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**Vnitrodruhový hnízdční parazitismus: případová studie poláka velkého a
vlaštovky obecné**

**Conspecific brood parasitism: a case study on the common pochard and the
barn swallow**

Disertační práce
Ph.D. Thesis

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I declare that this thesis has not been submitted for the purpose of obtaining the same or any other academic degree earlier or at another institution. My involvement in the research presented in this thesis is expressed through the authorship order of the included publications and manuscripts. All literature sources I used when writing this thesis have been properly cited.

In Prague, 30th April 2017

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Abstract

Presented thesis is mainly concerned with the conspecific brood parasitism (CBP) in birds. CBP is an alternative reproductive strategy when a parasitic female lay egg or eggs to other (host) female's nest of the same species. Then the parasitic female leaves the host's nest and does not provide any energetic investment in a subsequent parental care. Distinguish parasitic eggs or young is problematic because there are no obvious morphological differences. Thus, the use of molecular method is crucial for proper determination of CBP. CBP can be used as 'a best-of-bad-job' when female does not have her own nest or lost her nest for example through predation. Other option is that female can increase her fecundity ('fecundity enhancement' hypothesis) when she lay parasitic egg/eggs and care about her own clutch afterward.

Two different model species were studied. The first one was a precocial diving duck - the common pochard (*Aythya ferina*; Anseriformes; Anatidae). Protein fingerprinting was used for detection of CBP and for distinguishing between eggs of individual females. It was found that the rate of CBP was relatively high in this species (91%, 72%; **Chapter 1, 4**). Further results indicated that the host clutch size decreased with the number of parasitic eggs in the clutch. The study of individual reproductive tactics revealed that females used parasitism in different context. Some females laid eggs only parasitically but others combined parasitism and normal nesting. On the other hand, some females laid their eggs only in own nest and did not parasitize. These three reproductive tactics were overall in balance and females could change them between years. Moreover, it was found that females with different reproductive tactics varied in their reproductive effort. Finally, it was tested if a detection of parasitic eggs and parasitized nests is possible by using egg morphology (Eadie's method; **Chapter 3**). The results showed that the egg morphology was not suitable for a reliable determination of CBP in the common pochard and that the method could be impacted by relatedness between parasitic and host female.

The second species under study was an altricial songbird - the barn swallow (*Hirundo rustica rustica*; Passeriformes; Hirundinidae). For detection of parasitic young were used microsatellite DNA typing. The frequency of the CBP was lower than in the common pochard (22%; **Chapter 2**). Additionally, it was found that the rate of CBP increased with a breeding synchrony. About 28% of the parasitic young were fertilized by the nest attending male (quasi-parasitism = QP). Parasitic females had more offspring per breeding attempt than was the population average as same as the quasi parasitic males. On the other hand, host females suffered decrease in the number of offspring per breeding attempt.

In conclusion, the presented thesis brings new information about CBP in two different study species (the common pochard and the barn swallow) revealed by molecular methods.

Abstrakt

Tato disertační práce se zabývá vnitrodruhovým hnízdním parazitismem u ptáků (VHP). VHP je alternativní reprodukční strategie, kdy parazitická samice klade vejce do hnízda cizí hostitelské samice stejného druhu. Parazitická samice následně hnízdo hostitele opouští a ušetří tak energii, kterou by jinak musela investovat do rodičovské péče. Jelikož mezi parazitickým a hostitelským vejcem či mládětem není znatelný morfologický rozdíl, je problematické VHP rozpoznat. Proto je pro jeho určení vhodné použít molekulární metodiku. VHP může být použit jako „a best-of-bad-job“ strategie, kdy samice nemá vlastní hnízdo a vejce snáší pouze paraziticky, nebo o hnízdo přišla např. kvůli predaci. Další možnost je, že samice mohou zvýšit svoji fekunditu („fecundity enhancement“). V tomto případě samice často klade parazitická vejce a později zakládá vlastní snůšku.

V rámci této disertační práce byly studovány dva modelové druhy. Prvním druhem byla prekociální potápivá kachna – polák velký (*Aythya ferina*; Anseriformes; Anatidae). Parazitická vejce byla určena pomocí proteinového fingerprintingu a díky této metodě bylo také možné rozlišit vejce jednotlivých samic. Míra VHP byla u poláka velkého relativně vysoká (91 %, 72 %; **Kapitola 1, 4**). Velikost snůšky hostitelské samice byla negativně ovlivněna počtem cizích vajec ve snůšce. Ve studii, která se zabývala jednotlivými reprodukčními taktikami samic, bylo zjištěno, že samice poláka využívají parazitismus v různém kontextu. Některé samice snášely vejce pouze paraziticky, jiné samice kombinovaly parazitismus s péčí o vlastní snůšku. Na druhou stranu některé samice snášely vejce pouze do vlastní snůšky. Tyto tři reprodukční taktiky byly během tří let zastoupeny rovnoměrně a samice je během let měnily. Zároveň bylo zjištěno, že reprodukční úsilí se mezi samicemi lišilo v závislosti na reprodukční taktice. V neposlední řadě bylo testováno, zda je možné určit VHP pomocí morfologie vajec (tzv. ‚Eadiho metoda‘, **Kapitola 3**). Výsledky naznačují, že použití morfologie vajec není vhodné pro určení VHP, a navíc bylo zjištěno, že výsledek může být ovlivněn příbuzností mezi parazitem a hostitelem.

