# Interspecific Feeding in Birds: A Short Overview

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# Interspecific feeding in birds: a short overview

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**Abstract.** Interspecific feeding is an uncommon behaviour where an individual of one species feeds individuals (mostly offspring) of another species. Observations have been made in many avian species but causes of this behaviour remain unknown and no hypothesis was proposed to fully explain its occurrence. In this review, I collected observations of interspecific feeding in birds reported during the last 40 years and compiled a comprehensive dataset based on all published reports of interspecific feeding. It consists of 186 cases observed in 107 species worldwide and summarizes the information on involved species, their age, sex, and possible causes of this misdirected parental care. Additionally, I report a case of Great Spotted Woodpeckers' *Dendrocopos major* young fed by Eurasian Nuthatches *Sitta europaea*. Observations of interspecific feeding are highly skewed in favour of North American and European species, probably due to historical (long research and ornithology traditions) and language issues (publishing in English). Interspecific feeding does not seem to be related to nest type but is mostly associated with males allured by loud calls of nestlings from nearby allospecific nests. However, most of the observations remain only anecdotic and an empirical research that would try to find plausible explanations of the evolutionary advantages of this behaviour still remains to be carried out.

**Key words:** allofeeding, alloparents, database, interspecific helpers, misdirected parental care

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## INTRODUCTION

Feeding of offspring in birds is usually conducted by one or both of their parents, but there are some instances where other individuals beside the biological parents help raising the young (helpers; Skutch 1961). While intraspecific help is relatively common and cooperative breeding occurs in 9% of avian species (Cockburn 2006, Griesser et al. 2017), interspecific occurrences are much rarer (Krištín 2009). They are usually limited to obligate and facultative brood parasites, such as cuckoos Cuculidae, cowbirds Icteridae, ducks Anatidae, and fowl Galliformes (Krüger & Pauli 2017). However, there are known instances of occasional interspecific helpers even in species with no social breeding or parasitic tendencies (Shy 1982).

Shy (1982) reviewed known cases of interspecific help (in particular feeding) and listed 139 cases of interspecific feeding across 67 species and 27 families of birds (counts include only helper species and were adjusted according to the updated taxonomy by Gill & Donsker 2020). Shy (1982) also proposed eight categories of possible causes of this behaviour resulting from (i) mixed clutches in one nest, (ii) shifting attention of an adult to other nest due to their inability to find a mate, (iii) own lost clutch, (iv) close nest vicinity, (v) incubating mate, (vi) loud call of young, (vii) adopting orphans or (viii) other, miscellaneous reasons. According to the author, the last category was found most frequently (30% of listed cases), closely followed by close nests (25%) and mixed clutches (22%; Appendix 1).

Shy's (1982) review is still the most comprehensive work focused on interspecific feeding in birds. However, the collected cases are mostly focused on North American and European species of birds with no observations from other parts of the world (with only some exceptions from Costa Rica and South Africa). Grangé et al. (2010) reviewed and listed new studies concerning interspecific feeding, but only in breeding species of European birds. Besides, the paper might meet a language barrier as it was written in French and some of the studies reporting interspecific feeding in European species were missing (e.g. Yoerg & O'Halloran 1991, Krištín 2009, Pugacewicz 2009). Thus, an up to date compilation of observations of interspecific feeding across the whole world still

remains to be composed. Here, I collected and examined cases of interspecific feeding reported worldwide since the publication of Shy's (1982) review. Additionally, I also report my own observation of interspecific feeding of Great Spotted Woodpeckers' *Dendrocopos major* nestlings fed by Eurasian Nuthatches *Sitta europaea.*

## METHODS

I searched literature published in years 1983–2020 (since the release of Shy's 1982 review) for reports of the interspecific feeding in birds worldwide. First, I used keywords 'interspecific feeding' birds, 'misdirected parental care' birds, 'alloparental feeding' birds, 'interspecific parents' birds, and 'heterospecific alloparents' birds for a search in Google Scholar database. I used Google Scholar instead of other scientific databases (i.e. Scopus, Web of Science) because it is the most inclusive of results for theses, books, short reports in local journals, and it searches the whole text of the articles and not only titles and abstracts. The search was completed on 11 June 2020 and gave 665 results. I scanned titles and abstracts to determine whether they potentially contained information on the interspecific feeding in birds, or were unrelated to the topic. Second, I manually checked articles citing Shy's (1982) review and all references in relevant articles found by the database search for additional literature.

I categorized involved species as hosts (species being fed) or helpers (species providing food to allospecific hosts). I also recorded the age of hosts at the time they were fed (nestlings, fledglings, both, adults, or unknown), the sex of helpers (male, female, both, or unknown), the continent on which the observation was made (Europe, Africa, Asia, Australia and Oceania with Hawaiian islands included, North America, and South America), nest types of host and helper species, and a possible cause of the behaviour based on authors' notes in the text. Nest types were divided into four categories according to nest site and visibility of nestlings as cavity (usually tree holes or nest boxes with narrow entrances with nestlings being hidden; e.g. woodpeckers and tits), crevice (nests hidden in fissures, under crevices or in open nest boxes, nestlings might be visible, this category also includes species with variable nesting sites that range from cavities to crevices and woven nests hidden in bushes; e.g. redstarts, sparrows, and wrens), domed (woven or clay nests with either narrow or wide entrances, nestlings might be visible; e.g. Long-tailed Tit *Aegithalos caudatus* and some swallows), and open (open cups in vegetation or nests on ground with visible nestlings; e.g. thrushes, raptors, and grebes). The probable causes of interspecific feeding behaviour were based on Shy's (1982) categories: (i) lost nest — birds tending to other broods after their own was destroyed, (ii) close nest — birds taking interest in a nest that is in close vicinity to their own, (iii) calling young — birds stimulated by callings of others' offspring, (iv) orphan — feeding and/or adoption of an orphaned brood, (vi) mate incubates — a bird (usually a male) being eager to care for nestlings so that it feeds others' young while its mate still incubates their own eggs, (vii) mateless — a bird without a mate or its own brood taking care of others' offspring.

I did not consider captive birds, brood parasites, and, unlike Shy (1982), neither the category 'mixed broods' that originated (according to authors) from competition for nests that already contained eggs of another species. Such cases are not uncommon, especially in cavity breeders competing for nest sites (e.g. up to 7.2% of mixed broods can be find in Blue Tits *Cyanistes caeruleus* and Great Tits *Parus major*; Barrientos et al. 2015). Because parents usually do not discriminate between young inside their nest (Beecher 2012), these cases might not fall into the category of misdirected parental care *per se*. In some cases, I recorded two categories as the reasons were not mutually exclusive, e.g. a bird can feed offspring of other species both due to close vicinity of nests and allurement of young's calls. The final database consists of all reported cases of interspecific feeding in birds based on literature collected by Shy (1982), Grangé et al. (2010), and my own search and observation. For the purposes of a uniform database I omitted observations of mixed clutches cited in these studies and merged categories 'unknown' and 'miscellaneous' in probable causes of the behaviour.

I also compared whether old (from Shy 1982 and Grangé et al. 2010) and new data (collected in this study) differ in terms of species' taxonomy, origin of the observations, age of hosts, sex of helpers, and reasons causing the interspecific feeding. Due to low counts in some categories, I used Fisher's exact test to compare whether frequencies of category counts between old and new observations are similar or differ. Finally, since the majority of hosts were young fed by the allospecific parent on a nest (Shy 1982), nest visibility, its

accessibility, and similarity of nest types between hosts and helpers may play a role in triggering the interspecific feeding. Thus, I expected a positive correlation between nest types of hosts and helpers and/or that a majority of hosts would have open nests. Due to low counts in some categories, I also used Fisher's exact test to compare frequencies of nest types between host and helper species. All analyses were performed in R version 4.0.3 (R Core Development Team 2020).

## RESULTS

Combining records from Shy (1982) and Grangé et al. (2010) with my own search resulted in 186 cases of interspecific feeding across 107 helper species in 41 families and ten orders, and 105 host species in 42 families and nine orders of birds (Fig. 1, Appendix 1). In my search of new worldwide records of interspecific feeding I found 47 observations (25% of all records) in 42 studies (including my own observation) published in years 1984–2019. These records involved 44 species (41% of all records) of helpers from 27 families and five orders and 40 species (38%) of hosts from 27 families and five orders (Fig. 1). Out of these records, 31 species of helpers (29% of all records) and 32 species of hosts (30%) were newly registered in cases of interspecific feeding that were not included in Shy (1982) or Grangé et al. (2010).

