zpět do našich budek.

ABSTRAKT

Práce se zabývá faktory, které na vnitrodruhové a mezidruhové úrovni ovlivňují inkubačních chování pěvců. Na vnitrodruhové úrovni probíhal výzkum na sýkoře koňadře (*Parus major*). Na úrovni mezidruhové byli jako studijní systém zvoleni pěvci Austrálie a Nového Zélandu. Větší pozornost je dále věnována dvěma faktorům, které se na rozdílech v inkubačním chování mohou významně podílet. Na vnitrodruhové úrovni se jedná o míru exprese karotenoidových a melaninových ornamentů jakožto indikátorů kvality jejich nositelů. Na úrovni mezidruhové pak o míru hnízdní predace.

U sýkory koňadry inkubuje pouze samice, ale samec ji během inkubace krmí. U samic jsme se tak při výzkumu faktorů ovlivňujících míru rodičovského úsilí během inkubace zaměřili na intenzitu inkubace, u samců pak na intenzitu inkubačního krmení. Dále nás zajímalo, zda samčí inkubační krmení ovlivňuje intenzitu inkubace a ta následně líhnivost, jak předpokládá hypotéza samičí výživy. Zjistili jsme, že se intenzita inkubačního krmení snižovala s teplotou vnějšího prostředí, denní dobou a věkem snůšky. Pozitivní vliv na inkubační krmení měla v naší studii kvalita hnízdního teritoria, ale pouze v letech s nízkou potravní nabídkou. Naproti tomu věk samce, samčí ornamenty či věk snůšky nebyly dobrými indikátory intenzity inkubačního krmení. Co se týče intenzity inkubace, tak ji pozitivně ovlivňovala velikost snůšky a negativně pak teplota vnějšího prostředí. Věk snůšky, datum zahájení snůšky, kvalita hnízdního teritoria, intenzita inkubačního krmení, věk samice a její ornamenty intenzitu inkubace nepredikovaly. Inkubační krmení v naší populaci nemělo vliv na intenzitu inkubace a ta také neovlivňovala líhnivost. Naše data tak nejsou ve shodě s hypotézou samičí výživy.

Co se samotného výzkumu ornamentů týče, tak abychom zjistili, jak se kvalita jedince projevuje při zátěžové situaci, hendikepovali jsme pomocí stříhaní rýdovacích per a letek samice sýkory koňadry během inkubace. Předpokládali jsme, že si samice s výraznějšími ornamenty poradí s experimentálním hendikepem lépe, tj. dojde u nich k nižšímu poklesu hmotnosti během inkubace a menší změně v intenzitě inkubace před a po experimentálním zásahu. Náš předpoklad se ale nepotvrdil a míra exprese samičích ornamentů o jejich schopnosti se vyrovnat se zátěží během inkubace nevypovídala.

K ornamentům jsme se vrátili během výzkumu ptilochronologie jako možné metody určování kondice u sýkory koňadry. Zjišťovali jsme, zda míra exprese karotenoidových a melaninových ornamentů, jež jsou u sýkory koňadry považovány za kondičně závislé, koreluje s rychlostí růstu jejich per. Zjistili jsme negativní vztah mezi rychlostí růstu per a množstvím karotenoidů v peří a nezjistili vztah mezi rychlosti růstu a plochou melaninového ornamentu. Z výsledku našeho výzkumu a z porovnání našich závěrů se závěry podobných studií jsme usoudili, že se ptilochronologie jako metoda k určení kondice u sýkory koňadry nehodí.

Na mezidruhové úrovni jsme zkoumali faktory, které potenciálně ovlivnily evoluci inkubačního krmení u pěvců Austrálie a Nového Zélandu. Nejlépe vysvětlovala rozdíly v míře inkubačního krmení mezi druhy míra hnízdní predace, která s frekvencí inkubačního krmení korelovala pozitivně. Další faktory (tělesná velikosti druhu a sociální struktura) se na rozdílech ve frekvenci inkubačního krmení u zkoumaných druhů nepodílely.

V další studii jsme se zaměřili na hnízdní predaci samotnou. Našim záměrem bylo zjistit nejdůležitější koreláty, které vysvětlují míru hnízdní predace u australských a novozélandských pěvců. Zjistili jsme, že rozdíly mezi druhy jsou částečně vysvětleny tělesnou velikostí druhu, která korelovala s mírou predace negativně. Dalším významným korelátem byl typ hnízda, kdy nejnižší byla predace u dutinohnízdičů, nejvyšší pak u druhů hnízdících v hnízdech otevřených. Míra predace také významně negativně korelovala se zeměpisnou šířkou studie. Posledním významným korelátem byl rok, ve kterém byl výzkum prováděn a se kterým predace korelovala pozitivně.

ABSTRACT - Reproductive strategies in songbirds during incubation

This study focuses on the factors influencing incubation behavior of songbirds on both intraspecific and interspecific level. The Great Tit (*Parus major*) was chosen as a model species for the research conducted on the intraspecific level. The research on the interspecific level was done on Australian and New Zealand songbirds using literature data. Moreover, special attention was paid to two factors, which can significantly influence incubation behavior. The first is the expression of carotenoid- and melanin-based ornaments, which are supposed to be good indicators of individual quality and thus could influence the incubation behavior on intraspecific level. The second is the rate of nest predation, which can affect incubation behavior on the interspecific level.

Female is responsible for incubation in the Great Tit. However, male assists the female by feeding her, a behavior called the incubation feeding. Therefore, while studying the factors influencing parental effort during incubation, we focused on the rate of incubation feeding in males and the intensity of nest attentiveness in females. Furthermore, we wanted to find out whether incubation feeding affects nest attentiveness and nest attentiveness hatching success, which would be in agreement with the Female nutrition hypothesis. In our population, the intensity of incubation feeding decreased with increasing ambient temperature, time of day and clutch size. We found a positive relationship between incubation feeding rate and territory quality, but only in years with poor food supply. On the other hand, male age, male ornamentation and age of the clutch were not correlated with the intensity of incubation feeding. Female nest attentiveness correlated positively with clutch size and negatively with ambient temperature. There was no effect of age of the clutch, date in the season, territory quality, rate of incubation feeding, female age and female ornamentation on nest attentiveness. Incubation feeding did not correlate with nest

attentiveness and nest attentiveness did not correlate with hatching success. Thus, our findings were not in agreement with the Female nutrition hypothesis.

With respect to the research on ornamentation itself, we handicapped females of the Great Tit by feather clipping to find out how individual quality manifests during challenging situations. We expected females with more elaborate carotenoid-based ornamentation to deal with experimental treatment better. We expected them to loose less weight during incubation. Moreover, we predicted that these females would experience smaller change in the nest attentiveness before and after treatment. However, our findings did not confirm these predictions. The elaboration of carotenoid-based ornaments in Great Tit females did not predict their ability to cope with the challenging situation.

We returned to the problem of ornamentation during our study of ptilochronology. We aimed to find out whether the expression of carotenoid- and melanin-based ornaments, which are considered to be condition-dependent in the Great Tit, correlate with the growth rate of feathers and hence whether ptilochronology is an acceptable method to assess body condition in the Great Tit. There was a negative relationship between feather growth rate and the amount of carotenoids in the breast feathers and no relationship between feather growth rate and the size of the melanin ornament. It follows from these results and from the comparison of our conclusions with the conclusions of other similar studies that ptilochronology is not a suitable method to assess body condition in the Great Tit.

On the interspecific level we focused on factors, which could affect the evolution of incubation feeding in Australian and New Zealand songbirds. The differences in the rate of incubation feeding among species were best explained by the rate of the nest predation, which correlated with the rate of the incubation feeding positively. Other factors (species body mass and social structure) did not correlate with the rate of incubation feeding.

In the next study we focused on the nest predation itself. Our aim was to find out the most important correlates of the nest predation rate in Australian and New Zealand songbirds. Differences among species were partly explained by species body mass, which correlated with nest predation rate negatively. Another important correlate was nest type, with the lowest rates of nest predation in cavity nesters and the highest in open nesting species. The rate of the nest predation significantly negatively correlated with latitude of the study as well. The last important factor, which correlated with nest predation rate positively, was the year in which the study was conducted.

OBSAH

1. SEZNAM PŘILOŽENÝCH PŘÍSPĚVKŮ

Dizertační práce je založena na následujících příspěvcích:

Příspěvek I. Matysioková B. 2010: Inkubační krmení u ptáků. Sylvia, *in press.*

Příspěvek II. Matysioková B. & Remeš V.: Incubation feeding in Australian a New Zealand songbirds. *Zasláno do recenzního řízení* (Emu).

Příspěvek III. Matysioková B. & Remeš V. 2010: Incubation feeding and nest attentiveness in a socially monogamous songbird: role of feather colouration, territory quality, and ambient environment. Ethology 116: 596–607.

Příspěvek IV. Remeš V., Matysioková B. & Cockburn A.: Long-Term and Large-Scale Analyses of Nest Predation and Failure Patterns in the Southern Hemisphere: a Study of Australian and New Zealand Songbirds. *Zasláno do recenzního řízení* (PLoS ONE).

Příspěvek V. Matysioková B. & Remeš V. 2010: Responses to increased costs of activity during incubation in a songbird with female-only incubation. Journal of Ornithology, *in press.*

Příspěvek VI. Matysioková B. & Remeš V. 2010: Assessing the usefulness of ptilochronology in the study of melanin- and carotenoid-based ornaments in the Great Tit *Parus major*. Ibis 152: 397–401.

2. ÚVOD A CÍLE PRÁCE

Období hnízdění je klíčovou součástí životního cyklu ptáků. Obecně zahrnuje předinkubační chování (výběr a obhajoba hnízdního teritoria, námluvy, stavba hnízda), kladení vajec, inkubaci, období péče o mláďata na hnízdě a v době po vylétnutí. Jednotlivé druhy ptáků se liší jak přítomností či nepřítomností některých částí reprodukčního cyklu, jako je kupříkladu absence péče o mláďata u tabonů, tak délkou a charakterem jednotlivých fází. Délka období péče o mláďata na hnízdě se například u pěvců pohybuje zpravidla v řádech dnů či týdnů, zatímco u trubkonosých či tučňáků se jedná až o několik měsíců (Kendeigh 1952, Brooke 2004). Menší rozdíly pak nacházíme i v rámci jednotlivých druhů, kdy například rozdíl v délce inkubační periody může mezi jednotlivými páry činit i několik dní (Nilsson & Smith 1988, Moreno 1989).

Důvodů, proč se druhy či jedinci v reprodukčních strategiích a parametrech liší, může být více. Na mezidruhové úrovni je asi nejdůležitějším faktorem přežívání dospělců (Roff 1992, Martin 2002). Krátkověké druhy mají nižší šance na další hnízdění v následujících hnízdních sezónách ve srovnání s druhy dlouhověkými, a proto by měly investovat do současné snůšky více. Na vnitrodruhové úrovni se spíše uplatňují faktory, jako je kvalita hnízdního teritoria či kvalita hnízdících jedinců (např. Siikamäki 1998). Jak na vnitrodruhové, tak i na mezidruhové úrovni hraje zřejmě významnou roli míra hnízdní predace (Martin & Briskie 2009).

Ve své dizertační práci jsem se zaměřila hlavně na období inkubace. Mým cílem bylo zjistit, jaké faktory mají vliv na samčí a samičí inkubační chování na vnitrodruhové a mezidruhové úrovni. Dále jsem se hlouběji zabývala dvěma faktory potenciálně ovlivňujícími reprodukční chování ptáků. Na vnitrodruhové úrovni se jednalo o kvalitu jedinců, definovanou jako míra exprese jejich ornamentů, a na mezidruhové úrovni pak šlo o míru hnízdní predace. Veškerý výzkum byl prováděn na pěvcích, jakožto nejpočetnější skupině ptáků s širokou škálou reprodukčních strategií. Během svého výzkumu jsem použila více metodických přístupů (srovnávací studie, experiment, observační data) a technik (hendikepování, ptilochronologie, spektrofotometrie). Bližší informace týkající se metod užitých v jednotlivých fázích mého výzkumu jsou prezentovány v přiložených článcích a nebudou zde proto probírány.

3. INKUBACE

Inkubace je jednou z nejdůležitějších součástí ptačího reprodukčního cyklu (Deeming 2002a). S nějakou formou inkubačního chování se setkáme u naprosté většiny ptačích druhů. Výjimku tvoří hnízdní parazité, kteří tento úkol přenechávají na starost hostitelům (Sealy *et al.* 2002), a taboni, kde teplo potřebné pro inkubaci vajec vytváří tlející rostlinný materiál (Booth & Jones 2002). Dříve byla inkubace považována za období, během něhož mají ptáci pouze nízké energetické výdaje (Walsberg 1983, Murphy & Haukioja 1986), ale novější studie ukazují, že energetické výdaje během inkubace jsou stejné nebo dokonce ještě vyšší než energetické výdaje během péče o mláďata (Williams 1996, Tinbergen & Williams 2002). Inkubující jedinec má kromě zvýšených energetických výdajů navíc redukován čas, který by mohl věnovat sběru potravy a péči o sebe sama (Drent 1975, Mertens 1977). Inkubace tak může negativně ovlivňovat tělesnou kondici inkubujícího ptáka či jeho přežívání do následující hnízdní sezóny (Heinsohn & Cockburn 1994, Heaney & Monaghan 1996, Reid *et al.* 2000, Visser & Lessells 2001, de Heij *et al.* 2006). Délka inkubační periody se výrazně liší mezi druhy. Například u pěvců se pohybuje v rozmezí asi 10–50 dní (Lill 1979, Lloyd 2004a). Na její délku má vliv především fylogenetická příslušnost (Ricklefs 1993), ale také velikost vajec (Rahn & Ar 1974) či typ vývoje mláďat (altriciální nebo prekociální; Ricklefs & Starck 1998).

3.1. Samčí inkubační chování – inkubační krmení

U téměř 50 % ptačích čeledí se na inkubaci podílejí oba rodiče. V případě, že inkubuje pouze jeden jedinec, je to v naprosté většině případů samice (Skutch 1957, Deeming 2002b). U mnoha různých druhů však samec asistuje samici během inkubace tím, že ji krmí (Lack 1940). Toto chování se jmenuje inkubační krmení a setkáme se s ním u pěvců, dravců, sov, papoušků a zoborožců (Kendeigh 1952).

Existuje několik hypotéz navržených k vysvětlení významu inkubačního krmení u ptáků. V dnešní době je nejrozšířenější hypotéza samičí výživy (*female nutrition hypothesis*, von Haartman 1958, **Příspěvek I**), podle níž inkubační krmení umožňuje samici strávit méně času sběrem potravy. Samice tak může zvýšit intenzitu inkubace, tj. procento času během dne, které věnuje inkubaci (Martin & Ghalambor 1999, Tewksbury *et al.* 2002, **Příspěvek II**). Vyšší intenzita inkubace vede k vyšší líhnivosti a/nebo ke zkrácení inkubační periody (Lyon & Montgomerie 1985, Martin *et al.* 2007). Zkrácení vývojových period obecně snižuje riziko hnízdní predace (Bosque & Bosque 1995, Remeš & Martin 2002). Inkubační krmení tak patří mezi faktory, které se významně podílejí na reprodukční úspěšnosti hnízdícího páru.

Hypotézu samičí výživy jsme testovali u sýkory koňadry (*Parus major*, **Příspěvek III**). U tohoto druhu inkubuje pouze samice a samec jí během této doby asistuje v podobě inkubačního krmení jak na hnízdě, tak i mimo něj (Perrins 1979). Zjišťovali jsme, zda inkubační krmení ovlivňuje intenzitu inkubace a ta následně líhnivost vajec. Kromě toho jsme se zaměřili na faktory, které mohou mít na vnitrodruhové úrovni na inkubační krmení vliv. Jednalo se o velikost a stáří snůšky, datum zahájení hnízdění, denní dobu, teplotu vnějšího prostředí, věk a kvalitu samce definovanou mírou exprese jeho karotenoidových a melaninových ornamentů a kvalitu hnízdního teritoria. Zjistili jsme, že samci snižovali intenzitu inkubačního krmení se zvyšující se teplotou vnějšího prostředí. Jelikož se energetické výdaje inkubující samice se zvyšující se teplotou snižují (Biebach 1981, Haftorn & Reinertsen 1985, de Heij *et al.* 2008), není překvapivé, že se zároveň snižuje i frekvence inkubačního krmení (Lifjeld *et al.* 1987, Nilsson & Smith 1988, Pearse *et al.* 2004). Teplota vnějšího prostředí je také parametr, který nejčastěji negativně koreloval s intenzitou inkubačního krmení v dalších studiích zkoumajících tuto problematiku (**Příspěvek I**). Frekvence inkubačního krmení se snižovala i s denní dobou a věkem snůšky, stejně jak u sýkory koňadry zjistily i jiné studie (Kluijver 1950, Hinde 1952, Royama 1966). Vliv na inkubační krmení měla v naší studii i kvalita hnízdního teritoria. Samci z kvalitnějších teritorií krmili samice s větší intenzitou než samci z teritorií méně kvalitních. Tento vztah se ale projevoval pouze v letech s nízkou potravní nabídkou. Naproti tomu věk samce, samčí ornamenty či věk snůšky nebyly dobrými prediktory intenzity inkubačního krmení v naší populaci. Z našeho výzkumu tedy vyplývá, že inkubační krmení je u sýkory koňadry ovlivněno spíše vnějšími podmínkami (kvalita hnízdního teritoria, vnější teplota) než charakteristikami samce (ornamenty, věk). Jelikož jsme nenašli vztah mezi inkubačním krmením, intenzitou inkubace a líhnivostí, můžeme také říct, že naše výsledky nejsou ve shodě s hypotézou samičí výživy.

Intenzita inkubačního krmení není variabilní jen v rámci druhů (Sedgwick 1993, **Příspěvek III**), ale jeho frekvence se výrazně liší i mezi jednotlivými druhy (Martin & Ghalambor 1999, **Příspěvek II**). Proč a jak se liší druhy v intenzitě inkubačního krmení, jsme zkoumali u australských a novozélandských pěvců (**Příspěvek II**). Zaměřili jsme se hlavně na vliv míry hnízdní predace, tělesné velikosti druhu a sociální struktury, tj. zda se jednalo o kooperativní hnízdiče nebo o druhy hnízdící v páru. Druhy se mezi sebou výrazně liší v míře hnízdní predace (Ricklefs 1969, Conway & Martin 2000a), a to platí i u našeho studijního systému (viz kap. 5, **Příspěvek IV**). Vysoká míra inkubačního krmení vede k vysoké aktivitě kolem hnízda, takže lze očekávat evoluci nízké aktivity u hnízda u druhů trpících vysokou mírou hnízdní predace (Skutch 1949, Conway & Martin 2000a). Rozdílná míra hnízdní predace může být jedním z vysvětlení různé intenzity inkubačního krmení na mezidruhové úrovni. Výsledky studií, které se zaměřily na vztah mezi rizikem hnízdní predace a intenzitou inkubačního krmení mezi jednotlivými druhy, se však liší. U severoamerických pěvců bylo zjištěno, že se intenzita inkubačního krmení se zvyšujícím se rizikem hnízdní predace snižuje (Martin & Ghalambor 1999, Fontaine *et al.* 2007), případně nemění (Conway & Martin 2000a). Naše studie odhalila, že intenzita inkubačního krmení u australských a novozélandských pěvců je naopak nejvyšší u druhů, které trpí nejvyšší mírou hnízdní predace (**Příspěvek II**). V případě práce Conwaye a Martina (2000a) však nebyl k určení intenzity inkubačního krmení pro daný druh použit skutečný kvantitativní údaj, ale pouze kvalitativní popis (Conway & Martin 2000a). Je proto sporné, zda je možno výsledky této práce srovnávat s výsledky ostatních studií, které použily údaje kvantitativní (Martin & Ghalambor 1999, Fontaine *et al.* 2007, **Příspěvek II**).

Možným vysvětlením kontraintuitivního vztahu, který jsme zjistili u pěvců Austrálie a Nového Zélandu, je korelace vyššího inkubačního krmení s vyšší intenzitou inkubace, která byla nalezena jak mezi jedinci (Tewskubry *et al.* 2002, Lloyd *et al.* 2009), tak mezi druhy

(Martin & Ghalambor 1999, Fontaine *et al.* 2007, **Příspěvek II**). Zvýšení intenzity inkubace (umožněné vyšší frekvencí inkubačního krmení) může následně zkrátit inkubační periodu, jak bylo demonstrováno opět v rámci jednotlivých druhů (Haftorn 1983, Lyon & Montgomerie 1985, **Příspěvek V**) i mezi druhy (Martin 2002, Martin *et al.* 2007). Zkrácení délky vývojové periody je efektivní způsob zvyšování fitness (Lack 1968, Remeš & Martin 2002). Selekce u druhů s vysokou mírou hnízdní predace proto může preferovat zvyšování intenzity inkubace a následně i frekvence inkubačního krmení (Fontaine & Martin 2006). O důvodech, proč by měl vyšší predační tlak vést k jedné strategii v Severní Americe a k opačné v Austrálii a na Novém Zélandu, lze pouze spekulovat. Jedním z možných vysvětlení může být rozdíl ve způsobu orientace predátorů. Pokud se v Severní Americe řídí většina predátorů zrakem, pak se ptákům vyplatí snížit intenzitu aktivity u hnízda a tím i nápadnost hnízda pro případného predátora. Pokud se však v Austrálii a na Novém Zélandu predátoři řídí spíše čichem nebo nacházejí hnízda náhodou, je naopak výhodnější co nejvíce zkrátit vývojové periody, což ale vede k vyšší intenzitě rodičovské aktivity v okolí hnízda. Bohužel určení skutečné identity predátorů za použití videí je velmi náročné (Weidinger 2008) a takových studií je dosud málo (např. Brown *et al.* 1998, Morgan *et al.* 2006). Je proto velmi obtížné činit jakékoli závěry. Dále na intenzitu inkubačního krmení neměla u australských a novozélandských pěvců vliv tělesná velikost druhu (**Příspěvek II**). Stejný výsledek byl zjištěn i pro pěvce Arizony a Montany (Martin & Ghalambor 1999) a malé pěvce hnízdící v dutinách (Ghalambor 1998). Podobně se v naší studii intenzita inkubačního krmení nelišila mezi druhy hnízdícími kooperativně a v páru. Zdá se tedy, že nejvýznamnějším faktorem ovlivňujícím evoluci intenzity inkubačního krmení u pěvců Austrálie a Nového Zélandu je míra hnízdní predace.

3.2. Samičí inkubační chování – intenzita inkubace

Pro zdárný vývoj ptačího embrya je důležité, aby se vyvíjelo v teplotním rozmezí 36–40.5 °C. Při teplotách nižších než 26 °C dochází až k zastavení vývoje, delší vystavení teplotám překračujícím 40.5 °C je letální. Teploty v rozmezí 26–36 °C vedou ke zpomalení vývoje (Webb 1987, Conway & Martin 2000b). Samice[1] tak musí vyvážit teplotní potřeby vyvíjejícího se embrya se svými vlastními energetickými potřebami, které jsou navíc během inkubace poměrně vysoké (Williams 1996, Thomson *et al.* 1998). Intenzita inkubace se mezi druhy výrazně liší. Například u australských a novozélandských pěvců se pohybuje v rozmezí od 31 do 100 % (n = 100 druhů; **Matysioková, nepubl**.), u severoamerických pěvců v rozmezí od 32 do 97 % (Conway & Martin 2000a). Výrazné rozdíly však můžeme najít i v rámci jednotlivých druhů (Hałupka 1994, Boulton *et al.* 2010). Například u sýkory koňadry se intenzita inkubace jednotlivých samic pohybuje v rozmezí 61–89 % (**Příspěvek III**).

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[1] Přestože u několika druhů inkubují výhradně samci, používám pro zpřehlednění pro inkubujícího jedince výraz samice, jelikož se jedná o nejčastěji inkubující pohlaví (Skutch 1957, Deeming 2002).

Důvodů, proč se samice mezi sebou liší v intenzitě inkubace, může být hned několik. Jedná se jak o faktory vnějšího prostředí, jako je například kvalita hnízdního teritoria či teplota vnějšího prostředí (Skutch 1962, Sedgwick 1993, Rauter & Ryer 1997), tak o charakteristiky inkubující samice, jako je věk nebo kondice (Aldrich & Raveling 1983, Hegyi & Sasvári 1998). V našem výzkumu intenzity inkubace u sýkory koňadry jsme se zaměřili na několik faktorů, které by mohly samičí inkubační chování ovlivňovat (**Příspěvek III).** Jako faktory vnějšího prostředí jsme zvolili velikost a věk snůšky, datum zahájení snůšky, teplotu vnějšího prostředí, kvalitu hnízdního teritoria a míru, do jaké byla samice během inkubace krmena samcem (tj. inkubační krmení, viz 3.1.). Jako charakteristiky samice pak kondici definovanou jako exprese karotenoidových a melaninových ornamentů a věk samice. Ze všech námi zkoumaných faktorů ovlivňovala intenzitu inkubace v naší populaci pouze velikost snůšky a teplota vnějšího prostředí. Samice inkubující větší snůšky trávily na hnízdě více času než samice inkubující snůšky menší.

Samice se může během inkubace řídit buď svými potřebami a ukončit inkubační interval[2] ve chvíli, kdy vyčerpá energetické zásoby (Chaurand & Weimerskirch 1995, Reid *et al.* 1999) nebo aktuálním stavem snůšky a ukončit inkubační interval ve chvíli, kdy snůška dosáhne určité teploty (White & Kinney 1974). V prvním případě bude vztah mezi velikostí snůšky a intenzitou inkubace pozitivní. Větší snůšky pomaleji chladnou (Frost & Siegfred 1977, Reid *et al.* 2002) a samice tak na jejich opětovné zahřátí (které je energeticky náročnější než pouhé udržování teploty; Vleck 1981) potřebuje vydat méně energie než u rychleji chladnoucích snůšek menších. Pomalejší vyčerpání energetických zásob tak samici umožňuje prodloužit délku jednotlivých inkubačních intervalů (bez nutnosti zároveň prodlužovat délku intervalů potravních) a tím i zvýšit intenzitu inkubace. Pokud se však samice řídí aktuálním stavem snůšky, lze očekávat vztah přesně opačný. V takovém případě by totiž větší, pomaleji chladnoucí snůška umožňovala samici zkrátit délku inkubačních intervalů, protože dosáhne kritické teploty dříve, a tím snížit intenzitu inkubace (Reid *et al.* 2002). Naše výsledky naznačují, že samice sýkory koňadry se během inkubace řídí vlastními potřebami spíše než aktuálním stavem snůšky. Podobné chování bylo pozorováno například u sýkory modřinky (*Cyanistes caeruleus*; Jones 1987, Tripet *et al.* 2002) či lejska černohlavého (*Ficedula hypoleuca*; Blagosklonov 1977). Intenzita inkubace se v naší populaci také snižovala se zvyšující se teplotou vnějšího prostředí. Obdobné výsledky byly zjištěny i v jiných studiích (Hinde 1952, Sanz 1997, Camfield & Martin 2009). Tento výsledek je předvídatelný. Embryo se potřebuje vyvíjet v úzkém rozmezí teplot (viz výše), proto by samice měla zabránit vystavení snůšky nízkým teplotám v případě, že dochází ke snížení teploty vnějšího prostředí. Toho může dosáhnout právě zvýšením intenzity inkubace při snižující se teplotě vnějšího prostředí (Conway & Martin 2000b, **Příspěvek III**). Ani jeden ze zbývajících faktorů na

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[2] Jelikož čeština nemá adekvátní výraz pro anglické „bout“ ve spojení „incubation bout“ či „foraging bout“ používám v těchto případech slovo „interval“. V případě inkubačního intervalu se tak jedná o dobu mezi příletem inkubující samice na hnízdo a jejím odletem. V případě potravního intervalu se naopak jedná o periodu mezi ukončením jednoho inkubačního intervalu a zahájením druhého.

intenzitu inkubace vliv neměl. Z našeho výzkumu tak vyplývá, že podobně jako samčí inkubační chování (viz 3.1.) i samičí inkubační chování je u sýkory koňadry více ovlivněno podmínkami vnějšího prostředí (velikost snůšky, vnější teplota), než samičími charakteristikami (ornamenty, věk).

4. ORNAMENTACE A PTILOCHRONOLOGIE ANEB JAK (NE)MĚŘIT KVALITU

Kvalita jedinců je jedním z faktorů, jež může různým způsobem ovlivnit inkubační chování samců i samic. Kvalitní samci mohou být schopni investovat do snůšky více (Hill 1991, Senar *et al.* 2002, Griggio *et al.* 2010), ale k vyšší investici nemusí být nutně ochotni (Magrath & Komdeur 2003). Další možností je, že samec je ochoten více investovat do snůšky, pokud je spárovaný s kvalitnější či atraktivnější samicí (Burley 1988). Naopak samec může více krmit méně kvalitní samici, která má větší energetické nároky než samice kvalitnější (Hałupka 1994). Podobně jako u samce i u samice mohou být investice do současné snůšky závislé na její kvalitě (Aldrich & Raveling 1983, Hegyi & Sasvári 1998, Hanssen *et al.* 2003, Broggi & Senar 2009).

Je mnoho způsobů, jak měřit kvalitu či kondici u ptáků (Brown 1996, Stejskalová 2001). Kromě nejčastěji používaných parametrů, jako jsou biometrická data (délka běháku, křídla, zobáku, tělesná hmotnost) či na nich založené indexy, je jednou z možností i ptilochronologie. Tato metoda spočívá v určování nutriční kondice na základě šířky denního přírůstku per. Široké růstové proužky znamenají rychlý růst per, a jelikož růst pera je nákladný, předpokládá se, že šířka růstových proužků odráží kondici ptáků v období během přepeřování (Grubb 1989). Skutečnost, že se jedná o jednoduchou a finančně dostupnou metodu, která je navíc šetrná k ptákům samotným, dělá z ptilochronologie metodu velmi vhodnou pro terénní výzkum (Grubb 2006). Platnost této metody však byla některými vědci zpochybněna (Murphy & King 1991). Rozhodli jsme se proto zjistit, zda by ji bylo možno použít k určování kondice u našeho modelového druhu, sýkory koňadry. U tohoto druhu se setkáme hlavně se dvěma druhy ornamentů – melaninovými a karotenoidovými. Oba tyto typy ornamentů jsou obecně považovány za kondičně závislé (von Schantz *et al.* 1999, Hill 2002, Griffith *et al.* 2006, Galván & Alonso-Alvarez 2008). Očekávali jsme proto, že pokud rychlost růstu per skutečně odráží kondici ptáků během přepeřování, nalezneme pozitivní vztah mezi šířkou růstových proužků a expresí ornamentů.

Mezi plochou melaninového ornamentu a šířkou růstových proužků jsme nezjistili žádný vztah (**Příspěvek VI**). Toto zjištění odpovídá výsledkům jiných studií týkajících se stejného druhu (Senar *et al.* 2003, Hegyi *et al.* 2007). Proti veškerému očekávání jsme ale zjistili negativní vztah mezi karotenoidovými ornamenty a rychlostí růstu per, tzn. jedinci s nejvyšším obsahem karotenoidů v peří měli růstové proužky nejužší (**Příspěvek VI**). Výsledky prací, které zkoumaly vztah mezi karotenoidovými ornamenty a rychlosti růstu per u sýkory koňadry, se tedy výrazně liší. Některé z těchto prací našly vztah mezi rychlosti růstu per a expresí karotenoidových ornamentů pozitivní (Senar *et al.* 2003), jiné negativní (**Příspěvek VI**) a zbývající nenašly vztah žádný (Eeva *et al.* 1998, Senar *et al.* 2003, Hegyi *et al.* 2007). Z naší studie tak vyplývá, že u sýkory koňadry nelze ptilochronologii považovat za spolehlivou metodu k určení nutriční kondice. V dalším výzkumu jsme se proto rozhodli nadále používat jako indikátor kvality jedinců expresi jejich ornamentů (viz také 3.1., 3.2.).

U ptáků se můžeme setkat s více druhy ornamentů. Kromě zpěvu a různých typů výrůstků mezi ně patří i zbarvení peří. Nejčastěji se setkáme se zbarvením založeným na karotenoidech, melaninech a strukturních mechanismech (Hill & McGraw 2006). Běžnými ornamenty u ptáků jsou ornamenty karotenoidové (Olson & Owens 2005). Živočichové nedokáží karotenoidy sami syntetizovat, a musí je proto přijímat z vnějšího prostředí s potravou (Olson & Owens 1998). Karotenoidy jsou často navíc před uložením do ornamentu metabolizovány (Hill 2002). Nižší dostupnost karotenoidů a případná nutnost energeticky nákladné přeměny vede k tomu, že je exprese karotenoidových ornamentů nákladná (McGraw 2006a). Karotenoidové ornamenty jsou proto považovány za indikátory kvality a/nebo kondice jedince (Møller *et al.* 2000). Melaninové ornamenty nebyly dříve považovány za vhodné indikátory pro určení kondice, protože melaniny si organismy dokáží samy syntetizovat (McGraw 2006b). Z recentních studií však vyplývá, že mohou odrážet kondici stejně dobře jako ornamenty karotenoidové (Griffith *et al.* 2006, Galván & Alonso-Alvarez 2008). Vztah mezi expresí strukturního zbarvení a kondicí jedince (Hill 2006) byl prokázán v několika studiích, avšak mechanismus tohoto vztahu je nejasný (Prum 2006).