Druhý modelový druh byl atriciální pěvec – vlaštovka obecná (*Hirundo rustica rustica*; Passeriformes; Hirundinidae). Parazitická mláďata byla určena pomocí mikrosatelitů DNA. Míra VHP byla nižší než u poláka velkého (22 %, **Kapitola 2**). Dále bylo zjištěno, že míra hnízdního parazitismu byla pozitivně ovlivněna mírou synchronicity v hnízdění. Zhruba 28 % parazitických mláďat bylo oplodněno rezidentním samcem z hostitelského hnízda (Quasi parazitismus = QP). Samice, které kombinovaly normální hnízdění a parazitismus měly v průměru o jedno mládě více než ostatní samice v populaci. Stejně tak i QP samci měli zhruba

o jednoho potomka více než průměrný samec v populaci. Oproti tomu hostitelské samice měly zhruba o jedno mládě méně než byl průměr v rámci populace.

Předložená disertační práce přináší nové poznatky o VHP u dvou studovaných druhů (polák velký a vlaštovka obecná), které byly získány pomocí molekulárních metod.

Introduction

Brood parasitism is a generally known behaviour in birds. The most famous example is the common cuckoo (*Cuculus canorus*), where a female lays an egg in a nest of different species. After the female lays her egg she leaves the nest and thus breaks free from energetic costs connected with a subsequent parental care (as an incubation and a care for young; Payne 1977; Davies 2000). Because cuckoos are not able to build their own nest and their reproduction depends entirely on other host species this brood parasitism is termed obligate (OBP). But it is not only the common cuckoo that leaves its young entirely in the care of other birds. The brown headed-cowbird (*Molothrus ater*) is probably a more known brood parasite in America. Altogether there is about 1% of bird species that are obligate brood parasites (Payne 1977). OBP prevails in birds with altricial mode of parental care and there is only one known species with precocial mode of parental care (black-headed duck, *Heteronetta atricapilla*, Payne 1977; Davies 2000).

Furthermore, there are bird species that have adopted a facultative brood parasitism (FBP) in which a parasitic female lays its egg or eggs in another female's nest as an alternative in contrast to normal breeding in own nest (Payne 1977; Yom-Tov 1980; Rohwer and Freeman 1989; Petrie and Møller 1991; Davies 2000). Two forms of FBP are known. Firstly, it is an interspecific brood parasitism (IBP) when a female parasitizes different bird species. Sometimes it is thought to be an adaptive strategy (the redhead duck, *Aythya americana*; Sorenson 1991, 1993, 1997) but it can be also considered a maladaptive behaviour (Eadie and Lumsden 1985) when females are not able to distinguish between conspecific and heterospecific nests (the common goldeneye *Bucephala clangula*; Pöysä 2003). IBP is often present in species in which the second form of facultative brood parasitism occurs - a conspecific (or intraspecific) brood parasitism (Lyon and Eadie 1991; Krakauer and Kimball 2009).

Presented thesis is primarily concerned with the conspecific brood parasitism (CBP). Conspecific brood parasites are females that exploit the parental care from other individuals of the same species (Payne 1977; Davies 2000). Previous studies suggested this phenomenon was rare against OBP (Payne 1977; MacWhirter 1989; Yom-Tov 1980), probably because recognition of a parasitic egg laid by conspecific parasite has been problematic in contrast with recognition of a parasitic egg in OBP. When a female lays its parasitic egg in the nest of interspecific hosts, even though obligate brood parasites use often egg mimicry (Payne 1977; Davies 2000), an experienced researcher can distinguish the egg of parasite in the nest. But, in