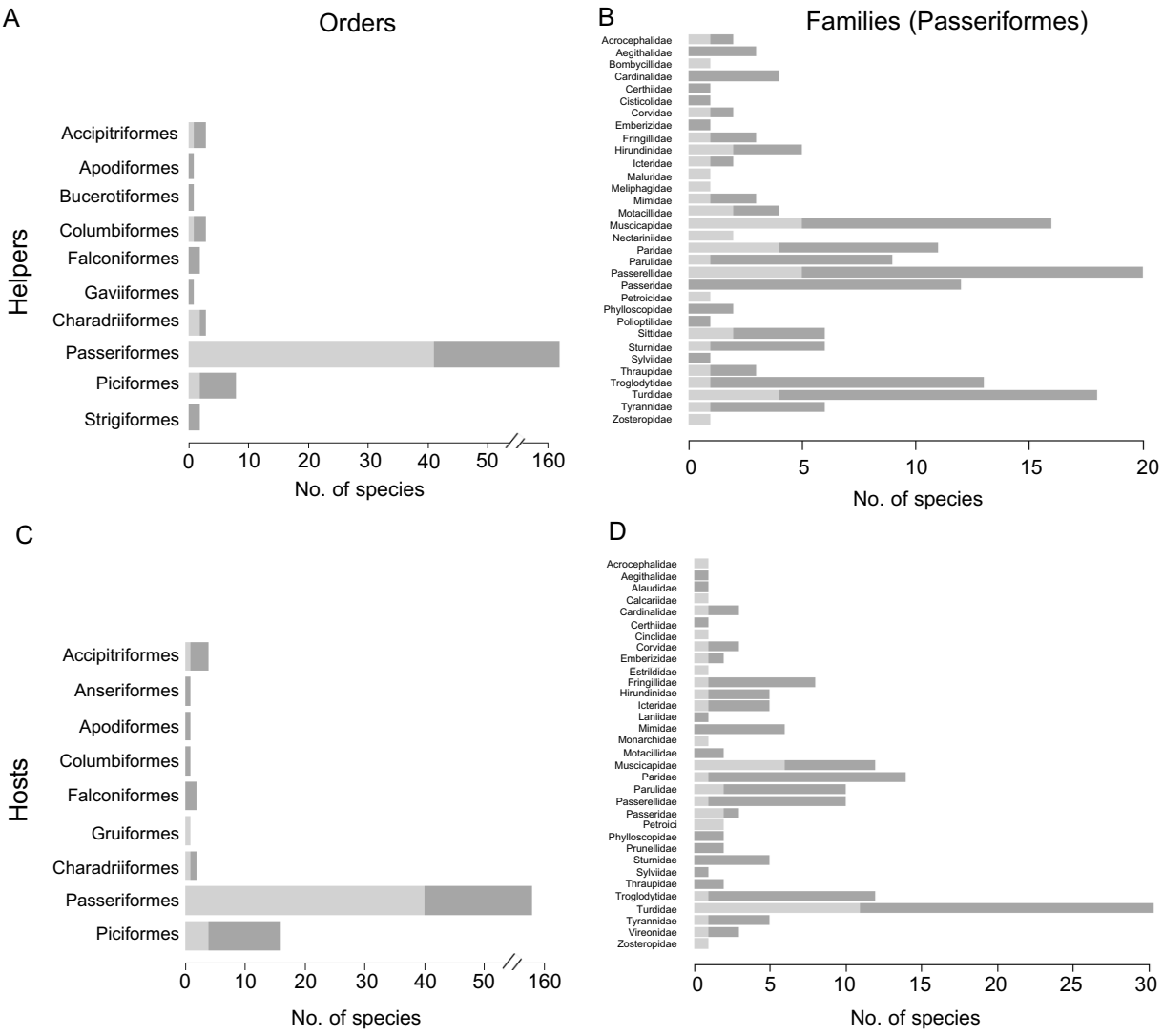


Fig. 1. Distributions of helper (A, B) and host (C, D) species in avian orders (A, C) and in families of the Passeriformes order (B, D). Dark colour represents all known observations, light colour represents worldwide observations since 1983 compiled by the author of this study.

There was a large imbalance between orders as 162 helper species (87% of all records) and 158 host species (85%) belonged in songbirds (order Passeriformes; Fig. 1A and 1C). While there were almost no differences in representation of orders between old and newly searched records in both helper (Fisher's exact test: p-value = 0.842) and host species (p-value = 0.755; Fig. 1A and 1C), differences in the proportion of observations between families (Fig. 1B and 1D) were considerable (helpers: p-value = 0.006, hosts: p-value = 0.001).

Most records originated from North America (including Central America, excluding the Hawaiian Islands) and Europe (including Iceland and Russia; Fig. 2A). Other parts of the world comprised of countries in South America, Asia, and Australia and Oceania, but there were no published cases from Africa in my search (Fig. 2A). As expected, North America and Europe were predominant also in occurrences collected by Shy (1982) and Grangé et al. (2010; Fig. 2A), yet the discrepancy in continents between old and new observations was large (Fisher's exact test: p-value < 0.001). In observations where the helper's sex was known, it was in most cases a male (Fig. 2B), but the frequencies of observations differed between old and new data (Fisher's exact test: p-value = 0.006). The most prevalent of possible reasons for the interspecific feeding according to the authors was 'calling young' in my search and 'close nest', when all known observations were considered (Fig. 2C). These two reasons also appeared to be the ones causing interspecific feeding in my own observation. The proportion of observations between old and new searches also differed significantly (p-value = 0.011). Finally, most of the host species were in the nestling phase when they were fed by the allospecific parent (Fig. 2D), which did not differ between the previous reviews and my own search (p-value = 0.125).

The proportion of nest types in helper and host species differed significantly (Fisher's exact

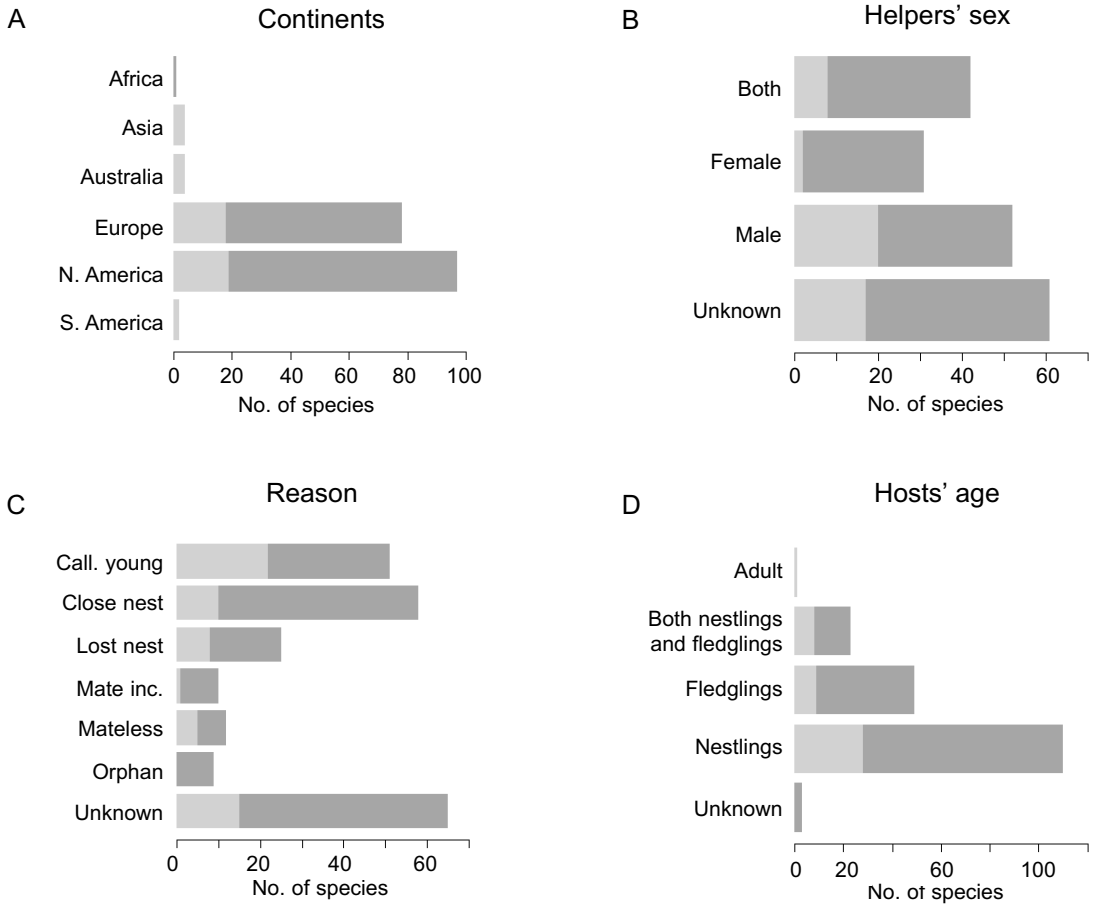


Fig. 2. Distributions of species in categories of continents where the observations were made (A), sex of helper species (B), presumed reasons behind the interspecific feeding (C), and age of host species when being provisioned (D). Dark colour represents all known observations, light colour represents worldwide observations since 1983 compiled by the author of this study.

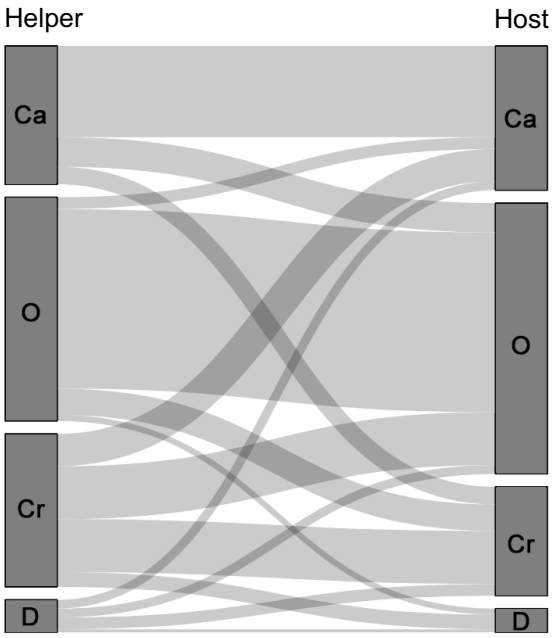


Fig. 3. Flow diagram connecting pairs of helper and host species according to their nest types (Ca — cavity, O — open cup, Cr — crevice, D — domed). For detailed description of these categories see Methods.

test: p-value < 0.001), thus, species were not obstructed by the same nest type when becoming allospecific helpers. The most common nest type was an open cup in both helper (41% of all records) and host species (50%), much less frequent were cavity nesters (helpers: 25%, hosts: 26%) and nest located in crevices (helpers: 28%, hosts: 20%). Only a fraction of interspecific interactions was observed in species with domed nests (helpers: 6%, hosts: 4%; Fig. 3).

**Field observation**

My own observation of the interspecific feeding was conducted in a small wood (3.7 ha, 280 m a.s.l.) overgrowing a greywacke waste tip situated between a greywacke quarry and an express highway near Hrabůvka, Czech Republic (49°34'30.9"N, 17°42'10.9"E). The wood consisted mainly of Common Oaks *Quercus robur*, Common Hornbeams *Carpinus betulus*, and Common Beeches *Fagus sylvatica*. On 12 May 2018, I found a cavity on a Wild Cherry tree *Prunus avium* occupied by Eurasian Nuthatches (3 m a.g.l, west orientation). There were nestlings in the cavity (acoustic confirmation; number and age of nestlings unknown) that were fed by both parents. On the same tree was also situated another cavity, apparently unoccupied (3.2 m a.g.l., south) and a third cavity (4 m a.g.l, east) occupied by a pair of Great Spotted Woodpeckers that were probably incubating eggs (frequent visits of male, flushed female, no audible noise; number of eggs unknown).