V našem výzkumu vztahu mezi ornamentací a inkubačním chováním u sýkory koňadry jsme se zaměřili na karotenoidové (**Příspěvek III**, **Příspěvek V**) i melaninové ornamenty (**Příspěvek III**). Zkoumali jsme, zda míra exprese těchto dvou typů ornamentů predikuje samčí a samičí inkubační chování (**Příspěvek III**). Zjistili jsme, že za běžných podmínek ornamenty nebyly dobrými prediktory inkubačního chování ani u jednoho pohlaví (viz 3.1., 3.2.). Jelikož se kvalita jedince může projevit až při zátěžové situaci (Ardia & Clotfelter 2007), rozhodli jsme se experimentálně ztížit podmínky samicím sýkory koňadry pomocí tzv. hendikepování a zkoumali jsme, jak se zvýšená zátěž projeví na jejich inkubačním chování (**Příspěvek V**). Z možných metod hendikepování (upevňování závaží, slepování per, stříhání per) jsme zvolili stříhání ručních a ocasních per, jelikož zlomená či chybějící pera patří mezi nejčastější přirozené hendikepy u divoce žijících ptáků (Dawson *et al.* 2001). Schopnost vyrovnat se s takovýmto hendikepem vypovídá o individuální kvalitě jedince (Harding *et al.* 2009). Protože nás zajímala zejména role ornamentů ve schopnosti vyrovnat se s experimentální zátěží, zjišťovali jsme, jak se změnila intenzita inkubace a tělesná hmotnost hendikepovaných samic ve vztahu k expresi jejich karotenoidových ornamentů. Předpokládali jsme, že se samice s výraznějšími karotenoidovými ornamenty s experimentálním zásahem vyrovnají lépe (tj. dojde k nižšímu poklesu tělesné hmotnosti a menší změně v intenzitě inkubace) než samice s ornamenty méně výraznými. Nenašli jsme však rozdíl ve změně tělesné hmotnosti či změně v intenzitě inkubace mezi samicemi s méně a více výraznými karotenoidovými ornamenty. Zdá se tedy, že míra exprese karotenoidových ornamentů není dobrým prediktorem schopnosti vyrovnat se se zátěžovou situací během inkubace. Význam ornamentů se pravděpodobně uplatňuje spíše v jiných částech hnízdního cyklu, jako je například období péče o mláďata (Griffith & Pryke 2006) nebo období mimo hnízdění (Senar 2006, Broggi & Senar 2009), než během období inkubace (**Příspěvek V, Příspěvek III**).

5. HNÍZDNÍ PREDACE

Predace je nejdůležitější faktor ovlivňující reprodukční úspěšnost u ptáků, protože způsobuje většinu hnízdních ztrát (Ricklefs 1969, Martin 1993, Thompson 2007). Druhy se mezi sebou významně liší v míře hnízdní predace (Ricklefs 1969, Conway & Martin 2000a). Dosavadní výzkumy ukazují, že hlavní rozdíly jsou způsobené typem hnízda (Nice 1957, Lack 1968, Martin & Li 1992, Wesołowski & Tomiałojć 2005, Fontaine *et al.* 2007), vegetačním patrem (Martin 1993), typem vegetace (Tewksbury *et al.* 2006), nadmořskou výškou (Boyle 2008) a geografickou polohou (Thompson 2007). Předchozí výzkumy však byly prováděny téměř výlučně na ptácích severního mírného pásu. Není proto jasné, zda tyto závěry platí i pro ptáky tropické, subtropické a ptáky jižní polokoule (Martin 1996, Stutchbury & Morton 2001).

Cílem mého výzkumu bylo zjistit, zda (a pokud ano, tak jakým způsobem) mohla predace formovat evoluci inkubačního chování u pěvců Austrálie a Nového Zélandu. O tom, jak se míra predace mezi jednotlivými druhy na jižní polokouli liší a co ji ovlivňuje, je jen velmi málo známo (viz výše). Výzkumu vlivu predace na inkubační chování tak předcházel výzkum samotné predace u australských a novozélandských pěvců a snaha o identifikaci nejdůležitějších korelátů s ní souvisejících.

I přesto, že celkové hnízdní ztráty byly podobné jako v jiných oblastech (58 %), proporce ztrát způsobená predátory byla v Austrálii a na Novém Zélandu překvapivě nižší (69 %; **Příspěvek IV)** než v jiných oblastech mírného (84–92 %; Mezquida & Marone 2001, BBIRD 2003, Wesołowski & Tomiałojć 2005), tropického a subtropického pásu (65–94 %; Marchant 1960, Oniki 1979, Robinson *et al.* 2000, Lloyd 2004b, Auer *et al.* 2007). Míra hnízdní predace byla vyšší u menších druhů. Tento výsledek se zdá být intuitivní, protože větší druhy se mohou lépe bránit. I přesto je to jediná studie, která takovýto vztah odhalila (Ricklefs 1969, Remeš 2006, Lyer 2008). Stejně jako v jiných regionech i v Austrálii a na Novém Zélandu má na riziko predace významný vliv typ hnízda. Nejméně jsou predací postiženi dutinohnízdiči, více pak druhy obývajícími uzavřená hnízda a nejvíce otevřeně hnízdící druhy (**Příspěvek IV**). Hlavním důvodem větší bezpečnosti dutin je zřejmě nižší dostupnost pro predátory ve srovnání s ostatními typy hnízd (Paclík *et al.* 2009). Naše studie dále odhalila významný vliv zeměpisné šířky na míru hnízdní predace. Predace se snižovala se zvyšující se zeměpisnou šířkou, což je ve shodě s tradičním poznatkem, že míra predace je nejvyšší právě v tropech

(Martin 1996). Míra hnízdní predace také pozitivně korelovala s rokem, ve kterém byla studie prováděna. O tom, proč v Austrálii a na Novém Zélandu stoupá míra hnízdní predace se dá jen spekulovat. Může jít o fragmentaci prostředí případně šíření hnízdních predátorů. Z výše uvedených výsledků vyplývá, že mezi pěvci Austrálie a Nového Zélandu jsou hnízdní predací nejvíce postiženy malé druhy hnízdící v otevřených hnízdech a obývající nižší zeměpisné šířky a že se míra predace obecně zvyšuje. Typ hnízda, velikost těla a geografická lokace tak potenciálně mohou mít velký význam v určení míry hnízdní predace a následně v evoluci životních strategií u australských a novozélandských pěvců (**Příspěvek IV**). O tom, jak se predace mohla podílet na evoluci samčího inkubačního chování u pěvců Austrálie a Nového Zélandu viz kapitolu 3.1. (**Příspěvek II**). Budoucí plány na výzkum vlivu predace na evoluci samičího inkubačního chování jsou zmíněny níže.

6. ZÁVĚR

Hlavní závěry mého výzkumu významu ornamentů a predace u ptáků a vlivu různých faktorů na inkubační chování jsou následující: 1) u sýkory koňadry nepredikuje exprese karotenoidových ani melaninových ornamentů míru rodičovských investic během inkubace ani u jednoho pohlaví, 2) inkubační chování je u sýkory koňadry ovlivňováno převážně faktory vnějšího prostředí, 3) hypotéza samičí výživy nevysvětluje variabilitu v inkubačním krmení u sýkory koňadry, 4) přinejmenším u sýkory koňadry nelze ptilochronologii doporučit jako spolehlivou metodu k určení nutriční kondice, 5) míra hnízdní predace v Austrálii a na Novém Zélandu je ovlivněna hlavně tělesnou velikostí druhu, typem hnízda, geografickou polohou a rokem, 6) predace je zřejmě významný faktor, který ovlivnil evoluci inkubačního krmení u pěvců Austrálie a Nového Zélandu.

Ve svém dalším výzkumu bych se chtěla nadále věnovat pěvcům Austrálie a Nového Zélandu. Výchozími studiemi pro tento výzkum budou mé práce, v nichž se zabývám samčím inkubačním chování a problematikou predace u této skupiny pěvců (**Příspěvek II, Příspěvek IV**). Cílem výzkumu bude zjistit, jak se mezi sebou liší druhy v míře samičích rodičovských investic během inkubace ve vztahu k predaci a dalším faktorům, které se na formování evoluce samičího inkubačního chování mohou podílet (například teplota vnějšího prostředí). Získané údaje chci srovnat s údaji, které byly publikovány pro pěvce severní (Martin & Ghalambor 1999, Conway & Martin 2000a) a jižní polokoule (Auer *et al.* 2007).

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Příspěvek I.

Matysioková B. 2010: Inkubační krmení u ptáků. *Sylvia*, *in press.*

S nejextrémnějším případem inkubačního krmení se setkáme u zoborožců, kde je samice po celou dobu inkubace a část, či dokonce celé, období péče o mláďata „zazděna“ v hnízdě a samec ji krmí otvorem ve „zdi“. Foto ©J. M. Garg, GNU Free Documentation License

Inkubační krmení u ptáků

Incubation feeding in birds

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Matysioková B. 2010: Inkubační krmení u ptáků. *Sylvia 46: XX–XX.*

Inkubační krmení je takové chování, kdy samec krmí samici během inkubace. Vyskytuje se u celé řady skupin ptáků, nejčastější je u zoborožců, dravců, sov, papoušků a pěvců. V současnosti existuje několik hypotéz pokoušejících se vysvětlit jeho význam. V tomto přehledu představuji všechny hypotézy a shrnuji publikované práce zabývající se významem inkubačního krmení u ptáků. Nejprve shrnuji faktory, které ovlivňují intenzitu inkubačního krmení. Mezi ně patří kvalita hnízdního teritoria, kondice samice, charakteristiky samce, riziko predace, teplota vnějšího prostředí, denní doba, datum, velikost a stáří snůšky a sociální struktura. Dále pak faktory, které jsou samy inkubačním krmením ovlivňovány. Jedná se o intenzitu inkubace, riziko predace, kondici samice, inkubační periodu a reprodukční úspěšnost. Z faktorů, které ovlivňují inkubační krmení, byla nalezena nejčastěji negativní korelace s teplotou vnějšího prostředí a rizikem predace. Z faktorů, které jsou samy inkubačním krmením ovlivňovány, korelovalo inkubační krmení nejčastěji pozitivně s intenzitou inkubace. Většina studií zahrnutých do tohoto přehledu jsou však studie korelační, a proto je těžké najít příčinné vztahy mezi chováním, fenotypem a podmínkami vnějšího prostředím.

Incubation feeding is a behaviour whereby the male feeds his mate during incubation. This behaviour occurs in several groups of birds, most often in hornbills, raptors, owls, parrots and songbirds. This review presents all hypotheses, which were proposed to explain the function of incubation feeding and summarizes published studies dealing with this behaviour in birds. First, I summarise the factors that have an influence on the rate of incubation feeding. These include territory quality, female condition, male characteristics, risk of predation, ambient temperature, time of day, date, clutch size, age of the clutch and social structure. The second factors summarized are those, which are affected by incubation feeding. These include nest attentiveness, risk of predation, female condition, incubation period and reproductive success. Incubation feeding correlated most often negatively with ambient temperature and the risk of nest depredation and positively with female nest attentiveness. However, most of the studies included in this review are correlational and thus it is difficult to infer causal relationships between individual behavioural, phenotypic, and environmental characteristics.

Keywords: incubation behaviour, male provisioning, parental investment

ÚVOD

Inkubace je jedním z klíčových procesů ptačí reprodukce (White & Kinney 1974, Deeming 2002a). S nějakou formou inkubace se setkáme u naprosté většiny ptačích druhů. U druhů, kde inkubuje pouze jeden z rodičů (zpravidla se jedná o samici, Skutch 1957, Deeming 2002b), má inkubující jedinec omezený čas pro sběr potravy a péči o sebe sama (Drent 1975). Jelikož je inkubace energeticky náročná (Willams 1996, Thomson et al. 1998, Tinbergen & Williams 2002), může to mít negativní dopad na jeho kondici, následnou rodičovskou péči během stejného či následujícího hnízdního pokusu nebo jeho přežívání do další sezóny (Heinsohn & Cockburn 1994, Heaney & Monaghan 1996, Reid et al. 2000, Visser & Lessells 2001, de Heij et al. 2006).

U mnoha různých druhů ptáků samec krmí inkubující samici (Lack 1940, Ricklefs 1974). Tento typ inkubace se nazývá podporovaná samičí inkubace (*assisted gyneparental incubation*, Williams 1996) a samčí chování pak inkubační krmení (*incubation feeding*, Cottam 1941). U zoborožců a některých dravců, sov a papoušků jsou samice během inkubace na samčím krmení plně závislé (Moreau 1934, Poulsen 1970, Altenburg et al. 1982, Saunders 1982, Korpimäki 1987) a ztráta samce může vést až k opuštění snůšky samicí (Saunders 1982). Veškeré nebo většinu krmení poskytuje samec samici během inkubace také u některých pěvců, jako například u havrana polního *Corvus frugilegus* (Røskaft 1983), straky obecné *Pica pica* (Mugaas & King 1981, Buitron 1988) či straky žlutozobé *Pica nuttali* (Verbeek 1972). U mnoha dalších druhů ptáků pak samec poskytuje samici jen část jejího denního příjmu potravy, zbytek si samice zajišťuje sama (např. Davies 1977).

V tomto článku shrnuji veškeré mně známé publikované práce, které se otázkou inkubačního krmení zabývají. Jedním z problémů týkajících se získávání a zpracovávání informací o inkubačním krmení z literatury je skutečnost, že autoři někdy neodlišují krmení během inkubace, tj. inkubační krmení od krmení před zahájením inkubace, tj. krmení zásnubního (*courtship feeding*). Mnoho autorů tak pod pojmem zásnubní krmení rozumí jak krmení zásnubní v užším slova smyslu, tak krmení inkubační (např. Smith 1980, Silver et al. 1985), což je často velmi matoucí. Jelikož jsem se v této práci chtěla zabývat výhradně inkubačním krmením, opomenula jsem záměrně práce, z nichž není zcela zřejmé, o jaký druh krmení se jedná, či kde je inkubační a zásnubní krmení spojováno do jediného pojmu.

Kde se s inkubačním krmením můžeme setkat

Inkubační krmení se vyskytuje u celé řady ptačích druhů, například u pěvců Severní Ameriky se s ním můžeme setkat u více než 41 % druhů (Verner & Willson 1969). Je častější u pěvců než u nepěvců (Kendeigh 1952) a u druhů, kde inkubuje pouze samice (Lifjeld 1989). Také je častější u dutinových hnízdičů než u druhů využívajících k hnízdění otevřená hnízda (Lifjeld 1989), což pravděpodobně souvisí s nižší rizikem predace u dutinových hnízdičů (Martin & Li 1992). Pravděpodobnost, že se u daného druhu inkubační krmení vyskytuje, není závislá na tělesné velikosti daného druhu (Ghalambor 1998, Martin & Ghalambor 1999).

K čemu inkubační krmení slouží?

Výzkumem funkce inkubačního krmení se zabývalo mnoho autorů. Já zde uvádím čtyři hlavní hypotézy vysvětlující funkci inkubačního krmení. Pátá navrhnutá hypotéza (hypotéza vyžadujícího chování, *Demand behavior hypothesis*, Smith 1980) považuje inkubační krmení za projev samičí dominance nad samcem. Jedná se tak spíše o proximátní vysvětlení inkubačního krmení, které není v protikladu k ostatním hypotézám, a proto se jím dále nebudu zabývat.

1. Hypotéza upevňování páru (*Pair-bonding* či *Pair bond maintenance hypothesis*, Lack 1940, Kluijver 1950)

Podle této hypotézy se jedná o chování symbolické, jehož hlavní funkcí je stmelování páru.

Předpovídá, že samice při opakovaném hnízdění (například po neúspěchu prvního hnízdění) pravděpodobněji zůstane se samcem, který jí během inkubace poskytl relativně více potravy. Vztah mezi frekvencí inkubačního krmení a „rozvodovostí“ zkoumal Hatchwell et al. (1999) u mlynaříků dlouhoocasých (*Aegithalos caudatus*), experimentálně pak Lifjeld & Slagsvold (1986) u lejsků černohlavých (*Ficedula hypoleuca*). Ani v jednom případě nebyl tento vztah nalezen a hypotézu upevňování páru se tak nepodařilo podpořit.

2. Hypotéza samičí výživy (*Female nutrition hypothesis*, von Haartman 1958, Royama 1966)

V současné době se jedná o nejpopulárnější a nejčastěji testovanou hypotézu. Protože je inkubace energeticky náročná (Willams 1996, Thomson et al. 1998, Tinbergen & Williams 2002), zaměřila se většina autorů na význam inkubačního krmení jako důležitého zdroje energie pro inkubující samici. Inkubační krmení by pak mělo mít vliv na reprodukční úspěch a/nebo kondici samice. Samec poskytující samici část jejího denního příjmu potravy jí umožňuje strávit méně času hledáním potravy. Toto umožňuje samici zvýšit procento času během dne, který může věnovat inkubaci, tj. zvýšit inteznitu inkubace (Martin & Ghalambor 1999, Tewksbury et al. 2002). Vyšší intenzita inkubace pak může vést k vyšší líhnivosti a/nebo ke zkrácení inkubační periody (Lyon & Montgomerie 1985, Martin et al. 2007), což může mít za následek snížení rizika predace. Vyšší líhnivost i nižší predace pak pozitivně ovlivňují reprodukční úspěšnost celého páru.

3. Hypotéza samčí kvality (*Male-quality hypothesis*, Nisbet 1973)

Podle této hypotézy se jedná o indikátor kvality samce vypovídající o jeho schopnosti starat se o mláďata. Jestliže inkubační krmení indikuje schopnost či ochotu samce investovat do rodičovské péče, lze očekávat vztah mezi frekvencí krmení během inkubace a během péče o mláďata. Tento vztah byl opravdu potvrzen u hýla mexického (*Carpodacus mexicanus*) v Montaně, kde byla intenzita inkubačního krmení významným prediktorem pozdější intenzity krmení mláďat samcem (Badyaev & Hill 2002). U populace stejného druhu v Arizoně už však vztah mezi intenzitou inkubačního krmení a intenzitou krmení mláďat nalezen nebyl (Stein et al. 2010). Stejně tak intenzita inkubačního krmení nic nevypovídala o následné intenzitě krmení mláďat u lejska černohlavého, mlynaříka dlouhoocasého a kardinála červeného *Cardinalis cardinalis* (Lifjeld & Slagsvold 1986, Hatchwell et al. 1999, Jawor & Breitwisch 2006). U mlynaříka dlouhoocasého dokonce v těch případech, kdy hnízdnícímu páru pomáhali pomocníci byla korelace mezi intenzitou inkubačního krmení a následnou intenzitou krmení mláďat hnízdícím samcem negativní (Hatchwell et al. 1999). Nutno podotknout, že hypotéza samčí kvality se většinou udává spíše ve spojitosti se zásnubním krmením, tzn. krmením samice samcem v období ještě před kladením vajec, protože oceňovat samcovu kvalitu má smysl spíše před inkubací než až během ní. V této spojitosti také byla několikrát prokázána (Nisbet 1973, Niebuhr 1981, Tryjanowski & Hromada 2005).

4. Hypotéza předčasného přinášení potravy (*Anticipatory food-bringing hypothesis,* Skutch 1954)

Podle této hypotézy se jedná o omyl samce, který přináší potravu na hnízdo domnělým mláďatům. Je založena na víceméně anekdotických pozorováních samců přilétajících na hnízdo s potravou v době, kdy je samice mimo hnízdo (Skutch 1954, Nolan 1958). Je nutno podotknout, že ve všech případech ale samec přilétal s potravou i v době přítomnosti samice a samici na hnízdě prokazatelně krmil. Navíc někteří pozdější autoři i příklady skutečného inkubačního krmení apriori nazývají předčasným přinášením potravy (např. Davis 1960). Je to zřejmě způsobeno tím, že v době, kdy tyto práce vznikaly, byla inkubace pokládaná za energeticky nenáročnou (Tinbergen & Williams 2002), a tak autoři přehlíželi možný význam krmení samice samcem. Hypotéza nebyla experimentálně testována.

Jak často krmí samec inkubující samici?

Frekvence inkubačního krmení se liší mezi jednotlivými druhy, kdy u některých je velmi nízká (např. 0,48 zakrmení za hodinu u střízlíka zahradního *Troglodytes aedon*, Johnson & Kermott 1992), u jiných pak mnohem vyšší (např.13,9 zakrmení za hodinu u sýkory babky *Poecile palustris,* Nilsson & Smith 1988). Intenzita inkubačního krmení se liší nejen mezi druhy, ale i v rámci jednotlivých druhů. Variabilita mezi hnízdy v rámci druhu se může pohybovat například od 0 do 4,7 zakrmení za hodinu u lindušky luční (*Anthus pratensis*, Hałupka 1994) nebo dokonce od 0,6 do 13 zakrmení za hodinu u tyranovce Oberholserova (*Empidonax oberholseri*, Sedgwick 1993). Pak je zajímavé ptát se na příčiny a důsledky této variability.

Na čem je inkubační krmení závislé?

Ve snaze pochopit význam inkubačního krmení se různí autoři zaměřili na faktory, které mohou intenzitu inkubačního krmení ovlivňovat. Patří mezi ně kvalita hnízdního teritoria, kondice samice, charakteristiky samce, riziko predace, teplota vnějšího prostředí, denní doba, datum, velikost a stáří snůšky a sociální struktura.

Kvalita hnízdního teritoria

Kvalita teritoria je velmi důležitý faktor ovlivňující dostupnost potravy pro hnízdící pár. Samci obhajující kvalitnější teritoria by mohli být schopni zajistit více potravy než samci z teritorií chudších (Wilkin et al. 2009). Alternativním vysvětlením je, že pomocí inkubačního krmení samci kompenzují nižší kvalitu teritoria, a tudíž bychom mohli naopak očekávat negativní vztah mezi kvalitou teritoria a intenzitou inkubačního krmení (Lifjeld & Slagsvold 1986).

Pozitivní vztah mezi kvalitou teritoria a intenzitou inkubačního krmení byl nalezen u lejsčíka žlutého (*Eopsaltria australis*), kde samci z velkých fragmentů (v nichž je více potravy) krmili inkubující samice o 40 % více než samci z fragmentů malých (Zanette et al. 2000). Stejně tak ovlivňovala kvalita teritoria samčí inkubační krmení u sýkory koňadry (*Parus major*), ale pouze v letech s nízkou potravní nabídkou (Matysioková & Remeš 2010). V ostatních studiích rozdíl v intenzitě inkubačního krmení mezi různě kvalitními hnízdními teritorii (Lifjeld & Slagsvold 1986, Rauter & Reyer 1997) či typy prostředí (Lloyd et al. 2009) nebyl nalezen.

Kondice samice

Jestliže samec upravuje intenzitu inkubačního krmení podle skutečných potřeb samice, dalo by se očekávat, že nutriční požadavky samic v horší kondici budou větší než samic v kondici lepší, a tak budou krmeny s větší intenzitou. Další možností je, že samec nereaguje na okamžité potřeby samice, ale naopak bude ochotněji investovat do samice v lepší kondici či samice atraktivnější (Burley 1988).

Snížení kondice samic lejska černohlavého vytržením několika ručních letek (tzv. hendikepování) nemělo na inkubační krmení žádný vliv a hendikepované samice byly krmeny se stejnou intenzitou jako samice kontrolní (Lifjeld & Slagvold 1986). Naopak zlepšení nutričního stavu samic stejného druhu a samic střízlíka pokřovního (*Thryomanes bewickii*) pomocí suplementace potravou vedlo k tomu, že dokrmované samice byly samcem krmeny méně než samice kontrolní (Smith et al. 1989, Pearse et al. 2004). Podobně u jiné populace lejska černohlavého mělo dokrmování primární samice pozitivní vliv na intenzitu krmení samice sekundární. U párů, kde byla primární samice dokrmována, krmili samci více samici sekundární, zatímco u kontrolních párů byla primární a sekundární samice krmena stejně (Lifjeld & Slagvold 1989).

Charakteristiky samce

Jedním ze základních parametrů, který by mohl ovlivnit samčí inkubační chování, je kvalita či kondice samce. Kvalitnější samci mohou být schopni investovat více než samci méně kvalitní, ale na druhou stranu nemusí být k vyšší investici ochotní (Magrath & Komdeur 2003). K odhadu kondice u ptáků je používáno mnoho přístupů (Brown 1996). Při zkoumání inkubačního krmení jsou používána převážně biometrická data (hmotnost, délka běháku, délka křídla) či indexy na nich založené. O kvalitě jedince mohou také vypovídat jeho ornamenty. Sem patří zpěv, různé výrůstky a zbarvení peří. U ptáků se setkáváme hlavně se zbarvením založeným na karotenoidech, melaninech a strukturních mechanismech (Hill & McGraw 2006). Karotenoidové ornamenty jsou mezi ptáky hodně rozšířené (Olson & Owens 2005), a jelikož je jejich exprese nákladná a ovlivňována prostředím (McGraw 2006a), jsou považovány za indikátory kvality a/nebo kondice jedince (Møller et al. 2000). Melaninové ornamenty sice nebyly dříve považovány za vhodné indikátory pro určení kondice (McGraw 2006b), ale z recentních studií vyplývá, že mohou stejně dobře odrážet kondici jako ornamenty karotenoidové (Griffith et al. 2006, Galván & Alonso-Alvarez 2008). Několik studií prokázalo vztah mezi expresí strukturního zbarvení a kondicí jedince (Hill 2006), avšak mechanismus tohoto vztahu je zcela nejasný (Prum 2006). Reprodukční úspěch se u živočichů liší také mezi různými věkovými kategoriemi (Clutton-Brock 1988). Ptáci mohou s věkem zlepšovat své schopnosti ve sběru potravy (Desrochers 1992) nebo obsazují lepší teritoria

(Pärt 2001). Na druhou stranu hnízdní úspěch jedinců, kteří už přesáhnou určitou věkovou hranici, se snižuje (Newton 1989).

Biometrická data

Ze všech sledovaných parametrů kondice (délka běháku a křídla, hmotnost) u lejska černohlavého intenzita inkubačního krmení pozitivně korelovala pouze s hmotností samce. Délka běháku ani délka křídla statisticky významné nebyly (Lifjeld et al. 1987). U jiné populace stejného druhu nebyl nalezen statisticky významný vztah mezi inkubačním krmením a žádným z těchto parametrů kondice (Lifjeld & Slagsvold 1986).

Ornamentace

Vztah mezi samčí ornamentací a inkubačním krmením zkoumali Siefferman & Hill (2005) u salašníka modrého (*Sialia sialis*). Zjistili, že nejlepším prediktorem inkubačního krmení je jasnost strukturního zbarvení, zatímco melaninové ornamenty inkubační krmení nepredikovaly. Avšak titíž autoři nenašli v jiné studii téhož druhu žádný vztah mezi inkubačním krmením, a ani strukturním ani melaninovým zbarvením samců (Siefferman & Hill 2003). Melaninové ani karotenoidové ornamenty se také neuplatňovaly jako prediktory inkubačního krmení u sýkory koňadry (Matysioková & Remeš 2010). Jawor a Breitwisch (2006) zkoumali vztah mezi samčí ornamentací a inkubačním krmením u kardinála červeného. Nenašli vztah mezi žádným ze samčích ornamentů (délka chocholky, velikost masky, zbarvení zobáku, karotenoidové zbarvení peří) a intenzitou inkubačního krmení. Negativní vztah mezi samčí ornamentací a inkubačním krmením našli Badyaev & Hill (2002) u hýla mexického, kde samci s nejrozvinutějšími karotenoidovými ornamenty (tj. samci červení) krmili samici méně než samci s ornamentací rozvinutou méně (samci žlutí). Opačný výsledek však u stejného druhu zjistil Hill (1999), kde samci s větším množstvím karotenoidů v peří krmili samice více než samci světlejší. Vztah mezi celkovým zbarvením a inkubačním krmením nebyl nalezen u lejska černohlavého (Lifjeld & Slagsvold 1986, Lifjeld et al. 1987). Stejně tak nebyl nalezen vztah mezi charakteristikami zpěvu samce a jeho intenzitou inkubačního krmení u sněhule severní (*Plectrophenax nivalis*, Hofstad et al. 2002).

Věk

Věk samce nekoreloval s inkubačním krmením u salašníka modrého (Siefferman & Hill 2005) ani u sýkory koňadry (Matysioková & Remeš 2010), ale negativně koreloval s inkubačním krmením u havranů polních, kde dvouletí (tj. poprvé hnízdící) samci krmili samice více než samci starší (Røskaft et al. 1983). I přesto byly samice spárované s mladšími samci zřejmě hladovější, protože žadonily více než samice, spárované se samci staršími. Zdá se proto, že u havranů polních nejsou mladší samci tak efektivní v přinášení potravy jako samci starší (Røskaft et al. 1983). Inkubační krmení bylo na věku závislé i u lejska černohlavého, kde se však výsledky liší mezi lety a populacemi. V roce 1983 krmili starší samci více než samci mladší, zatímco následující rok tomu bylo naopak (Lifjeld & Slagsvold 1986). V jiné populaci nebyl vztah mezi věkem samce a intenzitou, s jakou krmí samici během inkubace, pozorován vůbec (Lifjeld et al. 1987).

Experimentální snížení kondice

Snížení kondice pomocí hendikepování u lejsků černohlavých nemělo vliv na inkubační krmení u prvního hnízdění, ale negativně ovlivnilo inkubační krmení u opakovaného hnízdění v jednom ze dvou sledovaných roků (Lifjeld & Slagsvold 1986).

Riziko predace

Predace je hlavní důvod hnízdního neúspěchu u ptáků (Ricklefs 1969, Martin 1995). Riziko predace vzrůstá s rodičovskou aktivitou u hnízda (Martin et al. 2000), proto by měla být intenzita inkubačního krmení nižší u druhů či populací trpících vyšší mírou predace.

Evoluci nižší intenzity inkubačního krmení u druhů ohrožených vyšším rizikem predace opravdu potvrdily srovnávací analýzy u severoamerických pěvců (Martin & Ghalambor 1999, Fontaine et al. 2007), ale už ji nepotvrdila další analýza na rozsáhlejším souboru druhů (Conway & Martin 2000). V posledně jmenované práci však nebyla analyzována skutečná frekvence inkubačního krmení vyjádřena jako počet zakrmení za hodinu, ale pouze kvalitativní popis pro frekvenci inkubačního krmení u jednotlivých druhů (málokdy nebo nikdy, vzácně, středně často, často). Jelikož se jedná o data sebraná z dříve publikovaných prací a tyto kvalitativní popisy tak byly navrženy různými autory, je takto zaznamenaná frekvence inkubačního krmení poněkud subjektivní. Je proto otázka, jak interpretovat výsledky této studie ve srovnání se studiemi Martina & Ghalambora (1999) a Fontaine et al. (2007), v nichž autoři počítali se skutečnou frekvencí inkubačního krmení.

Frekvence inkubačního krmení se také liší mezi jednotlivými typy hnízd (Lifjeld 1989, Martin & Ghalambor 1999, Fontaine et al. 2007), přičemž nejvyšší je u druhů tesajících vlastní dutiny, což jsou druhy, které obecně trpí nižší mírou predace, a nejnižší u otevřeně hnízdících druhů, které obecně trpí mírou predace vyšší (Martin & Li 1992).

Experimentálně pak vliv predace na plastiticitu v intenzitě inkubačního krmení dokázali Ghalambor & Martin (2002) u severoamerických pěvců, kdy pěti druhům dutinových hnízdičů předváděli u hnízda atrapu predátora. Druhy, které jsou přirozeně vystaveny vyššímu riziku predace, snížily intenzitu inkubačního krmení po předvedení atrapy více než ty, které mají predaci nižší. Míra predace je zřejmě také jedním z hlavních důvodů, proč se inkubační krmení vyskytuje u sněhule severní trpící přirozeně nižší mírou predace, ale už se s ním nesetkáme u blízce příbuzného strnada severního (*Calcarius lapponicus*), u nějž je míra predace vyšší (Lyon & Montgomerie 1987).

Experimentálně potvrdili změnu v inkubačním krmení se snižujícím se rizikem predace Fontaine & Martin (2006). Během čtyř let systematicky odstraňovali predátory z 10 výzkumných ploch, zatímco 10 dalších ploch nechali nedotčených jako plochy kontrolní. Zjistili, že intenzita inkubačního krmení u 12 zkoumaných druhů byla vyšší na plochách se sníženým množstvím predátorů než na plochách kontrolních. Zdá se proto, že ptáci upravují intenzitu inkubačního krmení, a tím aktivitu na hnízdě, podle aktuálního rizika predace.

Teplota vnějšího prostředí

Se snižující se teplotou vnějšího prostředí musí ptáci zvyšovat svůj metabolismus tak, aby jejich tělesná teplota neklesla pod kritickou hladinu. Zvýšený metabolismus je spojen se zvýšením příjmu energie (Johnston & Bennett 2008), proto je-li intenzita inkubačního krmení závislá na skutečných samičích potřebách, lze očekávat, že se bude se snižující se teplotou zvyšovat.

Výsledky prací týkajících se vlivu teploty na inkubační krmení však jsou nejednotné. V některých studiích bylo zjištěno, že se intenzita inkubačního krmení se snižující se teplotou vnějšího prostředí zvyšuje (Lifjeld et al. 1987, Nilsson & Smith 1988, Ghalambor 1998, Pearse et al. 2004, Matysioková & Remeš 2010), zatímco v jiných studiích se s teplotou neměnila (Hałupka 1994, Rauter & Reyer 1997, Ghalambor 1998, Hatchwell et al. 1999, Laiolo & Rolando 2001, Jawor & Breitwisch 2006). Stejně tak rozsáhlá srovnávací studie týkající se 97 druhů severoamerických pěvců neodhalila vliv teploty na inkubační krmení na mezidruhové úrovni (Conway & Martin 2000).