CBP eggs of host and parasite look alike and there is a need for more sophisticated methods to determine parasitized nest. Several traditional methods have been used for their recognition. (i) Abnormal clutch size is a potential clue that more than one female laid eggs in one nest. (ii) Or, because birds are able to lay only one egg per day (Sturkie 1965), the appearance of two eggs in a nest during one day may be another hint that a nest was parasitized. (iii) Alternative possibility is finding a new egg in a nest few days before clutch initiation or after clutch completion or (iv) CBP can be detected by differences in eggs size, shape, colour or egg pattern (Yom-Tov 1980; Møller 1987; MacWhirter 1989; Vedder et al. 2007, 2010). These methods can suggest appearance of CBP but often underestimate or overestimate the true frequency of CBP (McRae 1997b; Andersson and Åhlund 2001; Grønstøl et al. 2006; Waldeck and Andersson 2006; Griffith et al. 2009). A direct observation or a time-lapse photography of nests and marked females (Heusmann et al. 1980; Eadie 1989; Sorenson 1991; Forslund and Larsson 1995) has been thought to be more accurate but Andersson and Åhlund (2001) highlighted that the method is lacking in providing sufficient sample size and that it is time consuming.

At the end of the 20th century molecular methods were integrated into the field biology. During this period, the number of known CBP species increased from 53 (Yom-Tov 1980) on more than 200 (Yom-Tov 2001). The number of studies stemming from use of genetic data continued to grow with information about the ecology and the life-histories of hosts and parasites (for example: Andersson and Åhlund 2000, 2001; Åhlund and Andersson 2001; Nielsen et al. 2006b; Andersson and Waldeck 2007; Waldeck et al. 2008; Jaatinen et al. 2009a,b, 2011; Aderholm et al. 2009; Hoi et al. 2010; Pöysä et al. 2010; Reichart et al. 2010; Duda and Chętnicki 2012; Šťovíček et al. 2013). Further, molecular methods have helped to clarify the reliability of traditional methods and seems to be more precise in determination of CBP (McRae 1997b; Andersson and Åhlund 2001; Grønstøl et al. 2006; Griffith et al. 2009; Waldeck and Andersson 2006). This is also the reason why were used protein fingerprinting (**Chapter 1, 3, 4**) and microsatellite DNA typing (**Chapter 2**) in studies presented in this thesis.

But, even though molecular methods are probably the most accurate for measuring the rate of CBP at this time, there is an effort to develop a method based on egg morphology (Eadie 1989 - so called Eadie's method). Such an approach would be cheaper, faster, and accessible to a broader number of biologists. Additionally, its application would be possible on historical collections. The Eadie's method was developed on goldeneye ducks (*Bucephala* spp.; Eadie 1989). It is based on assumption that variation in egg size is greater among females than within them. It requires a comparison of the Euclidean distance calculated for all pairs of eggs within

a clutch using standardized egg measurements of length, width and weight. When a maximum Euclidean distance (MED) exceeds a threshold value, the clutch is classified as parasitized.

The Eadie's method was compared with molecular identification of parasitized clutches in goldeneyes and its reliability was confirmed (Pöysä et al. 2009; Eadie et al. 2010). But Ådahl et al. (2004) questioned the use of the Eadie's method. They provided an experimental study using the common goldeneye and two other bird species (zebra finch (*Taeniopygia guttata*), jackdaws (*Corvus monedula*)) as model organisms. The MED was measured in original clutches. Then the CBP was simulated by randomly moved eggs among the clutches and the MED in manipulated clutches were calculated again. The results showed that the MED increased in manipulated clutches but there was still a considerable overlap and it was problematic to set the threshold value. The MED also increased with the clutch size which meant that high MED could be a signal for parasitized nest but could be also a signal just for nest with a high number of eggs. The same results were found in other studies comparing molecular and Eadie's method in different bird species (Roy et al. 2009; Lemons et al. 2011).

The applicability of Eadie's method on the common pochard (*Aythya farina*) is tested in **Chapter 3** in presented thesis. The results showed the MED was higher in parasitized nests than in non-parasitized but the overlap between them was substantial. The MED was affected by clutch size too. In this study, it was possible to correctly distinguish between parasitized and non-parasitized nests in 76.4% and parasitic and non-parasitic eggs in 68.3%. According to previous studies (Ådahl et al. 2004; Roy et al. 2009; Lemons et al. 2011) and results that are presented in **Chapter 3**, I think that the Eadie's method is not automatically applicable for detection of CBP.

But, the recognition of parasitized clutches based on Eadie's method can be affected by another actuality. Because the egg size is thought to be highly heritable in birds (reviewed in Christians 2002) the relatedness between host and parasitic female can complicate distinguishing between their eggs on the bases of egg morphology. There is a case for such consideration because in several studies were found that the host and parasitic females were close kin (Andersson and Åhlund 2000; Andersson and Waldeck 2007; Jaatinen et al. 2009a; Duda and Chętnicki 2012). In such situation, the contrast in egg size between parasitic and host female decrease as same as the MED. Results in **Chapter 3** showed that the Euclidean distance was impacted by the relatedness between females and discuss the applicability of Eadie's method in the common pochard.