During the next visit on 26 May 2018, no nestling begging calls, or parental activity was recorded in the Nuthatch cavity. Whether the nesting was successful, and the nestlings fledged, or the nest was depredated, is unknown. There were audible voices of nestlings from the woodpecker cavity and both parents were frequently visiting the nest and bringing food. On this day, I also recorded Nuthatches coming with food to the entrance of the woodpecker cavity and feeding woodpecker nestlings (see material video: https://youtu.be/f2Tv5BFaxPQ). Due to the non-apparent differences between sexes of Nuthatches and seeing only one individual at the time, it was impossible to tell whether the helper was only one or both birds from the pair, or even other individual unrelated to the pair that nested in the same tree. Regarding small area of the wood and that no calls of other Nuthatches were recorded in the vicinity, I presume helpers were individuals previously breeding in the same tree. Woodpecker nestlings started begging loudly when any bird (either a Woodpecker or a Nuthatch) appeared in the cavity entrance. The observation lasted for an hour during which the frequency of visits of either Woodpeckers or Nuthatches was ca. every five minutes. The birds of these two species never met near the cavity entrance so the Nuthatches were not driven out by the Woodpeckers.

Assuming helpers belonged to the pair observed in the same tree, Nuthatches' behaviour was probably facilitated by the close distance between the nests and the begging of woodpeckers' young. Woodpecker nestlings are quite loud, and their begging could have stimulated Nuthatches to provide food even though their own offspring already fledged, or their clutch was lost. A similar case of Great Spotted Woodpeckers' nestlings being fed by Nuthatches was already reported from France (Grangé et al. 2010). In this case, reasons for this behaviour seemed to be also the stimulation by calls from a nearby cavity.

## DISCUSSION

Cases of interspecific feeding in birds provided by my search of literature published worldwide since the year 1982 made one-quarter of all records included in this review. Old records, derived from

works of Shy (1982) and Grangé et al. (2010), and new ones searched for the purpose of this study, showed high discrepancy in proportion of number of cases recorded between families, sex of helpers, possible reasons causing interspecific feeding, and on particular continents. Although I searched for literature on interspecific feeding in birds worldwide, I found only another ten studies from outside North American and European continents and no case from Africa (Fig. 2A). This might be caused by the long ornithological and research traditions in Europe and North America and notes describing interspecific feeding might be hidden in local journals not written in English language, thus challenging to find. Though I collected also as much non-English literature as possible, the few articles included in this study had at least an alternative name of title and/or abstract written in English. Furthermore, many observations of interspecific feeding might not even be published, as some of data (e. g. collected by Shy 1982) were from personal communications. Hopefully, more reports are to be expected in the future due to the internationalization of science and higher technological advances in research, such as using video recording, which could help to document these unusual behavioural cases (Luo et al. 2018).

Records of interspecific feeding showed a large imbalance also between orders, as the distinct majority of observations was done on songbirds (Fig. 1). This is probably caused simply by the ratio of species between individual orders, as 60% of all species of birds worldwide belong in order Passeriformes (Gill & Donsker 2020) so the probability of detecting the behaviour is a magnitude higher by definition. Moreover, most of the songbird species are altricial with profound parental care and feed their offspring. Usually, female is the one that incubates eggs and spends most of the time on a nest, while male defends the territory (Skutch 1957). This might leave him with more opportunities to encounter nests of other species and for venting the energy and need to care for nestlings elsewhere, before his own offspring hatch (Skutch 1961, Cockburn 1998). In some cases, the whole pair assisted at an interspecific nest, possibly lured by loud calls of nearby nestlings (Pranty 2010, Morozov 2014, Jiang et al. 2016, Burbidge 2018) or adopted the young after their own nest was destroyed (Eltzroth & Robinson 1984). Nest depredation was also probably the reason for the only observation of a female being the helper in my search (Heber 2013, Fig. 2B).

The discrepancy between old and new records of interspecific feeding was, however, not found in the case of hosts' age, where most of the hosts were nestlings or were fed during the whole breeding phase inside the nest and after fledging (Fig. 2D). This shows that interspecific feeding occurs mostly during breeding and its causes thus might be somehow tied to the changes or anomalies in nesting behaviour. This is reflected also by categories of possible causes set by Shy (1982), which are all related to breeding. Out of these categories, the care for orphaned birds was not mentioned in any study in my search and in many observations, authors did not specify or dared to contemplate the reason behind interspecific feeding. Categories 'mate incubates' and 'mateless' were not reported often, but it might be due to underrepresentation. To state these reasons, observations must be done on nests of both host and helper species, which is not always possible (helper's nest hard to find or not searched for) or require a long-time surveillance. Similarly, when only the feeding of fledglings was witnessed or the nest was observed for a short period of time and no parents were seen, it does not mean that hosts' young were deserted, thus the low number of observations falling into the 'orphan' category. Adoptions were mostly common not with young after they were orphaned, but when helpers assumed (shared) care for allospecific offspring and sometimes biological parents even left the nest entirely (Haucke 2015). Moreover, monitoring of nests and their stationarity might have also helped to increase the number of observations of interspecific feeding of nestlings above fledglings. Young birds disperse to the close surroundings of the nest after fledging which could make observations of parental care more difficult.

I expected that most cases of interspecific feeding will be carried out between species pairs with similar types of nests and/or that hosts would be species with open nests as the higher visibility of young could help with alluring the alloparent. However, the proportion of nest types between helper and host species pairs differed significantly and even species with open nests fed cavity nesters and the other way around (Fig. 3). Moreover, open nests were not predominant in either helper or host species. Thus, nest type does not seem to be a strong factor affecting interspecific feeding, but instead, the distance between nests of helper and host species together with young's loud begging might be more important, as they were reported as the most numerous

categories of possible causes of this behaviour (Fig. 2C).

Increased acoustic begging is often found in chicks of brood parasites (Davies et al. 1998, Dearborn & Lichtenstein 2002) and some authors observed interspecific feeding in nests parasitized by Shiny Cowbird *Molothrus bonariensis* (Batisteli & Sarmento 2016, Segura et al. 2016). The dominant presence of a brood parasite in a nest could potentially attract the attention of nearby birds. Sealy & Lorenzana (1997) found 46 cases of brood parasites being fed by other species than their hosts. Thus, interspecific feeding could be more likely carried out by species that fail to recognize their own offspring and belong to hosts coveted by brood parasites (Jiang et al. 2016). However, parents usually do not need individual recognition of their young inside the nest and consider all nestlings as their own (Beecher 2012). The parent-offspring recognition in interspecific interactions could be also biased not only in the case of helpers, but also in young. Some authors described cases of interspecific feeding following begging of fledglings that did not discriminate between their parents and allospecific individuals (McGowan 1990, McNair & Duyck 1991, Pierce 2005, Farmer et al. 2008, Fiss et al. 2016, Burbidge 2018). Non-specific begging of young could be a consequence of low food provisioning by their parents (Farmer et al. 2008) solicited with increased begging due to hunger (Reers & Jacot 2011). Moreover, young fed by alloparents could face problems with specific recognition when trying to find a mate later in life, as they could fail to identify their own species (Hansen et al. 2008).

Out of the original categories of presumed reasons causing interspecific feeding defined by Shy (1982) I did not include mixed broods resulting from nest site competition in this work, but such cases would probably not increase to a great extent the number of species in which the interspecific feeding was found (see the list of species in Shy 1982). Mixed broods are found in species well known for nest site competition and lead to interspecific feeding of young left by the previous owners of the nest, such as in cavity nesting tits Paridae (Suzuki & Tsuchiya 2010, Samplionius & Both 2014, Barrientos et al. 2015) and in swallows Hirundinidae (Butler & Campbell 1987). In raptors, although the nest competition is also known, mixed broods based on adopted young of the previous nest owners are rare (e.g. van Bergen & Riem Vis 2012). In some cases, mixed broods could have originated from attempted predation of allospecific young that was brought alive to the nest as a prey but then raised instead (Stefanek et al. 1992, Watson et al. 1993). Czubat et al. (2018) reported several observations with White-tailed Eagles' *Haliaeetus albicilla* nests containing young of Common Buzzards *Buteo buteo*. Alive buzzards were in some cases eaten later or fed by allospecific parents (probably confused by their begging) and managed to fledge. Some authors also reported joint egg laying and shared parental care of mixed clutches by both host and helper species on a single nest (Kozma & Mathews 1995, Govoni et al. 2009). Moreover, although I focused on interspecific feeding, there also exist some cases of misdirected parental care, such as brooding and protection, but without the food provision, e.g. in penguins (Oosthuizen & de Bruyn 2009, Kemper 2014) or waders and ducks that do not directly feed their young (Skutch 1961, Rönkä et al. 2002).

Finally, whereas alloparental care among conspecifics relates to kinship selection and has greater evolutionary consequences (Grangé et al. 2010), the significance of the interspecific feeding in an evolutionary context still remains unknown. Interspecific feeding might have potential benefits for helpers for acquiring parental care skills that could be useful in the future when taking care of their own offspring (Riedman 1982). Helpers thus should be mostly young birds gaining the experience (Shy 1982), but this remains to be proved. Second, reciprocal altruism does not seem to be prominent as there is a lack of understanding of how the helper would get the help back (Shy 1982). Third, Sealy & Lorenzana (1997) suggested that in case of close nests, birds could feed young of their neighbours to lessen their vocal begging, which in turn could decrease a chance to attract predators that could depredate both nests. Finally, interspecific feeding is probably just a non-adaptive behaviour that has no benefits for helpers and is triggered by other adaptive features, such as the strong drive to care for young that was misplaced on allospecific offspring (Shy 1982). However, these errors are probably too minor that such behaviour was not corrected by the evolution (Shy 1982).

In sum, the occurrence of interspecific feeding in birds is mostly tied to songbirds and nesting behaviour, as the allospecific feeders are usually males feeding nestlings and/or fledglings, lured to the alien nests by the loud begging. However, although some explanations of this behaviour were suggested, no empirical research was done in this field and cases of interspecific feeding are

still reported only as unusual incidences. Thorough observations of nests of both host and helper species, especially with video recordings, should shed a light on alloparents' sex, breeding status, fitness, and nesting success. Moreover, laboratory-controlled experiments should determine factors triggering this unusual behaviour and revel, whether is interspecific feeding adaptive or only a misplaced behaviour with no evolutionary significance.

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## REFERENCES

Barrientos R., Bueno-Enciso J., Serrano-Davies E., Sanz J. J. 2015. Facultative interspecific brood parasitism in tits: A last resort to coping with nest-hole shortage. Behav. Ecol. Sociobiol. 69: 1603–1615.