Někdy se mezi sebou lišily i výsledky z jedné populace, kdy například u lejska černohlavého se v jednom roce intenzita inkubačního krmení s teplotou zvyšovala, zatímco ve druhém snižovala (Lifjeld & Slagsvold 1986). Podobné rozdíly byly nalezeny v experimentu týkajícím se dokrmování inkubujících samic lejska černohlavého. U samic kontrolních byl nalezen negativní vztah mezi teplotou vnějšího prostředí a intenzitou inkubačního krmení, zatímco tento vztah úplně zmizel u samic experimentálně dokrmovaných (Smith et al. 1989). Podobně byly nalezeny i rozdíly mezi blízce příbuznými druhy. U experimentu, kde bylo uměle ochlazováno a oteplováno hnízdo, reagovali samci na změnu teploty u brhlíka kanadského (*Sitta canadensis*), ale u blízce příbuzného brhlíka běloprsého (*Sitta carolinensis*) k žádné odezvě ze strany samců nedošlo (Ghalambor 1998).

Denní doba

U ptáků se setkáváme s typickým vzorcem potravní aktivity během dne kdy nejvyšší aktivita je ráno, mírná během dne a střední až výrazná pozdě odpoledne (Bednekoff & Houston 1994). Zvýšená potřeba příjmu potravy hlavně v ranních a večerních hodinách by tak mohla výrazně ovlivnit míru inkubačního krmení.

Nejvyšší intenzita inkubačního krmení ráno byla skutečně pozorována u brhlíka kanadského (Ghalambor 1998) a sýkory koňadry (Kluijver 1950, Hinde 1952, Matysioková & Remeš 2010). U ostatních sledovaných druhů (havran polní, lejsek černohlavý, sýkora babka, brhlík běloprsý, lejsčík žlutý, dudkovec stromový *Phoeniculus purpureus*) však byla konstantní během celého dne (Røskaft 1981, Lifjeld & Slagsvold 1986, Lifjeld et al. 1987, Nilsson & Smith 1988, Ghalambor 1998, Smith et al. 1989, Zanette et al. 2000, Radford 2004). U havrana polního nastala změna až po 18. hodině, kdy intenzita inkubačního krmení statisticky významně klesla (Røskaft 1981).

Datum

U mnoha různých druhů ptáků se s postupující sezónou zkracuje délka inkubační periody (Runde & Barrett 1981, Murphy 1995, Hipfner et al. 2001). Samice mohou začít inkubovat dříve (Haftorn 1981, Rowe & Weatherhead 2009) či s větší intenzitou (Cresswell & McCleery 2003, Lloyd et al. 2009), což zřejmě odráží jejich snahu o co nejčasnější vylíhnutí pozdějších snůšek, a tím zvýšení pravděpodobnosti následného přežití mláďat (Perrins 1970, Monrós et al. 2002). Samec tak může vyšší intenzitou inkubačního krmení významně přispět k časnějšímu vylíhnutí mláďat, a tím k vyšší reprodukční úspěšnosti páru.

Překvapivě opačný výsledek zjistili Zanette et al. (2000) u lejsčíka žlutého, Lloyd et al. (2009) u pěvce jihoafrického (*Cercotrichas coryphaeus*) a Smith et al. (1989) u lejska černohlavého, kde se intenzita inkubačního krmení v průběhu sezóny snižovala. U ostatních zkoumaných druhů nebylo inkubační krmení na datu závislé vůbec (Lifjeld & Slagsvold 1986, Lifjeld et al. 1987, Nilsson & Smith 1988, Jawor & Breitwisch 2006, Matysioková & Remeš 2010).

Velikost snůšky

Energetické výdaje inkubující samice se zvyšují s velikostí snůšky (Thomson et al. 1998). Přirozená velikost snůšky však překvapivě negativně korelovala s frekvencí inkubačního krmení u lejska černohlavého (Moreno & Carlson 1989). U ostatních zkoumaných druhů vliv nalezen nebyl (červenka obecná *Erithacus rubecula*, East 1981; havran polní, Røskaft 1983; lejsek černohlavý, Smith et al. 1989; papoušíček vrabčí *Forpus passerinus,* Waltman & Beissinger 1992; lejsčík žlutý, Zanette et al. 2000; sýkora koňadra, Matysioková & Remeš 2010).

Naproti tomu experimentální zvětšení snůšky pozitivně ovlivnilo intenzitu inkubačního krmení u lejska černohlavého (Blagosklonov 1977), kdy se frekvence inkubačního krmení zvýšila z 0 zakrmení za hodinu u snůšek se čtyřmi vejci na 3,3 zakrmení u snůšek s osmi vejci a 5,3 zakrmení u snůšek s vejci dvanácti. Podobný výsledek u lejska černohlavého získal i Sanz (1997), v jehož experimentu zvětšení snůšky o dvě vejce vedlo k navýšení frekvence inkubačního krmení o 0,6 zakrmení za hodinu. Manipulace s velikostí snůšky však neovlivnila frekvenci inkubačního krmení u jiné populace stejného druhu (Moreno & Carlson 1989).

Stáří snůšky

Pokud platí hypotéza předčasného přinášení potravy a samec přináší potravu domnělým mláďatům, mělo by se inkubační krmení objevovat převážně ke konci inkubační periody.

U sýkory koňadry (Matysioková & Remeš 2010) však byla intenzita krmení naopak největší na začátku inkubační periody a s věkem snůšky se snižovala. Podobně ani u ostatních zkoumaných druhů nedošlo ke zvýšení frekvence inkubačního krmení ke konci inkubační periody, ale inkubační krmení bylo v průběhu celé inkubační periody konstantní (sýkora koňadra, Royama 1966; lejsek černohlavý, Lifjeld et al. 1987; sýkora babka, Nilsson & Smith 1988; střízlík zahradní, Johnson & Kermott 1992; lejsčík žlutý, Zanette et al. 2000; kavče žlutozobé a kavče červenozobé *Pyrrhocorax graculus* a *P. pyrrhocorax,* Laiolo & Rolando 2001; dudkovec stromový, Radford 2004; kardinál červený, Jawor & Breitwisch 2006).

Jedinou výjimkou, kde se intenzita inkubačního krmení s věkem snůšky zvyšovala, byl timáliovec šedotemenný (*Pomatostomus temporalis,* King 1980). Autorovi se však jen v 69 % případů podařilo určit, že samec přilétal opravdu s potravou. Není proto vyloučeno, že se s věkem snůšky mohla měnit frekvence návštěv bez potravy, což by výrazně ovlivnilo výsledek.

Sociální struktura

U kooperativně hnízdících druhů pomáhají s péčí o potomstvo rodičům zpravidla potomci z předchozích hnízdění, na rozdíl od druhů solitérně hnízdících, u kterých si hnízdní pár musí vystačit sám (Koenig & Dickinson 2004). U druhů polygynních jeden samec pomáhá během hnízdění více samicím. Počet jedinců ve skupině pomáhajících s hnízděním či počet samic, které musí samec zaopatřovat, může významně ovlivnit schopnost samce zásobovat samici potravou během inkubace.

Kooperativní hnízdění

U pěvce jihoafrického byla intenzita inkubačního krmení vyšší u kooperativně hnízdících skupin ve srovnání se solitérně hnízdícími páry (Lloyd et al. 2009). U australského lezčíka proužkobřichého (*Climacteris affinis*) se mezi kooperativně a solitérně hnízdícími páry intenzita inkubačního krmení nelišila (Radford 2002). U blízce příbuzného lezčíka hnědého (*Climacteris picumnus*) počet pomocníků pozitivně koreloval s celkovou intenzitou inkubačního krmení (Doerr & Doerr 2007). U dudkovce stromového, který hnízdí výhradně kooperativně, neměla velikost skupiny na celkovou intenzitu inkubačního krmení vliv (Radford 2004), ale negativně ovlivňovala intenzitu inkubačního krmení hnízdícím samcem (Ligon & Ligon 1978, Radford 2004). U dudkovce stromového, lezčíka hnědého a pěvce jihoafrického krmili hnízdící samci více než jednotliví pomocníci (Radford 2004, Doerr & Doerr 2007, Lloyd et al. 2009).

Párovací systém

Vliv párovacího systému na inkubační krmení byl zkoumán u lejsků černohlavých v Norsku. Samice, jejichž samci byli polygynní, dostávaly méně potravy než samice monogamních samců. Jednotlivé samice žijící s polygynním samcem však obdržely stejné množství potravy a celková intenzita inkubačního krmení polygynního samce se nelišila od intenzity krmení samce monogamního (Lifjeld et al. 1987, Lifjeld & Slagvold 1989). Podobně u motáka pochopa (*Circus aeruginosus*) krmil polygynní samec během inkubace primární samici (tj. samici, která zahnízdila dříve) stejně často jako samici sekundární. Narozdíl od samic lejsků však samice monogamních samců neobdržely více potravy než samice samců polygynních (Altenburg et al. 1982). V jiné studii tykající se opět lejska černohlavého krmil polyteritoriální samec (tj. samec, který obhajoval více než jednu hnízdní budku) samici méně než samec, který měl pouze jedno teritorium. Ve druhém roce však tento rozdíl nebyl významný (Lifjeld & Slagsvold 1986). Z práce bohužel není patrné, zdali byl polyteritoriální samec také polygamní nebo ne.

Na co má inkubační krmení vliv?

Existuje několik faktorů, které mohou být inkubačním krmením ovlivňovány, ať už přímo (intenzita inkubace, riziko predace, kondice samice) nebo nepřímo prostřednictvím zvýšené intenzity inkubace (inkubační perioda, reprodukční úspěšnost).

Intenzita inkubace

Intenzita inkubace ovlivňuje teplotu vajec (White & Kinney 1974), která dále ovlivňuje líhnivost (Webb 1987) a/nebo délku inkubační periody (Martin et al. 2007). Z těchto důvodů je intenzita inkubace velmi důležitým faktorem podílejícím se na celkové reprodukční úspěšnosti hnízdícího páru.

Pozitivní vztah mezi frekvencí inkubačního krmení a intenzitou inkubace byl nalezen u lindušky luční (Hałupka 1994), lejska černohlavého (Lifjeld & Slagvold 1986, Moreno & Carlson 1989), lesňáčka žlutého (*Dendroica petechia*, Tewksbury et al. 2002), ťuhýka šedohřbetého (*Lanius excubitoroides*, Zack 1986), tangary šarlatové (*Piranga olivacea*, Klatt et al. 2008), lejsčíka dlouhonohého (*Petroica australis*, Powlesland 1983) a pěvce jihoafrického (Lloyd et al. 2009). Podobně u tyranovce Oberholserova byla intenzita inkubace samic, které byly během inkubace alespoň jednou za hodinu krmeny samcem, vyšší než u samic, které nebyly krmeny vůbec (Sedgwick 1993). Experimentální dokrmování samic lejska černohlavého, střízlíka zahradního a střízlíka pokřovního vedlo k podobným výsledkům, kdy dokrmované samice vykazovaly větší intenzitu inkubace než samice kontrolní (Smith et al. 1989, Pearse et al. 2004).

Na mezidruhové úrovni pozitivní vztah mezi frekvencí inkubačního krmení a intenzitou inkubace odhalily i studie srovnávající severoamerické druhy pěvců (Martin & Ghalambor 1999, Conway & Martin 2000, Fontaine et al. 2007). Ve studii Conwaye & Martina (2000) byl ale tento vztah přítomen jen v případě, že byl zkoumán vztah pouze mezi intenzitou inkubačního krmení a intenzitou inkubace. Tento vztah však vymizel, když byly do analýzy přidány další vysvětlující proměnné (např. predace, velikost těla). To naznačuje, že vztah mezi intezitou inkubačního krmení a intenzitou inkubace byl nejspíše způsobený třetí proměnnou (např. korelací obou proměnných s predací), a proto přidání této proměnné do analýzy vedlo k jeho vymizení.

U střízlíka pokřovního (Pearse et al. 2004), kardinála červeného (Jawor & Breitwisch 2006), lindušky horské (*Anthus spinoletta*, Rauter & Ryer 1997), sýkory koňadry (Matysioková & Remeš 2010) a pěti druhů pěvců v Arizoně (Ghalambor & Martin 2002) vztah mezi intenzitou inkubačního krmení a intenzitou inkubace nalezen nebyl. Stejně tak inkubační krmení neovlivnilo průměrnou intenzitu inkubace u mlynaříka dlouhoocasého (Hatchwell et al. 1999) ani dudkovce stromového (Radford 2004). Když však u posledních dvou jmenovaných druhů nebyla brána v úvahu průměrná intenzita inkubace a inkubačního krmení, ale jednotlivá pozorování, zjistilo se, že inkubační krmení intenzitu inkubace na takto krátké časové škále ovlivňuje pozitivně.

Zajímavé je, že u papoušíčka vrabčího a sýkory modřinky (*Cyanistes caeruleus*) byl nalezen vztah negativní, tj. čím více samci inkubující samice krmili, tím nižší byla intenzita inkubace (Grenier & Beissinger 1999, Tripet et al. 2002). U papoušíčka vrabčího samice opouští hnízdo, aby mohla být nakrmena samcem. Jelikož samec potravu samici vyvrhuje, celé krmení trvá minimálně 10 minut. Čím častěji samec přilétal na hnízdo s potravou, tím častěji samice opouštěla hnízdo a tím delší dobu trávila mimo hnízdo (Grenier & Beissinger 1999). Negativní vztah mezi intenzitou inkubace a frekvencí inkubačního krmení tak zůstává nevysvětlen pouze v případě sýkory modřinky.

Nepřítomnost inkubačního krmení způsobená experimentálním odstraněním samce u sněhule severní, druhu, u nějž se inkubační krmení běžně vyskytuje, vedla ke snížení intenzity inkubace o 16,2 % ve srovnání s kontrolními samicemi (Lyon & Montgomerie 1985). Stejně tak odstranění samce u lejska černohlavého, a tím snížení intenzity inkubačního krmení z 8,5 na 0 zakrmení za hodinu vedlo k poklesu intenzity inkubace o 20,8 % (von Haartman 1958). Nutno však podotknout, že tento experiment byl proveden pouze na jednom hnízdě, a výsledky mají tudíž jen omezenou výpovědní hodnotu.

Na mezidruhové úrovni neměla přítomnost či nepřítomnost inkubačního krmení u zkoumaného druhu vliv na jeho intenzitu inkubace, jak bylo zjištěno ve srovnávací studii zaměřené na 18 druhů pěvců subtropické Argentiny (Auer et al. 2007).

Riziko predace

Riziko predace vzrůstá s rodičovskou aktivitou u hnízda (Martin et al. 2000), a proto může být vyšší míra inkubačního krmení doprovázena vyšší mírou predace.

Vzrůstající míra predace se zvyšující se intenzitou inkubačního krmení byla opravdu nalezena u lesňáčka žlutého (Tewksbury et al. 2002). Hnízda, která podlehla predaci, měla větší intenzitu inkubačního krmení (průměrně pět zakrmení za hodinu) než hnízda úspěšná, u nichž byla intenzita inkubačního krmení průměrně nižší (tři zakrmení za hodinu). Tento vztah už ale nebyl potvrzen u mlynaříků dlouhoocasých (Hatchwell et al. 1999) či tangary šarlatové (Klatt et al. 2008), kde se intenzita krmení samcem nelišila mezi hnízdy zničenými predátorem a hnízdy úspěšnými.

Kondice samice

Studií, které by zkoumaly vliv inkubačního krmení na kondici samice na konci inkubace, je velmi málo. Pozitivně ovlivnilo hmotnost samice u lejska černohlavého (Lifjeld & Slagvold 1986), ale pouze v jednom ze dvou sledovaných let. Ve druhém roce, stejně jako v další studii týkající se téhož druhu, frekvence inkubačního krmení s hmotností samice nekorelovala (Lifjeld & Slagvold 1986, 1987).

To, že inkubační krmení přesto může ovlivňovat kondici samice, naznačují dvě další práce. U havrana polního, kde je samice na krmení samcem plně závislá během celé inkubace i z počátku období péče o mláďata, prokázal Røskaft (1983) vztah mezi intenzitou inkubačního krmení a množstvím vylétlých mláďat. Samice, které dostávaly více potravy během inkubace, byly na začátku období péče o mláďata zřejmě v lepší kondici, což se projevilo na počtu vylétlých mláďat. U sněhulí severních vedlo experimentální odstranění samce (a tím i odstranění inkubačního krmení) k tomu, že v případě uhynutí dvou či více mláďat došlo k úhynu druhého mláděte statisticky významně dříve než u samic, které o inkubační krmení ochuzeny nebyly. Podle autorů tyto rozdíly v načasování redukce snůšky naznačují, že nepřítomnost inkubačního krmení snížila kondici inkubující samice, a tím i její schopnost péče o mláďata (Lyon & Montgomerie 1985).

Inkubační perioda

Délka inkubační periody je další parametr, který může významně ovlivnit hnízdní úspěšnost páru. Prodloužená inkubační perioda znamená delší dobu vystavení hnízda riziku predace a také pozdější líhnutí, které může negativně ovlivnit následné přežívání mláďat (Perrins 1970, Monrós et al. 2002). Délka inkubační periody se liší mezi druhy a v rámci jednotlivých druhů se odvíjí od různých parametrů, mezi něž patří i intenzita inkubace (Moreno 1989, Martin et al. 2007). Samec tak může ke zkrácení inkubační periody přispět zvýšenou intenzitou inkubačního krmení, a tím umožní samici strávit více času na hnízdě.

Intenzita inkubačního krmení korelovala s délkou inkubační periody u sýkory babky, kde zvýšení frekvence inkubačního krmení o každé jedno zakrmení za hodinu odpovídalo zkrácení délky inkubační periody o 0,7 dne. Rozdíl mezi nejkratší a nejdelší inkubační periodou činil čtyři dny (Nilsson & Smith 1988). Experimentální odstranění samce v době před inkubací, a tím i inkubačního krmení mělo za následek prodloužení délky inkubační periody u sněhule severní v průměru o 1,4 dne (Lyon & Montgomerie 1985). Naopak u lejska černohlavého, mlynaříka dlouhoocasého ani salašníka modrého vliv inkubačního krmení na délku inkubační periody prokázán nebyl (Lifjeld & Slagsvold 1986, Hatchwell et al. 1999, Siefferman & Hill 2005).

Podobně nekonzistentní jsou výsledky experimentálního dokrmování samic během inkubace, jež mělo simulovat inkubační krmení samcem. U střízlíka zahradního a střízlíka pokřovního neovlivnilo dokrmování samic délku inkubační periody (Pearse et al. 2004), zatímco u sýkory babky došlo k jejímu významnému zkrácení (Nilsson & Smith 1988).

Reprodukční úspěšnost

Má-li mít inkubační krmení podstatný význam pro reprodukční úspěšnost páru, mělo by pozitivně ovlivňovat úspěšnost líhnutí, případně i počet vylétlých mláďat. Možný vliv inkubačního krmení na úspěšnost líhnutí dokazuje i to, že experimentální dokrmování samic sýkory babky během inkubace vedlo ke zvýšení procenta vylíhlých vajec o 6 % (Nilsson & Smith 1988).

Úspěšnost líhnutí

Naprostá většina studií, které se na vztah mezi samčím inkubačním chováním a líhnivostí zaměřily, neodhalila žádný vztah mezi intenzitou inkubačního krmení a úspěšností líhnutí (Lifjeld & Slagsvold 1986, Hałupka 1994, Hatchwell et al. 1999, Siefferman & Hill 2005, Stein et al. 2010). Pozitivní vliv inkubačního krmení na úspěšnost líhnutí byl nalezen pouze u sněhule severní, kdy byl části samic experimentálně odebrán na začátku inkubace samec. Tyto samice tak na rozdíl od samic kontrolních byly ochuzeny o samčí asistenci v podobě inkubačního krmení. Úspěšnost líhnutí se u experimentálních samic snížila o 15,2 % ve srovnání se samicemi kontrolními (Lyon & Montgomerie 1985). V tomto případě však nešlo o vliv intenzity inkubačního krmení na úspěšnost líhnutí, ale o vliv jeho přítomnosti.

Počet vylétlých mláďat

Intenzita inkubačního krmení pozitivně korelovala s počtem vylétlých mláďat u lezčíka hnědého (Doerr & Doerr 2007) a havrana polního (Røskaft 1983). Jelikož u havranů je samice na samčím krmení plně závislá po celou dobu inkubace a prvních 2 týdnů po vylíhnutí mláďat, je možné, že samice, které byly více krmeny během inkubace, byly na začátku období péče o mláďata v lepší kondici. To mohlo mít za následek větší proporci vylétlých mláďat (Røskaft 1983). Zajímavé je, že u lindušky luční Hałupka (1994) našel mezi počtem mláďat těsně před vylétnutím a frekvencí inkubačního krmení vztah negativní. Autor toto překvapivé zjištění vysvětluje tak, že samice, které jsou krmeny více, mohou být ty, které jsou v horší kondici, a mají proto vyšší energetické nároky. Samci se tak vyšší intenzitou inkubačního krmení mohou snažit zachránit snůšku spíše než zvýšit reprodukční úspěšnost. Intenzita inkubačního krmení se ve stejné studii nelišila mezi hnízdy, která vyvedla alespoň jedno mládě, a těmi, která nebyla úspěšná.

Další studie už vliv intenzity (Lifjeld & Slagsvold 1986, Jawor & Breitwisch 2006, Klatt et al. 2008) či přítomnosti (Lyon & Montgomerie 1985) inkubačního krmení na počet vylétlých mláďat či mláďat těsně před vylétnutím neprokázaly.

ZÁVĚR

Přestože prací zabývajících se významem inkubačního krmení u ptáků je celá řada, je patrné, že se svými výsledky liší, a to nejen mezi druhy, ale i v rámci jednotlivých druhů, případně i populací. Nejvíce prací se zabývalo vlivem inkubačního krmení na intenzitu inkubace, nejméně pak vztahem mezi intenzitou inkubačního krmení a kondicí samice a intenzitou inkubačního krmení a kvalitou teritoria. Z faktorů, které mají vliv na inkubační krmení, byla nalezena negativní korelace nejčastěji s teplotou vnějšího prostředí, a to u poloviny z šestnácti druhů a rizikem predace, s nímž negativně korelovala u všech pěti sledovaných druhů. Z faktorů, které jsou samy inkubačním krmením ovlivňovány, nejčastěji inkubační krmení pozitivně korelovalo s intenzitou inkubace, a to u osmi z dvaceti druhů. Toto zjištění je ve shodě s hypotézou samičí výživy. Studie nepodpořily hypotézu upevňování párů, jelikož ani jedna z prací nenašla vztah mezi intenzitou inkubačního krmení a pravděpodobností dalšího zahnízdění se stejným samcem. Stejně tak nebyla podpořena hypotéza samčí kvality, jelikož intenzita krmení během inkubace predikovala intenzitu krmení mláďat pouze v jedné z šesti studií. V tomto případě navíc v jiné populaci stejného druhu už tento vztah nalezen nebyl. Podobně nebyla podpořena ani hypotéza předčasného přinášení potravy, protože ani u jednoho druhu nepřinášeli samci krmení samici častěji ke konci inkubace, jak tato hypotéza předpovídá.

Zdá se proto, že nejpravděpodobnějším vysvětlením funkce inkubačního krmení je umožnění samici strávit více času na hnízdě. Bohužel většina studií, které byly zahrnuty do tohoto přehledu, jsou studie observační, tj. nezaložené na pokusech, a proto je obtížné z nich odvodit příčinné vztahy mezi jednotlivými prvky chování. Do budoucna by tak další studie zkoumající inkubační krmení u ptáků měly být zaměřeny na provádění experimentů, jako je manipulace velkosti snůšky, kondice samice, rizika predace či například kvality hnízdního teritoria, protože pouze experimentální studie jsou schopny odhalit příčinné vztahy mezi zkoumanými proměnnými.

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SUMMARY

In bird species where only the female incubates the eggs, the male often feeds his mate during incubation. Such behavior is call incubation feeding. Several hypotheses were proposed to

explain its function. The *Pair-bond maintenance hypothesis* claims that incubation feeding is just a symbolic act, which serves to strengthen the pair bond. A female fed frequently by her mate during incubation should preferentially pair with this particular male during the next breeding attempt. According to the *Female nutrition hypothesis* food received by the female from her mate during incubation contributes significantly to her energy budget. This allows her to spend more time on the nest incubating the eggs leading to higher nest attentiveness. As higher nest attentiveness can result in higher hatching success and/or a shorter incubation period, incubation feeding can have significant positive impact on the reproductive success of the breeding pair. This hypothesis is currently the most popular one and was tested most often. The *Male-quality hypothesis* considers incubation feeding to be an indicator of male quality. The male that feeds his mate frequently during incubation should be able or willing to provide superior parental care to his offspring later during the nestling period. The *Anticipatory-food bringing hypothesis* claims that food brought by the male is not intended primarily for the incubating female but is an inadvertent result of the male bringing food to the young that have not yet hatched.

I summarized all published studies dealing with the variation in the rate and functional significance of incubation feeding in birds. First, I focused on factors that influence the rate of incubation feeding. They included territory quality, female condition, male characteristics (biometric measurements, ornamentation and age), risk of nest depredation, ambient temperature, time of day, date, clutch size, and age of the clutch. From these factors, incubation feeding correlated most often negatively with ambient temperature and the risk of nest depredation. Second, I focused on factors that are themselves affected by the rate of incubation feeding. These included nest attentiveness, risk of nest depredation, female condition, the length of incubation period and reproductive success. Incubation feeding correlated most often positively with female nest attentiveness, which agrees with the *Female nutrition hypothesis.* The *Pair-bond maintenance* hypothesis was not supported by the studies, because none of them found any relationship between the rate of incubation feeding and divorce rate. Similarly, the *Male-quality hypothesis* was not supported, because the rate of incubation feeding predicted nestling feeding rate just in one of six studies. Moreover, in another population of the same species this relationship was absent. Since the rate of incubation feeding was not highest during the end of incubation period in any species, the *Anticipatory food-bringing hypothesis* was not supported as well. Thus, the most probable explanation of the function of incubation feeding seems to be to allow the female to spend more time on the nest. However, it is important to mention that most of the studies included in this review are correlational and thus it is difficult to infer causal relationships between individual behavioral, phenotypic, and environmental characteristics.

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Příspěvek II.

Matysioková B. & Remeš V.: Incubation feeding in Australian and New Zealand songbirds. Zasláno do recenzního řízení (*Emu*).

S inkubačním krmením se můžeme setkat například u australských modropláštníků. Na obrázku dva samci a samice modropláštníka korunkatého (*Malurus coronatus*). Kresba ©John Gould

Incubation feeding in Australian a New Zealand songbirds

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Abstract

Incubation behaviour is an important component of avian reproduction. At the same time, we know very little about incubation behaviour of tropical and southern hemisphere birds. Thus, we collated all available data on the rate of incubation feeding in Australian and New Zealand songbirds (25 species from 12 families). Mean incubation feeding rate was 1.93 per hour across all populations (n = 29). The rate of incubation feeding differed between families. The rate of incubation feeding across species was not related to body mass, did not differ between cooperative and pair-breeding species but was positively correlated with nest predation rate. Across populations, the intensity of incubation feeding changed neither with latitude nor temperature prevailing during incubation, although the negative correlation with temperature approached statistical significance. Incubation intensity of females correlated positively with the rate of incubation feeding by males among species. We compare our results with those found in North American songbirds.

Running head: Incubation feeding in songbirds

Introduction

Understanding why species differ in reproductive strategies is a major focus of life history studies (Roff 1992). One of the key phases of avian reproduction is incubation (Deeming 2002). As incubation behaviour is energetically demanding (Williams 1996; Thomson *et al.* 1998) it can negatively influence condition and/or survival of the incubating individual (de Heij 2006, and references therein). In bird species with uniparental incubation, it is in most cases the female who is responsible for incubating the eggs (Deeming 2002). Hence, she faces a trade-off between time- and energy-consuming incubation behaviour on the one side and foraging for self-maintenance on the other side (Drent 1975; Mertens 1977).

From this perspective, a behaviour whereby the male feeds the female during incubation, called incubation feeding (Lack 1941), might be critical for maintaining female condition and incubation effort at the same time (von Haartman 1952; Røskaft 1983; Lyon and Montgomerie 1985). Incubation feeding is quite widespread in birds (Kendeigh 1952), but species differ in its intensity (Martin and Ghalambor 1999). Understanding selective forces shaping the occurrence and intensity of incubation feeding across species has been hindered by paucity of data on incubation feeding and its correlates. There are just a few studies dealing with incubation feeding on the interspecific level. Moreover, all of them focused on North American songbirds (Martin and Ghalambor 1999; Conway and Martin 2000; Fontaine *et al.* 2007) with the exception of Auer *et al.* (2007) who studied birds of subtropical Argentina. Besides, only two of the studies dealt with actual rate of incubation feeding (Martin and Ghalambor 1999; Fontaine *et al.* 2007). Remaining studies used just presence or absence of incubation feeding (Auer *et al.* 2007) or categorized the relative frequency of incubation feeding according to qualitative descriptions gained from the literature (Conway and Martin 2000).

To advance our understanding of the incubation feeding in birds, we focused on much less studied southern hemisphere species of songbirds. We used all published information to obtain the rate of incubation feeding in Australian and New Zealand songbirds. Furthermore, we investigated correlates of incubation feeding among species. We focused on geographic latitude, ambient temperature, adult body mass, sociality and risk of nest depredation. We also investigated whether incubation feeding predicts female incubation effort across species. Finally, we compared our results with previous studies conducted on northern hemisphere species.

Materials and methods

Data collection

We collected data for this study from the literature. We started with Handbook of Australian, New Zealand, and Antarctic Birds (HANZAB) vols. 5, 6, and 7 (Higgins *et al.* 2001; Higgins and Peter 2002; Higgins *et al.* 2006). Here, we located all studies in which incubation feeding was mentioned and, whenever possible, obtained the primary source. To find articles that were published after HANZAB had been published, we also went through all the articles between 2000 and 2008 in Australian Bird Watcher, Australian Field Ornithology, Austral

Ecology, Australian Journal of Zoology, Australian Zoologist, Canberra Bird Notes, Corella, Emu, New Zealand Journal of Ecology, New Zealand Journal of Zoology, Notornis, Pacific Conservation Biology, South Australian Ornithologist, Sunbird, VOGR Notes, Western Australian Naturalist, and Wildlife Research. Here we located all the articles dealing with incubation feeding in songbirds.

Moreover, we did a comprehensive search on databases unrestricted by the year of publication. On Web of Science (available since 1945) and Zoological Record Plus (since 1978), we searched with the scientific name of every species. We went through all the titles and abstracts and in majority of them obtained the primary article. We left out only articles that were not about the breeding biology of a particular species, or which were done in captivity, e.g. many studies of the zebra finch (*Taeniopygia guttata*). On Google, we searched for the combination of the scientific name of the species and following terms: incubation feeding, courtship feeding, incubation behaviour, male feeds female, and breeding biology. We also searched on the web pages of Emu, Notornis, New Zealand Journal of Zoology, and New Zealand Journal of Ecology, i.e. all volumes of these journals. We used the scientific name of the species, and separately the above-mentioned search terms concerning breeding biology. Subsequently, we searched the text of thus obtained articles to locate information on incubation feeding. All these searches were done from October 2008 to January 2009.

Original studies often provided only qualitative, verbal description of the intensity of incubation feeding rather than precise figures. This classification seemed to us to be subjective and not comparable across studies; thus we included only species with exact quantitative information available (i.e., the number of feedings per hour). To be able to meaningfully compare across species, we included only species with female-only incubation. As most studies provided only information on the rate of incubation feeding performed on the nest, we used this rate in all our analyses. Thus we excluded six studies where we could not distinguish between on- vs. off-nest incubation feeding. We also excluded three studies where we were not able to distinguish between the feeding having occurred before the incubation began and that occurring during incubation.

We extracted from all the studies information about the location of study site, and year(s) and months of the study. We used the information on the study site to find out the geographic latitude where the study was done using Google Earth. The year(s) and months of the study were used to find out the ambient temperature during the time when the rate of incubation feeding was quantified. Temperature information was extracted from the databases of the Australian Bureau of Meteorology for Australian study sites and the National Institute of Water and Atmospheric Research for New Zealand study sites. We obtained mean monthly temperature as the average of mean monthly minimum and maximum temperatures, which were available from the respective agencies. If the particular study covered a longer period of time than the incubation phase, we used just the months when the birds incubated to obtain temperature during incubation. We obtained data on nest attentiveness and nest losses caused by nest predators by a comprehensive literature search similar to that used for incubation feeding (B. Matysioková and V. Remeš, unpubl. data). Nest attentiveness was defined as percentage of daytime female spent by incubating the eggs. We transformed data on predator-caused nest losses to daily predation rates by the method of Ricklefs (1969). For this transformation, the length of the nest cycle was calculated as the sum of clutch size, incubation period, and nestling period of every species. For each species on our list, we obtained information on adult body mass (g) (Higgins *et al.* 2001; Higgins and Peter 2002; Higgins *et al.* 2006) and social organisation (cooperative vs. pair-breeding, Cockburn 2006).