Incidence of the CBP is highly variable between species (Yom-Tov 1980, 2001; Geffen and Yom-Tov 2001; Arnold and Owens 2002;). It has been suggested it is affected by high

fecundity rate, by the cost of parental care or by the increase period of time the nest is exposed (Andersson 1984; Rohwer and Freeman 1989; Sorenson 1992; Lyon and Everding 1996; Geffen and Yom-Tov 2001). In precocial species is known, they usually lay larger clutches than similar sized altricial species (Ar and Yom-Tov 1978) and they start an incubation at the end of a clutch completion. Both these actualities prolong the vulnerability of nests to parasitism. Also, parental care about precocial young is not as demanding as in altricial species, because it only consists from guiding young to feeding sites and protection against predators (Sorenson 1992; Öst et al. 2007).

Really, CBP was described in most of the precocial orders and in order Anseriformes almost in a half of the species (Yom-Tov 2001). This is the reason, why was the common pochard choose as a first model species. It is a precocial diving duck that belongs to order Anseriformes and it has an average clutch size between 8 and 10 (Cramp 2006). So, the CBP was highly expected to be found in this species and was even described before (Cramp and Simmons 1977) but never by any molecular method. For recognition of CBP and for distinguishing between eggs of individual females was used protein fingerprinting (**Chapter 1, 3, 4**). This method was firstly applied by Andersson and Åhlund (2001) and it is based on isoelectric focusing of egg white proteins in pH gradient. In presented thesis, samples from two different populations of the common pochard were examined: the first one located in Poodří Landscape Protected Area [49°45'N, 18°09'E] in Czech Republic during 2008 – 2010 (**Chapter 1**) and the second one found in Třeboň Biosphere Reserve in Czech Republic [49°09'03.43"N, 14°43'32.55"E] during 2004 – 2006 (**Chapter 3, 4**).

The frequency of CBP in the first study population was relatively high (92.9%, **Chapter 1**). The highest rate of CBP was probably described in the wood duck (*Aix sponsa*, 95%; Semel and Sherman 1986). Authors posit it was due to placing artificial nest boxes in unnaturally high proximity which made them more visible and thus finding of host nests was simplified for the parasitic female. In other bird species was found that CBP increased with a breeding synchrony (Yom-Tov 1980; Andersson 1984; McRae 1997a) or with a population density (Heusmann et al. 1980; Møller 1987; Eadie 1989; Jamieson et al. 2000), because a lot of host nests is available as same as a lot of parasitic females (Rohwer and Freeman 1989). These aspects may also explain the high rate of CBP in the first study (**Chapter 1**) because there were high number of breeding females and the breeding is relatively synchronized in the common pochard (from mid-May till the end of June; **Chapter 1**). Frequency of CBP was also relatively high in other population of the common pochard (89%, Šťovíček et al. 2013). Šťovíček et al. (2013)

suggested that females laid parasitically because of decreasing area of suitable nesting sites thanks to water management for fish production.

In the second study of the common pochard, the population number was relatively lower, which can explain slightly lower rate of CBP (71.9%, **Chapter 3**). But it was still higher than in other studies of precocial species (the common goldeneye 40-68% of parasitized nests, Andersson and Åhlund 2000; Pöysä et al. 2010; the ruddy duck *Oxyura jamaicensis* 67%, Reichart et al. 2010; the Barrow's goldeneye *Bucephala islandica* 58%, Jaatinen et al 2009 a,b). More information about the frequency of the CBP and host clutch size is available in **Chapter 1**.

In contrast against Anseriformes the CBP is present in only 1% of Passeriformes (Yom-Tov 2001). A reason of such a discrepancy is mainly because of above mentioned differences between altricial and precocial species. But partially, it may be fault of scientists because they focus mainly on studying CBP in birds with precocial mode of parental care where is high probability CBP is present. As a second model species was used the barn swallow (**Chapter 2**). It is a socially monogamous altricial bird that belongs to order Passeriformes. It nests in colonies usually in barns and other farm outbuildings in close proximity of humans. Their clutch contains up to 6 eggs and they often breed two times in one season (Møller 1994). Two different populations were studied in Třeboň Biosphere Reserve in the Czech Republic during 2010 – 2012. The first population was found in Šaloun, Lomnice nad Lužnicí [49° 4' 7.762" N, 14° 42' 36.521" E] and the second one in Hamr, Lužnice [49° 3' 25.288" N, 14° 46' 10.82" E]. The CBP was described in this species (Møller 1987, 1989) but never with use of molecular tools (but see Møller et al. 2003). For identification of parasitized young microsatellite DNA typing at six highly-polymorphic loci was used (Primmer et al. 1995; Tsyusko et al. 2007).