Batisteli A. F., Sarmento H. 2016. Interspecific parental care by a Rufous-collared sparrow (*Zonotrichia capensis*) at a nest of the Pale-breasted thrush (*Turdus leucomelas*) parasitized by a Cowbird (*Molothrus bonariensis*). Ornitol. Neotrop. 27: 253–257.

Beecher M. D. 2012. Development of parent-offspring recognition in birds. In: Aslin R. N., Alberts J. R., Petersen M. R. (eds). Development of perception. Psychobiological perspectives: Audition, somatic perception, and the chemical senses. Academic Press, New York, pp. 45–66.

Burbidge G. 2018. European Starling pair feeds a juvenile Downy Woodpecker. Ontario Birds 36: 170–173.

Butler R. W., Campbell C. A. 1987. Nest appropriation and interspecific feeding between Tree Swallows *Tachycineta bicolor* and Barn Swallows *Hirundo rustica*. Can. Field Nat. 101: 433–434.

Cockburn A. 1998. Evolution of helping behaviour in cooperatively breeding birds. Annu. Rev. Ecol. Syst. 29: 141–177.

Cockburn A. 2006. Prevalence of different modes of parental care in birds. Proc. R. Soc. B 273: 1375–1383.

Czubat A., Sierakowski M., Szubart-Chodorowska E., Świerad R. 2018. [Common Buzzard *Buteo buteo* nestlings in nests of White-tailed Eagles *Haliaeetus albicilla* as an example of interspecific adoption]. Ptaki Śląska 25: 139–148.

Davies N. B., Kilner R. M., Noble D. G. 1998. Nestling cuckoos, *Cuculus canorus*, exploit hosts with begging calls that mimic a brood. Proc. R. Soc. B 265: 673–678.

Dearborn D. C., Lichtenstein G. 2002. Begging behaviour and host exploitation in parasitic cowbirds. In: Wright J., Leonard M. L. (eds). The evolution of begging. Competition, cooperation & communication. Kluwer Academic Publishers, Dordrecht, pp. 361–387.

Eltzroth E. K., Robinson S. R. 1984. Violet-green Swallows help Western Bluebirds at the nest. J. Field Ornithol. 55: 259–261.

Farmer C., Frederick B. A., Banko P. C., Stephens R. M., Snow C. W. 2008. Palila (*Loxioides baillueui*) fledgling fed by Hawai'i 'Amakihi (*Hemignathus virens*). Wilson J. Ornithol. 120: 416–418.

Fiss C. J., McNeil D. J., Poole R. E., Rogers K. M., Larkin J. L. 2016. Prolonged interspecific care of two sibling Golden-winged Warblers (*Vermivora chrysoptera*) by a Black-and-white Warbler (*Mniotilta varia*). Wilson J. Ornithol. 128: 921–926.

Gill F., Donsker D. 2020 (eds). IOC World Bird List (v 10.1). Available at: www.worldbirdnames.org

Govoni P. W., Summerville K. S., Eaton M. D. 2009. Nest sharing between an American Robin and a Northern Cardinal. Wilson J. Ornithol. 121: 424–426.

Grangé J.-L., Magnin D., Potiron J.-L. 2010. À propos d'une aide au nourrissage interspécifique chez la Sitelle torchepot *Sitta europea*. Le Casseur d'os 10: 167–176.

Griesser M., Drobniak S. M., Nakagawa S., Botero C. A. 2017. Family living sets the stage for cooperative breeding and ecological resilience in birds. PLOS Biol. 15: e2000483.

Hansen B. T., Johannessen L. E., Slagsvold T. 2008. Imprinted species recognition lasts for life in free-living great tits and blue tits. Anim. Behav. 75: 921–927.

Haucke H. H. 2015. Interspecific feeding of Carolina Wren nestlings and fledglings by an Eastern Phoebe. Bulletin of the Texas Ornithological Society 48: 59–62.

Heber S. 2013. Anecdotal evidence of interspecific parental care: Feeding and brooding of Robin (*Petroica australis*) nestlings by a female Bellbird (*Anthornis melanura*). Notornis 60: 186–187.

Jiang A., Jiang D., Goodale E., Zhou F., Wen Y. 2016. Olive-backed Sunbird *Cinnyris jugularis* assisting Crested Bunting *Melophus lathami* at the nest: substantiated evidence for interspecific feeding, Guangxi, south-west China. Forktail 32: 93–96.

Kemper J. 2014. Chicknapped! Two Kelp Gull chicks brooded and defended by an African Penguin at Halifax Island, Namibia. Ornithol. Obs. 5: 11–16.

Kozma J. M., Mathews N. E. 1995. Interspecific cooperative nesting between Barn Swallows and Say's Phoebes in South-central New Mexico. Auk 112: 515–517.

Krištín A. 2009. Interspecific feeding at bird nests: *Ficedula albicollis* as a helper at the nest of *Turdus philomelos*. Tichodroma 21: 98–101.

Krüger O., Pauli M. 2017. Evolution of avian brood parasitism and phylogenetic history of brood parasites. In: Soler M. (ed.). Avian brood parasitism. Behaviour, ecology, evolution and coevolution. Springer, Cham, pp. 43–60.

Luo K., Hu Y., Lu Z., Li D. 2018. Interspecific feeding at a bird nest: Snowy-browed flycatcher (*Ficedula hyperythra*) as a helper at the Rufous-bellies niltava (*Niltava sundara*) nest, Yunnan, Southwest China. Wilson J. Ornithol. 130: 1003–1008.

McGowan K. J. 1990. Nesting Fish Crows adopt a fledgling Blue Jay. J. Field Ornithol. 61: 171–173.

McNair D. B., Duyck B. 1991. Interspecific feeding among some oscines. The Chat 55: 9–11.

Morozov N. S. 2014. [Involvement of Great Tits *Parus major* in feeding young of nearby nesting Blue Tits *Parus caeruleus*]. Russkiy Ornitologicheskiy Zhurnal 23: 1412–1416.

Oosthuizen W. C., de Bruyn P. J. N. 2009. King penguin brooding and defending a sub-Antarctic skua chick. Polar Biol. 32: 303–305.

Pierce A. J. 2005. Interspecific feeding of a White-Eye fledgling by a Little Spiderhunter. The Natural History Journal of Chulalongkorn University 5: 41.

Pranty B. 2010. Hairy Woodpeckers (*Picoides villosus*) feed Downy Woodpecker (*P. pubescens*) nestlings. Florida Field Naturalist 38: 71–72.

Pugacewicz E. 2009. [Cases of positive and probable interspecific altruism in birds observed in the northern Podlasie region]. Kulon 14: 129–132.
R Core Development Team 2020. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Available at: https://www.R-project.org
Reers H., Jacot A. 2011. The effect of hunger on the acoustic individuality in begging calls of a colonially breeding weaver bird. BMC Ecol. 11: 3.
Riedman M. L. 1982. The evolution of alloparental care and adoption in mammals and birds. Q. Rev. Biol. 57: 405–435.
Rönkä M. T. H., Rainio K. T., Lindroos R. G. 2002. Turnstones *Arenaria interpres* brooding Redshank *Tringa totanus* clutch. Ornis Fennica 79: 45–47.
Samplonius J. M., Both C. 2014. A case of a three species mixed brood after two interspecific nest takeovers. Ardea 102: 105–107.
Sealy S. G., Lorenzana J. C. 1997. Feeding of nestling and fledgling brood parasites by individuals other than the foster parents: A review. Can. J. Zool. 75: 1739–1752.
Segura L. N., Gonzales E., Jauregui A. 2016. Unusual nest and nestling appropriation by the Eared Dove (*Zenaida auriculata*). Ornitol. Neotrop. 27: 101–104.
Shy M. M. 1982. Interspecific feeding among birds: A review. J. Field Ornithol. 53: 370–393.
Skutch A. F. 1957. The incubation patterns of birds. Ibis 99: 69–93.
Skutch A. F. 1961. Helpers among birds. Condor 63: 198–226.
Stefanek P. R., Bowerman W. W., Grubb T. G., Holt J. B. 1992. Nestling Red-tailed hawk in occupied Bald Eagle nest. J. Raptor Res. 26: 40–41.
Suzuki T. N., Tsuchiya Y., 2010. Feeding a foreign chick: A case of a mixed brood of two Tit species. Wilson J. Ornithol. 122: 618–620.
van Bergen V., Riem Vis R. 2012. [Goshawk *Accipiter gentilis* raised by Buzzard *Buteo buteo*]. De Takkeling 20: 119–125.
Watson J. W., Davison M., Leschner L. L. 1993. Bald Eagles rear Red-tailed Hawks. J. Raptor Res. 27: 126–127.
Yoerg S. I., O'Halloran J. 1991. Dipper nestlings fed by a Gray Wagtail. Auk 108: 427–440

## STRESZCZENIE

**[Karmienie międzygatunkowe u ptaków]**
Karmienie międzygatunkowe to nietypowe zachowanie, polegające na tym, że osobnik jednego gatunku — zwanego pomocnikiem — karmi osobniki (najczęściej młode) innego gatunku — zwanego gospodarzem. Zachowania takie zostały zaobserwowane u wielu gatunków ptaków, jednak ich przyczyny pozostają nieznane i żadna z zaproponowanych dotychczas hipotez nie wyjaśnia w pełni ich występowania.