Data analysis

The primary aim of this study was to collate all available information on the rate of incubation feeding in Australian and New Zealand songbirds. However, we also performed some simple correlational analyses to infer possible factors responsible for the variation in the intensity of incubation feeding. We included factors that had been previously shown to be important (e.g. Conway and Martin 2000) or could be reasonably expected to be important based on the current understanding of the incubation behaviour in birds (reviewed in Deeming 2002). The factors included into the analyses are apparent from Tables 1 and 2. We conducted two types of analyses. First, in traits that do not vary among populations within species (social organisation) or in which we had data from populations different from those used to obtain incubation feeding rate (body mass and predation rate), we fitted models with the average incubation feeding rate for individual species. Second, in traits for which we had data from the same populations from which we obtained also data on incubation feeding (latitude and temperature), we fitted models based on these population-specific values. For both types of analyses (i.e., across species and across populations), we fitted both univariate and multivariate models. In all the analyses body mass was $\log_{10}$ transformed, incubation feeding rate was square root transformed, and latitude was raised to the power of two. As our analyses were exploratory, we did not attempt to control for phylogenetic relationships among species. However, in population-level analyses, we adjusted for multiple observations for the same species by treating species as a random factor in linear mixed models.

Results

Altogether, we collected data on the rate of incubation feeding performed on the nest from 29 different populations of 25 species of Australian and New Zealand songbirds coming from 12 families. We were able to find geographic latitude and temperature during incubation in 27 of these populations. From the 25 species, 11 were cooperative. We obtained data on nest predation rate for 16 species and on nest attentiveness for 21 species. Seven of the 12 families included just one species (Maluridae, Neosittidae, Pomatostomidae, Pachycephalidae, Callaeidae, Sylviidae, Muscicapidae), two families two species (Meliphagidae and Artamidae), one family three species (Climacteriidae), one four (Corvidae) and one family seven species (Petroicidae).

Incubation feeding rate ranged from 0.07 to 6.30 feedings per hour (mean = 1.93, sd = 1.47, median = 1.70, n = 29) across populations and from 0.07 to 5.21 (mean = 1.78, sd = 1.26, median = 1.63, n = 25) across species (i.e. averages for individual species weighed by sample size). Families significantly differed in the average species-specific incubation feeding rate ($F_{11,13} = 2.82$, $P = 0.039$, $n = 25$). Nest attentiveness ranged from 52.0 to 95.7 % (mean = 73.1, sd = 11.4, median = 74.3, $n = 21$).

In univariate analyses conducted on species averages, incubation feeding rate did not differ between cooperative and pair-breeding species. It did not correlate with body mass but was positively correlated with nest predation rate (Table 1, Fig. 1). Across populations, the intensity of incubation feeding changed neither with latitude nor temperature during incubation (Table 1).

In multivariate analyses conducted on species averages, incubation feeding rate again did not differ between cooperative and pair-breeding species. It was not related to body mass but was positively correlated with nest predation rate (Table 2). Across populations, the intensity of incubation feeding was related neither to latitude nor temperature during incubation, although the correlation with temperature approached statistical significance (Table 2). In all three population-level analyses, species as a random factor explained substantial proportion of variation (from 31.5 to 40.5 %, Tables 1 and 2).

Nest attentiveness correlated positively with adult body mass ($F_{2,18} = 7.73$, $P = 0.012$) and the rate of incubation feeding performed on the nest ($F_{2,18} = 4.60$, $P = 0.046$; whole model $R^2 = 0.37$, Fig. 2).

Discussion

In general, rates of male incubation feeding found in Australian and New Zealand songbirds were similar to those recorded in songbirds in North America, which averaged ca 1.44 per hour (19 species; Martin and Ghalambor 1999). They were higher in species suffering from increased risk of nest depredation. An increase of daily nest predation rate by 1 % was coupled with an increase of incubation feeding rate by ca 0.9 per hour. This finding is quite surprising. Higher incubation feeding rate results in comparatively higher activity around the nest. Therefore, we expected to find lower rate of incubation feeding in species suffering from higher risk of nest depredation, similarly as was found in North American songbirds (Martin and Ghalambor 1999; Fontaine *et al.* 2007), although the evidence is not unequivocal (Conway and Martin 2000).

A possible explanation is that higher incubation feeding rates correlate with higher nest attentiveness both within (Tewskubry *et al.* 2002; Lloyd *et al.* 2009) and among species (Martin and Ghalambor 1999; Fontaine *et al.* 2007; this study). An increase in nest attentiveness can subsequently lead to shorter incubation periods, which was again demonstrated both within (Haftorn 1983; Lyon and Montgomerie 1985) and among species (Martin 2002; Martin *et al.* 2007). Decreasing the length of the development period in the nest, which is typically the period of high offspring mortality (Roff *et al.* 2005), is an effective way to increase fitness (Lack 1968; Remeš and Martin 2002). Hence, selection can favour an increase in nest attentiveness and consequently in the rate of incubation feeding in species suffering from higher risk of nest depredation (Fontaine and Martin 2006). The difference between our results and patterns observed in North American songbirds may be caused by different predator-prey interactions. In our system, benefits of faster development might have outweighed costs of higher activity around the nest, whereas in North American songbirds benefits of low activity around the nest might be more important than benefits of faster development. Relative importance of these different costs and benefits will depend primarily on nest searching strategies of principal predators.

It is difficult to infer a cause and effect from comparative data alone. Thus, we do not know whether high incubation feeding is a cause or a consequence of high nest depredation risk. Traditionally, it has been assumed that high activity around the nest leads to high nest depredation risk within species and that this translates into a negative relationship between nest depredation risk and activity around the nest on the interspecific level (Martin *et al.* 2000). Contrary to this expectation, we found out a positive relationship between nest depredation risk and activity around the nest (i.e., on-nest incubation feeding rate) among species. We suggest that the above-mentioned model is valid for nestling feeding rates, where activity around the nest (i.e., nestling feeding rates) is generally much higher than during incubation (East 1981; Hofstad *et al.* 2002; Barg *et al.* 2006). Then, parental activity during nestling feeding might be a very important source of nest disclosure to potential predators. On the contrary, during incubation nests might be located by predators more at random, independently of relatively low parental activity on the nest. Consequently, it would be possible to increase incubation feeding rates with the benefit of increasing nest attentiveness and consequently shortening the development time without bearing the cost of nest disclosure.

We found a marginally non-significant negative relationship between incubation feeding rate and ambient temperature during incubation. An increase of ambient temperature by 10°C was coupled with a decrease of incubation feeding rate by ca 2.2 per hour. This negative relationship is typically found on the intraspecific level (Nilsson and Smith 1988; Pearse *et al.* 2004; Matysioková and Remeš 2010). Energetic expenditure of the incubating female increases with declining temperature (Biebach 1981; Haftorn and Reinertsen 1985; de Heij *et al.* 2008). Therefore it is not surprising that we found similar (though marginally non-significant) pattern on the interspecific level. In a large dataset of North American passerine species, Conway and Martin (2000) did not find any relationship between ambient temperature and male incubation feeding. However, they did not use the frequency of incubation feeding in the analyses, but instead used only qualitative descriptions. Similarly, they did not use actual ambient temperature from the same sites and time as the description of incubation feeding came from, but used the average temperature prevailing typically within the breeding range of the species during the breeding season (Conway and Martin 2000). This indirect estimation of both incubation feeding intensity and temperature might have obscured possible patterns in the data.

Annual reproductive effort typically declines with increasing adult survival rate (Roff 1992). This may be the cause of lower reproductive effort in the tropics and southern latitudes where adult mortality rate is generally lower compared to northern latitudes (Rowley and Russell 1991; Ghalambor and Martin 2001; Sanz 2001). Hence, we predicted that the rate of incubation feeding (a component of reproductive effort) would be increasing from the equator towards more temperate, southern latitudes. There was no such pattern in our data, suggesting that our sample size was probably too small to reveal such a pattern. Alternatively, southern latitudes experience typically milder climate compared to northern latitudes, and life-histories of southern birds are more similar to the tropical birds than to northern birds living at the same latitudes (Cody 1966; Russell *et al.* 2004). Thus, the gradient of environment and adult mortality rates from the equator to the south (ultimately to southern New Zealand) might have been too weak to generate a pattern in incubation feeding rate.

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Figure captions

Fig. 1. Relationship of the rate of incubation feeding to daily nest predation rate across species (n = 16).

Fig. 2. Relationship of nest attentiveness to the rate of incubation feeding across species (n = 21).

Table 1. Univariate analyses relating incubation feeding rate to individual environmental factors and covariates both across species and across populations. P-values of statistically significant factors are in bold.

Factor	Estimate (*SE*)	*DF*	*F*	*P*
Species-level				
Body mass	-0.04 (0.29)	1, 24	0.80	0.804
Sociality (pair)	cooperation: -0.01 (0.10)	1, 24	0.02	0.890
Nest predation	30.23 (11.56)	1, 15	6.84	**0.020**
Population-level				
Latitude	-0.0003 (0.0003)	1, 24.4	0.96	0.338
Species variance component	0.11 (0.13)			
Residual variance component	0.17 (0.12)			
Temperature	-0.05 (0.04)	1, 24.2	1.60	0.218
Species variance component	0.08 (0.13)			
Residual variance component	0.18 (0.13)			

Table 2. Multivariate analyses relating incubation feeding rate simultaneously to several environmental factors and covariates both across species and across populations. P-values of statistically significant factors are in bold.

Factor	Estimate (*SE*)	*DF*	*F*	*P*
Species-level				
Body mass	0.18 (0.36)	3, 12	0.24	0.630
Sociality (pair)	cooperation: 0.08 (0.15)	3, 12	0.31	0.586
Nest predation	35.00 (14.54)	3, 12	5.79	**0.033**
Population-level				
Latitude	-0.0006 (0.0004)	1, 22.4	2.81	0.107
Temperature	-0.08 (0.04)	1, 21.9	3.46	0.077
Species variance component	0.08 (0.15)			
Residual variance component	0.17 (0.14)			

Fig. 1

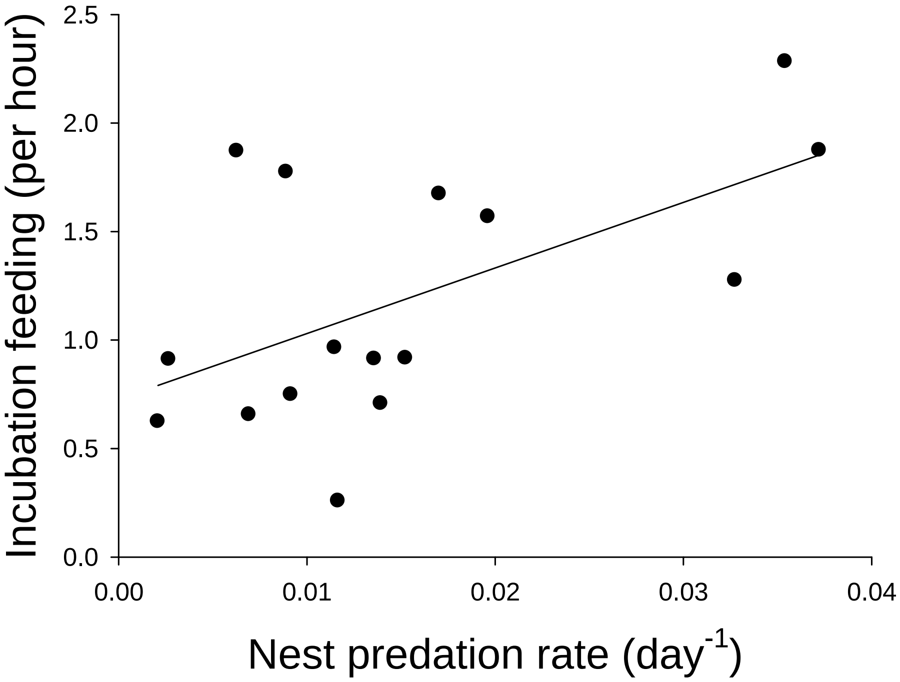
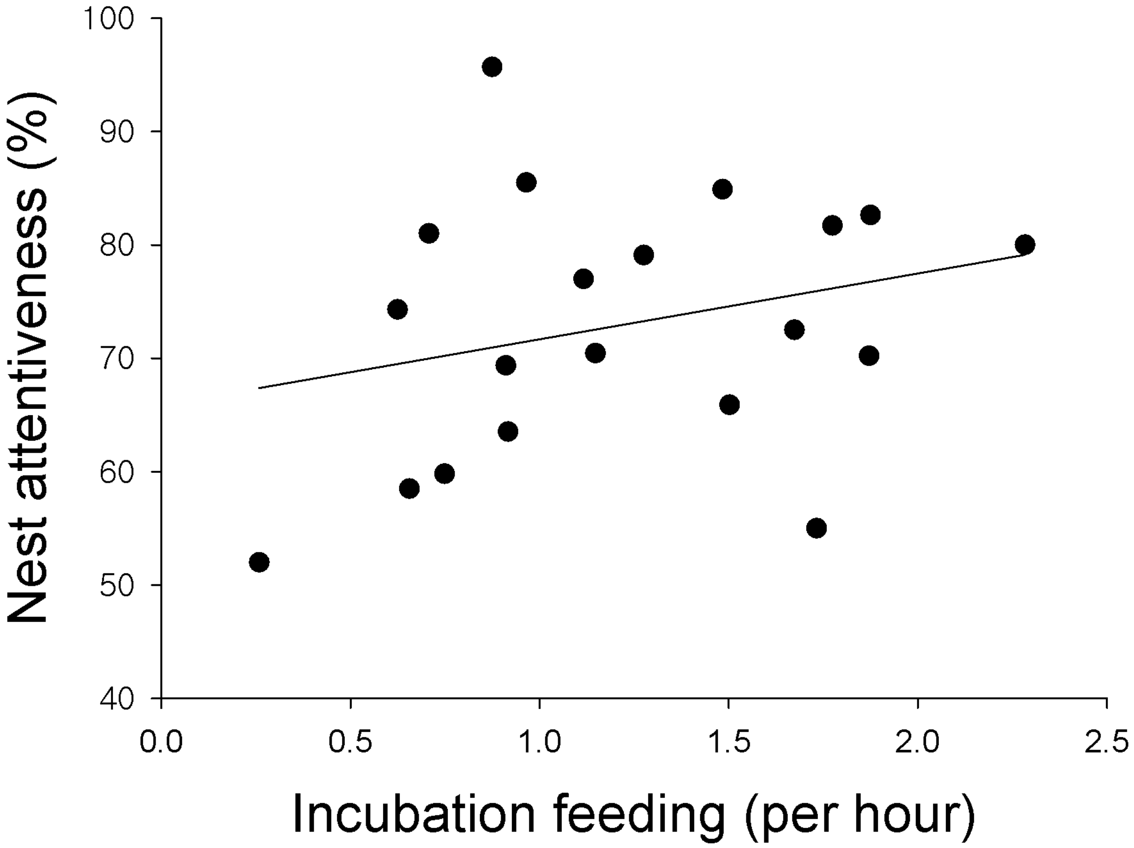

Incubation feeding (per hour)
2.5
2.0
1.5
1.0
0.5
0.0
0.00
0.01
0.02
0.03
0.04
Nest predation rate (day^{-1})

Fig. 2


100
90
80
70
60
50
40
Nest attentiveness (%)
0.0
0.5
1.0
1.5
2.0
2.5
Incubation feeding (per hour)

Příspěvek III.

Matysioková B. & Remeš V. 2010: Incubation feeding and nest attentiveness in a socially monogamous songbird: role of feather colouration, territory quality and ambient environment. *Ethology* 116: 596–607.

Melaninový ornament (černá náprsenka) u sýkory koňadry (*Parus major*). Z rozsahu černé barvy sahající v tomto případě až ke spodním krovkám ocasním je patrné, že se jedná o samce. Foto ©Vladimír Remeš

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Incubation Feeding and Nest Attentiveness in a Socially Monogamous Songbird: Role of Feather Colouration, Territory Quality and Ambient Environment

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Abstract

Parental investment and environmental conditions determine reproductive success in wild-ranging animals. Parental effort during incubation, and consequently factors driving it, has profound consequences for reproductive success in birds. The female nutrition hypothesis states that high male feeding enables the incubating female to spend more time on eggs, which can lead to higher hatching success. Moreover, both male and female parental investment during incubation might be signalled by plumage colouration. To test these hypotheses, we investigated relationships between male and female incubation behaviour and carotenoid and melanin-based plumage colouration, territory quality and ambient temperature in the Great Tit *Parus major*. We also studied the effect of female incubation behaviour on hatching success. Intensity of male incubation feeding increased with lower temperatures and was higher in territories with more food supply, but only in poor years with low overall food supply. Female nest attentiveness increased with lower temperatures. Plumage colouration did not predict incubation behaviour of either parent. Thus, incubation behaviour of both parents was related mainly to environmental conditions. Moreover, there was no relationship between male incubation feeding, female nest attentiveness and hatching success. Consequently, our data were not consistent with the female nutrition hypothesis.

Introduction

Parental investment and environmental conditions during reproduction are key determinants of reproductive output in free-ranging animals. Incubation is one of the key processes in avian reproduction (White & Kinney 1974; Deeming 2002a). Some form of incubation behaviour is present in 99% of all bird species. In species with uniparental incubation, which is usually done by females (Skutch 1957), the incubating individual has reduced time for foraging and self-maintenance (Drent 1975). As incubation is energetically demanding (Williams 1996; Thomson et al. 1998; Tinbergen & Williams 2002), this can have negative effects on body condition of the incubating parent, subsequent care during the same or next breeding attempt, or survival to the next breeding season (Heinsohn & Cockburn 1994; Heaney & Monaghan 1996; Reid et al. 2000; Visser & Lessells 2001; de Heij et al. 2006).

In many species in which the male does not participate directly in warming the eggs, he feeds the incubating female. This behaviour is called incubation feeding (Lack 1940; Kendeigh 1952). In hornbills, some raptors and some songbirds, the incubating female is completely dependent on incubation feeding (Kendeigh 1952; Poulsen 1970; Verbeek 1972). However, in the majority of species males provide only a certain part of the daily food intake of incubating females (Davies 1977). The intensity of incubation feeding differs both within and among species (Kendeigh 1952; Conway & Martin 2000), and can be influenced by various factors. Its intensity was found to increase with decreasing ambient temperature (Nilsson & Smith 1988; Smith et al. 1989; Pearse et al. 2004), higher male quality (Lifjeld et al. 1987; Siefferman & Hill 2005), or higher food supply on territory (Zanette et al. 2000). Currently, the most popular hypothesis to explain the occurrence and patterns of incubation feeding is the female nutrition hypothesis (von Haartman 1958; Royama 1966). It claims that incubation feeding is an important source of energy for the incubating female. Consequently, male provides female with an important part of her daily energy intake, that allows her to spend more time on eggs, i.e. to increase her nest attentiveness (Martin & Ghalambor 1999; Tewksbury et al. 2002).

As higher nest attentiveness can lead to higher hatching success (Lyon & Montgomerie 1985; Webb 1987), incubation feeding can significantly affect reproductive performance of birds. However, nest attentiveness can be influenced by other factors in addition to incubation feeding. Females increase nest attentiveness in cold temperatures to keep eggs within temperature limits necessary for successful development of the embryo (Yom-Tov et al. 1978; Webb 1987; Sanz 1997). High-quality territories with superior food supply enable females to spend more time on eggs (Rauter & Reyer 1997; Zanette et al. 2000; Zimmerling & Ankney 2005). Apart from environmental conditions, higher quality females also spend more time on eggs (Ardia & Clotfelter 2007), which is also evidenced by a positive relationship between clutch size and nest attentiveness found in some species of birds (Blagosklonov 1977; Jones 1987; Deeming 2002b).

Individual quality and ability to provide parental care and invest in a given breeding attempt can be signalled by plumage colouration (Hill & McGraw 2006). Carotenoid-based feather colouration is widespread in birds (Olson & Owens 2005). Carotenoids cannot be synthesized by birds, and thus their concentration in feathers is dependent on both food availability and foraging efficiency (McGraw 2006a). Moreover, when deposited into feathers they cannot be used for important physiological functions, including immunological defence or mitigating oxidative stress. Consequently, carotenoids allocated to feathers should indicate individual quality and/or condition (Møller et al. 2000). Although melanin ornaments are often claimed not to reflect condition (McGraw 2006b), recent evidence suggests that in certain conditions they might be as condition-dependent as carotenoid-based ornaments (Griffith et al. 2006). Potential proximate mechanisms of condition-dependence might include corticosterone-mediated stress (Roulin et al. 2008), oxidative stress (Galván & Alonso-Alvarez 2008, 2009), allocation of calcium among competing physiological functions (Roulin et al. 2006) or hormonal control of melanin deposition (McGraw 2008). Thus, both types of plumage colouration can be important in signalling capability of parental investment.

In our study, we examined male and female incubation behaviour in the Great Tit *Parus major*, a typical socially monogamous passerine with female-only incubation. Our aims were to find out: (1) which factors affect the intensity of male incubation behaviour, i.e. incubation feeding, (2) what is the effect of incubation feeding and other factors on female incubation behaviour, i.e. nest attentiveness, (3) what is the effect of nest attentiveness on hatching success, and (4) whether carotenoid- and melanin-based plumage colouration predicts parental effort during incubation in both males and females. Based on the predictions of the female nutrition hypothesis, we expected to find a positive relationship between incubation feeding and nest attentiveness; we also expected a positive relationship between nest attentiveness and hatching success. We expected that parental effort will be positively related to the intensity of both carotenoid- and melanin-based plumage colourations.

Methods

General Fieldwork

This work was conducted on three adjacent nest-box plots (188 nest-boxes in total), in a deciduous forest near Grygov (49°31′N, 17°19′E) in eastern Czech Republic. The forest is dominated by lime *Tilia* spp. and oak *Quercus* spp. with interspersed ash *Fraxinus excelsior*, hornbeam *Carpinus betulus*, and alder *Alnus glutinosa*. Nest boxes are placed about 1.5 m above ground and besides Great Tit are inhabited by Blue Tit *Cyanistes caeruleus*, Collared Flycatcher *Ficedula albicollis*, and Nuthatch *Sitta europea*. Fieldwork was carried out between 2005 and 2007 from early Apr. until mid-Jun. We checked nest-boxes daily to record the laying of the first egg and final clutch size. Later, we checked which eggs hatched to determine the hatching success. We defined hatching success as the percentage of eggs that hatched. We used only nests where we knew the exact fate of all the eggs.

Incubation Behaviour

During incubation, we monitored nest attentiveness of females and incubation feeding by males. We obtained one sample from each nest. To determine nest attentiveness, we deployed temperature data loggers (Hobo H8 Temp/External; Onset Computer Corp., Pocasset, MA, USA), by putting their first probe (1.8 m cable) through the nest wall into the bottom of the nest cup. The data logger itself with the second, inner probe was mounted under the nest-box. These probes measured inner and outer temperature at every nest from 06.00 until 12.00 hours (i.e. for 6 h) in 9-s intervals. This interval is the shortest possible to enable the coverage of 6 h of recording with respect to the memory capacity of our data loggers. To determine incubation feeding, we placed video cameras about 5 m in front of the nest-box on the ground and recorded bird activity for 90 min. This is a standard recording period in studies of incubation feeding in songbirds (e.g. Zanette et al. 2000; Badyaev & Hill 2002; Doerr & Doerr 2007). We deployed cameras in the morning, between 07.30 and 12.00 hours. We took ambient temperature during incubation feeding from a local meteorological station. Both data loggers and cameras were deployed early in the incubation period. Median was day 4 (range 1–8) for data loggers and day 3 (1–9) for cameras, where day 0 means the day when the last egg was laid. Female Great Tits were in full incubation already on day 1, as evidenced by no significant effect of the day of incubation on nest attentiveness (see Results). In 80 nests, cameras were deployed on the same morning when data loggers were recording temperature. Setting cameras took very short time (<1 min). However, to check for potential disturbance, we compared nest attentiveness for nests, where cameras and data loggers were recording on the same morning vs. on different days; there was no difference ($F_{1,159} = 0.02$; $p = 0.900$) excluding any potential systematic bias in the data.

On the nest temperature recordings, time when the incubating female is away from the nest, is recognisable by downward spikes (Fig. 1). Temperature drops quickly when the female leaves the clutch (off-bout) and then starts to increase sharply when she returns (on-bout). Consequently, it is easy to make the difference between an attended and an empty nest (Zimmerling & Ankney 2005). From the pattern of nest temperatures, we calculated nest attentiveness during the 6 morning hours. It was calculated as time (in seconds) the female was inferred to be on the eggs divided by total monitoring time and expressed in percents. To evaluate reliability of temperature data loggers in monitoring nest attentiveness, we calculated the number of minutes on the temperature recording that was wrongly identified as either on-bout or off-bout by direct comparison with video tapes taken at the same time. Only 3.3% of 7 200 minutes were misidentified (n = 80 nests). To get ambient temperature for every nest, we took outer temperature for the start of each on- and off-bout and averaged it across the 6 h of monitoring.

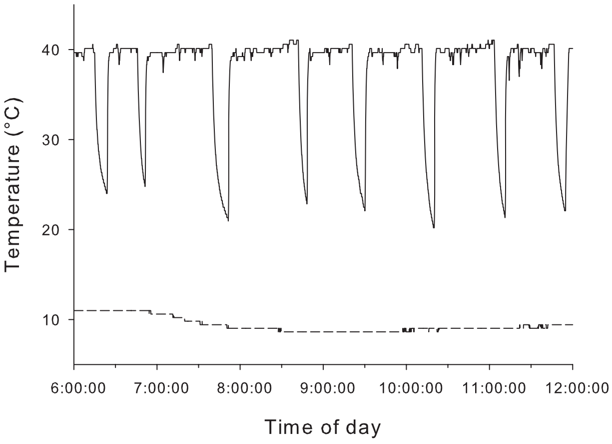

Fig. 1: Graph of a typical incubation profile of the Great Tit (temperature in the nest cup: full line, ambient temperature: dashed line).

Adults

During feeding of nestlings (median age of young for females = 7 days, for males = 9 days), we captured parents in the nest-box. We captured females on almost all the nests (n = 165). However, because of time constraints, we captured males only on a subset of nests (n = 109). We took from 10 to 15 yellow feathers from the upper right part of breast for later spectrophotometric analysis. We photographed the breast by a digital camera (Panasonic DMC-FZ5). When taking the picture of the breast, we held the bird outstretched by its tarsi and beak; we photographed it form a standard distance fixed by a tripode, together with a standard following procedures given by Figuerola & Senar (2000). All these measurements and photographs were taken by VR. We also determined the age of birds based on their plumage as 1 yr old or older (Svensson 1992).

Territory Quality

We characterized territory quality by assessing food supply during incubation of every pair in the vicinity of its nest-box. As the main food consumed by Great Tit during incubation, which takes place in our population mostly in early May, is caterpillars (Betts 1955), we characterized food supply as the amount of caterpillars on trees within the territory. We determined (1) relative food supply on each of the five most numerous tree species by the frass fall method (Zandt 1994) and (2) counted all trees with a diameter above 10 cm at breast height in a circle with 20-m radius around every occupied nest-box. We put three plates (0.15 m^2) around an occupied box during incubation under randomly chosen trees, always ca. 5 m from the box in three equidistant directions. We collected fallen frass after 48 h into small plastic bags that were sealed and stored in a cold place. After the field season, we let the contents dry overnight under room temperature and humidity, removed large debris and weighed the rest to the nearest 0.0001 g.

We analysed the amount of frass fallen on the plate in relation to tree species and controlled for canopy height (three categories: low, medium, high), year and date. There was a significant effect of tree species ($F_{4,170} = 11.7$, $p < 0.001$, $n = 179$). Least squares means for the five tree species were 0.075 for oak, 0.060 for hornbeam, 0.031 for lime, 0.026 for alder, and 0.016 for ash (in g/48 h/0.15 m^2). We recalculated these means so that ash, species with the least frass, had coefficient of 1. Other species had accordingly higher coefficients: 4.6 for oak, 3.7 for hornbeam, 1.9 for lime and 1.6 for alder. Thus, for example one oak was equivalent to 4.6 individuals of ash, because our data indicated that it had 4.6 times more caterpillars as compared to ash, when controlled for possible confounding effects of sampling. Our results concerning relative food supply on different species of trees agree with previous analyses (Keller & van Noordwijk 1994; Naef-Daenzer 2000). To determine territory quality, we summed the number of trees within 20-m radius around the nest multiplied by their respective coefficients. Tit parents do not limit their foraging exclusively to 20 m around their nest. The distance where the great majority of their foraging takes place is given in literature, variously as within 25 m (Naef-Daenzer 2000), 30 m (Smith & Sweatman 1974) or 45 m from the nest (Naef–Daenzer & Keller 1999) in similar habitats to ours. These figures come from studies done during feeding of the young; comparable figures for the incubation period are currently lacking. The radius of 20 m was chosen as a compromise between biological plausibility and the workload of counting trees.

Analyses of Samples

We measured the area of the black breast stripe from photos in Adobe Photoshop CS3 Extended. We used the quick selection tool to roughly delimit the breast stripe. Then, we manually finished the selection so that it was as precise as possible and measured its area. We used a ruler photographed together with every bird to adjust the scale of each photo and to obtain absolute area (in cm^2). We defined stripe area as the area of the black band between the point of inflexion, where the ventral stripe widens to a throat patch, and the posterior end of the stripe (Figuerola & Senar 2000). All measurements were taken by BM. To assess repeatability, a different observer measured a subsample of photos. Repeatability, calculated as an intraclass correlation coefficient (Lessels & Boag 1987), was high ($r_i = 0.87$, $p < 0.001$, $n = 75$).

According to standard procedures (Andersson & Prager 2006), we quantified reflectance spectra of yellow feathers sampled from the breast. We used 10–15 feathers from each bird, which is enough to obtain reliable values in Great Tit (Quesada & Senar 2006). We used Avantes AvaSpec-2048 fiber optic spectrometer (Avantes BV, Eerbeek, The Netherlands) together with AvaLight-XE xenon pulsed light source and WS-2 white reference tile. The probe was used both to provide light and to sample reflected light stream, and was held perpendicular to feather surface. We took five readings, each from different part of each set of feathers. Feathers were arranged on black, non-reflective surface so that they overlapped extensively.

We needed a spectrophotometric measure of the amount of carotenoids in the breast feathers. Senar et al. (2008) showed that hue, measured by a Minolta colorimeter (Minolta CR200 colorimeter; Konica Minolta, Tokyo, Japan), correlated with lutein content of breast feathers in the Great Tit. Similarly, Isaksson & Andersson (2008) and Isaksson et al. (2008) showed that so called carotenoid chroma correlated positively with feather carotenoids in the Great Tit. Carotenoids present in Great Tit breast feathers (lutein, zeaxanthin) absorb the most at around 450 nm, and theoretical modelling also showed that carotenoid chroma directly reflects the amount of carotenoids in feathers (Andersson & Prager 2006). As we used a spectrophotometric approach equal to that of Isaksson & Andersson (2008) and Isaksson et al. (2008), and as the hue calculated from spectrophotometric measurement of feathers does not correlate with the amount of carotenoids in feathers (Isaksson et al. 2008), we use here carotenoid chroma. We obtained reflectance (in %) from the wavelength of 320–700 nm in 1-nm increments. We calculated carotenoid chroma as $(R_{700}–R_{450})/R_{700}$, where R_{700} is reflectance at 700 nm and R_{450} reflectance at 450 nm. In statistical analyses, we used the average carotenoid chroma calculated from the five readings from each set of feathers. To assess the repeatability of our measurements, in a subsample of feathers, we arranged feathers anew and took another five readings and again averaged the carotenoid chroma calculated from them. We calculated repeatability of these two average carotenoid chroma estimates, calculated as intraclass correlation coefficient (Lessels & Boag 1987), which was high ($r_i = 0.85$, $p < 0.001$, n = 55).

Statistical Analyses

Due to the fidelity of birds to their breeding grounds, some females were sampled in more than 1 yr (22 females two times, 4 females three times, n = 143). Thus, we adjusted for this by fitting female identity as a random effect in mixed models for repeated measurements. In contrast, only three males were sampled two times (n = 93). As their treatment as repeated measurements would lead to strongly unbalanced data, we instead excluded at random one observation for each of these three males.

We used general linear mixed models to explain variation in female nest attentiveness (Proc Mixed of SAS 9.1, SAS Institute Inc., Cary, NC, USA). We used generalized linear mixed models with binomial distribution and logit link function for hatching success (Proc Glimmix of SAS 9.1), which was coded as number of eggs hatched/clutch size. Finally, we used generalized linear models with Poisson distribution and log link function for male incubation feeding (the response variable was no. of feedings per 90 min, Proc Genmod of SAS 9.1). These models fit the data well and the overdispersion of data in generalized linear models was reasonable (deviance/df = 1.3 for hatching success and 1.9 for incubation feeding). Chi-square values from the models of incubation feeding are likelihood ratio test statistics for type 3 tests.