The rate of the CBP in altricial species is generally lower (cliff swallow *Petrochelidon pyrrhonota* 4% - ~ 40% of parasitized nests (Brown 1984; Brown and Brown 1989; Smyth et al. 1993); zebra finch *Taeniopygia guttata* 17.5% - 36% (Birkhead et al. 1990; Griffith et al. 2010); bearded tit *Panurus biarmicus* 20% (Hoi et al. 2010)). Together in both study populations of the barn swallow was found about 22% of nests with at least one parasitic young (**Chapter 2**). Slightly lower rate of CBP was reported in other study of the barn swallow (16.5%, Møller 1987). This contrast can be ascribed to different methodology of distinguishing parasitized nests. Møller (1987) used traditional method of appearance of two or three eggs in one day that may underestimate the frequency of brood parasitism. For example, if a parasite laid an egg right before a clutch initiation or after a clutch completion the egg would stay

undetected. Other explanation could be attributed to a high population number. It was described even in the barn swallow that the CBP increased with a colony size (Møller 1987).

Additionally, some socio-ecological aspects of CBP were tested in the barn swallow (**Chapter 2**). It was found that the frequency of CBP does not depend on the timing during the breeding season but it does depend on a breeding synchrony (the number of simultaneously breeding females). Moreover, there are studies that found females may avoid parasitism by breeding solitarily (Møller 1987) or at hidden places (Fujita and Higuchi 2007). Interestingly, we did not find any difference in the frequency of the CBP between females nesting solitarily or in colonies, even though the solitary nests were rarely parasitized. The discussion about the CBP in the barn swallow is presented in **Chapter 2**.

Several hypotheses have been proposed to explain the adaptive function of CBP and they are based on a reaction to different environmental and physiological conditions (reviewed in Petrie and Møller 1991; Sorenson 1991; Lyon and Eadie 2008). Firstly, females may use CBP as ‘the best of a bad job’ strategy (Dawkins 1980) when they are constrained by unfavourable environment (e. g. floods, drought) or by poor physiological conditions (impacting e.g. inexperienced, young or weak females). Under such circumstances some individuals are not able to gain a nest site or a territory, the critical resource for nesting, leading them to lay eggs to other female’s nests (‘a pure parasite’; Yom-Tov 1980; Andersson 1984; Rohwer and Freeman 1989). In such situation, a parasitic egg laying is the only option how to gain some reproductive effort. In some species, a majority of parasitic females or all parasitic females do not have a nest of their own (Eadie and Fryxell 1992; Forslund and Larsson 1995; Sandell and Diemer 1999; Anderholm et al. 2009). In the common pochard, where individual breeding tactics were studied (**Chapter 4**), some of the parasitic females also did not have a nest of their own and laid eggs only parasitically. These females had the lowest reproductive effort in the population. It suggests that those can be females of low reproductive quality as it was found in other studies (Eadie 1989; Sorenson 1991, 1993; Weigmann and Lamprecht 1991; Semel and Sherman 2001). ‘The best of a bad job’ hypothesis includes also females that lost their nest, for example because of predation (Emlen and Wrege 1986; McRae 1997a). Under these conditions a parasitic egg laying is a relatively unproductive strategy but enables females at least to salvage some reproductive effort.

Second hypothesis predicts increase in total fecundity against other members of the population – ‘a fecundity enhancement’ hypothesis (Kendra et al. 1988). Females in good condition increase their annual fecundity by laying extra eggs parasitically alongside having their own nest (‘a nesting parasites’). By laying parasitic eggs a female bypasses extra energetic

costs tied up with incubation of enlarged clutch and subsequent parental care (Andersson 1984; Sorenson 1991; Lyon and Eadie 2008). In the common pochard was found that ‘nesting parasites’ had higher reproductive effort than other females from the population (**Chapter 4**). Further, 18 identified females in the barn swallow that laid parasitic eggs additionally to normal nesting had about one nestling more than was the average of other females from the rest of the population (**Chapter 2**). Thus, we recorded an increase in the reproductive effort by ‘nesting parasites’ in our both model species as was described also in other studies (McRae 1998; Møller 1987; Sorenson 1991; Åhlund and Andersson 2001). ‘Nesting parasites’ usually lay parasitic eggs before their initiated their own clutch (Lyon 1993; McRae 1998; Møller 1987; Sorenson 1991; Åhlund and Andersson 2001) as was found in the common pochard too (**Chapter 4**).

There is a hypothesis that a female may completely avoid costs of normal nesting and become a life-long specialist. Such female would never build a nest of her own and instead, she would lay all her eggs parasitically (Payne 1977). But to my knowledge there is any reference to lifelong specialist in the literature. In contrast in many species there is an evidence that females can switch reproductive tactic across years (Heusmann et al. 1980; Eadie 1989; Forslund and Larsson 1995; Sorenson 1991; McRae 1998; Åhlund and Andersson 2001) as same as in the common pochard (**Chapter 4**).