W pracy przedstawiono zestawienie dotychczasowych obserwacji karmienia międzygatunkowego u ptaków. Znalazły się w nim obserwacje zidentyfikowane w wyniku przeszukania bazy literaturowej obejmującej ostatnich 40 lat. Dla każdej obserwacji odnotowano gatunek pomocnika i gospodarza, wiek gospodarza, płeć pomocnika, kontynent, na którym dokonano obserwacji, rodzaj gniazda gospodarza i pomocnika oraz możliwe przyczyny błędnego ukierunkowania opieki rodzicielskiej przez pomocników. Dodatkowo, w zestawieniu umieszczono obserwacje zebrane w dwóch poprzednich pracach przeglądowych dotyczących zagadnienia karmienia międzygatunkowego u ptaków. W zestawieniu pominięto ptaki hodowlane, pasożyty lęgowe oraz lęgi mieszane, które powstały w wyniku konkurencji o miejsca gniazdowe, w których znajdowało się już gniazdo z jajami. W sumie, w zestawieniu znalazło się 186 obserwacji karmienia międzygatunkowego, obejmujących 107 gatunków pomocników z 41 rodzin i 10 rzędów oraz 105 gatunków gospodarzy z 42 rodzin i 9 rzędów ptaków (Fig. 1, Apendyks 1). Następnie przeprowadzono analizy porównując m. in. nowy zestaw danych z danymi zebranymi w dwóch poprzednich pracach przeglądowych (używając roku 1983 jako cezury), oraz czy rodzaj miejsca gniazdowego pomocników i gospodarzy wpływa na występowanie zjawiska karmienia międzygatunkowego. Analizując potencjalne powody nietypowego zachowania pomocników wzięto pod uwagę sześć czynników: utratę własnego lęgu, bliskie położenie gniazda gospodarza, głos żebrzących młodych stymulujący przedstawicieli innych gatunków ptaków do karmienia, adopcję osieroconego lęgu gospodarza przez pomocnika, brak partnera, etap okresu gniazdowego, gdy jeden z partnerów wysiaduje jaja, a drugi partner (zwykle samiec), będąc gotowym do opieki nad potomstwem, karmi obce pisklęta.

Dodatkowo w pracy został opisany przypadek karmienia piskląt dzięcioła dużego przez kowalika w niewielkim zadrzewieniu we wschodnich Czechach. Obie pary ptaków — kowaliki i dzięcioły gniazdowały w dziuplach znajdujących się w tym samym drzewie. W dniu, kiedy zaobserwowano kowaliki karmiące młode dzięcioły, nie zaobserwowano ani karmienia własnych młodych ani ich głosów dochodzących z dziupli.

Większość gatunków gospodarzy, jak i pomocników należało do wróblowych (Fig. 1). Dotychczasowe obserwacje karmienia międzygatunkowego dotyczą przede wszystkim gatunków północnoamerykańskich i europejskich (Fig. 2A), co prawdopodobnie wynika z uwarunkowań historycznych (długie tradycje badań i obserwacji ornitologicznych) oraz językowych (publikacje w języku angielskim). W przypadkach, gdy znana była płeć pomocnika najczęściej był to samiec, choć proporcja płci różniła się dla obserwacji sprzed i po roku 1983 (Fig. 2B). Pomocnicy

najczęściej karmili pisklęta, a w następnej kolejności podloty gospodarzy (Fig. 2D). Najczęściej wymienianą potencjalną przyczyną karmienia międzygatunkowego było głośne nawoływanie piskląt, szczególnie, gdy dochodziło ono z gniazda gospodarza położonego w pobliżu gniazda pomocnika (jak miało to miejsce w przypadku opisywanej obserwacji kowalika karmiącego młode dzięcioły) (Fig. 2C). Wydaje się, że karmienie międzygatunkowe nie jest związane z typem gniazda — tj. pomocnicy nie muszą gniazdować w podobny sposób lub podobnych miejscach, jak gospodarze, żeby karmić ich pisklęta (Fig. 3).

Większość dotychczasowych obserwacji karmienia międzygatunkowego ma charakter anegdotyczny i przypadkowy, brak jest badań empirycznych, które próbowałyby znaleźć wiarygodne wytłumaczenie tego zachowania.

Appendix 1. A list of collected records of interspecific feeding in birds. Taxonomic names are adopted from Gill & Donsker 2020. Helper species are characterized as species providing food, while host species receive food from the helpers. Reasons state a presumed cause of the interspecific feeding as provided by the authors of the source literature up to two reasons. Host age — age of the host species: A — adult, B — both nestlings and fledglings, F — fledglings, N — nestlings, U — unknown; Helper sex — sex of the helper species: B — both male and female, F — female, M — male, U — unknown; CON — a continent where the instance of interspecific feeding was observed Af — Africa, As — Asia, Au — Australia and Oceania, Eu — Europe, NA — North America, SA — South America. Records were collected by the author of this study from the original sources, except for Shy 1982 and Grangé et al. 2010, which are secondary sources from which were the records adopted.

| Helper | | Host | | Reasons | Host | Helper | Nest site | | CON | Source |
|---|---|---|---|---|---|---|---|---|---|---|
| Species | Family | Species | Family | | Age | sex | Helper | Host | | |
| *Accipiter gentilis* | Accipitridae | *Buteo jamaicensis* | Accipitridae | close nest | N | F | O | O | NA | 39 |
| *Acrocephalus scirpaceus* | Acrocephalidae | *Carduelis carduelis* | Fringillidae | close nest, calling young | N | U | O | O | Eu | 22 |
| *Acrocephalus schoenobaenus* | Acrocephalidae | *Acrocephalus arundinaceus* | Acrocephalidae | unknown | F | U | O | O | Eu | 35 |
| *Aegithalos caudatus* | Aegithalidae | *Dendrocopos major* | Picidae | calling young | N | B | D | C | Eu | 22 |
| *Aegithalos caudatus* | Aegithalidae | *Parus major* | Paridae | mateless | N | U | D | C | Eu | 39 |
| *Aegithalos caudatus* | Aegithalidae | *Parus major* | Paridae | unknown | N | U | D | C | Eu | 22 |
| *Ammodramus maritimus* | Passerellidae | *Agelaius phoeniceus* | Icteridae | mateless | F | M | O | O | NA | 39 |
| *Anthornis melanura* | Meliphagidae | *Petroica australis* | Petroicidae | lost nest, calling young | N | F | O | O | Au | 17 |
| *Arachnothera longirostra* | Nectariniidae | *Zosterops* sp. | Zosteropidae | unknown | F | U | D | O | As | 33 |
| *Bombycilla cedrorum* | Bombycillidae | *Vireo olivaceus* | Vireonidae | calling young | F | U | O | O | NA | 28 |
| Bubo virginianus | Strigidae | *Buteo jamaicensis* | Accipitridae | unknown | N | F | O | O | NA | 39 |
| *Cardinalis cardinalis* | Cardinalidae | *Turdus migratorius* | Turdidae | lost nest, mate incubates | F | M | O | O | NA | 39 |
| *Cardinalis cardinalis* | Cardinalidae | *Dumetella carolinensis* | Mimidae | calling young | F | M | O | O | NA | 39 |
| *Cardinalis cardinalis* | Cardinalidae | *Icteria virens* | Icteridae | close nest | N | M | O | O | NA | 39 |
| *Catharus ustulatus* | Turdidae | *Turdus migratorius* | Turdidae | calling young | N | U | O | O | NA | 39 |
| *Certhia familiaris* | Certhiidae | *Cyanistes caeruleus* | Paridae | lost nest, calling young | N | B | R | C | Eu | 22 |
| *Cinnyris jugularis* | Nectariniidae | *Emberiza lathami* | Emberizidae | close nest, calling young | N | B | D | O | As | 19 |
| *Circus aeruginosus* | Accipitridae | *Circus pygargus* | Accipitridae | mateless | N | M | O | O | Eu | 35 |
| *Circus pygargus* | Accipitridae | *Circus aeruginosus* | Accipitridae | lost nest, calling young | F | M | O | O | Eu | 22 |
| *Colaptes auratus* | Picidae | *Sturnus vulgaris* | Sturnidae | unknown | N | F | C | C | NA | 39 |
| *Colibri cyanotus* | Trochilidae | *Basilinna leucotis* | Trochilidae | unknown | U | U | O | O | NA | 39 |
| *Columba livia* | Columbidae | *Coloeus monedula* | Corvidae | close nest | N | U | R | C | Eu | 22 |
| *Contopus virens* | Tyrannidae | *Tyrannus tyrannus* | Tyrannidae | calling young, orphan | N | U | O | O | NA | 39 |
| *Corvus ossifragus* | Corvidae | *Cyanocitta cristata* | Corvidae | unknown | F | B | O | O | NA | 27 |
| *Cyanerpes cyaneus* | Thraupidae | *Vireo flavoviridis* | Vireonidae | unknown | U | F | O | O | NA | 39 |
| *Cardinalis cardinalis* | Thraupidae | *Ramphocelus passerinii* | Thraupidae | unknown | F | M | O | O | NA | 39 |
| *Cardinalis cardinalis* | Paridae | *Phoenicurus ochruros* | Muscicapidae | calling young | N | U | C | R | Eu | 27 |
| *Cardinalis cardinalis* | Paridae | *Certhia* sp. | Certhiidae | close nest | B | M | C | R | Eu | 39 |
| *Cardinalis cardinalis* | Paridae | *Erithacus rubecula* | Muscicapidae | close nest | N | B | C | R | Eu | 39 |
| *Cardinalis cardinalis* | Paridae | *Troglodytes troglodytes* | Troglodytidae | unknown | N | B | C | R | Eu | 39 |
| *Cardinalis cardinalis* | Paridae | *Turdus merula* | Turdidae | unknown | N | U | C | O | Eu | 20 |
| *Delichon urbicum* | Hirundinidae | *Passer domesticus* | Passeridae | calling young | A | U | D | R | Eu | 7 |
| *Dendrocopos major* | Picidae | *Jynx torquilla* | Picidae | lost nest, calling young | N | F | C | C | Eu | 22 |
| *Dendrocopos major* | Picidae | *Sturnus vulgaris* | Sturnidae | close nest | N | F | C | C | Eu | 22 |
| *Dendrocoptes medius* | Picidae | *Passer domesticus* | Passeridae | calling young | N | M | C | R | Eu | 30 |