To keep the number of predictors low, we included only predictors that have been previously shown to affect our dependent variables. We always started with a set of variables that were either factors of interest (feather colouration and age of adults, nest attentiveness, incubation feeding), characteristics of the environment (laying date, ambient temperature, territory quality) or covariates (year, clutch size, age of clutch, time of day). In the analyses of

Table 1: Results of a generalised linear model explaining male incubation feeding (n = 90)

	Incubation feeding			
Factor	χ^2	df	p	Estimate (SE)
Intercept				4.44 (0.941)
Year	11.06	2, 81	0.004	0.38 (0.688): 2005 2.42 (0.744): 2006
Clutch size	2.03	1, 80	0.154	+
Laying date	1.63	1, 79	0.202	+
Age of clutch	4.1	1, 81	**0.043**	−0.22 (0.115)
Time of day	20.78	1, 81	**<0.001**	−0.38 (0.088)
Ambient temperature	6.35	1, 81	**0.012**	−0.07 (0.029)
Territory quality	0.29	1, 81	0.592	0.01 (0.002)
Male age	<0.01	1, 76	0.989	1 yr old > older
Male stripe area	0.66	1, 78	0.418	−
Male carotenoid chroma	0.38	1, 77	0.539	+
Territory quality × year	7.69	1, 81	**0.021**	0.002 (0.0053): 2005 −0.014 (0.0057): 2006
Territory quality × male stripe area	0.70	1, 74	0.404	
Territory quality × male carotenoid chroma	2.21	1, 75	0.137	

p-values of the final model are in bold. Sign (+ or −) or text in Estimate show the direction of the non-significant effects; exact parameter estimates are listed only for variables retained in the final model.

Table 2: Results of a general linear mixed model explaining female nest attentiveness (n = 143)

	Nest attentiveness			
Factor	*F*	df	p	Estimate (SE)
Intercept				0.76 (0.034)
Year	2.20	2, 137	0.114	2007 > 2005 > 2006
Clutch size	6.76	1, 140	**0.010**	0.01 (0.003)
Laying date	1.37	1, 139	0.244	+
Age of clutch	0.04	1, 131	0.852	+
Ambient temperature	38.04	1, 140	**<0.001**	−0.01 (0.001)
Territory quality	1.83	1, 135	0.179	−
Female age	0.26	1, 134	0.608	1 yr old > older
Female stripe area	2.07	1, 136	0.153	−
Female carotenoid chroma	0.13	1, 132	0.720	−
Male incubation feeding	0.14	1, 133	0.710	−
Territory quality × year	0.18	2, 125	0.832	
Territory quality × female stripe area	1.00	1, 130	0.320	
Territory quality × female carotenoid chroma	0.02	1, 124	0.900	
Territory quality × male incubation feeding	0.12	1, 129	0.730	
Male incubation feeding × year	0.48	2, 127	0.618	

p-values of the final model are in bold. Sign (+ or −) or text in Estimate show the direction of the non-significant effects; exact parameter estimates are listed only for variables retained in the final model.

male incubation feeding, we fitted interactions of territory quality with year, male breast stripe area and male breast carotenoid chroma (Table 1). In the analyses of female nest attentiveness, we also fitted interactions of territory quality with year, female breast stripe area, female breast carotenoid chroma and male incubation feeding, and the interaction of male incubation feeding with year (Table 2). We included these interactions because we wanted to know whether effects of territory quality and male incubation feeding differ with year, and whether the effects of male and female colouration and male incubation feeding depend on territory quality. Variables included into models differed according to the dependent variable and are apparent from Tables 1–3. We did not include male incubation feeding as a predictor in the analysis of hatching success, because the only way incubation feeding could affect hatching success is through nest attentiveness. We also did not include male plumage colouration as a predictor in the analysis of female nest attentiveness, because we did not want to test hypotheses on differential allocation or compensation. Male plumage colouration was not likely to bias the results obtained on the effects of female colouration on nest attentiveness, because there was no assortative pairing in relation to colouration in our population (correlation between mates: carotenoid chroma $r = -0.15$, p = 0.121, n = 104; breast stripe size $r = 0.07$, p = 0.487, n = 104). We subsequently removed one by one the least significant factors until we ended with only statistically significant variables of the final model (Grafen & Hails 2002). In tables, we give *F*, χ^2, df and p-values of non-significant predictors, immediately before they were removed from the model. Residuals were always checked to conform to the requirements of a particular model. Denominator df were estimated by Satterthwaite method.

Table 3: Results of a generalised linear mixed model explaining hatching success (n = 119)

	Hatching success			
Factor	*F*	df	p	Estimate (SE)
Intercept				0.21 (1.167)
Year	0.15	2, 110	0.860	2005 > 2006 > 2007
Clutch size	4.98	1, 117	**0.028**	0.27 (0.121)
Laying date	0.01	1, 112	0.927	+
Female age	0.58	1, 116	0.446	1 yr old > older
Female stripe area	0.10	1, 114	0.751	+
Female carotenoid chroma	0.12	1, 113	0.729	−
Nest attentiveness	0.25	1, 115	0.619	+

p-values of the final model are in bold. Sign (+ or −) or text in Estimate show the direction of the non-significant effects; exact parameter estimates are listed only for variables retained in the final model.

Ethical Note

We used standard methods in capturing and handling birds used in the research of cavity-nesting passerines. We captured adults in the nest-box. We handled them for as short time as possible to minimize any distress. We plucked the smallest number of feathers possible to obtain reliable results based on a previous methodological study (Quesada & Senar 2006). Our temperature probes had no adverse effects on birds.

This study complies with the current law of the Czech Republic. We had all necessary permits for this study and it was overseen by the Ethical Committee of Palacky University.

Results

Altogether we had 176 active nests over the 3 yr. However, we did not obtain all measurements for all the nests and thus, sample sizes for individual analyses differ. Clutch size was 10.6 ± 1.34 eggs (mean ± SD, range 7–16, n = 174), nest attentiveness 75 ± 6% (range 61–89, n = 161), incubation feeding 0.86 ± 1.19 per hour (range 0–5.4, n = 166), and hatching success was 94 ± 9.5% (range = 44–100, n = 136).

Incubation Feeding

Male incubation feeding was negatively associated with ambient temperature (Fig. 2a), time of day and age of the clutch. Thus, the intensity of incubation feeding decreased with higher temperatures, later time of the day and advancing age of the clutch. The frequency of incubation feeding increased with territory quality, but only in years with low overall food supply (2005 and 2007; Fig 3). Frass fall amounted to 0.14 (g/48 h/1 m^2) in 2005, 0.11 in 2007 and 0.51 in 2006. Thus, year 2006 had about five times more frass compared with years 2005 and 2007. Other effects were not significant (Table 1).

Nest Attentiveness

Nest attentiveness was negatively related to ambient temperature (Fig. 2b) and positively to clutch size. Thus, percentage of time females spent on eggs increased with lower temperatures and a higher number of eggs in the nest. Other factors were not significant (Table 2; Fig. 4a).

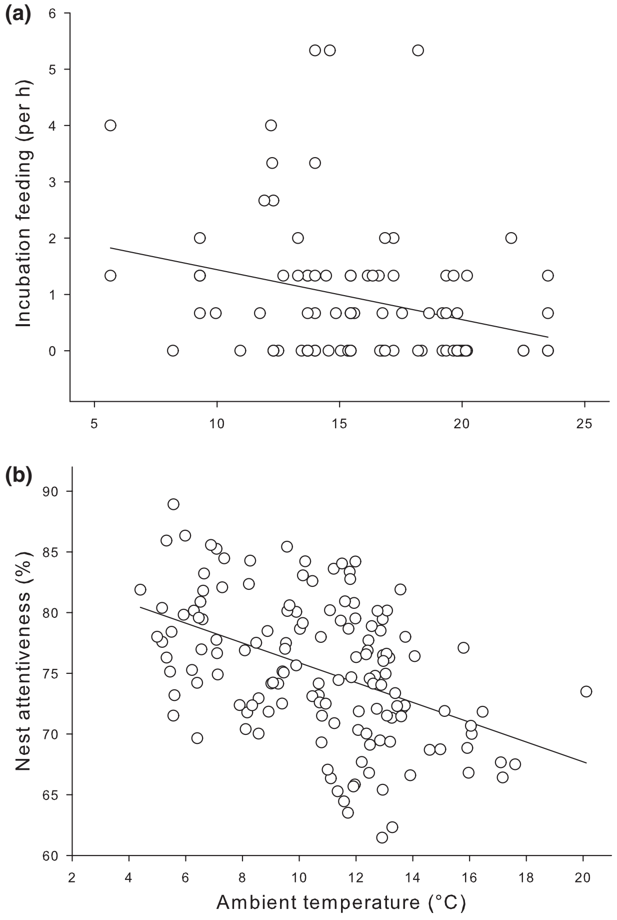

Fig. 2: Relationships of (a) incubation feeding (n = 90) and (b) nest attentiveness (n = 143) to ambient temperature. Lines are least squares regression fits to the data.

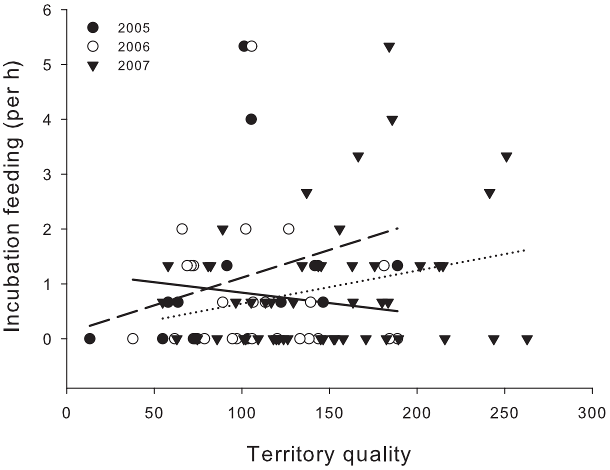

Fig. 3: Relationship between incubation feeding and territory quality (for units see Methods) separately for years 2005 (dashed line), 2006 (full line) and 2007 (dotted line; n = 90).

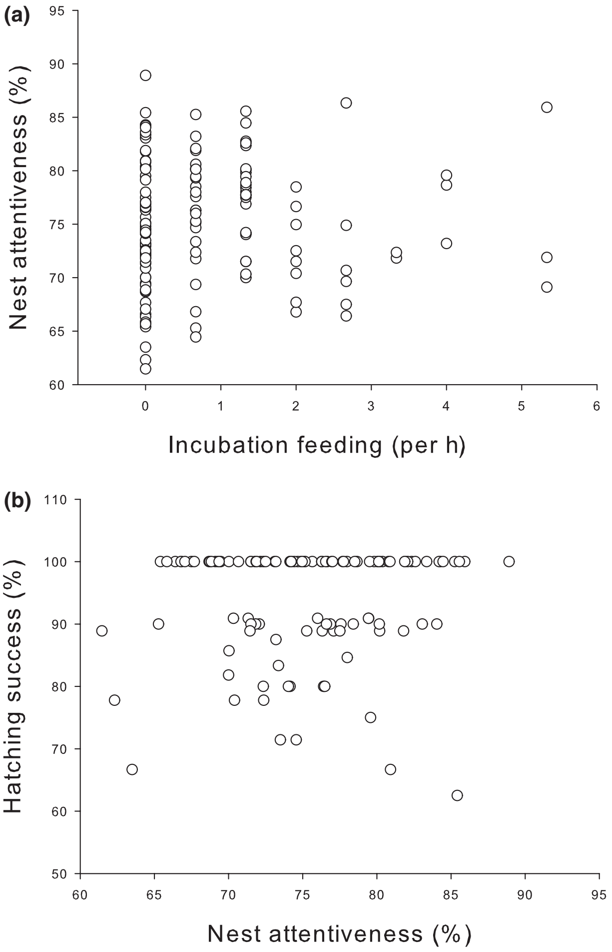

Fig. 4: Relationships between (a) female nest attentiveness and male incubation feeding (n = 143) and (b) hatching success and nest attentiveness (n = 114). These relationships are predicted to be positive under the female nutrition hypothesis.

Hatching Success

Hatching success was positively related to clutch size; other factors were not significant (Table 3; Fig. 4b).

Discussion

Incubation feeding rate in our population was similar to that observed in other secondary cavity nesters (e.g. Moreno & Carlson 1989; Siefferman & Hill 2005) and varied substantially among males (0–5.4 per hour). Neither of male characteristics (plumage colouration, age) predicted the rate of incubation feeding, whereas environmental conditions and characteristics of the nesting attempt did (ambient temperature, territory quality, time of day and age of the clutch). Incubation feeding did not predict nest attentiveness (Fig. 4a). Nest attentiveness was associated neither with any of the female characteristics (plumage colouration, age), nor territory quality, but it was associated with ambient temperature and clutch size. Nest attentiveness did not predict hatching success (Fig. 4b).

Predictors of Incubation Behaviour

Carotenoid and melanin-based ornaments can signal male quality and his capacity to invest in a given breeding attempt (Griffith & Pryke 2006). However, in our population of Great Tit neither of the examined colouration traits predicted male incubation behaviour. This agrees with results obtained for the same type of feather colouration in Northern Cardinal *Cardinalis cardinalis* (Jawor & Breitwisch 2006) and Eastern Bluebird *Sialia sialis* (Siefferman & Hill 2003, 2005), although structural feather colour predicted incubation feeding in Eastern Bluebird. The only species where a positive relationship between carotenoid-based feather colouration and incubation feeding was observed is House Finch *Carpodacus mexicanus* (Hill 1991; Badyaev & Hill 2002). Male age did not correlate with incubation feeding in our population, whereas it did so in some other species (Røskaft et al. 1983; Lifjeld & Slagsvold 1986). Statistically significant predictors of incubation feeding in our population of Great Tit were ambient temperature, territory quality, time of day and age of the clutch. Thus, male incubation feeding in our population was related to environmental conditions rather than to male characteristics.

All studies examining female parental care and/or breeding success in relation to female plumage colouration have focused on nestling period (Amundsen & Pärn 2006). Our study is the first that focused on the relationship between female plumage colouration and female behaviour during incubation. Neither carotenoid-based nor melanin-based female plumage colouration predicted female nest attentiveness in our population of Great Tit. In species where male does not participate directly in incubating the eggs, he can increase female nest attentiveness, and hence probably hatching success, by higher intensity of incubation feeding (Sedgwick 1993; Tewksbury et al. 2002; Fontaine et al. 2007). However, we did not find such a relationship. Female incubation behaviour in our population was related only to ambient temperature and clutch size and not to male behaviour, female characteristics, or quality of the breeding territory.

Environmental conditions were the main correlates of incubation behaviour in both male and female Great Tit. In particular, females increased nest attentiveness with colder temperatures (see also Hinde 1952; White & Kinney 1974; Sanz 1997), which was mirrored by increased male incubation feeding. Attentiveness increased on average from 68% at 20°C to 81% at 4°C. Variation between females at the same temperature was about 20% (Fig. 2b). Similarly, male incubation feeding increased from 0.2 to 1.8 per hour with temperature drop from 24 to 6°C, whereas variation among males at the same temperature might have been as high as from 0 to 5 per hour (Fig. 2a).

Male incubation feeding increased with territory quality, but only in years with low overall food supply. Zanette et al. (2000) found out that male Eastern Yellow Robins *Eopsaltria australis* fed their incubating females more in a habitat with higher food supply. The effect of territory food supply on male incubation feeding agrees with previous observations that Great Tit parents on territories with higher food supply have lower energy expenditure during nestling feeding (Tinbergen & Dietz 1994), breed early (Wilkin et al. 2007) or have better growing nestlings that fledge in higher body weight (Naef–Daenzer & Keller 1999). Thus, territories with higher food supply enable parents to invest more in current breeding attempt and rear higher quality young or to save energy. It is remarkable that this effect was apparent only in years with low overall food supply. It seems that in a good year, all males had territories with enough food to supply their incubating mate and male provisioning capacity played a role only in poor years. On the other hand, nest attentiveness was not related to territory quality in our study, whereas in some other species it was (Rauter & Reyer 1997; Zanette et al. 2000). Extra resources obtained by females on good territories could be allocated to self-maintenance rather than to incubation effort. Thus, females foraging in good territories during incubation off-bouts and receiving more food from males during on-bouts might have lost less weight during incubation, suffered less costs to other functions (physiological, behavioural) or increased their parental effort in other parts of the breeding cycle or in future breeding bouts.

Female Nutrition Hypothesis

Incubation feeding did not predict nest attentiveness, which in turn was not related to hatching success (Fig. 4). Thus, our data were not consistent with the female nutrition hypothesis. However, three alternatives should be mentioned here. First, as mentioned above, females might have allocated extra food obtained from males into self-maintenance instead of incubation effort. Second, female nest attentiveness might respond to the amount or quality of food brought by the male on the nest. Any patterns that could arise from the effects of food load or quality would be missed by our approach. Third, Great Tit male feeds his female also while she is off the nest (Hinde 1952; Royama 1966; de Heij 2006). Incubation feeding off the nest is very difficult to record (Hinde 1952; Nilsson & Smith 1988; Pearse et al. 2004). We were not able to follow females during off-bouts in the dense canopy of our flood-plain forest (B. Matysioková & V. Remeš, unpubl. data). Similarly, most of the previous studies focused exclusively on feeding on the nest, even in species with off-nest incubation feeding occurring (e.g. Hinde 1952; Lifjeld et al. 1987; Nilsson & Smith 1988; Smith et al. 1989; Sanz 1997; Pearse et al. 2004; de Heij 2006; Lloyd et al. 2009; but see Klatt et al. 2008). However, rate of incubation feeding on the nest need not fully correspond to overall incubation feeding rate. In the only study that quantified incubation feeding both on and off the nest, which was done on Scarlet Tanager *Piranga olivacea*, no significant relationship between incubation feeding on and off the nest was found (Klatt et al. 2008; B. Stutchbury, pers. comm.). Thus, if incubation feeding off the nest were more important for the female, we would have missed some important patterns in our population. On the other hand, food load delivered to female when on the nest might be larger, i.e. more important, than that delivered to female outside of nest (Nilsson & Smith 1988). However, these questions remain unresolved.

Conclusions

In summary, our work is one of the first studies that deal with relationships between feather colouration and incubation behaviour in birds. Our data suggest that neither carotenoid-based nor melanin-based colouration predict bird behaviour during incubation, which agrees with previous findings in other species (Siefferman & Hill 2003, 2005; Jawor & Breitwisch 2006; but see Hill 1991). However, it is possible that they play a role in other parts of the breeding cycle, e.g. in nestling period (Senar et al. 2002; Doutrelant et al. 2008; Quesada & Senar 2007; review in Griffith & Pryke 2006), or during non-breeding season (review in Senar 2006). On the contrary, we revealed significant relationships with environmental conditions, including ambient temperature and territory quality. There was no relationship between incubation feeding, nest attentiveness and hatching success. Consequently, although alternative explanations are possible, our data are not consistent with the female nutrition hypothesis conceived to explain the occurrence and rate of male incubation feeding in birds.

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Příspěvek IV.

Remeš V., Matysioková B. & Cockburn A.: Long-Term and Large-Scale Analyses of Nest Predation and Failure Patterns in the Southern Hemisphere: a Study of Australian and New Zealand Songbirds. Zasláno do recenzního řízení (*PLoS ONE*).

Krysa (*Rattus rattus*) požírající mládě pávíka popelavého (*Rhipidura fuliginosa*). Na Nový Zéland byly krysy zavlečeny v polovině 19. století. Dnes se zde jedná o významného predátora ptačích hnízd. Foto ©David Mudge

Long-Term and Large-Scale Analyses of Nest Predation and Failure Patterns in the Southern Hemisphere: a Study of Australian and New Zealand Songbirds

Short title: Nest Predation in Australia and New Zealand

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Abstract

Background

Juvenile mortality is one of crucial drivers of life-history evolution. At the same time, predation is the main cause of nest loss in birds. Thus, identifying factors influencing the risk of depredation is crucial for better understanding life history evolution and, moreover, for effective conservation.

Methodology/Principal Findings

We used published data and unpublished records to study factors influencing nest predation and total failure rates in 226 populations of 115 Australian and New Zealand species of songbirds. Predation (average 42.3%) and failure rates (57.6%) increased over the last four decades, particularly in eastern Australia. Predation and failure rates also increased from temperate regions to the tropics and were highest in eastern Australia, lowest in south-western Australia and intermediate in New Zealand. Predation and failure were higher in smaller species, lower in cavity nesters than in species with open nests, and higher in introduced species. Contrary to previous studies, there was no effect of habitat type and nest site (ground, shrub, canopy). Nest predation caused on average 70% of total nest failure, lower than in other tropical, subtropical, and temperate areas. The contribution of nest predators to failure is at least 1.2 times higher now than 40 years ago.

Conclusions/Significance

In the first study of nest predation and failure spanning from the tropics to temperate regions conducted on almost 17000 nests, we confirmed that tropical birds faced higher nest failure rates. We identified a steep increase in nest depredation rates in the last four decades, suggesting that a large-scale ecological phenomenon must be responsible. It may include increases in predator abundances and/or ranges or habitat fragmentation. We further discuss implications of our results for the evolution of reproductive strategies and for the conservation of Australian and New Zealand birds.

Introduction

Juvenile mortality is one of crucial drivers of the evolution and plasticity of life-history traits [1]. Thus, identification of robust predictors of juvenile mortality across a broad range of species is critical for better understanding of variation in life-history and behavioural traits [2–4]. For example, nest predation is the main source of nest failure in most birds [5–7] and has been identified as an important correlate of a suite of life-history traits across species [8,9]. Additionally, population growth of especially shorter-lived species (e.g. songbirds as opposed to long-lived seabirds) is particularly sensitive to reproductive failure [10]. Thus, effective conservation efforts require robust estimates of species vulnerability to nest predation as a potential limit on population growth rates.

Many nest predation studies have been conducted on northern temperate songbirds [reviewed in refs. 5,7] including detailed studies of nest predators using video cameras [reviewed in ref. 11]. These studies identified several consistent correlates of nest predation, including nest type [12–15], vegetation layer [6], habitat [16], elevation [17], and geography [7]. However, these studies were conducted on limited and non-overlapping samples of species. Moreover, how these results apply in tropical, subtropical and southern hemisphere birds with their distinctive life histories is not clear [18,19]. Although nest predation studies of tropical and southern hemisphere birds have a long tradition [20–22], they are certainly much less numerous. The only correlate of nest predation that has been studied to some extent in these birds is nest type, with some studies reporting lower nest predation in cavity compared to open nesters [21–23] while others reporting no difference [24] or mixed results [25].

For a major advance in identifying predictors of nest predation and failure in tropical and southern hemisphere birds, we need studies on a broad and varied sample of species on a large number of nests. Australian and New Zealand songbirds provide a unique opportunity to achieve these aims, because local avifauna is diverse and comparatively well studied. Moreover, songbirds are here mostly phylogenetically distinct from well-studied European and North American species [26] with typically slow life-history more similar to that of tropical species than to northern temperate species living at corresponding latitudes [27]. Additionally, in Australia and New Zealand both observational and experimental studies show that introduced predators hamper reproductive success of native songbirds [28–30]. Consequently, identification of populations and species that are particularly vulnerable to nest predation might help in their conservation.

In this study we accumulated detailed data on nest predation and total nest failure in Australian and New Zealand songbirds based on published studies. Subsequently, we searched for predictors of nest predation and failure rates on large spatial and temporal scales. Specifically, we asked which of the traits identified previously to correlate with nest predation risk in northern temperate birds (see above) are important in Australian and New Zealand songbirds. This also provides assessment of the determinants of species vulnerability to nest predation that could be used in conservation. We provide comparisons with other published large-scale datasets elsewhere in the world to advance our general understanding of similarities and differences in nest predation patterns on a global scale.

Methods

Data collection

We collected data for this study from the literature. We focused on intensive field studies of single or several species and avoided published accounts based on Nest Record Scheme from Australia or New Zealand. We started with Handbook of Australian, New Zealand, and Antarctic Birds (HANZAB) vols. 5, 6, and 7 [31–33]. Here, we located all studies dealing with nest failure and predation and obtained the primary source. To find articles that were published after HANZAB had been published, we also surveyed all the articles between 2000 and 2008 in Australian Bird Watcher, Australian Field Ornithology, Austral Ecology, Australian Journal of Zoology, Australian Zoologist, Canberra Bird Notes, Corella, Emu, New Zealand Journal of Ecology, New Zealand Journal of Zoology, Notornis, Pacific Conservation Biology, South Australian Ornithologist, Sunbird, VOGR Notes, Western Australian Naturalist, and Wildlife Research. Here we located all the articles dealing with nest failure and predation in songbirds.

Moreover, we did a comprehensive search on databases unrestricted by the year of publication. On Web of Science (available since 1945) and Zoological Record Plus (since 1978), we searched with the scientific name of every species. We went through all the titles and abstracts and in majority of them obtained the primary article. We left out only articles that were obviously not about the breeding biology of a particular species, or which were obviously done in captivity, e.g. many studies of the zebra finch (*Taeniopygia guttata*). On Google, we searched for the combination of the scientific name of the species and following terms: predation, nest failure, breeding success, and breeding biology. We also searched on the web pages of Emu, Notornis, New Zealand Journal of Zoology, and New Zealand Journal of Ecology, i.e. all volumes of these journals. We used the scientific name of the species, and separately the above-mentioned search terms concerning breeding biology. Subsequently, we searched the text of thus obtained articles to locate information on nest failure and predation. All these searches were done from October 2008 to January 2009.

From the resulting articles we extracted where possible: the number of nests failed, number of nests destroyed by predators, number of nests studied, and when and where the study was done. An obvious constraint on the data is that it is not always possible to assign a particular nest loss to predation without direct evidence obtained by video-taping. Here we relied on two approaches to identify nest losses caused by predators. First, if the author(s) explicitly stated how many nests were taken by predators, we accepted this claim. Second, if nests lost to predators were not explicitly enumerated, we assigned a loss to nest predation if the total clutch or brood disappeared suddenly without other obvious reasons (e.g. storm or human interference). We did not include partial losses unless losses were reported as total number of eggs or nestling lost instead of the number of nests affected. In such cases, there was no way of teasing apart partial and total losses. We calculated the number of nests studied as number of eggs divided by clutch size reported for that particular study. Because this method includes partial predation, total losses will be overestimated in these populations.

Besides analysing proportion of failed nests and nests lost to predators, we also transformed these data to daily nest failure (DFR) and predation rates (DPR) by the method of ref. 5. To validate the values thus obtained, we also calculated daily failure rates by two other approaches [34; V. Remeš, unpubl. results), which were based on the nest survival model of ref. 35. Estimates produced by all three methods were highly correlated (r = 0.99–1.00, n = 225) and we used only values obtained by the method of ref. 5 in all statistical analyses. For all these estimates, length of the nest cycle was calculated as the sum of incubation period, nestling period, and clutch size. This assumes that eggs are laid daily, which is true in most of the species (81 of 107 species where known, the rest lay in intervals of 2 days) and thus provides a reasonable approximation. None of these methods estimates true daily rates that can be obtained by applying the Mayfield method [35] on original data sets – these are obviously not available when working with literature data. However, we included the best available estimates of DFR and DPR into our analyses, because overall nest failure is a product of daily failure rate and the length of exposure. Thus, excluding daily rates might lead to biased estimates of selection pressures on anti-predation adaptations [9].

For each species in our database, we obtained its typical habitat (forest, shrubland, open, and "various" for generalist species), nest type (open, domed, and cavity), nest height (in meters), nest location (ground, shrub, and canopy), adult body mass (g), and whether the species is native or introduced [31–33]. To put our data from Australia and New Zealand into perspective, we compared it with published large-scale datasets elsewhere in the world.

Data analysis

We used two approaches to modelling the data, in both cases carrying out the analyses in SAS 9.2. First, we used generalised linear mixed models (GLMM) with binomial distribution and logit link. Depending on the analysis, the response was the number of nest depredated or failed and the binomial denominator was the number of nests studied or failed. Coding the response variable as a binomial proportion weighed these analyses by sample size. We included species as a random factor and analysed the data in the Glimmix procedure. Second, we modelled daily predation and failure rates in linear mixed models (LMM) weighed by sample size. We again included species as a random factor and analysed the data in the Mixed procedure. In all these analyses, one estimate of nest loss for a set of nests reported in a literature source was always treated as one data point (i.e., population estimate). Because of high variation of nest failure and predation rates and very weak predictive power of species (and taxonomic family, results not shown) in population-level analyses (see Results), we did not try to correct for phylogenetic relationships among species. The application of phylogenetic comparative methods is only useful and feasible when traits vary minimally within species as compared to across species variation [36].

We adopted two approaches to deal with potential spatial autocorrelation in our data. First, we were interested in broad-scale geographical trends. We thus included latitude and longitude as explanatory variables into our statistical models. This technique is known as trend surface analysis. However, it is well suited to model broad-scale trends and not small-scale autocorrelation in residuals [37]. Ignoring this potential small-scale autocorrelation could lead to biased parameter estimates and inflated Type I error rates [38]. Thus, second, we tested for potential remaining autocorrelation in residuals from trend surface analyses. We calculated semivariograms and spatial correlograms using Moran's I [39]. Both these techniques agreed on the absence of small-scale autocorrelation in residuals from the trend surface analyses (Appendix 1). Thus, we fitted GLMM and LMM with a trend surface component (i.e. including latitude and longitude) but with spatially uncorrelated error terms (using variance components matrix). However, sometimes several studies were conducted at the same place over the years (e.g. a natural reserve, university research station). Thus, to account for potential site effects, we included study site as a random factor. There were 125 different study sites.

We fit the models with the predictors we considered interesting and worth including based on our experience and past studies (see Introduction), which are apparent from Tables below. Graphical inspection of data revealed a non-linear effect of longitude reflecting strong differences among broadly defined regions and different trends with time across regions. Since we did not predict and test these patterns a priori their general validity might be questioned. However, because of their interest we report on them. All tests were two-tailed. In GLMMs, we checked for potential overdispersion of the data. As the variance of Pearson residuals was 0.9–1.4 (depending on the model), there was no overdispersion [40]. In LMMs, we checked residuals for any deviations from normality, equal variance, and linearity. Residuals always conformed to all these requirements. Body mass and nest height were $\log_{10}$ transformed, and daily predation and failure rates square root transformed. Denominator degrees of freedom were estimated by the Satterthwaite method. Besides tests of significance we always report parameter estimates for use in potential future metaanalyses and for judging biological significance of our results (see Tables).

Results

In total, we located 226 population estimates of nest predation (n = 16972 nests) in 115 species of Australian and New Zealand songbirds belonging to 75 genera and 31 families.

Families with the highest number of studies were Meliphagidae (42 studies), Petroicidae (32), Pardalotidae (23), Maluridae (22), and Turdidae (17), whereas there were 10 families with only one study. Our sample of species includes members of almost all 38 songbird families living in Australia and New Zealand, except representatives of four native and three introduced families. It represents 33.2% of 346 breeding species of Australian and New Zealand songbirds.

The number of nests studied varied considerably among studies (Table 1) but did not change with the year when the study was published ($r = 0.08$, $P = 0.227$, $n = 216$). When assessed by the midpoint of the study period the earliest study was conducted in 1943. However, all other studies had a midpoint after 1960 and availability of data increased steadily until the present (Figure S1). More studies were done in Australia ($n = 149$) than in New Zealand ($n = 77$; Figure S2). Most studies were done on native species ($n = 202$), as compared to introduced species ($n = 24$).

Nest failure, nest predation, daily failure and predation rates, and proportion of losses caused by predators varied considerably among studies (Table 1). Proportion of losses caused by predators increased with total nest failure (Table 2). It increased from ca. 0.45 at 10% nest failure to ca. 0.85 at 90% failure ($r = 0.40$, $P < 0.001$, $n = 202$).

Environmental predictors and covariates

Both the proportion of nests destroyed by predators and those that failed declined with body mass and latitude (Figure 1), but increased with year (Figure 3a) and in introduced species (Table 3). Proportion of total nest losses caused by predators increased with the year of study and total nest failure (Table 2, Figure 3b). Simple proportions showed that the fraction of nest losses caused by predators increased from 0.43 between 1965 and 1975 ($n = 16$) to 0.73 between 1995 and 2005 ($n = 87$; see Figure 3b). The model in Table 2 predicted a lower increase over the last 40 years, from 0.67 in 1965 to 0.82 in 2005. Results for daily nest predation and failure rates were similar as those for binomial proportions. There was an additional effect of species nesting in cavities to be less prone to nest failure (Table 4, Figure 4).

Visual inspection of scatterplots suggested that both nest failure and nest predation were lowest in south-western (SW) Australia and higher in eastern (E) Australia and New Zealand (Figure 2). This was supported by a significant quadratic effect of longitude after accounting for other predictors (GLMM: No depredated, $F_{1,108.3} = 10.5$, $P = 0.002$; No failed, $F_{1,109.7} = 9.6$, $P = 0.003$; LMM: DPR, $F_{1,113} = 9.7$, $P = 0.002$; DFR, $F_{1,113} = 9.0$, $P = 0.003$). Moreover, the proportion of nest losses caused by predators was also highest in E Australia (quadratic effect GLMM: $F_{1,92.4} = 6.5$, $P = 0.013$).

Nest predation increased more steeply with year in E Australia (logit slope = 0.026, SE = 0.011) than in the other two regions (SW Australia slope = 0.012, SE = 0.013; New Zealand slope = 0.004, SE = 0.005). These differences were statistically significant even when accounting for all other predictors (year by region interaction: $F_{2,85.6} = 6.4$, $P = 0.002$). The same results were obtained with daily predation rates (year by region interaction: $F_{2,97.7} = 5.8$, $P = 0.004$). The logit slopes translated into increases in nest predation between 1965 and 2005 from 36.4 to 62.0% in E Australia, from 25.6 to 35.3% in SW Australia, and from 17.1 to 19.4% in New Zealand.

The random effect of species accounted for very little variance in all the analyses (generally less than 5%; Tables 3 and 4) with the exception of the analysis of the proportion of total failure caused by predators (20%, Table 2). The random effect of study site explained between 1.5 and 12% of variance (Tables 2, 3, and 4).