Drawing from these hypotheses and from an observation of reproductive behaviour in the redhead duck led Sorenson (1991) to provide a decision model of reproductive tactics. This model connects single reproductive options in one continuum and present them as a flexible life history strategy. The model allows to predict before every breeding season which tactic is the most advantageous and maximizes female’s lifetime reproductive success. (i) Firstly, female may resign on breeding completely and do not lay eggs at all (‘non-breeding females’). (ii) Secondly,

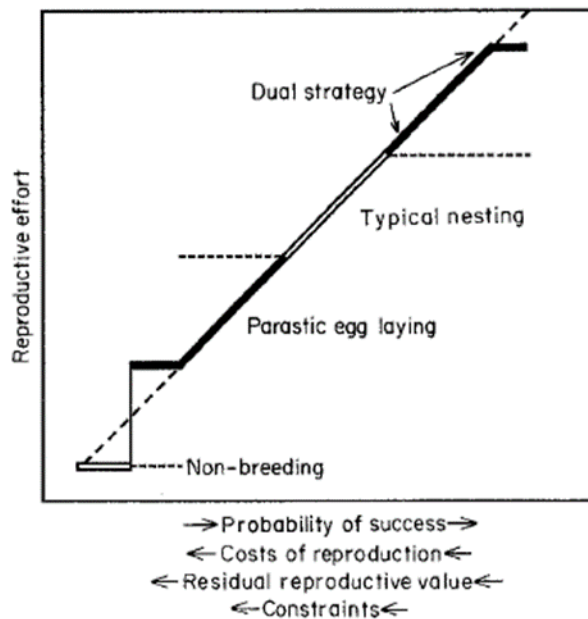


Figure 1. ‘Reproductive options available to redhead females at the beginning of the breeding season. In addition to the probability of success, females may alter reproductive effort in response to changes in the costs of reproduction and their own residual reproductive value, while constraints may directly affect reproductive performance.’ (Sorenson 1991)

she may lay her eggs only parasitically (Parasitic egg laying = ‘pure parasites’), or (iii) as the third option she may have just a nest of her own (Typical nesting = ‘non-parasitic females’). (iv) The last possibility is she would have a nest of her own and in addition lay some of her eggs parasitically (dual strategy = ‘nesting parasites’; Fig 1. Sorenson 1991).

Three reproductive tactics of females that laid at least one egg were found in the redhead duck (Sorenson 1991) and the common goldeneye (Andersson and Åhlund 2001). With the protein fingerprinting it was not possible to detect ‘non-breeding females’ in our study population of the common pochard. But, as was mentioned above both parasitic tactics were present and some of the females laid their eggs only in own nest (**Chapter 4**). The proportion of the individual breeding tactics was overall in balance. But in 2006 proportion of ‘nesting parasites’ decreased from 34% in 2004 and 38% in 2005 to only 8%. On the other hand, the proportion of ‘non-parasitic females’ increased from 17% in 2004 and 27% in 2005 to 50% in 2006 (**Chapter 4**). In the redhead duck (Sorenson 1991) were found that females chose a different breeding tactic in their reaction to unfavourable environmental conditions. During one year when there was a drought and a lack of food, females did not opt for nesting or a dual strategy of nesting and parasitism – both considered energetically costly. Instead, they resorted predominantly to pure parasitism. In the study of the common pochard (**Chapter 4**) the change between the proportion of ‘non-parasitic females’ and ‘nesting parasites’ can be caused by the high predation pressure due to American mink (*Neovison vison*). In a population with low number of individuals can be hard to find a host nest. Thus, the number of breeding females decreased and low population size could let to decrease in the number of ‘nesting parasites’. For more information, see **Chapter 4** which is devoted to reproductive tactics in the common pochard.

There are additional hypotheses explaining CBP. By parasitic egg laying in different nests a female can spread a risk of predation and thus increase chances of its eggs hatching and its offspring surviving until reaching independence (The risk spreading hypothesis; e.g., Rubenstein 1982; Petrie and Møller 1991; Davies 2000). The risk spreading hypothesis was rejected in some studies (Bulmer 1984; Sorenson 1991; Lyon and Eadie 2008) but the role of nest predation in evolution of the CBP is still discussed (Pöysä and Pesonen 2007; Andersson and Åhlund 2012). Another hypothesis predicts that kin selection (Hamilton 1964) can play role in evolution of CBP (Andersson and Eriksson 1982; Andersson 1984) mainly in birds where female natal philopatry occurs as in ducks (Anderson et al. 1992). A host female can tolerate eggs from related parasitic female and thus increase its own inclusive fitness (Andersson and Eriksson 1982; Andersson 1984). For example, Tiedemann et al. (2011) found