Continued on the next page

| Helper | | Host | | Reasons | Host | Helper | Nest site | | CON | Source |
|---|---|---|---|---|---|---|---|---|---|---|
| Species | Family | Species | Family | | Age | sex | Helper | Host | | |
| *Dumetella carolinensis* | Mimidae | *Colaptes auratus* | Picidae | orphan | N | U | O | C | NA | 39 |
| *Dumetella carolinensis* | Mimidae | *Troglodytes aedon* | Troglodytidae | unknown | N | F | O | C | NA | 39 |
| *Emberiza citrinella* | Emberizidae | *Lanius excubitor* | Laniidae | calling young | F | B | O | O | Eu | 22 |
| *Empidonax minimus* | Tyrannidae | *Spizella passerina* | Passerellidae | close nest | N | U | O | O | NA | 39 |
| *Erithacus rubecula* | Muscicapidae | *Aegithalos caudatus* | Aegithalidae | lost nest, close nest | N | U | R | D | Eu | 22 |
| *Erithacus rubecula* | Muscicapidae | *Phylloscopus trochilus* | Phylloscopidae | calling young, mate incubates | N | U | R | D | Eu | 22 |
| *Erithacus rubecula* | Muscicapidae | *Turdus merula* | Turdidae | mate incubates, orphan | N | M | R | O | Eu | 39 |
| *Erithacus rubecula* | Muscicapidae | *Turdus philomelos* | Turdidae | lost nest | N | B | R | O | Eu | 39 |
| *Erithacus rubecula* | Muscicapidae | *Troglodytes troglodytes* | Troglodytidae | unknown | N | U | R | R | Eu | 39 |
| *Erithacus rubecula* | Muscicapidae | *Troglodytes troglodytes* | Troglodytidae | unknown | F | F | R | R | Eu | 39 |
| *Erithacus rubecula* | Muscicapidae | *Troglodytes troglodytes* | Troglodytidae | unknown | F | B | R | R | Eu | 39 |
| *Erithacus rubecula* | Muscicapidae | *Turdus merula* | Turdidae | unknown | F | B | R | O | Eu | 39 |
| *Falco peregrinus* | Falconidae | *Falco tinnunculus* | Falconidae | close nest, calling young | N | F | R | R | Eu | 22 |
| *Falco peregrinus* | Falconidae | *Falco tinnunculus* | Falconidae | lost nest, close nest | B | B | R | R | Eu | 22 |
| *Ficedula albicollis* | Muscicapidae | *Turdus philomelos* | Turdidae | lost nest, calling young | N | M | C | O | Eu | 22 |
| *Ficedula hyperythra* | Muscicapidae | *Niltava sundara* | Muscicapidae | calling young | N | M | R | R | As | 25 |
| *Fringilla coelebs* | Fringillidae | *Coccothraustes coccothraustes* | Fringillidae | calling young | F | M | O | O | Eu | 39 |
| *Gavia arctica* | Gaviidae | *Somateria fischeri* | Anatidae | close nest | F | B | R | O | NA | 39 |
| *Haemorhous mexicanus* | Fringillidae | *Turdus migratorius* | Turdidae | unknown | N | B | R | O | NA | 39 |
| *Helmitheros vermivorum* | Parulidae | *Geothlypis formosa* | Parulidae | calling young | F | U | O | O | NA | 39 |
| *Helmitheros vermivorum* | Parulidae | *Seiurus aurocapilla* | Parulidae | mateless | N | U | O | D | NA | 39 |
| *Hylocichla mustelina* | Turdidae | *Catharus fuscescens* | Turdidae | unknown | N | U | O | O | NA | 15 |
| *Chlidonias hybrida* | Laridae | *Fulica atra* | Rallidae | calling young, mateless | F | U | O | O | Eu | 3 |
| *Chlorodrepanis virens* | Fringillidae | *Loxioides bailleui* | Fringillidae | lost nest, calling young | F | M | O | O | Au | 9 |
| *Chroicocephalus ridibundus* | Laridae | *Ichthyaetus melanocephalus* | Laridae | orphan | F | B | O | O | Eu | 22 |
| *Icterus galbula* | Icteridae | *Icterus spurius* | Icteridae | unknown | N | M | D | D | NA | 28 |
| *Ichthyaetus melanocephalus* | Laridae | *Chroicocephalus ridibundus* | Laridae | mateless | N | M | O | O | Eu | 40 |
| *Junco hyemalis* | Passerellidae | *Thryomanes bewickii* | Troglodytidae | close nest, mate incubates | N | M | R | R | NA | 39 |
| *Leuconotopicus villosus* | Picidae | *Dryobates pubescens* | Picidae | close nest, calling young | N | B | C | C | NA | 34 |
| *Leuconotopicus villosus* | Picidae | *Dryobates pubescens* | Picidae | calling young | F | M | C | C | NA | 39 |
| *Lophophanes cristatus* | Paridae | *Dendrocopos major* | Picidae | lost nest | N | B | C | C | Eu | 22 |
| *Malurus coronatus* | Maluridae | *Neochmia phaeton* | Estrildidae | lost nest, close nest | N | M | D | R | Au | 14 |
| *Megascops asio* | Strigidae | *Colaptes auratus* | Picidae | lost nest | N | F | C | C | NA | 39 |
| *Melanerpes carolinus* | Picidae | *Baeolophus bicolor* | Paridae | calling young | F | U | C | C | NA | 39 |
| *Melospiza melodia* | Passerellidae | *Setophaga aestiva* | Parulidae | close nest | B | B | O | O | NA | 39 |
| *Melospiza melodia* | Passerellidae | *Turdus migratorius* | Turdidae | close nest | B | B | O | O | NA | 39 |
| *Melospiza melodia* | Passerellidae | *Troglodytes aedon* | Troglodytidae | orphan | F | U | O | C | NA | 39 |
| *Melospiza melodia* | Passerellidae | *Setophaga aestiva* | Parulidae | unknown | N | B | O | O | NA | 24 |
| *Melozone crissalis* | Passerellidae | *Cardinalis cardinalis* | Cardinalidae | unknown | F | M | O | O | NA | 39 |
| *Melozone crissalis* | Passerellidae | *Toxostoma curvirostre* | Mimidae | unknown | F | U | O | O | NA | 39 |
| *Mniotilta varia* | Parulidae | *Seiurus aurocapilla* | Parulidae | calling young, orphan | F | B | R | D | NA | 39 |
| *Mniotilta varia* | Parulidae | *Vermivora chrysoptera* | Parulidae | calling young | F | M | R | O | NA | 10 |
| *Mniotilta varia* | Parulidae | *Helmitheros vermivorum* | Parulidae | unknown | N | M | R | O | NA | 39 |
| *Motacilla alba* | Motacillidae | *Phoenicurus ochruros* | Muscicapidae | close nest | N | B | R | R | Eu | 18 |
| *Motacilla cinerea* | Motacillidae | *Cinclus cinclus* | Cinclidae | calling young | N | M | R | R | Eu | 43 |
| *Motacilla cinerea* | Motacillidae | *Turdus philomelos* | Turdidae | close nest | N | U | R | O | Eu | 39 |
| *Motacilla flava* | Motacillidae | *Galerida cristata* | Alaudidae | orphan | F | M | O | O | Eu | 22 |
| *Muscicapa striata* | Muscicapidae | *Turdus merula* | Turdidae | lost nest, close nest | N | B | R | O | Eu | 39 |
| *Muscicapa striata* | Muscicapidae | *Troglodytes troglodytes* | Troglodytidae | close nest | B | B | R | R | Eu | 22 |
| *Muscicapa striata* | Muscicapidae | *Turdus merula* | Turdidae | unknown | N | U | R | O | Eu | 22 |
| *Parus major* | Paridae | *Cyanistes caeruleus* | Paridae | close nest | N | B | C | C | Eu | 29 |
| *Passer domesticus* | Passeridae | *Baeolophus bicolor* | Paridae | close nest, calling young | N | F | R | C | NA | 39 |
| *Passer domesticus* | Passeridae | *Prunella modularis* | Prunellidae | calling young | B | F | R | O | Eu | 39 |
| *Passer domesticus* | Passeridae | *Petrochelidon pyrrhonota* | Hirundinidae | close nest | N | F | R | D | NA | 39 |