Comparison with other regions

We compared the data reported in this study with multi-species studies or reviews based on substantial samples of species and nests for other regions. Overall nest failure in Australia and New Zealand was similar to other regions (Figure 5). However, the proportion of nest losses caused by predators was quite low both in Australia and New Zealand compared with other studies (Table 1, Figure 5).

Discussion

Nest predation and failure in Australian and New Zealand songbirds have increased in recent decades, particularly in E Australia. Nest predation and failure increased towards the equator and were highest in E Australia. They were highest in smaller birds, in birds with open and domed nests, and in introduced species. Proportion of nest losses caused by predators increased with time and was highest in E Australia. Overall patterns in nest failure were driven primarily by nest predation. Our data do not support the hypothesis that predation and failure regimes affecting Australian and New Zealand birds are radically different from those of other regions for which large-scale surveys are available. In the following discussion we first address the necessary restrictions to the quality of our data, and then address explanations for the broad-scale patterns we have identified.

Limits to data

Although we assembled a large and very detailed dataset on nest failure and predation in Australian and New Zealand songbirds, there remain problems with our data. As has been reported previously [41], the geographical distribution of studies is biased towards more populated areas. Most studies originated from E and SW Australia and New Zealand with few studies coming from tropical north and no studies from arid central Australia (Figure S2). Taxonomic coverage of families and species seemed reasonable. Most studies came from the last four decades and the frequency of study has increased over that time (Figure S1). While this is encouraging, sample size of most of the studies is modest (median = 40 nests; Table 1) with no improvement over the years. Most studies also had short timespans (median = 2 years). This certainly introduces substantial sampling variation into the data. Data demonstrated high within species variation as compared to among species variation, which was reflected by low proportion of variation explained by species. However, despite this high sampling variation our analyses revealed several robust predictors of nest failure and we discuss them in turn below.

Time

Nest predation and failure, daily nest predation and failure rates, and proportion of nest losses caused by predators all increased over the last five decades (Figure 3). At least two related explanations are possible. First, as nest predation studies has become more common in recent decades (see Figure S1) there might have been more studies in places that are fragmented or otherwise impacted by anthropogenic disturbance. Second, population changes of important nest predators might be the driver of this pattern. As an example that is best documented we discuss here the case of the pied currawong (*Strepera graculina,* ca. 300g bird, family Cracticidae), which increased in abundance and colonised new areas during last decades. There was an increase of 62% in reporting rate between 1980s and 2000s across the range of this species [42]. The pied currawong has been identified as a significant nest predator by studies using both artificial nests [43,44] and natural nests of woodland songbirds [45]. Although adult pied currawongs are largely insectivorous during spring and summer, nestlings of other species are the primary food provided by pied currawong to their own young [46]. Pied currawongs live exclusively in eastern Australia, which is compatible with the more striking increase in predation rates in this region. However, the large-scale increases in nest predation rates identified here are not likely to be explained by a single predator species. This is supported by our finding that nest predation increased also in SW Australia and New Zealand where the pied currawong does not live.

It has been recently estimated that about two-thirds of Australia's bird species are showing significant long-term declines [47], and nest predation has been implicated in many of these declines [48]. However, increased nest predation does not automatically imply negative impacts on songbird populations [49]. There are many other factors that may be causing declines of small birds, including insecticides, cats, increasingly fragmented vegetation, and spread of other abundant and aggressive native species like noisy miner (*Manorina melanocephala*, ref. 50) Moreover, birds might compensate higher nest losses by more frequent renesting, especially given long breeding seasons typical of Australian birds [27]. A clear demonstration of a causative effect of nest predation in songbird declines would have to involve predator removal and monitoring of songbird demography [51,52]. So far, only one study followed the effects of nest predator (pied currawong) exclusion on the breeding success of two woodland songbirds (eastern yellow robin, *Eopsaltria australis* and scarlet robin, *Petroica multicolor*) and the effects were strong and positive [45]. Moreover, there is growing evidence that low production of recruits caused by high nest predation might be behind long-term declines of some small songbirds (e.g. hooded robin, *Melanodryas cucullata*; ref. 48).

Geography

Avian life-history attributes usually vary across latitude [53] and this variation has often been ascribed to nest predation rates being higher closer to the equator [18]. However, some studies based on comparison of phylogenetically and ecologically related species suggested that nest predation is not in fact higher in the subtropics/tropics [54,55]. In our dataset, nest predation and failure did increase towards the equator (Figure 1), consistent with the traditional view. However, the causes of this pattern remain questionable. One possibility is increasing diversity or changing composition of predator communities towards the equator. For instance, in North America the relative importance of snakes as predators decreases with increasing latitude (i.e. away from the equator), in concert with their decreasing diversity and abundance [7].

Geographical patterns in our data were more complex than just this latitudinal trend. Nest failure and predation were higher in E Australia and New Zealand than in SW Australia (Figure 2). Again, different abundance and/or diversity of nest predators might be the clue. We know that biogeography [7], habitat type [56], and habitat fragmentation [57] all affect nest predation rates. However, effects of habitat fragmentation might be dependent on landscape context, being more profound in certain habitat types [16] or geographic areas than in others [58]. One tentative explanation might be that nest predation is kept high by pied currawongs and other widespread nest predators in E Australia and many introduced predators, mainly mustelids [e.g. 59], in New Zealand. SW Australia lacks pied currawongs and the abundance of introduced mammalian predators has been restricted using large-scale poisoning with sodium monofluouracetate, to which native mammals are resistant because of high levels of the toxin in native vegetation [60]. However, before robust data on real nest predators are acquired, which requires substantial sampling effort [11], no definite explanation for the geographic patterns can be offered.

Nest type

It has repeatedly been shown that nests in cavities are safer from predators and suffer from lower predation pressure, and that this is not just because cavity nesters are often studied in nest-boxes [14,15,21–23,25]. Higher safety of cavities is also traditionally suggested as one of the main reasons for high nest success of typical primary cavity nesters, e.g. woodpeckers [61]. Our data for daily failure and predation rates tend to confirm this pattern, but there was no evidence that simple proportion of nests failed or depredated is lower for cavity nesters. This can be explained by the fact that nest failure is a product of daily failure rate and exposure time. Cavity nesters have larger clutches and longer incubation and nestling periods, which has been demonstrated in North America [9,14] and is true also in our sample of species (V. Remeš, unpubl. results). This exposes cavity nesters to the risk of failure for longer time. Thus, although their daily failure rates are lower, their greater duration of exposure generates overall failure similar to that of open and domed nests. Nest sites did not differ in the proportion of losses caused by predators. Thus, cavities tend to be generally safer against predators and no compensatory nest failure occurs in cavity nesters.

Trends in daily failure rates across nest types agreed with differences in nest construction. Cavity nests had the lowest daily failure rates, open nests the highest with domed nests in between (Figure 4a; see also ref. 23). This agrees with the idea that domed nests are better protected from predators by their construction and are more defendable by a parent sitting on the nest as compared to open nests, but are less resistant to predator attack than true cavities [62]. However, parents might also adopt other compensatory behavioural strategies besides nest defence, e.g. watching for predators and luring them away from the nest. Interactions between nest site, size and parental behaviour in determining nest survival are complex and require further attention [63–65]. Overall, our results tend to confirm nest type as a significant correlate of clutch and brood safety and thus potential driver of the evolution of life-history characteristics [2,66].

Other factors

Body mass was a consistent predictor of nest failure and predation rates. Large species suffered less from nest losses. This indicates that large species might be better able to defend their nest against predators. For example, nests of large and aggressive noisy friarbird (*Philemon corniculatus*) with a good view of surroundings were more successful than more hidden nests, suggesting that this species might be able to defend its nests against at least some nest predators [67]. However, this pattern is by no means general. Although Ricklefs [ref. 5] also found decreasing daily nest failure rate with body mass, his analysis included both songbirds and raptorial birds. The pattern would not have been apparent had he analysed only songbirds [ref. 5: Fig. 11]. Similarly, there was no relationship between body mass and daily predation rates in North American ($r = -0.05$, $P = 0.596$, $n = 129$, data from ref. 68) or European songbirds ($r = -0.03$, $P = 0.836$, $n = 62$, data from ref. 69). Thus, the generality of this pattern remains uncertain.

Native species suffered from lower nest predation rates than introduced species (Figure 4b). This might be caused by their longer coevolution with native predators and consequent evolution of more effective antipredator strategies. On the other hand, a large part of predation on songbird nests is inflicted by introduced predators [28], which weakens the validity of this argument. Another possibility is that introduced species are just by accident a sample of species (*n* = 10) particularly vulnerable to nest predation. Except common myna (*Acridotheres tristis*), all of them are open nesters that suffer from heavy nest predation also in their native ranges in Europe [69].

There was no relationship of nest predation and failure to either habitat type or nest height. This was true also when nest categories (ground, shrub, canopy) instead of nest height were used, which would allow for non-linear effects of nest height. Our results are quite surprising, because traditionally predation rates were linked to habitat type and nest strata [5,6]. They show that broad regions might differ in nest failure patterns. However, without knowledge of the identity and foraging behaviour of nest predators, we are not able to provide an explanation of these differences.

Comparison with other regions

Nest failure rates for Australia and New Zealand lay close to the average of reported values for other regions (Figure 5). There seems to be no clear-cut difference between temperate and tropical/subtropical regions in total nest failure. Results of some earlier, small-scale studies also questioned the paradigm of higher nest failure in tropical/subtropical regions [54,70]. There is substantial variation in nest failure risk within regions. It might be more fruitful to search for population- and species-specific predictors of nest failure and predation risk rather than focus on broad-scale differences among distant geographical regions. This will be also productive for looking at fine-scale life-history adaptations in species from different regions [55].

By contrast with the fairly weak differences affecting total nest failure, the contribution of predation to nest loss is surprisingly low in Australia and New Zealand compared to other areas for which data are available (Figure 5). Comparably low share of predator-caused nest losses is rather surprising given large numbers and densities of introduced predators in Australia and New Zealand. However, other potential predators declined dramatically, e.g. numerous mammals [71], and Australian and New Zealand faunas underwent such dramatic changes that it is difficult to infer what the net effects on populations of potential nest predators (snakes, large birds, mammals) were [72]. Another possibility is that nest abandonment is high, due to either long breeding seasons [27] or well developed desertion strategies against brood parasites [73], leaving less opportunities for nest predation. However, some abandonments are certainly caused by nest predators [74] and these losses should be ascribed to predation. Unfortunately, we did not quantify proportion of nest failure due to nest abandonment and identifying nest abandonments due to predators would be extremely difficult. Although very interesting, this question thus remains unanswered.

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Author contributions

Conceived and designed the experiments: VR BM AC. Collected the data: BM VR. Analysed the data: VR. Wrote the paper: VR BM AC.

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Figure legends

Figure 1. Predation and failure rates across latitude. For the sake of convenience raw data are shown and thus we depicted the lines from GLMM analyses with species and site as random factors but unadjusted for other predictors.

Figure 2. Predation and failure rates across longitude. For the sake of convenience raw data are shown and thus we depicted the lines from GLMM analyses with species and site as random factors, with a quadratic effect of longitude but unadjusted for other predictors.

Figure 3. Predation and failure (a) and nest losses caused by predators (b) over the years. For the sake of convenience raw data are shown and thus we depicted the lines from GLMM analyses with species and site as random factors but unadjusted for other predictors.

Figure 4. Daily predation and failure rates in relation to nest type (a) and species origin (b). We depicted least squares means (95% CI) from LMM analyses adjusted for random effects of species and site and all other predictors.

Figure 5. Comparison of nest failure and proportion of failure due to predators across regions. (a) Overall nest failure (1 SD) in Australia and New Zealand compared to temperate areas (white), and tropics and subtropics (grey). Figures within bars indicate number of species, with number of nests in brackets. (b) Proportion of nest failure caused by predators (1 SD; unknown for two studies). Localities are arrayed roughly from north to south (from top to bottom). Data come from following studies: North America [75], Europe [15], Ecuador [20], Panama [25], Amazonia [21], subtropical Argentina [23], South Africa [24], and temperate Argentina [76].

Supporting Information

Appendix 1 Analyses of potential small-scale spatial autocorrelation in nest predation and failure data in Australia and New Zealand.

Figure S1 Distribution of studies across years when they were published (*n* = 169).

Figure S2 Geographical distribution of individual population estimates (*n* = 222). Colours indicate broad geographic regions: south-western Australia (orange), eastern Australia (blue), New Zealand (red), and other (green).

Tables

Table 1. Descriptive characteristics of nest failure data in Australian (Au) and New Zealand (NZ) songbirds.

	Mean		sd		Median		Range		No studies	
	Au	NZ	Au	NZ	Au	NZ	Au	NZ	Au	NZ
No of studied nests	79.6	66.3	100.4	76.4	41.0	42.0	5 to 656	5 to 521	149	77
Length of the study (years)	3.3	2.5	3.6	1.8	2.0	2.0	1 to 22	1 to 9	136	72
Nests that failed (%)	57.4	57.8	19.4	19.6	57.9	58.5	8.3 to 100	8.8 to 93.1	140	62
Nests destroyed by predators (%)	43.7	39.6	22.9	21.7	42.9	36.7	0 to 100	0 to 88.9	149	77
Failed nests that failed due to predation (proportion)	0.72	0.63	0.24	0.27	0.76	0.69	0 to 1	0 to 1	140	62
Daily predation rate (day^{-1})	0.020	0.017	0.015	0.013	0.017	0.015	0 to 0.077	0 to 0.058	148	77
Daily failure rate (day^{-1})	0.029	0.028	0.016	0.016	0.026	0.024	0.002 to 0.077	0.004 to 0.075	139	62

Table 2. Results of GLMM relating proportion of nest failure caused by predators to environmental factors and covariates.

RESPONSE	No Depredated / No Failed			
FIXED EFFECTS	*df*	*F*	*P*	Estimate (SE)
Intercept				–39.67 (15.68)
Body mass	1, 84.4	0.5	0.488	0.210 (0.301)
Habitat (Various)	3, 64.8	1.0	0.412	Forest: –0.334 (0.457) Open: –0.747 (0.518) Shrubland: –0.659 (0.464)
Latitude	1, 88.7	0.2	0.703	–0.007 (0.018)
Longitude	1, 117.0	1.5	0.227	–0.010 (0.009)
Native vs Introduced (Native)	1, 79.2	0.6	0.458	Introduced: 0.405 (0.543)
Nest height[a]	1, 88.2	1.0	0.325	–0.489 (0.494)
Nest type (Open)	2, 99.5	0.3	0.743	Domed: –0.094 (0.327) Cavity: 0.329 (0.464)
Year[b]	1, 106.0	7.0	**0.009**	0.021 (0.008)
Total failure	1, 166.5	21.5	**<0.001**	0.026 (0.006)
RANDOM EFFECTS	Estimate	SE		
Species	0.609	0.240		
Site	0.360	0.208		
Residual	3.031	0.551		
N	193			

P values of statistically significant factors are in bold. Reference levels of categorical variables are given in brackets.

[a] The same results were obtained when nest height categories were used (ground, shrub, canopy).

[b] Year of study publication (to increase sample size). However, correlation with midpoint of the study period was very high: r = 0.95, P < 0.001, N = 210.

Table 3. Results of GLMM relating nest predation and nest failure to environmental factors and covariates.

RESPONSE	No Depredated / No Studied				No Failed / No Studied			
FIXED EFFECTS	*df*	*F*	*P*	Estimate (SE)	*df*	*F*	*P*	Estimate (SE)
Intercept				–33.98 (9.63)				–29.72 (9.61)
Body mass	1, 95.1	8.0	**0.006**	–0.587 (0.206)	1, 95.7	15.0	**<0.001**	–0.622 (0.161)
Habitat (Various)	3, 66.7	1.9	0.132	Forest: –0.132 (0.289)	3, 66.3	1.7	0.167	Forest: 0.278 (0.226)
				Open: –0.519 (0.356)				Open: –0.182 (0.268)
				Shrubland: –0.256 (0.297)				Shrubland: –0.005 (0.232)
Latitude	1, 108.9	3.7	**0.056**	–0.027 (0.014)	1, 98.9	5.6	**0.020**	–0.026 (0.011)
Longitude	1, 126.6	1.2	0.285	0.007 (0.006)	1, 117.6	5.8	**0.018**	0.012 (0.005)
Native vs Introduced (Native)	1, 66.1	8.0	**0.006**	Introduced: 0.938 (0.331)	1, 83.0	21.4	**<0.001**	Introduced: 1.37 (0.30)
Nest height[a]	1, 97.6	0.1	0.800	–0.089 (0.350)	1, 98.8	0.2	0.648	–0.124 (0.271)
Nest type (Open)	2, 113.8	0.4	0.691	Domed: –0.038 (0.233)	2, 107.5	1.6	0.205	Domed: 0.011 (0.180)
				Cavity: –0.293 (0.345)				Cavity: –0.465 (0.260)
Year[b]	1, 171.0	13.0	**<0.001**	0.017 (0.005)	1, 161.5	9.9	**0.002**	0.015 (0.005)
RANDOM EFFECTS	Estimate	SE			Estimate	SE		
Species	0.228	0.094			0.116	0.054		
Site	0.289	0.102			0.185	0.067		
Residual	4.663	0.736			2.806	0.472		
N	216				193			

P values of statistically significant factors are in bold. Reference levels of categorical variables are given in brackets.

[a] The same results were obtained when nest height categories were used (ground, shrub, canopy).

[b] Year of study publication (to increase sample size). However, correlation with midpoint of the study period was very high: r = 0.95, P < 0.001, N = 210.

Table 4. Results of LMM relating daily predation and failure rates to environmental factors and covariates.

RESPONSE	Daily predation rate				Daily failure rate			
FIXED EFFECTS	*df*	*F*	*P*	Estimate (SE)	*df*	*F*	*P*	Estimate (SE)
Intercept				–1.81 (0.50)				–1.73 (0.52)
Body mass	1, 95	19.2	**<0.001**	–0.046 (0.010)	1, 103	33.6	**<0.001**	–0.051 (0.009)
Habitat (Various)	3, 64	1.1	0.354	Forest: 0.005 (0.014) Open: –0.021 (0.018) Shrubland: –0.008 (0.015)	3, 75.6	1.3	0.279	Forest: 0.011 (0.012) Open: –0.012 (0.015) Shrubland: 0.002 (0.013)
Latitude	1, 112	3.8	**0.055**	–0.001 (0.001)	1, 104	7.3	**0.008**	–0.002 (0.001)
Longitude	1, 119	0.2	0.672	0.0001 (0.0003)	1, 120	2.3	0.130	0.0004 (0.0003)
Native vs Introduced (Native)	1, 61.2	11.2	**0.001**	Introduced: 0.055 (0.017)	1, 89.7	27.4	**<0.001**	Introduced: 0.083 (0.016)
Nest height[a]	1, 94.6	0.3	0.572	–0.010 (0.018)	1, 105	2.2	0.144	–0.022 (0.015)
Nest type (Open)	2, 110	2.3	0.109	Domed: –0.016 (0.012) Cavity: –0.029 (0.017)	2, 115	5.2	**0.007**	Domed: –0.019 (0.010) Cavity: –0.037 (0.014)
Year[b]	1, 183	17.2	**<0.001**	0.001 (0.0002)	1, 163	14.6	**<0.001**	0.001 (0.0003)
RANDOM EFFECTS	Estimate	SE			Estimate	SE		
Species	0.0005	0.0002			0.0004	0.0002		
Site	0.0009	0.0003			0.0006	0.0002		
Residual	0.056	0.009			0.036	0.006		
N	215				192			

P values of statistically significant factors are in bold. Reference levels of categorical variables are given in brackets.

[a] The same results were obtained when nest height categories were used (ground, shrub, canopy).

[b] Year of study publication (to increase sample size). However, correlation with midpoint of the study period was very high: r = 0.95, P < 0.001, N = 210.

Fig. 1

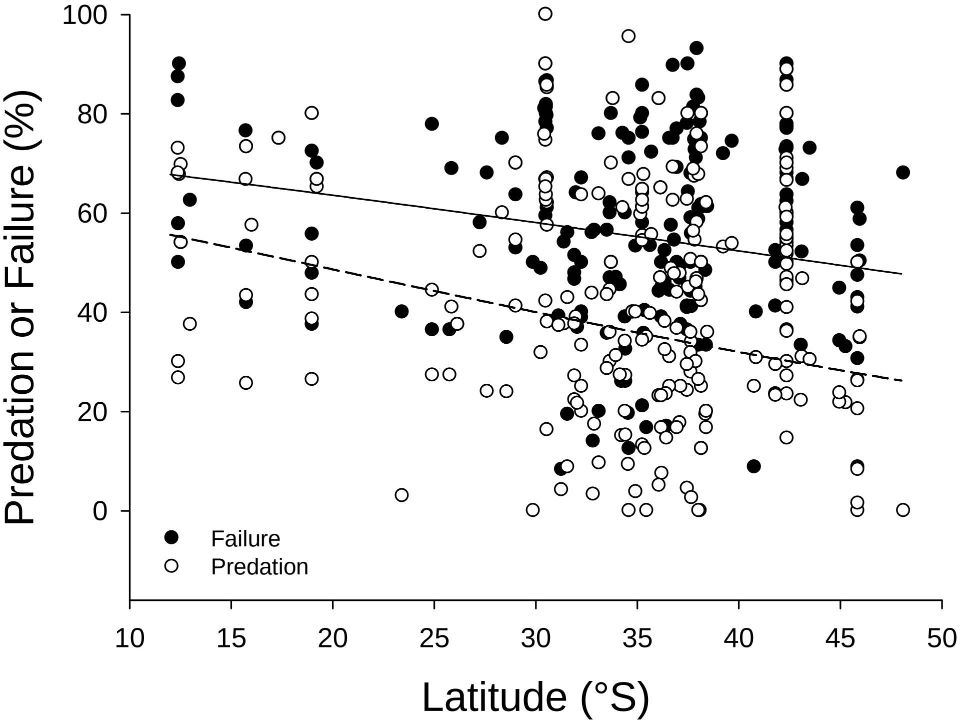

Predation or Failure (%)
100
80
60
40
20
0
10
15
20
25
30
35
40
45
50
Latitude (°S)
● Failure
○ Predation

Fig. 2

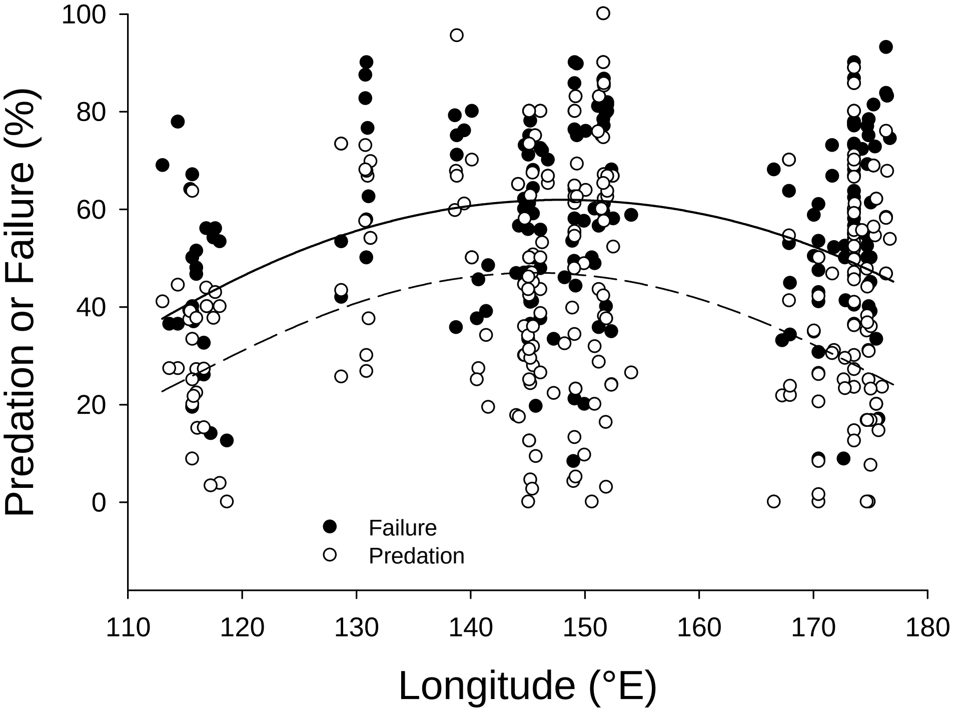

100
80
60
40
20
0
Predation or Failure (%)
● Failure
○ Predation
110
120
130
140
150
160
170
180
Longitude (°E)

Fig. 3

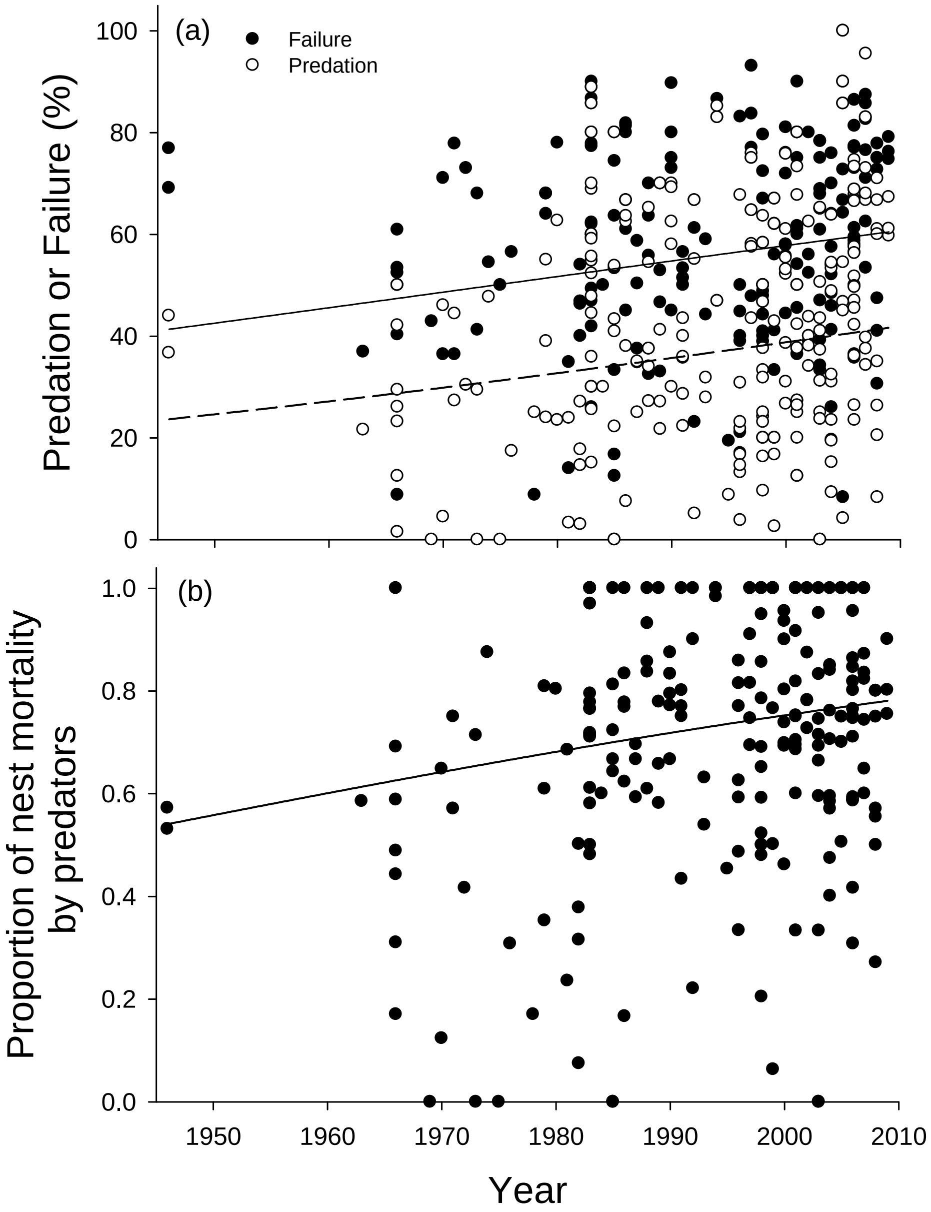

(a)
● Failure
○ Predation
Predation or Failure (%)
0
20
40
60
80
100
(b)
Proportion of nest mortality by predators
0.0
0.2
0.4
0.6
0.8
1.0
1950
1960
1970
1980
1990
2000
2010
Year

Fig. 4

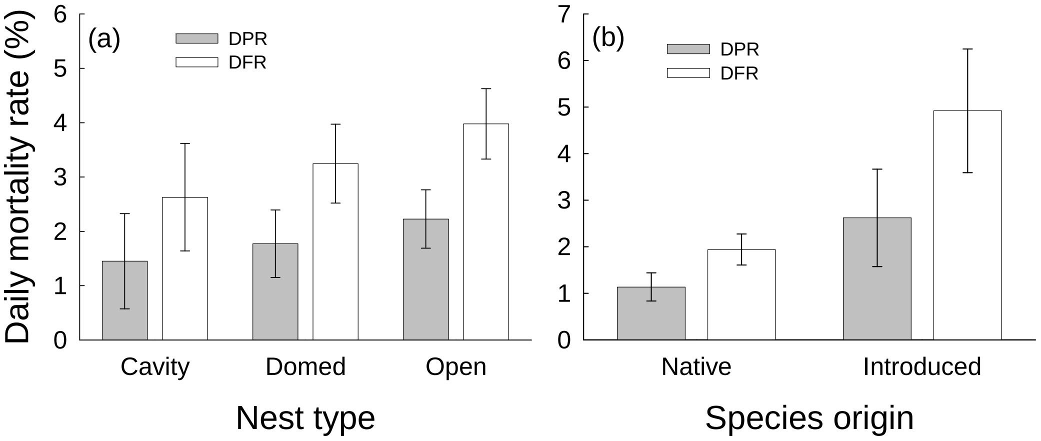
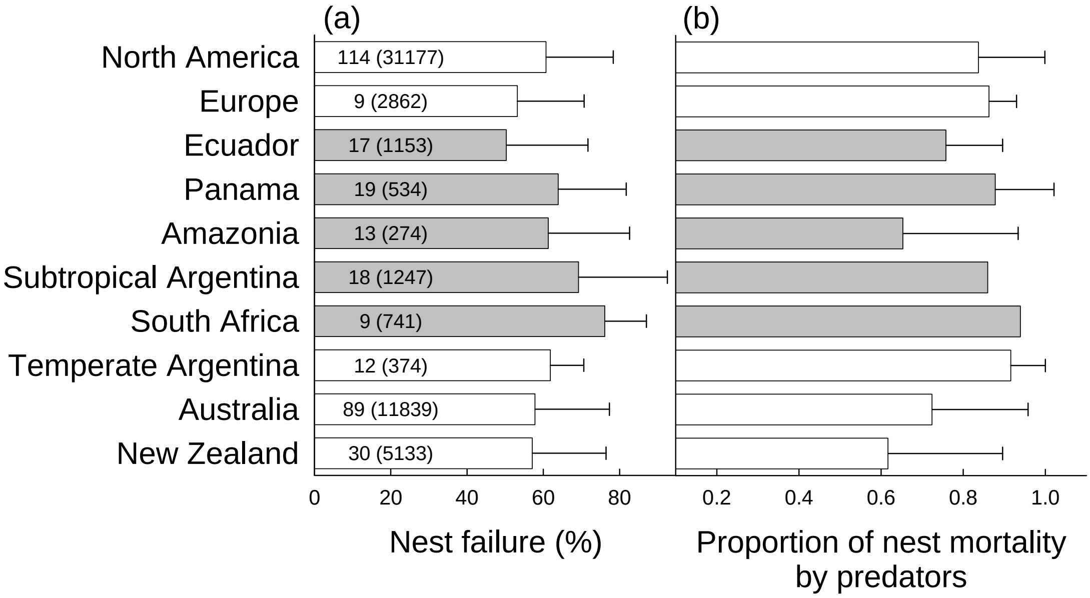

Daily mortality rate (%)
(a)
DPR
DFR
0
1
2
3
4
5
6
Cavity
Domed
Open
Nest type
(b)
DPR
DFR
0
1
2
3
4
5
6
7
Native
Introduced
Species origin

Fig. 5

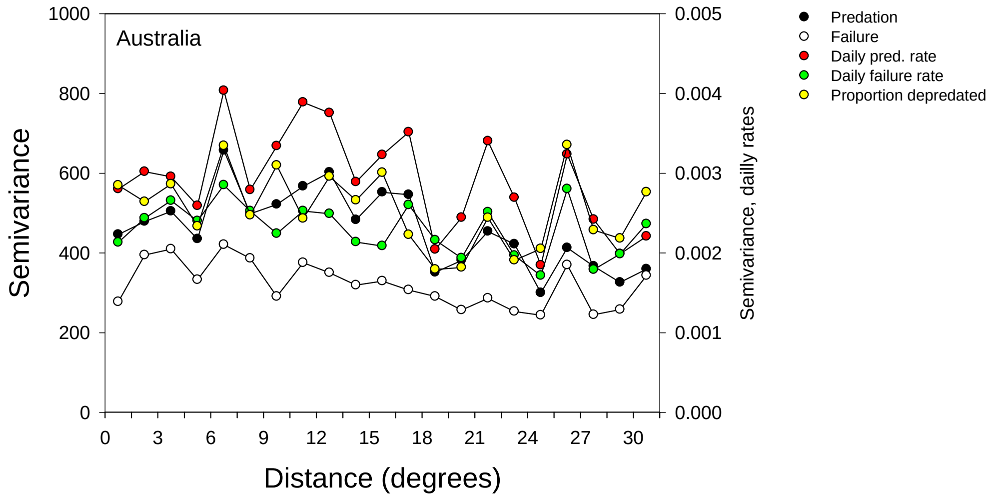

(a)
(b)
North America
Europe
Ecuador
Panama
Amazonia
Subtropical Argentina
South Africa
Temperate Argentina
Australia
New Zealand
114 (31177)
9 (2862)
17 (1153)
19 (534)
13 (274)
18 (1247)
9 (741)
12 (374)
89 (11839)
30 (5133)
0
20
40
60
80
0.2
0.4
0.6
0.8
1.0
Nest failure (%)
Proportion of nest mortality by predators

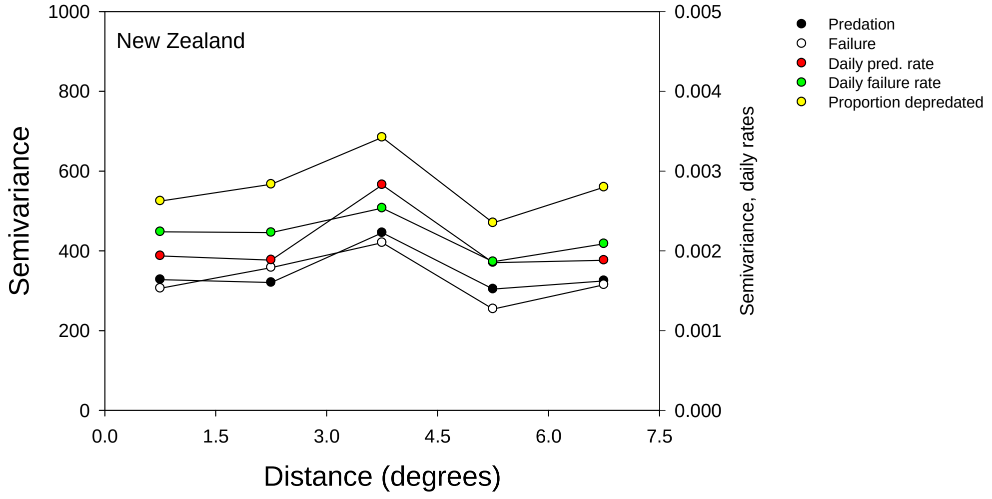
Appendix 1 Analyses of potential small-scale spatial autocorrelation in nest predation and failure data in Australia and New Zealand.