in the common eider that the relatedness between a host and a parasite is higher than between other female's pairs in a population. Moreover, parasitized females were older than non-parasitized and had more parasitic eggs in the nest. Authors (Tiedemann et al. 2011) proposed that close related females may cooperate across generations and thus help hatch extra eggs of their younger kin. Besides, a high relatedness between a host and a parasite was described in other studies (Andersson and Åhlund 2000; Nielsen et al. 2006b; Andersson and Waldeck 2007; Waldeck et al. 2008; Duda and Chętnicki 2012) but such interaction was not found by others (Semel and Sherman 2001; Anderholm et al. 2009). In the wood ducks, adult females even refuse to parasite close kin (Semmel and Sherman 2001).

Advantages of CBP for a parasite seem to be obvious, but a host may suffer appreciable costs. The parasite may damage or remove some of the host egg/eggs during parasitism (Lombardo et al. 1989). A clutch of the host is thus decreased and a host reproductive effort too. Moreover, it was suggested, in species where CBP appears commonly, individuals may manipulate with own clutch size (Weller 1959). Thus, if parasitic eggs appear in host nest in the beginning of laying, host female can decrease the number of her own eggs and the number of eggs in the nest does not differ between parasitized and non-parasitized nests. Such a response to experimental addition of eggs was found in the common goldeneye (Andersson and Eriksson 1982) and the common eider (Erikstad and Bustnes 1994). Thus, host female pays the cost by laying smaller clutch than it would maximize her fitness (Andersson and Eriksson 1982). When the number of eggs in the clutch is not decreased by a parasite or a host it may lead to enlarged clutch size. To avoid the cost of incubation of large clutch, a female may desert her nest. The nest desertion of enlarged clutches was observed in experimental study where eggs were added by researchers (Andersson and Eriksson 1982) as same as in study where clutches were enlarged by natural parasitism (Jaatinen et al. 2009b). If a host female does not desert her parasitized nest, other costs connected with incubation of large clutch may follow. It may cause: (i) a reduction of hatchlings or fledglings success (Eadie 1989; Weigmann and Lamprecht 1991; Lyon 1993; Semel and Sherman 2001; Lyon et al. 2002), (ii) a prolonged incubation and thus a higher risk of predation (Gibbons 1986; Nielsen et al. 2006a) and (iii) higher energetic investment in terms of incubation and parental care (Kilpi and Lindstrom 1997; Visser and Lessells 2001; Hanssen et al. 2005). Furthermore, the host female can have a lower adult survival (Brown and Brown 1991, 1998) or lower future reproduction (Milonoff et al. 2004). As was mentioned before the costs of parasitism for precocial birds are probably not as demanding as for altricial (Rohwer and Freeman 1989; Sorenson 1992) but still were found in

some studies (Andersson and Eriksson 1982; Sorenson 1997; Jaatinen et al. 2009b; Deng et al. 2011; Waldeck et al. 2011).

In the first research of the common pochard, the clutch size of the host females decreased with the number of parasitic eggs (**Chapter 1**). On the other hand, we did not find such relationship between the number of parasitic and host eggs in the second study population (unpublished data), probably because the frequency of CBP was lower (**Chapter 3**). But still the clutch size of parasitized females was significantly higher than the clutch size of females that were not parasitized (unpublished data). The discussion about clutch size of the common pochard can be found in **Chapter 1**.

Still, there is no evidence that female's fitness is impacted by incubation of an enlarged clutch in the common pochard. Another study of the same species suggested that the host female does not suffer by moderate levels of parasitism because neither clutch size nor hatching probability were affected by experimental addition of eggs (Dugger and Blums 2001). The only noticeable cost of parasitism in the common pochard seems to be nest desertion after brood parasitism (Neužilová and Musil 2010; Šťovíček et al. 2013). Thus, the costs for the host are probably small but other studies evaluating the effect of CBP on host female and her young would help to clarify this question.

If selection pressure is considerably high, then the host should evolve anti-parasitic tactic to avoid these costs of parasitism (Petrie and Møller 1991; Davies 2000). In some species, a host can recognize a parasitic egg and eject it from the nest or buried it into a nest material (Lyon 1993, 2003; Sorenson 1995; Jamieson et al. 2000). Mostly, the foreign egg is rejected if it is laid before a host clutch initiation (Brown 1984; Emlen and Wrege 1986; Møller 1987; McRae 1995). The nest abandoned is also considered as an anti-parasitic strategy (McRae 1995; Hoi et al. 2010; Šťovíček et al. 2013). Additionally, a host may also repulse the parasitism by a territoriality and nest guarding and by displaying aggressive behaviour against a female intruder (Emlen and Wrege 1986; Møller 1987, 1989; Gowaty and Wagner 1988).