Continued on the next page

| Helper | | Host | | Reasons | Host | Helper | Nest site | | CON | Source |
|---|---|---|---|---|---|---|---|---|---|---|
| Species | Family | Species | Family | | Age | sex | Helper | Host | | |
| *Passer domesticus* | Passeridae | *Anthus petrosus* | Motacillidae | unknown | F | M | R | R | Eu | 22 |
| *Passer domesticus* | Passeridae | *Serinus serinus* | Fringillidae | unknown | N | F | R | O | Eu | 39 |
| *Passer domesticus* | Passeridae | *Turdus merula* | Turdidae | unknown | F | F | R | O | Eu | 39 |
| *Passer domesticus* | Passeridae | *Muscicapa striata* | Muscicapidae | unknown | N | F | R | R | Eu | 39 |
| *Passer domesticus* | Passeridae | *Vireo olivaceus* | Vireonidae | unknown | N | U | R | O | NA | 39 |
| *Passer domesticus* | Passeridae | *Setophaga aestiva* | Parulidae | unknown | N | U | R | O | NA | 39 |
| *Passer domesticus* | Passeridae | *Tyrannus tyrannus* | Tyrannidae | unknown | F | F | R | O | NA | 39 |
| *Passer domesticus* | Passeridae | *Tyrannus tyrannus* | Tyrannidae | unknown | F | F | R | O | NA | 39 |
| *Passer domesticus* | Passeridae | *Tachycineta bicolor* | Hirundinidae | unknown | N | U | R | C | NA | 39 |
| *Passerculus sandwichensis* | Passerellidae | *Calcarius lapponicus* | Calcariidae | unknown | N | U | O | O | NA | 31 |
| *Periparus ater* | Paridae | *Cyanistes caeruleus* | Paridae | unknown | F | U | C | C | Eu | 22 |
| *Petroica australis* | Petroicidae | *Petroica macrocephala* | Petroicidae | close nest, calling young | B | M | O | R | Au | 26 |
| *Phoenicurus phoenicurus* | Muscicapidae | *Phoenicurus ochruros* | Muscicapidae | calling young, close nest | B | M | R | R | Eu | 21 |
| *Phoenicurus phoenicurus* | Muscicapidae | *Phoenicurus ochruros* | Muscicapidae | mateless | B | M | R | R | Eu | 6 |
| *Phylloscopus collybita* | Phylloscopidae | *Troglodytes troglodytes* | Troglodytidae | unknown | F | B | D | R | Eu | 22 |
| *Phylloscopus sibilatrix* | Phylloscopidae | *Erithacus rubecula* | Muscicapidae | lost nest, close nest | B | M | D | R | Eu | 22 |
| *Picoides dorsalis* | Picidae | *Picoides arcticus* | Picidae | calling young, mateless | N | F | C | C | NA | 39 |
| *Pipilo erythrophthalmus* | Passerellidae | *Spizella pusilla* | Passerellidae | close nest | N | M | O | O | NA | 39 |
| *Pipilo erythrophthalmus* | Passerellidae | *Haemorhous mexicanus* | Fringillidae | unknown | F | B | O | R | NA | 39 |
| *Pipilo erythrophthalmus* | Passerellidae | *Mimus polyglottos* | Mimidae | unknown | F | F | O | O | NA | 39 |
| *Pipilo erythrophthalmus* | Passerellidae | *Spizella pusilla* | Passerellidae | unknown | F | F | O | O | NA | 39 |
| *Pipilo erythrophthalmus* | Passerellidae | *Hylocichla mustelina* | Turdidae | unknown | B | M | O | O | NA | 37 |
| *Pipilo maculatus* | Passerellidae | *Junco hyemalis* | Passerellidae | calling young | N | M | O | R | NA | 39 |
| *Piranga olivacea* | Cardinalidae | *Spizella passerina* | Passerellidae | mate incubates | N | M | O | O | NA | 39 |
| *Poecile atricapillus* | Paridae | *Catharus guttatus* | Turdidae | unknown | N | U | C | O | NA | 36 |
| *Poecile gambeli* | Paridae | *Sphyrapicus thyroideus* | Picidae | lost nest, close nest | N | B | C | C | NA | 39 |
| *Poecile montanus* | Paridae | *Lophophanes cristatus* | Paridae | lost nest, calling young | N | B | C | C | Eu | 13 |
| *Polioptila plumbea* | Polioptilidae | *Tangara larvata* | Thraupidae | close nest | N | F | O | O | NA | 39 |
| *Prinia maculosa* | Cisticolidae | *Sylvia layardi* | Sylviidae | close nest | N | B | D | O | Af | 39 |
| *Progne subis* | Hirundinidae | *Passer domesticus* | Passeridae | unknown | F | M | C | R | NA | 39 |
| *Progne subis* | Hirundinidae | *Sturnus vulgaris* | Sturnidae | unknown | N | B | C | C | NA | 39 |
| *Protonotaria citrea* | Parulidae | *Setophaga pinus* | Parulidae | unknown | F | U | C | O | NA | 39 |
| *Pyrrhocorax graculus* | Corvidae | *Pyrrhocorax pyrrhocorax* | Corvidae | calling young | F | U | R | R | Eu | 13 |
| *Quiscalus quiscula* | Icteridae | *Spizella passerina* | Passerellidae | unknown | B | U | O | O | NA | 39 |
| *Ramphocelus passerinii* | Thraupidae | *Turdus grayi* | Turdidae | unknown | B | M | O | O | NA | 5 |
| *Saxicola rubicola* | Muscicapidae | *Phoenicurus ochruros* | Muscicapidae | unknown | B | M | O | R | Eu | 35 |
| *Sayornis phoebe* | Tyrannidae | *Thryothorus ludovicianus* | Troglodytidae | lost nest | B | U | R | R | NA | 16 |
| *Sayornis phoebe* | Tyrannidae | *Tachycineta bicolor* | Hirundinidae | unknown | N | F | R | C | NA | 39 |
| *Setophaga fusca* | Parulidae | *Setophaga coronata* | Parulidae | close nest, calling young | N | F | O | O | NA | 39 |
| *Setophaga ruticilla* | Parulidae | *Turdus migratorius* | Turdidae | close nest | N | B | O | O | NA | 39 |
| *Sialia sialis* | Turdidae | *Tachycineta bicolor* | Hirundinidae | close nest, calling young | N | M | C | C | NA | 42 |
| *Sialia sialis* | Turdidae | *Troglodytes aedon* | Troglodytidae | close nest, mate incubates | N | M | C | C | NA | 39 |
| *Sialia sialis* | Turdidae | *Troglodytes aedon* | Troglodytidae | close nest | N | M | C | C | NA | 39 |
| *Sialia sialis* | Turdidae | *Sialia currucoides* | Turdidae | mateless | N | M | C | C | NA | 39 |
| *Sialia sialis* | Turdidae | *Mimus polyglottos* | Mimidae | unknown | B | B | C | O | NA | 39 |
| *Sitta europaea* | Sittidae | *Dendrocopos major* | Picidae | close nest, calling young | N | U | C | C | Eu | 13 |
| *Sitta europaea* | Sittidae | *Dendrocopos major* | Picidae | close nest, calling young | N | U | C | C | Eu | this study |
| *Sitta europaea* | Sittidae | *Dendrocopos major* | Picidae | calling young | N | F | C | C | Eu | 13 |
| *Sitta europaea* | Sittidae | *Sturnus vulgaris* | Sturnidae | close nest | N | U | C | C | Eu | 39 |
| *Sitta europaea* | Sittidae | *Sturnus vulgaris* | Sturnidae | close nest | N | U | C | C | Eu | 39 |
| *Sitta pygmaea* | Sittidae | *Sialia currucoides* | Turdidae | close nest, calling young | N | M | C | C | NA | 39 |
| *Spizella passerina* | Passerellidae | *Haemorhous purpureus* | Fringillidae | close nest, orphan | F | B | O | O | NA | 39 |
| *Spizella passerina* | Passerellidae | *Tyrannus tyrannus* | Tyrannidae | unknown | B | M | O | O | NA | 11 |
| *Spizella pusilla* | Passerellidae | *Pipilo erythrophthalmus* | Passerellidae | close nest | N | U | O | O | NA | 39 |

Continued on the next page

| Helper | | Host | | Reasons | Host | Helper | Nest site | | CON | Source |
|---|---|---|---|---|---|---|---|---|---|---|
| Species | Family | Species | Family | | Age | sex | Helper | Host | | |
| *Sturnus vulgaris* | Sturnidae | *Dryobates pubescens* | Picidae | calling young | F | B | C | C | NA | 4 |
| *Sturnus vulgaris* | Sturnidae | *Colaptes auratus* | Picidae | close nest | N | B | C | C | NA | 39 |
| *Sturnus vulgaris* | Sturnidae | *Progne subis* | Hirundinidae | lost nest | N | U | C | C | NA | 39 |
| *Sturnus vulgaris* | Sturnidae | *Turdus migratorius* | Turdidae | lost nest | N | B | C | O | NA | 39 |
| *Sturnus vulgaris* | Sturnidae | *Parus major* | Paridae | unknown | N | U | C | C | Eu | 13 |
| *Sturnus vulgaris* | Sturnidae | *Turdus migratorius* | Turdidae | unknown | N | U | C | O | NA | 39 |
| *Sylvia atricapilla* | Sylviidae | *Emberiza citrinella* | Emberizidae | orphan | N | F | O | O | Eu | 13 |
| *Tachycineta bicolor* | Hirundinidae | *Turdus migratorius* | Turdidae | close nest | N | M | C | O | NA | 39 |
| *Tachycineta thalassina* | Hirundinidae | *Sialia mexicana* | Turdidae | lost nest | N | B | C | C | NA | 8 |
| *Thryothorus ludovicianus* | Troglodytidae | *Myiarchus crinitus* | Tyrannidae | close nest, mate incubates | N | M | R | C | NA | 39 |
| *Thryothorus ludovicianus* | Troglodytidae | *Baeolophus bicolor* | Paridae | unknown | N | U | R | C | NA | 39 |
| *Toxostoma rufum* | Mimidae | *Pipilo erythrophthalmus* | Passerellidae | unknown | F | U | O | O | NA | 28 |
| *Troglodytes aedon* | Troglodytidae | *Cardinalis cardinalis* | Cardinalidae | close nest, calling young | N | M | C | O | NA | 23 |
| *Troglodytes aedon* | Troglodytidae | *Colaptes auratus* | Picidae | close nest, mate incubates | N | M | C | C | NA | 39 |
| *Troglodytes aedon* | Troglodytidae | *Pheucticus melanocephalus* | Cardinalidae | mateless | B | M | C | O | NA | 39 |
| *Troglodytes hiemalis* | Troglodytidae | *Myadestes townsendi* | Turdidae | unknown | B | U | R | R | NA | 39 |
| *Troglodytes troglodytes* | Troglodytidae | *Parus major* | Paridae | close nest, mate incubates | N | M | R | C | Eu | 39 |
| *Troglodytes troglodytes* | Troglodytidae | *Parus major* | Paridae | close nest | N | F | R | C | Eu | 13 |
| *Troglodytes troglodytes* | Troglodytidae | *Muscicapa striata* | Muscicapidae | close nest | F | U | R | R | Eu | 39 |
| *Troglodytes troglodytes* | Troglodytidae | *Linaria cannabina* | Fringillidae | close nest | N | B | R | O | Eu | 39 |
| *Troglodytes troglodytes* | Troglodytidae | *Cyanistes caeruleus* | Paridae | unknown | N | U | R | C | Eu | 39 |
| *Troglodytes troglodytes* | Troglodytidae | *Periparus ater* | Paridae | unknown | N | U | R | C | Eu | 39 |
| *Troglodytes troglodytes* | Troglodytidae | *Phylloscopus trochilus* | Phylloscopidae | unknown | F | U | R | D | Eu | 39 |
| *Turdus merula* | Turdidae | *Erithacus rubecula* | Muscicapidae | close nest, calling young | B | B | O | R | Eu | 22 |
| *Turdus merula* | Turdidae | *Turdus philomelos* | Turdidae | lost nest, close nest | F | M | O | O | Eu | 22 |
| *Turdus merula* | Turdidae | *Motacilla alba* | Motacillidae | calling young | F | M | O | R | Eu | 39 |
| *Turdus merula* | Turdidae | *Turdus philomelos* | Turdidae | mateless | B | M | O | O | Eu | 39 |
| *Turdus merula* | Turdidae | *Turdus iliacus* | Turdidae | mateless | N | M | O | O | Eu | 32 |
| *Turdus merula* | Turdidae | *Erithacus rubecula* | Muscicapidae | unknown | F | F | O | R | Eu | 39 |
| *Turdus migratorius* | Turdidae | *Haemorhous mexicanus* | Fringillidae | close nest | N | B | O | R | NA | 39 |
| *Turdus migratorius* | Turdidae | *Dumetella carolinensis* | Mimidae | close nest | N | B | O | O | NA | 39 |
| *Turdus migratorius* | Turdidae | *Toxostoma rufum* | Mimidae | unknown | U | U | O | O | NA | 39 |
| *Turdus migratorius* | Turdidae | *Sialia sialis* | Turdidae | unknown | B | U | O | C | NA | 28 |
| *Turdus philomelos* | Turdidae | *Prunella modularis* | Prunellidae | calling young | F | U | O | O | Eu | 22 |
| *Tyrannus forficatus* | Tyrannidae | *Quiscalus quiscula* | Icteridae | close nest | N | U | O | O | NA | 39 |
| *Tyrannus tyrannus* | Tyrannidae | *Icterus galbula* | Icteridae | unknown | B | F | O | D | NA | 39 |
| *Upupa epops* | Upupidae | *Jynx torquilla* | Picidae | lost nest, calling young | N | B | C | C | Eu | 22 |
| *Vermivora cyanoptera* | Parulidae | *Spizella pusilla* | Passerellidae | unknown | N | U | O | O | NA | 39 |
| *Zenaida auriculata* | Columbidae | *Turdus amaurochalinus* | Turdidae | lost nest | N | U | O | O | SA | 38 |
| *Zenaida macroura* | Columbidae | *Zenaida asiatica* | Columbidae | unknown | N | F | O | O | NA | 39 |
| *Zonotrichia albicollis* | Passerellidae | *Junco hyemalis* | Passerellidae | unknown | F | U | O | R | NA | 39 |
| *Zonotrichia capensis* | Passerellidae | *Turdus leucomelas* | Turdidae | lost nest, calling young | N | U | O | O | SA | 2 |
| *Zosterops palpebrosus* | Zosteropidae | *Terpsiphone paradisi* | Monarchidae | calling young, mate incubates | N | U | O | O | As | 1 |