1) Semivariograms

We calculated empirical semivariograms using function variogram in gstat package of R language. We used residuals from trend surface analyses of daily predation/failure rates (square root transformed), percent of depredated/failed nests, and proportion of nests failed due to depredation (i.e., regressions with latitude and longitude as predictors). When residuals from full models presented in Results were used, the outcomes were identical. To account for the fact that potential spatial processes cannot extend across ocean, we calculated semivariograms separately for Australia and New Zealand. We divided the data into lag classes so that pair number in individual lag classes exceeded 100. We calculated semivariograms for 1/2 of the longest spatial extent of data, which led to lag classes measuring 1.5 degrees of geographical coordinates. This translates into ca. 166 km in latitude and from ca. 162 km (at 13°S) to ca. 112 km (at 48°S) in longitude.

Flat shape of semivariograms indicated that there was virtually no small-scale autocorrelation in residuals from trend surface analyses (e.g. Fortin MJ, Dale M. 2005. Spatial analysis. A guide for ecologists. Cambridge University Press, Cambridge).

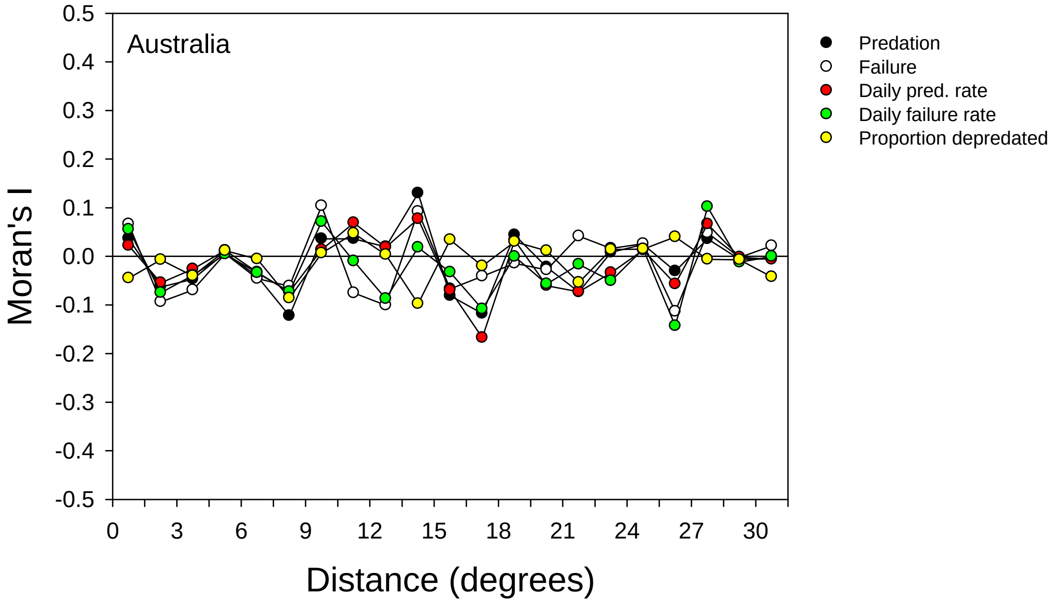




2) Spatial correlograms based on Moran's I

We calculated spatial correlograms for the same data and lag classes as above. We used function correlog in ncf package of R language.

Flat shape of the spatial correlograms also confirmed that small-scale autocorrelation in the residuals from trend surface analyses was absent (e.g. Fortin MJ, Dale M. 2005. Spatial analysis. A guide for ecologists. Cambridge University Press, Cambridge).



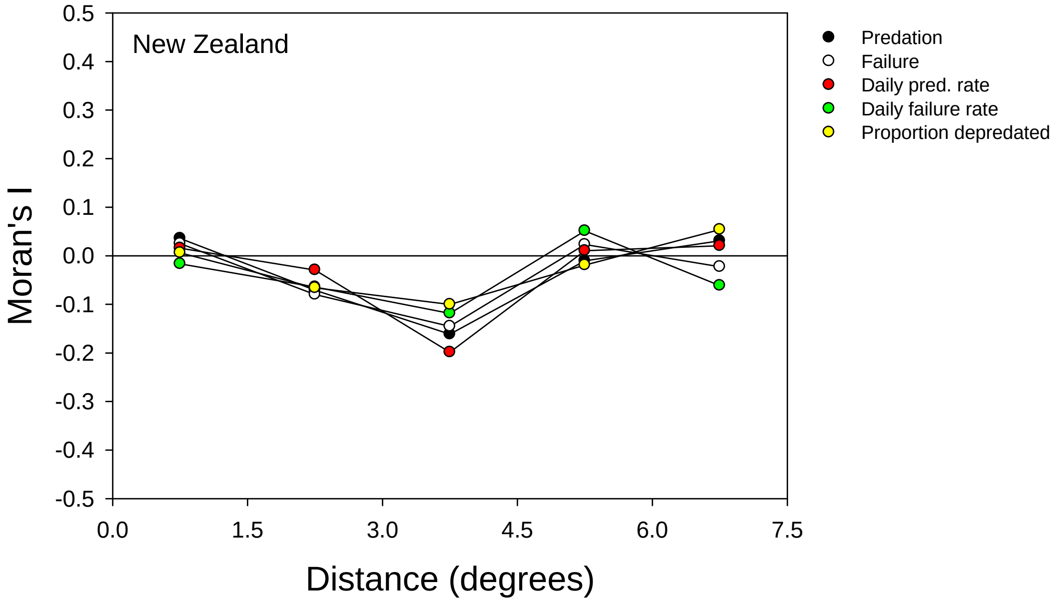


Figure S1 Distribution of studies across years when they were published (*n* = 169).

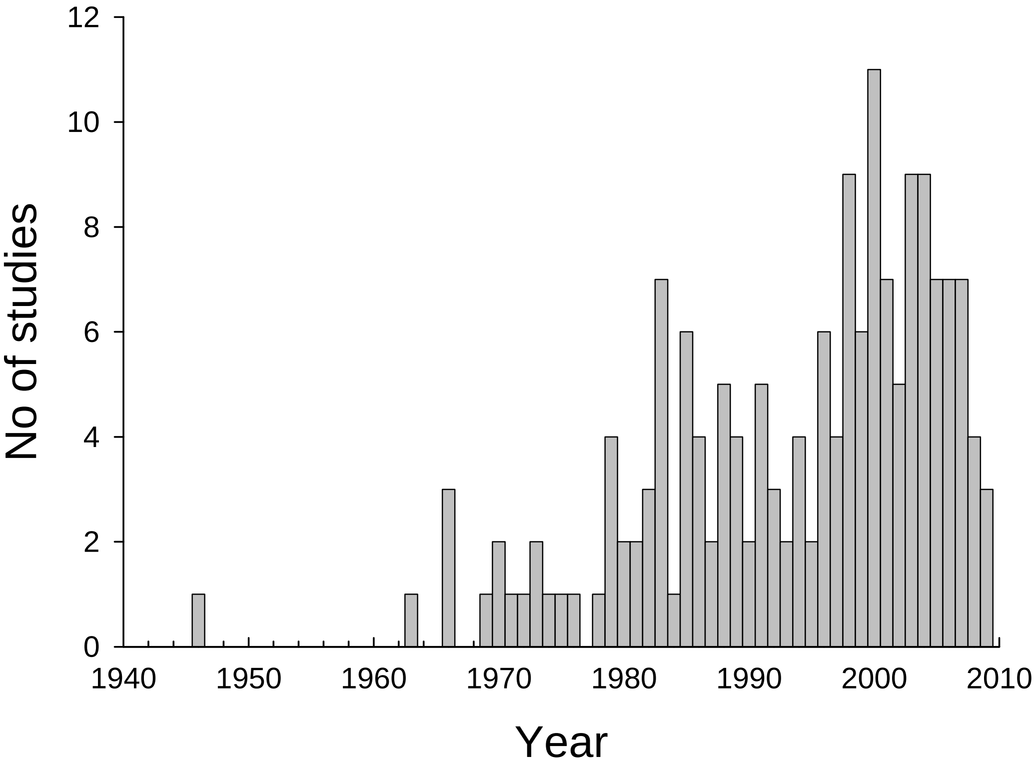
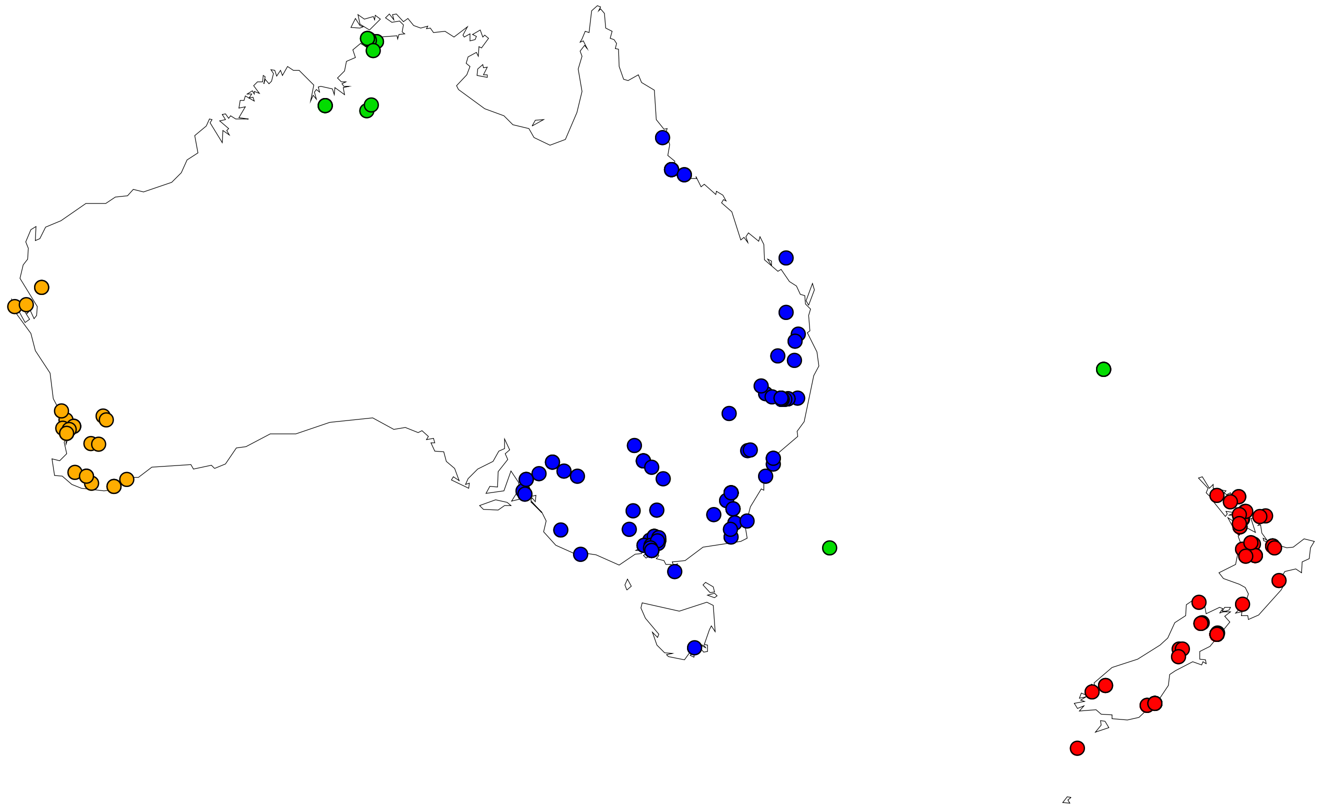


Figure S2 Geographical distribution of individual population estimates (n = 222). Colours indicate broad geographic regions: south-western Australia (orange), eastern Australia (blue), New Zealand (red), and other (green).



Příspěvek V.

Matysioková B. and Remeš V.: Responses to increased costs of activity during incubation in a songbird with female-only incubation: does feather colour signal coping ability? *Journal of Ornithology, in press.*

Samice sýkory koňadry (*Parus major*) po experimentálním hendikepování. Odstraněné letky záhy po vyhnízdění dorostou. Foto ©Beata Matysioková

Beata Matysioková and Vladimír Remeš

Responses to increased costs of activity during incubation in a songbird with female-only incubation: does feather colour signal coping ability?

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Abstract

Individuals differ in their ability to cope with energetically demanding situations while caring for the current brood and they can signal this ability by their colouration. We examined the impact of handicapping (clipping of wing and tail feathers) on an energetically demanding care behaviour (incubation) in the Great Tit (*Parus major*) females. We hypothesised that the intensity of carotenoid-based breast feather colouration signals the ability to cope with impaired flight ability and consequent increased energetic demands. If this is the case, females with more intensely coloured feathers should cope better with the handicap compared with less intensely coloured females, i.e. the impact of handicapping on mass loss and nest attentiveness should be negatively correlated with colouration. Handicapped females lost more weight than control females but did not decrease nest attentiveness to a greater extent, suggesting that females take the costs of handicapping on themselves. Females in poor condition were more severely influenced by handicapping. Intensity of female breast feather colouration did not correlate with either change in nest attentiveness or body mass loss during incubation. Intensity of breast feather colouration therefore does not appear to signal female ability to cope with this energetically demanding situation during incubation.

Keywords

Feather colouration, female ornaments, Great Tit, handicapping, incubation behaviour, nest attentiveness

Introduction

One of the basic tenets of evolutionary biology is that individuals differ in their ability to survive and cope with challenging environmental conditions. This ability can be influenced by the quality, age and condition of the individual (Fox et al. 2001). Individual quality and condition can be signalled to potential mates or rivals by various types of ornaments including those based on carotenoids (Searcy and Nowicki 2005). Carotenoid-based colouration is widespread in animals, including feathers and bare parts in birds (Olson and Owens 2005). Carotenoids cannot be synthesised by animals, must be obtained from food, and thus are potentially in short supply (Olson and Owens 1998). Full expression of carotenoid-based colouration is costly and carotenoids are involved in a number of trade offs with important physiological functions, including immune function and the level of oxidative stress (von Schantz et al. 1999; McGraw 2006). Consequently, intensity of carotenoid-based colouration is expected to indicate individual quality, condition, and/or capability of parental effort (Møller et al. 2000; Griffith et al. 2006).

The role of feather ornaments as indicators of quality, condition, and parental effort has been traditionally studied in males (reviewed in Griffith and Pryke 2006). However, there has been a recent surge of interest in the function and evolution of female ornaments (reviewed in Amundsen 2000; Amundsen and Pärn 2006; Kraaijeveld et al. 2007; Clutton-Brock 2009). Recent studies have demonstrated that female ornaments might work as badges of status enabling better access to resources (Murphy et al. 2009; Griggio et al. 2010) or as signals of good parenting abilities (Linville et al. 1998; Siefferman and Hill 2005; but see Smiseth and Amundsen 2000; Griggio et al. 2010). It has been even demonstrated that breeding success might be correlated with female ornament expression (Morales et al. 2007; Bitton et al. 2008) and males might base their mate choice at least partly on the degree of female ornamentation (Griggio et al. 2009; but see Murphy et al. 2009). However, studies examining female ornaments during reproduction in birds have been carried out during the nestling period while incubation was almost completely neglected (Amundsen 2000; Amundsen and Pärn 2006; but see Hanssen et al. 2006).

Incubation is a very important part of the breeding cycle in birds and parental effort during incubation can have strong consequences for the reproductive success of the pair (Deeming 2002). Normal embryo development requires eggs to be kept within a narrow range of temperatures (Webb 1987). Non-optimal temperatures can lead to reduced hatchability and longer incubation periods (Lyon and Montgomerie 1985; Webb 1987; Martin 2008). At the same time, incubation is energetically demanding for the incubating individual (Willams 1996; Thomson et al. 1998; Tinbergen and Williams 2002), who has to split its time between warming the eggs and foraging for itself. Hence, the ability to cope with energetically challenging situations during incubation can be very important for the reproductive success of the pair. In species with female-only incubation females can signal this ability by their carotenoid-based feather colouration and males might accordingly base their mate choice on the intensity of female's colouration (Amundsen and Pärn 2006; Kraaijeveld et al. 2007).

Handicapping is a useful and widely employed method to study the effects of energetically challenging situations on bird behaviour (Harrison et al. 2009). Birds can be handicapped by adding weights (Wright and Cuthill 1989; Griggio et al. 2005), taping their feathers (Senar et al. 2002a) or feather clipping (Slagsvold and Lifjeld 1988; Sanz et al. 2000). The last method is particularly suitable because it simulates events that can happen in the wild due to attacks by predators, and hence represents a risk to which birds might have become adapted (Slagsvold and Lifjled 1990). Broken or missing feathers are among the most often encountered natural handicaps in free ranging birds (Dawson et al. 2001). The ability to cope with such a handicap might therefore reveal an important component of individual quality (Harding et al. 2009).

In our study, we examined effects of handicapping (feather clipping) on incubation behaviour in the Great Tit (*Parus major*), a small, short-lived songbird with female-only incubation. In particular, we determined whether females differed in their responses to this energetic constraint in relation to the intensity of their yellow, carotenoid-based feather colouration. We predicted that impaired flight ability caused by handicapping would 1) extend the time females spent foraging off the nest and hence decrease time they spent on the nest, and/or 2) lead to higher body mass loss during incubation compared with controls. Moreover, if carotenoid-based feather colouration of the Great Tit females indicates ability to cope with such energetic constraint, females with more intense feather colour can be expected to be less affected by the challenge (Smiseth and Amundsen 2000; Doutrelant et al. 2008).

Methods

General field work

This work was conducted on three adjacent nest-box plots which are ca. 1 km apart in a broad-leaved forest dominated by oak (*Quercus petraea*) on Velký Kosíř in the east of the Czech Republic (49°32′N, 17°04′E). There are 300 nest-boxes in total placed about 1.5 m above ground and besides Great Tits they are inhabited by Collared Flycatchers (*Ficedula albicollis*), Blue Tits (*Cyanistes caeruleus*), Nuthatches (*Sitta europea*) and Coal Tits (*Periparus ater*). Fieldwork was carried out in 2008 from early April until May. We checked nest-boxes daily to record laying of the first egg and final clutch size. Day 0 was the day when the last egg was laid. Eggs in our population usually start to hatch on days 11–13 and hatching lasts for 2–3 days.

Cross-fostering

We wanted to isolate the direct effects of female incubation behaviour (i.e. egg warming) on hatching success and incubation period length, excluding any genetic or maternal effects. Therefore, we matched pairs of nests by their age and clutch size and exchanged clutches between pairs of nests. Clutches were exchanged as soon as, or immediately after, egg laying ended. We took the whole clutch from a nest, weighed it on a digital balance to the nearest 0.01 g and swapped it within the dyad (in 67 out of 82 nests on day 1, range 0–3). Nests were always exactly matched by the date when the last egg was laid. There was no difference in clutch size in 52 nests, a difference of one egg in 28 nests and of two eggs in two nests. The transfer of eggs took on average 8 min (range = 3–14 min).

Nest attentiveness

During incubation, we monitored the percentage of time incubating females spent on eggs, i.e. nest attentiveness. We deployed temperature data loggers by inserting a probe through the nest wall into the bottom of the nest cup. A second probe was mounted under the nest-box. We measured inner and outer temperature from 5 a.m. until 10:40 p.m. in 16-s intervals. On the nest temperature recordings, time when the incubating female is away from the nest is recognizable by downward spikes. Temperature drops quickly when the female leaves the clutch (off-bout) and then starts to increase sharply when she returns (on-bout; Fig. 1). Consequently, it is easy to make the difference between an attended and an empty nest (e.g. Zimmerling and Ankney 2005). From the pattern of nest temperatures, we calculated nest attentiveness throughout the day. To get ambient temperature for every nest, we took outer temperature for the start of each on- and off-bout and averaged it across the day. The data loggers were deployed on day 3 or 4 of incubation and the nest attentiveness was measured on the subsequent day (i.e., on days 4–5). Four days after experimental treatment (see below), we measured nest attentiveness again in the same way (i.e., on days 9–10).

Experimental treatment

The day after nest attentiveness was measured for the first time we captured females in the nest-box (i.e., on days 5–6) and weighed them on a spring Pesola balance (to the nearest 0.25 g). We handicapped every first and second female and left every third female as a control. In experimental females, we clipped primaries number 5, 6 and 8 (out of the total of 10 primaries, counted from the outside) on both wings, together with the four central tail feathers (out of the total of 12 tail feathers). We clipped the feathers as close to their bases as possible. This methodology was modified from Slagsvold and Lifjeld (1990). We handled control females in the same way as experimental females except that we did not clip the feathers. We returned all the females back to the nest-box through the entrance. Then we covered the entrance and waited for about one minute before leaving. The effect of handicapping was temporary and lasted until the post-breeding moult. Experimental and control females did not differ significantly in their initial body weight ($F_{1,75} = 1.2$, $P = 0.283$).

Females and clutches

The day after nest attentiveness was measured for the second time we captured females in the nest-box again (i.e., on days 10–11). We aged them (one year old or older, Svensson 1992), weighed them on a spring Pesola balance (nearest 0.25 g), and measured their tarsus by a digital calliper (nearest 0.01 mm). We took 10 to 15 yellow feathers from the upper right part of breast for later spectrophotometric analysis. Experimental and control females did not differ significantly in their tarsus length ($F_{1,54} = 0.14$, $P = 0.706$). After this day we checked nest-boxes daily to determine hatching success. We removed eggs that did not hatch and dissected them to determine the cause of hatching failure, i.e. eggs with no sign of embryo development or apparent dead embryo. We defined hatching success as percentage of fertilised eggs that hatched. Since we were interested in the effects of incubation behaviour on hatching success, we excluded eggs with no sign of embryo development from the analyses. Some unhatched eggs disappeared from the nest before we were able to dissect them. We removed these nests from the analyses of hatching success and thus the sample size was reduced. We calculated incubation period as the time from laying of the last egg to hatching of the first egg (Lyon and Montgomerie 1985).

Laboratory analyses

We quantified reflectance spectra of yellow feathers sampled from the breast using standard procedures (Andersson and Prager 2006). We used 10–15 feathers from each bird, which is sufficient to obtain reliable values from our species (Quesada and Senar 2006). We used an Avantes AvaSpec-2048 fibre optic spectrometer together with an AvaLight-XE xenon pulsed light source and a WS-2 white reference tile. The probe was used both to provide light and to sample the reflected light and was held perpendicular to the feather surface. We took five readings, each from a different part of each set of feathers. Feathers were arranged on black, nonreflective surface so that they overlapped extensively.

We obtained reflectance (%) from the wavelength of 320 to 700 nm in 1-nm increments (Fig. 2). We calculated so called carotenoid chroma, because it has been demonstrated that it correlated positively with the amount of carotenoids deposited in feathers in the Great Tit (Isaksson et al. 2008, Isaksson and Andersson 2008, see also Andersson and Prager 2006). Carotenoid chroma is a preferable index of the concentration of carotenoids in feathers in unsaturated carotenoid-based colours (Andersson and Prager 2006). Carotenoids present in Great Tit breast feathers (lutein, zeaxanthin) absorb maximally at around 450 nm (Andersson and Prager 2006) and the colour of our Great Tits was unsaturated, because we still had reasonable reflectance around 450 nm (see Fig. 2). We calculated carotenoid chroma as (R_{700} minus R_{450}) divided by R_{700}, where R_{700} is reflectance at 700 nm and R_{450} reflectance at 450 nm. In statistical analyses, we used the average carotenoid chroma calculated from the five readings from each set of feathers. To assess repeatability of our measurements, in a subsample of feathers, we arranged feathers anew and took other five readings and again averaged the carotenoid chroma calculated from them. We calculated repeatability of these two average carotenoid chroma estimates using the intraclass correlation coefficient (Lessels and Boag 1987), which was high ($r_i = 0.85$, $P < 0.001$, $n = 55$). As previous studies used also other characteristics derived from reflectance spectra, we also calculated brightness (R_{avg}), hue (λ_{R50}), and UV-chroma (see Montgomerie 2006). We calculated brightness (R_{avg}) and hue (λ_{R50}) according to Andersson and Prager (2006, p. 78). R_{avg} is reflectance averaged over the interval from 320 to 700 nm. λ_{R50} is wavelength halfway between R_{max} and R_{min}, where R_{max} is maximum reflectance and R_{min} is minimum reflectance between 320 and 700 nm. We also calculated UV-chroma as reflectance between 320 and 400 nm divided by reflectance between 320 and 700 nm. Experimental and control females did not differ significantly in either of the four colour characteristics: carotenoid chroma ($F_{1,54}$ = 0.02, P = 0.883), brightness ($F_{1,54}$ = 0.78, P = 0.381), hue ($F_{1,54}$ = 1.49, P = 0.227), and UV-chroma ($F_{1,54}$ = 1.43, P = 0.237).

Statistical analyses

We analysed the effects of experimental treatment on desertion rate (Likelihood-ratio test), change in nest attentiveness and female mass, incubation period length (general linear models), and hatching success (generalised linear models with binomial error distribution and logit link). We analysed all data using JMP software, with the exception of hatching success where we used SAS. Binomial models were fitted as the number of eggs that hatched / clutch size. We confirmed that the data met the assumptions of general linear models where these were used (Grafen and Hails 2002). We also checked that data in the binomial model were not overdispersed (deviance / *df* = 1.30).

Initial models included treatment and relevant other factors as predictors, which are apparent from Tables 1 and 2. In the analyses of the change in nest attentiveness (attentiveness before treatment minus after treatment) and body mass (mass after treatment minus before treatment), we fitted also interactions of treatment with female initial condition and breast carotenoid chroma (see Table 1). We did this because we wanted to know whether females differed in their response to handicapping based on their initial condition and yellow colouration. In the analyses of incubation period length and hatching success, we fitted only the interaction of treatment with female breast carotenoid chroma (see Table 2). We also re-ran all the models with other colour characteristics (hue, brightness, UV-chroma) instead of carotenoid chroma (see Table 3). Date of experiment was set so that the day of first experiment = 1. Body condition for each female was calculated as the residual from the linear regression of initial body mass on tarsus length. We always retained treatment in the final model as our main factor of interest whatever its statistical significance (see Grafen and Hails 2002). Other predictors were removed from the models starting with interactions. We removed non-significant predictors until we ended only with factors significant at $\alpha = 0.05$. In tables, we give *F*, *DF*, and *P* values of nonsignificant predictors immediately before they were removed from the model. Data are presented as mean ± *SD*.

Nest attentiveness is strongly affected by ambient temperature in the Great Tit (Kluijver 1950). Thus, when using attentiveness as a predictor in the analyses of incubation period length and hatching success, we adjusted for variation in ambient temperature among nests during sampling as follows. We fitted a regression of nest attentiveness on ambient temperature separately for both measurements (i.e., before and after treatment). In both cases there was a significant negative relationship (linear regression: before treatment $F_{1,75}$ = 13.3, P = 0.001, R^2 = 0.15; after treatment $F_{1,50}$ = 18.6, P < 0.001, R^2 = 0.27). We calculated the residual nest attentiveness and averaged the residuals from these two regressions. In this way, we obtained temperature-independent attentiveness for each female as a predictor variable.

When analysing observational data on mass decrease, it is necessary to take into account the problem of the regression toward the mean. Regression toward the mean occurs in repeated-measures analyses where subsets of population are compared based on their initial measurements. Thus, for instance it follows from this effect that initially heavy individuals will loose more mass than initially light individuals. However, since regression to the mean will affect both experimental and control groups, experimental studies are not subject to this problem (Kelly and Price 2005). Accordingly, in our study we interpret only the difference in mass loss between handicapped and control females, not the pattern in control females itself, which might be subject to the problem of the regression to the mean. However, this does not seem to be the case, because our results are the same even when the data is mathematically adjusted according to Kelly and Price (2005: Equation 6; results not shown).

Results

Altogether we performed cross-fostering on 82 nests. Five females deserted their nests after cross-fostering, leaving 77 females for our experiment (54 experimental and 23 control). There was a strong tendency for experimental females to desert their nests more often after treatment compared to control females (18 experimental and three control, $\chi^2 = 3.68$, $P = 0.055$, $n = 77$). Clutch size in our population was 10.4 ± 1.20 eggs ($n = 82$). Carotenoid chroma of yellow breast feathers was 0.64 ± 0.06 (range: 0.44 – 0.75), brightness was 0.24 ± 0.038 (0.17 – 0.33), hue was 501.3 ± 3.95 (495.0 – 505.6), and UV-chroma was 0.14 ± 0.008 (0.12 – 0.16, $n = 56$ in all four cases).

Nest attentiveness

Nest attentiveness before the treatment was 76.6 ± 4.77% ($n = 77$) and did not differ between experimental and control females ($F_{1,75} < 0.1$, $P = 0.875$). On average, nest attentiveness decreased between the first and second measurement by 1.4 ± 5.52% ($n = 52$). Treatment had no influence on the amount of change in nest attentiveness. However, although our nests were highly synchronised and differed by less than 14 days, there was a significant effect of date. In the first nests of the breeding season, nest attentiveness increased by about 5%, whereas in the last nests, it on the contrary decreased by about 5% (Table 1). No other factor had any influence on the change in nest attentiveness (Table 1, Fig 3a).

Body mass loss

Female body mass before the experiment was 20.37 ± 0.88 g ($n = 77$). Body mass loss between the first and the second weighing was 0.66 ± 0.58 g ($n = 56$). Mass loss was significantly higher in experimental females (0.81 ± 0.52 g, $n = 36$) than in control females (0.38 ± 0.59 g, $n = 20$; simple effect of treatment: $F_{1,54} = 8.0$, $P = 0.007$, Fig 3b). Mass loss was, however, also related to the initial condition of the female and the relationship differed between experimental and control females, as evidenced by the significant interaction between treatment and initial female condition (Table 1, Fig 4). No other factors were significant (Table 1).

Incubation period

Length of the incubation period was 11.8 ± 0.97 days (*n* = 48). Treatment had no effect on the length of the incubation period. It was negatively related to season and temperature-independent nest attentiveness; other factors were not significant (Table 2).

Hatching success

Overall hatching success was 91.1 ± 11.52% (*n* = 51). There was no effect of treatment on hatching success; similarly, no other factor was significant (Table 2).

It follows from the above results that female carotenoid-based feather colouration expressed as carotenoid-chroma was not correlated with her ability to cope with energetic handicap during incubation (see also Table 1). Similarly, no other colour characteristic (hue, brightness, and UV-chroma) was correlated with female coping ability, incubation period length or hatching success (Table 3).

Discussion

Handicapping had no influence on female incubation behaviour, the length of incubation period or hatching success. However, during incubation handicapped females lost overall more body weight than control females. Females in poor condition were more severely influenced by handicapping. Intensity of female breast feather colouration did not correlate with either female incubation behaviour, body mass loss during incubation, incubation period length or hatching success.