## REFERENCES


(1) Balar R. 2009. Interspecific feeding of Asian Paradise-Flycatcher *Terpsiphone paradise* nestlings by Oriental White-eye *Zosterops palpebrosus*. Indian Birds 4: 163–164.

(2) Batisteli A. F., Sarmento H. 2016. Interspecific parental care by a Rufous-collared sparrow (*Zonotrichia capensis*) at a nest of the Pale-breasted thrush (*Turdus leucomelas*) parasitized by a Cowbird (*Molothrus bonariensis*). Ornitol. Neotrop. 27: 253–257.

(3) Bruni G., Menchetti M., Ricciardi G., Vannini A., Mori E. 2014. An unexpected case of heterospecific altruistic behaviour in a non-breeding migrant tern (Charadriformes, Sternidae). Ornis Hungarica 22: 76–80.

(4) Burbidge G. 2018. European Starling pair feeds a juvenile Downy Woodpecker. Ontario Birds 36: 170–173.

(5) Chaves-Bonilla L., Sandoval L. 2015. [*Ramphocelus passerinii* feeding *Turdus grayi* chicks and notes about reproduction in other *Ramphocelus* species]. Boletín SAO 24: 4–8.

(6) Diviš T. 2018. Male of Common Redstart (*Phoenicurus phoenicurus*) helped parents of Black Redstart (*Phoenicurus ochruros*) to feed their nestlings. Panurus 27: 57–60.

(7) Dula P. 2019. [Feeding of an adult House Sparrow *Passer domesticus* by the House Martin *Delichon urbicum* – An attempt to interpret the phenomenon]. Kulon 24: 82–87.
(8) Eltzroth E. K., Robinson S. R. 1984. Violet-green Swallows help Western Bluebirds at the nest. J. Field Ornithol. 55: 259–261.
(9) Farmer C., Frederick B. A., Banko P. C., Stephens R. M., Snow C. W. 2008. Palila (*Loxioides baillueui*) fledgling fed by Hawai'i 'Amakihi (*Hemignathus virens*). Wilson J. Ornithol. 120: 416–418.
(10) Fiss C. J., McNeil D. J., Poole R. E., Rogers K. M., Larkin J. L. 2016. Prolonged interspecific care of two sibling Golden-winged Warblers (*Vermivora chrysoptera*) by a Black-and-white Warbler (*Mniotilta varia*). Wilson J. Ornithol. 128: 921–926.
(11) Foster J., Tozer R. 2001. Chipping Sparrow feeds young of Eastern Kingbird. Ontario Birds 19: 79–83.
(12) Gill F., Donsker D. 2020 (eds). IOC World Bird List (v 10.1). Accessible at: www.worldbirdnames.org [accessed 16.06. 2020].
(13) Grangé J.-L., Magnin D., Potiron J.-L. 2010. À propos d'une aide au nourrissage interspécifique chez la Sitelle torchepot *Sitta europea*. Le Casseur d'os 10: 167–176.
(14) Hall M. L., Murphy S. A., Churchwell R. T., Milenkaya O. 2010. Interspecific feeding between an insectivore and a granivore – male Purple-crowned Fairy-wren *Malurus coronatus* feeds nestling Crimson Finches *Neochmia phaeton*. Corella 34: 49–50.
(15) Halley M. R., Heckscher C. M. 2013. Interspecific parental care by a Wood Thrush (*Hylocichla mustelina*) at a nest of the Veery (*Catharus fuscescens*). Wilson J. Ornithol. 125: 823–828.
(16) Haucke H. H. 2015. Interspecific feeding of Carolina Wren nestlings and fledglings by an Eastern Phoebe. Bulletin of the Texas Ornithological Society 48: 59–62.
(17) Heber S. 2013. Anecdotal evidence of interspecific parental care: Feeding and brooding of Robin (*Petroica australis*) nestlings by a female Bellbird (*Anthornis melanura*). Notornis 60: 186–187.
(18) von Hirschheydt J. 1998. Adoption of Black Redstart nestlings by a pair of White Wagtails leads to the loss of their own young. Ornithol. Beob. 95: 66-68.
(19) Jiang A., Jiang D., Goodale E., Zhou F., Wen Y. 2016. Olive-backed Sunbird *Cinnyris jugularis* assisting Crested Bunting *Melophus lathami* at the nest: substantiated evidence for interspecific feeding, Guangxi, south-west China. Forktail 32: 93–96.
(20) Klvaňová A. 2017. Mezidruhové krmení. Ptačí svět 3/2017: 3.
(21) Král M. 2001. Conflict between the Redstart (*Phoenicurus phoenicurus*) and the Black Redstart (*Phoenicurus ochruros*) at a shared nest site. Sylvia 37: 153–155.
(22) Krištín A. 2009. Interspecific feeding at bird nests: *Ficedula albicollis* as a helper at the nest of *Turdus philomelos*. Tichodroma 21: 98–101.
(23) LaBarbera K., Spencer R. 2016. House Wren (*Troglodytes aedon*) provisions nestlings of Northern Cardinal (*Cardinalis cardinalis*). Wilson J. Ornithol. 128: 676–678.
(24) Lozano G. A., Lemon R. E. 1998. Adoption of Yellow Warbler nestlings by Song Sparrows. Wilson Bull. 110: 131–133.
(25) Luo K., Hu Y., Lu Z., Li D. 2018. Interspecific feeding at a bird nest: Snowy-browed flycatcher (*Ficedula hyperythra*) as a helper at the Rufous-bellies niltava (*Niltava sundara*) nest, Yunnan, Southwest China. Wilson J. Ornithol. 130: 1003–1008.
(26) Masuda B. M. 2011. Interspecific feeding of South Island Tomtit (*Petroica macrocephala macrocephala*) nestlings and fledglings by a male Stewart Island Robin (*P. australis rakiura*). Notornis 58: 95–97.
(27) McGowan K. J. 1990. Nesting Fish Crows adopt a fledgling Blue Jay. J. Field Ornithol. 61: 171–173.
(28) McNair D. B., Duyck B. 1991. Interspecific feeding among some oscines. The Chat 55: 9–11.
(29) Morozov N. S. 2014. [Involvement of Great Tits *Parus major* in feeding young of nearby nesting Blue Tits *Parus caeruleus*]. Russkiy Ornitologicheskiy Zhurnal 23: 1412–1416.
(30) Nicolai B. 2003. Middle Spotted Woodpecker *Picoides medius* feeds young House Sparrow *Passer domesticus*. Ornithol. Jber. Mus. Heineanum 21: 1–4.
(31) Ouellet H. 1990. Savannah Sparrow attends nest of Lapland Longspur. Bird Behav. 9: 30–33.
(32) Petersen Ć. 2014. [A male Black Bird helper at Redwing nests]. Náttúrufræðingurinn 84: 61–64.
(33) Pierce A. J. 2005. Interspecific feeding of a White-Eye fledgling by a Little Spiderhunter. The Natural History Journal of Chulalongkorn University 5: 41.
(34) Pranty B. 2010. Hairy Woodpeckers (*Picoides villosus*) feed Downy Woodpecker (*P. pubescens*) nestlings. Florida Field Naturalist 38: 71–72.
(35) Pugacewicz E. 2009. [Cases of positive and probable interspecific altruism in birds observed in the northern Podlasie region]. Kulon 14: 129–132.
(36) Reitsma L. R., Burns C., Sullivan J. 2019. *Poecile atricapillus* (Black-capped Chickadee) feeding *Catharus guttatus* (Hermit Thrush) nestlings. Northeast. Nat. 26: N15–N17.
(37) Schaeffer K. M., Brown W. P., Shriver W. G. 2009. Misdirected parental care by a male Eastern Towhee at a Wood Thrush nest. Wilson J. Ornithol. 121: 427–429.
(38) Segura L. N., Gonzales E., Jauregui A. 2016. Unusual nest and nestling appropriation by the Eared Dove (*Zenaida auriculata*). Ornitol. Neotrop. 27: 101–104.
(39) Shy M. M. 1982. Interspecific feeding among birds: A review. J. Field Ornithol. 53: 370–393.
(40) Van Impe J. 1997. La mouette mélanocéphale *Larus melanocephalus* comme aide à la mouette rieuse *L. ridibundus* pendant sa reproduction. Alauda 65: 7–12.
(41) Vernet P. 2013. Une mésange bleue *Cyanystes caeruleus* nourrit une nichée de rougequeues noirs *Phoenicurus ochruros*. Le Tiercelet 22: 28–29.
(42) Williams D. P. Brittingham M. C., Avery J. D. 2019. Eastern Bluebird (*Sialia sialis*) feeds Tree Swallow (*Tachycineta bicolor*) nestlings: Support for location-based decision rule. Wilson J. Ornithol. 131: 633–637.
(43) Yoerg S. I., O'Halloran J. 1991. Dipper nestlings fed by a Gray Wagtail. Auk 108: 427–440.