It seems that most of the costs of handicapping were channelled to female mass loss. This agrees with a previous study of the Great Tit, where handicapped females kept feeding rates to the nestlings unchanged at the cost of deteriorating own body condition (Sanz et al. 2000). Similar results were obtained in a study of the Tree Swallow *Tachycineta bicolor* where the costs of handicapping were paid through the loss of female body mass while nestling condition was unaffected (Winkler and Allen 1995). However, in incubating Tree Swallows, handicapped females both lost more mass than control females and also slightly decreased nest attentiveness (Ardia and Clotfelter 2007). In some other species handicapping did not influence female body mass or body condition but it did influence feeding rate and consequently nestling condition and growth, e.g. in Antarctic Petrels *Thalassoica antarctica*, Leach's Storm-petrels *Oceanodroma leucorhoa*, Cory's Shearwaters *Calonectris diomedea*, and tropical House Wrens *Troglodytes aedon* (Sæther et al. 1993; Mauck and Grubb 1995; Navarro and Gonzáles-Solís 2007; Tieleman et al. 2008). The two species where females invested into current brood at the expense of their own condition (Great Tits and Tree Swallows) are both short-lived with low probabilities of future reproduction, which selects for increased investment into current breeding attempt. On the contrary, long-lived species with a high probability of future reproduction, including Antarctic Petrels, Leach's Storm-petrels, Cory's Shearwaters, and tropical House Wrens, are expected to reduce any increases of investment into current brood to maximise their own survival (Roff 1992; Ghalambor and Martin 2001).

Our experimental treatment affected females that were in poor condition disproportionately more than those in good condition (see Fig. 4). The importance of good overall state of females for successful incubation in the Great Tit is further supported by our finding that handicapped females deserted their clutches more often than control females. Similar relationships between female condition and nest desertion have been also found in other species (Wiggins et al. 1994; Yorio and Dee Boersma 1994; Merilä and Wiggins 1997; but see Bleeker et al. 2005). An obvious explanation for this pattern is that incubation is energetically demanding and females in poor condition, caused by low body mass or impaired flight abilities, are not able to withstand the energetic stress (Willams 1996; Thomson et al. 1998; Tinbergen and Williams 2002).

Intensity of yellow breast feather colouration was not related to the ability of females to cope with the handicap. One might ask how female colouration could help prevent a change in body mass. Handicapping is a standard way of testing whether an individual is of higher quality, i.e., is better able to cope with a challenging situation. Our experimental approach was motivated by a widespread finding that individual quality often shows up only under unfavourable conditions (e.g. brood size manipulations, various forms of handicapping, food restrictions; e.g. Ardia and Clotfelter 2007; Doutrelant et al. 2008). We conjecture that handicapped females could overcome the handicap by working harder. On a mechanistic basis, it means to put more energy into flight to get resources (self-maintenance) and simultaneously care for the clutch (incubate), without these functions being compromised. Of course, this higher effort is expected to bear costs, e.g. higher metabolic rate and higher oxidative stress generated by heavy work. This can be presumably achieved only by higher-quality individuals. There certainly was a variation among females in the degree of their body mass loss (see Figs 3 and 4), i.e., in their ability to cope. We were interested whether this variation could be ascribed to female colouration and found out that this was not the case.

We would like to mention three potential problems when generalizing our results. First, costs of the manipulation could have also been observed after hatching. This might have been particularly true during nestling feeding, when females have to fly more. Previously, all studies examining female feather colouration during reproduction in birds have been carried out during the nestling period (Amundsen and Pärn 2006; but see Hanssen et al. 2006). Several of them investigated the function of yellow breast feather colouration in Great and Blue Tits but generated mixed results. Some found a positive relationship between the intensity of female yellow colouration and breeding success, whereas others found no or even a negative relationship (correlative studies: Senar et al. 2002b; Mänd et al. 2005; Hidalgo-Garcia 2006; experiment: Doutrelant et al. 2008). Hence, information content of female yellow colouration might differ between parts of the breeding cycle, i.e., incubation vs. feeding of young. Second, the coloration of the females that deserted just after the manipulation is missing. It is possible that these deserting females had low carotenoid chroma values and were of inferior quality. Consequently, if we were left with only higher-quality individuals, our test of the indicator potential of the carotenoid-based coloration in females would have been weakened. Third, males feed females during incubation in the Great Tit. If we found better coping ability in more colourful females, we would not be sure whether they cope better because they are able to work harder, or because they are more helped by their males. However, male incubation feeding is not a source of potential bias in our study, because we found no effect of female colour on the ability to cope with energetic stress. Moreover, we have studied this problem during three years in a nearby population and there was no effect of female colour on male incubation feeding (Matysioková and Remeš 2010).

While bearing the above-mentioned reservations in mind, our results are not consistent with a role for feather carotenoids as indicators of female quality or capacity for extra parental effort, as has been demonstrated by several other studies (see above). Differences in the results of multiple studies investigating feather ornaments in the same species are known to occur due to population differences in the information content of the ornamental traits (Dunn et al. 2008; Galván and Moreno 2009) and different expression of ornaments in different populations and subspecies (Hill 2002). Great Tit subspecies differ strongly in the intensity of yellow breast colouration (Harrap and Quinn 1996). However, there is no work quantifying differences in yellow colouration and in the functional ecology of feather ornaments among populations of the Great Tit. Nevertheless, it is at least possible that different populations are subject to different constraints on the expression of yellow colouration and that the information content of feather ornaments varies in space. Only rigorous studies conducted in an explicitly comparative framework might provide answers to the heterogeneity of studies conducted so far (Senar et al. 2002b; Mänd et al. 2005; Hidalgo-Garcia 2006; Doutrelant et al. 2008; this study).

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Figure captions

Fig. 1 Graph of a typical incubation profile of the Great Tit.

Fig. 2 Average (± SD) reflectance spectrum of yellow breast feathers of female Great Tits in 1-nm increments (*n* = 56).

Fig. 3 Nest attentiveness (a; mean ± SE) and body mass of incubating females (b) in control and experimental nests before and after handicapping (feather clipping)

Fig. 4 Body mass change of incubating Great Tit females in relation to female condition before experiment (mass residuals in relation to tarsus) separately for control and experimental (clipped feathers) nests. More negative values of mass change mean higher mass loss over incubation

Fig 1

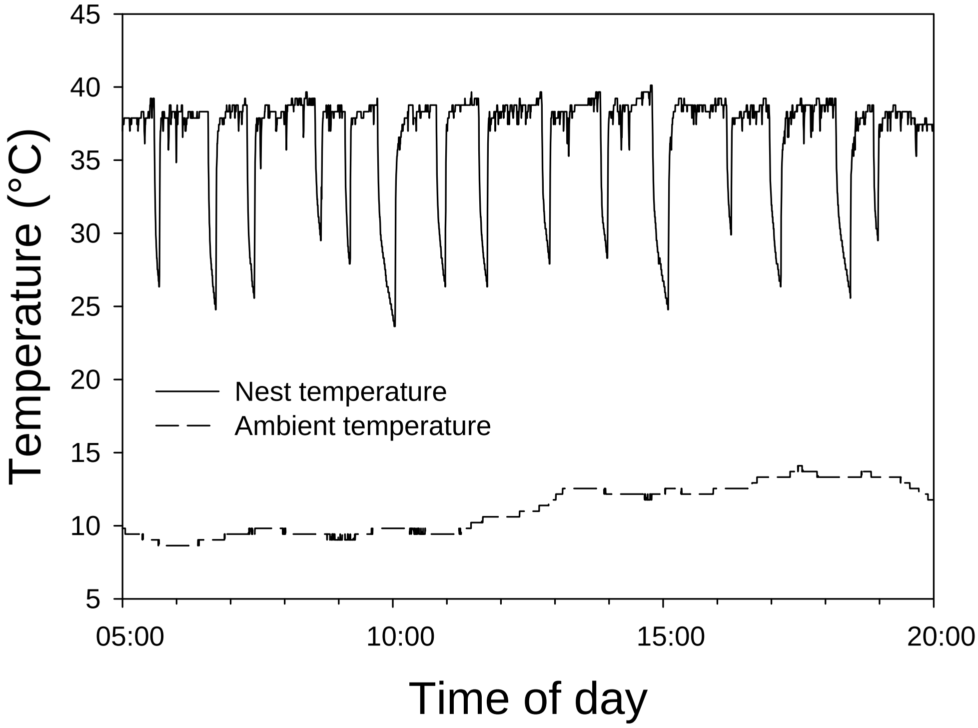
45
40
35
30
25
20
15
10
5
Temperature (°C)
Nest temperature
Ambient temperature
05:00
10:00
15:00
20:00
Time of day

Fig 2

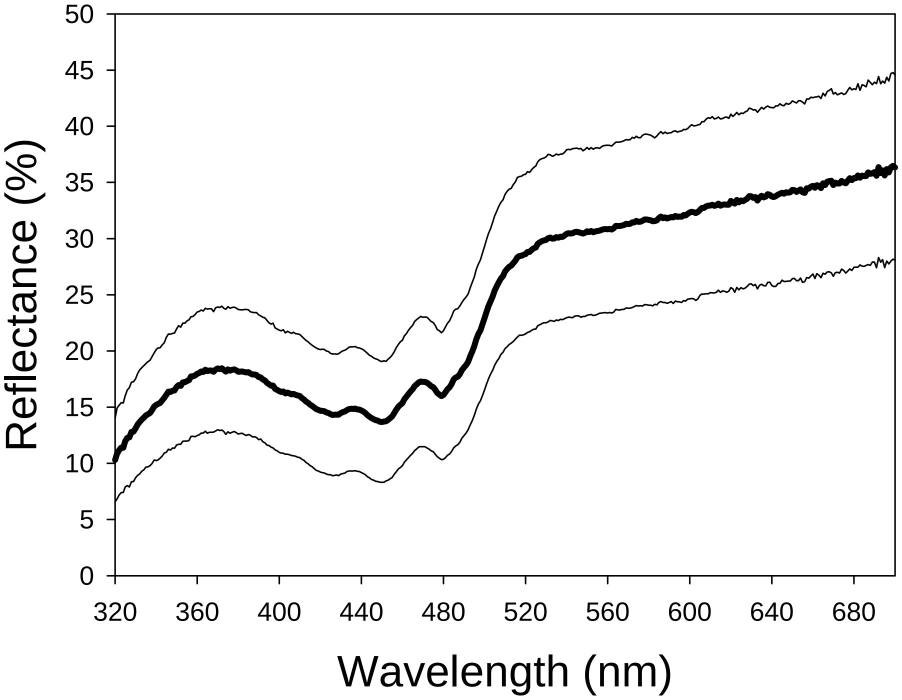
Reflectance (%)
0
5
10
15
20
25
30
35
40
45
50
320
360
400
440
480
520
560
600
640
680
Wavelength (nm)

Fig 3

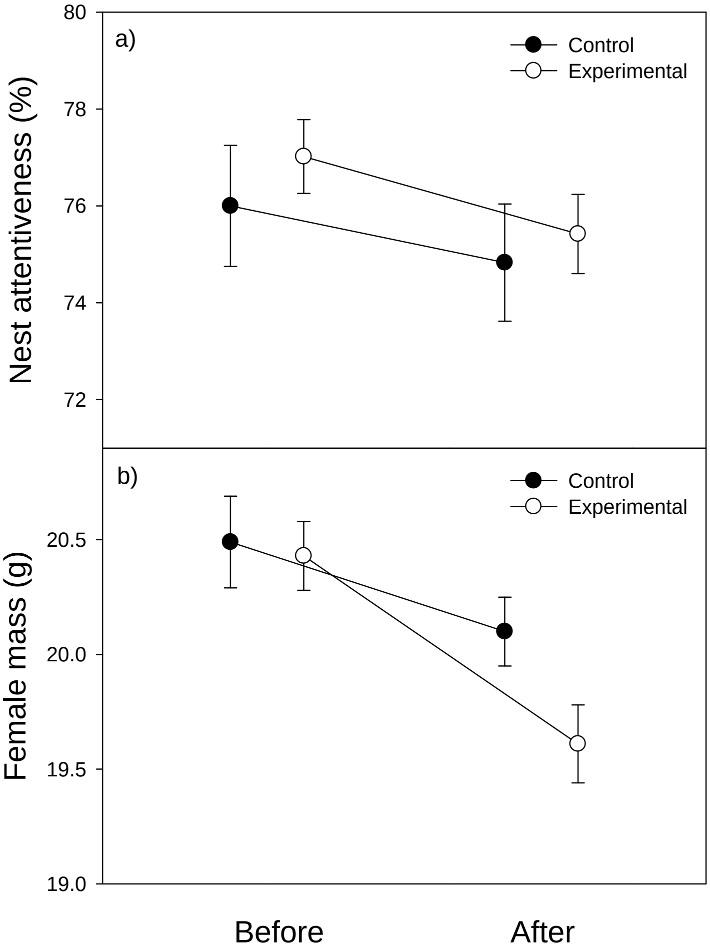
a)
Control
Experimental
Nest attentiveness (%)
80
78
76
74
72
b)
Control
Experimental
Female mass (g)
20.5
20.0
19.5
19.0
Before
After

Fig 4

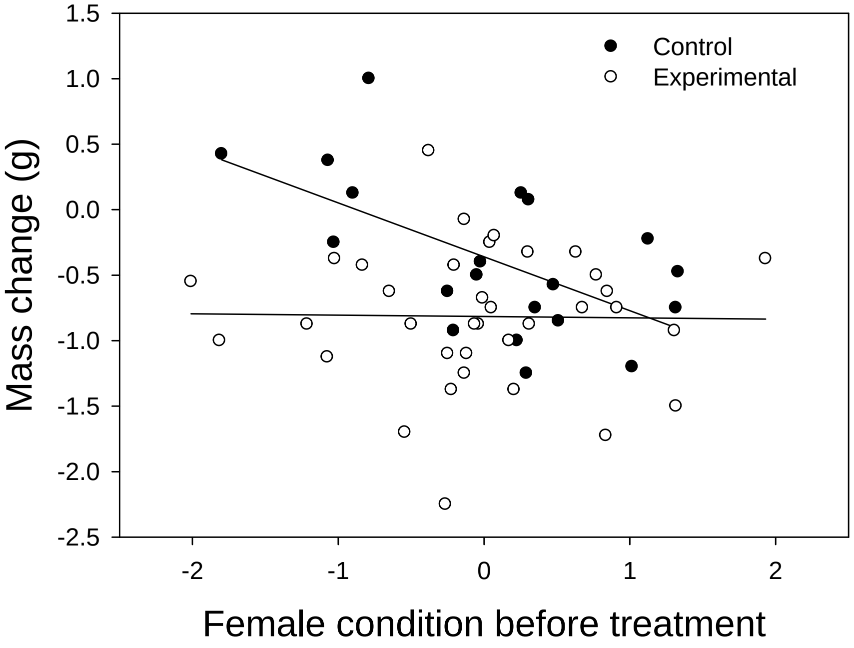
Mass change (g)
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
-2.5
-2
-1
0
1
2
Female condition before treatment
● Control
○ Experimental

Table 1 Models explaining the change in nest attentiveness and in female body mass during incubation

	Change in nest attentiveness (%)[a]				Change in body mass (g)[b]			
Factor	*F*	*DF*	*P*[c]	Estimate (*SE*)[d]	*F*	*DF*	*P*[c]	Estimate (*SE*)[d]
Intercept				-4.71 (2.370)				-0.36 (0.116)
Treatment	0.1	1,49	**0.818**	0.35 (1.531) (handic.)	10.0	1,52	**0.003**	-0.46 (0.144) (handic.)
Date of experiment	7.4	1,49	**0.009**	0.84 (0.308)	0.3	1,49	0.601	+
Female carotenoid chroma	<0.1	1,46	0.952	+	1.6	1,50	0.213	-
Female age	3.6	1,48	0.064	older>1y old	3.1	1,51	0.086	older>1y old
Female condition	2.2	1,47	0.144	+	5.8	1,52	**0.020**	-0.41 (0.140)
Female condition x Treatment	0.1	1,44	0.719		5.2	1,52	**0.026**	0.40 (0.175) (handic.)
Female carotenoid chroma x Treatment	0.6	1,45	0.461		0.6	1,48	0.425	

Final models: [a] $F_{2,49} = 3.7$, $P = 0.031$, $R^2 = 0.13$, $n = 52$; [b] $F_{3,52} = 5.9$, $P = 0.002$, $R^2 = 0.25$, $n = 56$.

[c] *P*-values of the final models are in bold.

[d] Sign (+ or -) or text in Estimate show the direction of the nonsignificant effects; exact parameter estimates are listed only for variables retained in final models, including treatment whatever its significance.

Table 2 Models explaining incubation period length and hatching success

	Incubation period (day)[a]				Hatching success (logit scale)[b]			
Factor	*F*	*DF*	P^c	Estimate (*SE*)[d]	χ^2	*DF*	P^c	Estimate (*SE*)[d]
Intercept				13.43 (0.358)				3.74 (0.584)
Treatment	0.8	1,44	**0.372**	0.21 (0.236) (handic.)	0.3	1,39	**0.570**	0.44 (0.771) (handic.)
Date of experiment	24.1	1,44	**<0.001**	-0.23 (0.047)	0.1	1,35	0.925	-
Temperature-indep. nest attentiveness	4.6	1,44	**0.037**	-7.14 (3.325)	0.4	1,37	0.515	+
Clutch size	1.47	1,43	0.232	+	1.8	1,38	0.186	+
Female carotenoid chroma	0.333	1,42	0.567	+	0.3	1,36	0.592	-
Female carotenoid chroma x Treatment	0.12	1,41	0.730		3.5	1,34	0.063	

Final models: [a] $F_{3,44} = 10.3$, $P < 0.001$, $R^2 = 0.41$, $n = 48$; [b] $n = 41$.

[c] *P*-values of the final models are in bold.

[d] Sign (+ or -) in Estimate shows the direction of nonsignificant effects; exact parameter estimates are listed only for variables retained in final models, including treatment whatever its significance.

Table 3 Tests of the effects of brightness (R_{avg}), hue (λ_{R50}), and UV-chroma, together with their interaction with handicapping, on the change in nest attentiveness and body mass, incubation period length, and hatching success. Colour characteristics were tested while added in turn to full models presented in Tables 1 and 2 (without carotenoid chroma).

	Attentiveness (%)			Body mass (g)			Incubation period (day)			Hatching success (logit scale)		
	F	*DF*	*P*	*F*	*DF*	*P*	*F*	*DF*	*P*	χ^2	*DF*	*P*
R_{avg}	1,45	<0.1	0.838	1,49	0.3	0.59	0.4	1,42	0.543	0.7	1,35	0.407
R_{avg} x Treatment	1,44	0.3	0.564	1,48	0.1	0.753	0.7	1,41	0.406	<0.1	1,34	0.879
λ_{R50}	1,45	<0.1	0.874	1,49	1.2	0.286	0.1	1,42	0.778	0.1	1,35	0.769
λ_{R50} x Treatment	1,44	0.1	0.795	1,48	0.2	0.701	0.2	1,41	0.621	0.5	1,34	0.472
UV-chroma	1,45	0.8	0.386	1,49	0.9	0.336	<0.1	1,42	0.870	<0.1	1,35	0.930
UV-chroma x Treatment	1,44	0.1	0.733	1,48	1.1	0.299	0.9	1,41	0.353	2.5	1,34	0.115

Příspěvek VI.

Matysioková B. & Remeš V. 2010: Assessing the usefulness of ptilochronology in the study of melanin- and carotenoid-based ornaments in the Great Tit *Parus major*. *Ibis 152: 397–401.*

Ptilochronologie je metoda využívající k určení nutriční kondice ptáků rychlost růstu per. Ta je odvozena ze šířky růstových proužků. Na obrázku jsou rýdovací pera rákosníka zpěvného (*Acrocephalus palustris*) s patrnými růstovými proužky. Foto ©Vladimír Remeš

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Short communication

Assessing the usefulness of ptilochronology in the study of melanin- and carotenoid-based ornaments in the Great Tit *Parus major*

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Keywords: feather growth, nutritional condition, signalling.

Ptilochronology is a method for assessing the nutritional condition of birds based on the width of daily growth bars on feathers. Wide growth bars reflect fast feather growth and as feather growth is costly, the width of the bars reflects the condition of a bird during moult (Grubb 1989). It is a very simple and inexpensive method, which makes it ideal for field research (Grubb 2006). In addition, as a sampled feather is soon replaced by a new feather, a process that would take place during natural moult, this method is also harmless to the bird.

Ptilochronology has therefore become a popular method for assessing the nutritional state of birds in the wild (Grubb 2006). However, the efficacy of the method might differ, for example, between sexes (Grubb 1989, Takaki *et al.* 2001, Bostrom & Ritchison 2006) or age categories (Grubb *et al.* 1991). Kern and Cowie (2002) failed to find any relationship between the growth of different types of feathers taken from the same individual. Furthermore, other studies have concluded that the general validity of the method is unclear and that it can be used only under strictly controlled conditions (Murphy & King 1991).

Despite these reservations, ptilochronology has been used in several studies of feather ornaments as an indicator of condition (Hill & Montgomerie 1994, Eeva *et al.* 1998, Keyser & Hill 1999, Doucet 2002, Senar *et al.* 2003, van Oort & Dawson 2005, Hegyi *et al.* 2007, Siefferman *et al.* 2008, Kimball 2009). The assumption is that these species moult body and contour feathers at the same time. Thus, if both ornaments and feather growth bars reflect condition (Griffith *et al.* 2006, Grubb 2006, Hill & McGraw 2006), then these two traits should covary. Carotenoid-based feather ornaments are expected to reflect a bird's condition and there is evidence supporting this claim (von Schantz *et al.* 1999, Hill 2002, McGraw 2006a). Although melanin ornaments were thought not to reflect condition (McGraw 2006b), recent evidence suggests that they might be as condition-dependent as carotenoid-based ornaments (Griffith *et al.* 2006, Galván & Alonso-Alvarez 2008).

No clear-cut relationship between feather ornaments and feather growth has emerged from studies to date (see above). As ptilochronology is a very simple method and has great potential in field ornithology, we examined the relationships between both carotenoid- and melanin-based ornaments and feather growth in a large sample of individuals of a wild passerine. We chose the Great Tit *Parus major* because expression of its carotenoid-based (Hõrak *et al.* 2000, Tschierren *et al.* 2003, but see Fitze & Richner 2002) and melanin-based ornaments (Fitze & Richner 2002, Galván & Alonso-Alvarez 2008) is known to depend on condition during moult and feather growth. Thus, if feather growth also reflects condition during moult, we expected a positive correlation between the width of feather growth bars and the expression of both carotenoid- and melanin-based ornaments.

METHODS

This research was conducted at three adjacent nestbox plots (188 nestboxes in total) in a deciduous forest near the village of Grygov (49°31′N, 17°19′E) in eastern Czech Republic. Nestboxes were placed 1.5 m above the ground and, besides Great Tits, were also inhabited by Blue Tits *Cyanistes caeruleus*, Collared Flycatchers *Ficedula albicollis* and Nuthatches *Sitta europaea*. Fieldwork was carried out between 2005 and 2007 from early April until mid-June.

During feeding of nestlings (median age of young females = 7 days, males = 9 days), we captured parents in the nestbox. We captured females at almost all the nests (*n* = 165). However, because of time constraints, we captured males only from a subset of nests (*n* = 109). We measured their tarsus-length with digital callipers (to the nearest 0.01 mm) and weighed them on a spring Pesola balance to the nearest 0.125 g. From each bird we took 10–15 yellow feathers from the upper right part of the breast for spectrophotometric analysis. We photographed the bird's breast with a digital camera (Panasonic DMC-FZ5). When taking a picture of the breast, we held the bird outstretched by its tarsi and beak and photographed it together with a ruler from a standard distance following the protocol of

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Figuerola and Senar (2000). All measurements and photographs were taken by V.R. We also plucked the second outer rectrix from the right side of the tail for later measurement of growth bars on feathers. We determined the age of the birds based on their plumage as 1 year old or older (Jenni & Winkler 1994). For each bird, we calculated its condition as the residual from the linear regression of body mass on tarsus-length (Brown 1996).

Analyses of samples

We quantified reflectance spectra of yellow feathers sampled from the breast using standard procedures (Andersson & Prager 2006). We used 10–15 feathers from each bird, which is sufficient to obtain reliable values from our study species (Quesada & Senar 2006). We used an Avantes AvaSpec-2048 fibre-optic spectrometer together with an AvaLight-XE xenon pulsed light source and WS-2 white reference tile. The probe was used both to provide light and to sample reflected light and was held perpendicular to the feather surface. We took five readings from different parts of each feather. Feathers were arranged on a black, non-reflective surface so that they overlapped extensively.

We obtained reflectance (%) from 320 to 700 nm in 1-nm increments. We calculated carotenoid chroma as (R700–R450)/R700, where R700 is the reflectance at 700 nm and R450 the reflectance at 450 nm. In statistical analyses we used the average carotenoid chroma calculated from the five readings from each set of feathers. To assess repeatability of our measurements, in a subsample of feathers we rearranged feathers and took another five readings, and again averaged the carotenoid chroma calculated from them. We calculated repeatability of these two average carotenoid chroma estimates as an intraclass correlation coefficient (Lessels & Boag 1987), which was sufficiently high ($r_i = 0.85$, $P < 0.001$, $n = 55$). We use carotenoid chroma here because it reflects the amount of yellow carotenoids (lutein and zeaxanthin) in breast feathers in the Great Tit (Isaksson & Andersson 2008, Isaksson *et al.* 2008).

We analysed photographs of breast feathers in Adobe PHOTOSHOP CS3 Extended. We used the quick selection tool to roughly delimit the black stripe. Then we manually finished the selection so that it was as precise as possible and measured the surface area of the stripe. We used a standard in photographs of each bird to adjust the scale of each photograph and to obtain absolute surface area (cm^2). We defined stripe surface as the area of the black feathers between the point of inflexion, where the ventral stripe widens to a throat patch, and the posterior end of the stripe (Figuerola & Senar 2000). All measurements were taken by B.M. To assess repeatability, a different observer measured a subsample of photographs; repeatability was high ($r_i = 0.87$, $P < 0.001$, $n = 75$).

As it is not possible to use the standard technique (see Grubb 1989, 2006) to determine the width of feather growth bars in the Great Tit (Senar *et al.* 2003), we used the modification suggested by Carrascal *et al.* (1998). We measured the length of the feather and overall width of the first 10 measurable distal growth bars to the nearest 0.1 mm. Growth bars were not apparent in all the feathers and we excluded these feathers from the analyses. All measurements were taken twice. To obtain the width of one growth bar (mm) we divided the average of the two measurements by 10. Repeatability of the two measurements was high ($r_i = 0.99$, $P < 0.001$, $n = 210$). All measurements were taken by B.M.

Statistical analyses

We analysed variation in growth bar width using general linear mixed models (GLMM). As we sampled some individuals repeatedly across years, we included individual identity as a repeated factor in the mixed procedure of SAS. First, we fitted a model with the following factors and covariates: year, sex, age, carotenoid chroma, black stripe, length of tail feather and condition. We subsequently removed non-significant factors (age, black stripe, condition) until we had only statistically significant variables at the level of $\alpha = 0.05$ in the model. F and P values for non-significant factors given in the Results section are those immediately before the factor was removed from the model. Growth bar width was transformed to the power of four to normalize its originally left-skewed distribution and all the analyses were conducted using this transformation. Residuals from each linear model were checked to conform to the requirements of normal distribution, equal variance and linearity (Grafen & Hails 2002).

RESULTS

We obtained tail feathers from 238 birds over 3 years (146 females, 92 males). Average length of tail feathers was 65.9 mm (mean ± 3.15 sd, $n = 238$) and was larger in males than in females ($F_{1,236} = 226.27$, $P < 0.001$). Individual identity as a random repeated factor was significant (estimate = 5.089 ± 0.4685 se, $z = 10.86$, $P < 0.001$).

The width of feather growth bars was 2.87 mm (mean ± 0.23 sd, $n = 210$), being larger in females than in males ($F_{1,202} = 13.14$, $P < 0.001$) and differed with year ($F_{2,202} = 4.82$, $P = 0.009$). The growth bar width also correlated negatively with the carotenoid chroma of yellow breast feathers ($F_{1,202} = 5.82$, $P = 0.017$; Fig. 1a) and positively with the total length of the feather ($F_{1,202} = 57.91$, $P < 0.001$; whole model $R^2 = 0.56$). There was no significant relationship of growth bar width to the size of the black breast stripe ($F_{1,199} < 0.01$, $P = 0.971$; Fig. 1b), to condition

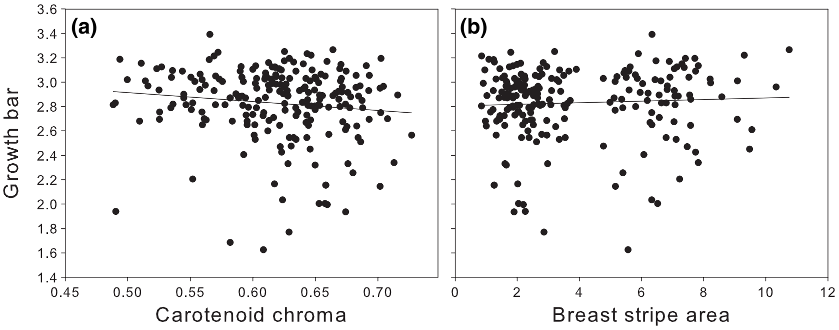

Figure 1. Relationship between the width of growth bars of tail feathers (mm) and (a) carotenoid chroma of yellow breast feathers (for definition see Methods; $n = 210$), and (b) black breast stripe area (cm^2, $n = 210$). For the sake of convenience, untransformed data not adjusted for other covariates are presented. However, note that all analyses were conducted on transformed data.

($F_{1,200} = 0.83$, $P = 0.362$) or to age ($F_{1,201} = 1.06$, $P = 0.305$).

Individual identity as a random repeated factor was significant in the analysis of feather growth in both the full model (estimate = 332.8 ± 33.88 se, $z = 9.82$, $P < 0.001$) and the final model after non-significant fixed-factors were removed (estimate = 322.6 ± 32.10 se, $z = 10.05$, $P < 0.001$).

DISCUSSION

We found no relationship of growth bar width to the size of the melanin ornament but, unexpectedly, a negative relationship to the chroma of the carotenoid ornament. Thus, the growth rate of tail feathers declined as carotenoid levels in breast feathers increased.

The available evidence suggests that carotenoid-rich feather ornaments are a reflection of good body condition during feather growth (von Schantz *et al.* 1999, Hill 2002, McGraw 2006a). This is also true for the Great Tit (Hõrak *et al.* 2000, Tschierren *et al.* 2003, but see Fitze & Richner 2002). Given comparatively well-established condition-dependence of carotenoid-based feather ornaments, we expected positive relationships between their expression and the growth rate of tail feathers. However, contrary to our expectations, there was a significant negative relationship between the carotenoid chroma of yellow breast feathers and growth rate of tail feathers. This runs contrary to previous studies, where the correlation between the intensity of carotenoid-based ornaments and feather growth rate was either positive (Hill & Montgomerie 1994, Senar *et al.* 2003) or absent (Eeva *et al.* 1998, van Oort & Dawson 2005, Hegyi *et al.* 2007). However, the significance of our results should not be overstated, because the relationship between carotenoid content and feather growth was not very strong ($r = -0.16$; see also Fig. 1).

Melanin-based ornaments were thought not to be condition-dependent (McGraw 2006b). However, recent evidence suggests that they might be as condition-dependent as carotenoid-based ornaments (Griffith *et al.* 2006). Potential proximate mechanisms of condition-dependence might include corticosterone-mediated stress (Roulin *et al.* 2008), oxidative stress (Galván & Alonso-Alvarez 2008), or the allocation of calcium among competing physiological functions (Roulin *et al.* 2006). However, we found no relationship of growth bar width to the size of the melanin-based black breast stripe, commensurate with the findings of previous studies (Senar *et al.* 2003, Hegyi *et al.* 2007, Kimball 2009). Thus, our study adds to a growing body of evidence that feather growth does not correlate with the expression of melanin ornaments, at least in small songbirds.

The usefulness of ptilochronology has been challenged (Murphy & King 1991, Takaki *et al.* 2001, Kern & Cowie 2002, van Oort & Otter 2005, Bostrom & Ritchison 2006). Here, we did not test methods of conducting ptilochronology but used standard methods to compare the relationship between feather ornaments and feather growth from a large sample of birds. Results of studies conducted to date are highly inconsistent, even when conducted on the same species. For instance, in the Great Tit, feather growth has been shown to correlate positively with hue of yellow breast feathers (Senar *et al.* 2003), negatively with chroma (this study), or not at all with either brightness (Eeva *et al.* 1998, Senar *et al.* 2003, Hegyi *et al.* 2007) or chroma (Senar *et al.* 2003, Hegyi *et al.* 2007). Similar inconsistencies can be found in studies of other bird species (Hill & Montgomerie 1994, van Oort & Dawson 2005). At least two possible conclusions can be drawn from these studies. First, ptilochronology may be an unreliable approach for assessing condition in wild-ranging birds, at least until rigorous methodological studies demonstrate otherwise. Secondly, ptilochronology may be reliable in certain species or for application to certain types of ornaments, but to reveal interspecific patterns would require many more studies to be conducted on a broader spectrum of species. Moreover, differences in results within a species are known to occur due to population differences in the information content of the ornamental traits (Dunn *et al.* 2008, Galván & Moreno 2009) and different expression of ornaments in different populations and subspecies (Hill 2002). Again, studies conducted on populations differing in resource limitation (e.g. carotenoids, see Hill 2002) or expression and information content of feather ornaments could reveal interesting patterns. The usefulness of ptilochronology as a simple field method to estimate a bird's condition during moult could still emerge from future studies, especially if these are done in an explicitly inter- or intraspecific comparative framework.

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