Under certain circumstances there is a possibility for a parasitic female to avoid aggressive behaviour that is connected with the nest guarding. In species with bi-parental care where extra-pair copulations (EPC) are a part of the reproduction system a quasi-parasitism may occur (reviewed in Griffith et al. 2004). If a female copulates with a male from the different pair bond (EPC) he may afterward allow her an access in his nest (Petrie 1986; Quasi parasitism = QP, Wrege and Emlen 1987). Such cooperation between parasitic female and nest attending male can be understood as adaptive QP. On the other hand, in populations where extra-pair paternity (EPP = when EPC leads to successful fertilization) and CBP are present at certain

level the QP may arise by chance (Alves and Bryant 1998). The studies about the incidence of QP are scarce (reviewed in Griffith et al. 2004) but their number is slowly growing (Krakauer 2008; Li et al. 2009; Du and Lu 2010; Mészáros 2010; Hoi et al. 2010).

Still, there are many unanswered questions that are crucial for understanding this phenomenon. For example, what are the benefits and costs for all the participants (a host female, a nest attending male (a father of the quasi-parasitic young) and a quasi-parasitic female; Lyon et al. 2002; Griffith et al. 2004). The host female would probably suffer the highest cost of being parasitized because she is the one who cares about alien young ('extra-pair maternity'). The quasi-parasitic female may obtain genetic benefits (Alves and Bryant 1998), but that would be the same benefits as she can achieve from the EPP (good genes, genetic variation, and decreased inbreeding depression – advantages that are mutual for EPP; Petrie and Kempenaers 1998; Griffith et al. 2002). Therefore, the main benefit would be probably access to the nest of her extra-pair mate. The attending male may also gain genetic benefits as the quasi-parasitic female (Alves and Bryant 1998) and, additionally, if the quasi-parasitic female has a nest of her own, he may fertilize some of her eggs in her nest (McRae and Burke 1996; Alves and Bryant 1998). But the quasi-parasitic male can also suffer from increased intra-clutch competition between half-siblings in his own nest (Lyon et al. 2002).

The barn swallow is social monogamous bird, where both parents guard the nest (Møller 1994). Also, it is well known that EPP is present in this species (Møller et al. 2003; Kleven et al. 2005; Safran et al. 2005). In the population that was under study in presented thesis was detected 17.2 % of extra-pair young (EPY, **Chapter 2**). Møller et al. (2003) found in other barn swallow population similar percentage of EPY (17.8 %) but no case of CBP. On the other hand, they detected 17 quasi-parasitic young in 5 nests. Because there was no evidence of CBP and the number of QP young per parasitized nest was high (3.4) Griffith et al. (2004) speculated these QP young can be a reason of rapid mate switching or misidentification. This conclusion was a motivation for investigation whether QP is really present in the barn swallow.

In presented study was found 17 QPY in barn swallow population which represents about 30% of CBP young (**Chapter 2**). They were distributed in 16 nests. Even though the proportion of QPY was only ~2 % results suggests that QP did not arise by chance. Based on Griffith et al. (2004), the estimated frequency for QPY should be between 0.2% and 0.1% and so the detected frequency of QPY highly exceeds this estimation. Additionally, even though it was found that swallows lay parasitically in neighbour's nests (Brown 1984; Møller 1987; but see Møller 1989), presented study suggests the opposite result. In examples where the position of host's and parasite's nests were identified females did not lay parasitic eggs to the nearest

nests (**Chapter 2**). Moreover, males that participate in QP had about one young more than was average per other males from the population. Results about QP in the barn swallow is discussed in **Chapter 2**.

In conclusion, this thesis brings new information about CBP described by molecular methods in two study species: the common pochard (**Chapter 1, 4**) and the barn swallow (**Chapter 2**). Specifically, CBP is present in studied populations of the common pochard in relatively high frequency (71.9 % and 92.9 % of parasitized nests; **Chapter 1, 4**). Most of the parasitic eggs were laid before the peak of the breeding season (**Chapter 1**). The number of host eggs in the nest decreased with the number of parasitic eggs in the nest (**Chapter 1**). Parasitic females of the common pochard use different breeding tactics ('pure parasites', 'non-parasitic females', 'nesting parasites') and they could switch them between years (**Chapter 4**). The reproductive effort differed between females according to their reproductive tactic. 'Nesting parasites' had the higher reproductive effort and on the other hand 'pure parasites' had the lowest reproductive effort (**Chapter 4**). Additionally, it was tested if egg morphology is reliable for detection of CBP in the common pochard. Results demonstrated that Eadie's method uncovered about 76 % of parasitized nests and 68 % of parasitic eggs. Moreover, relatedness between females may affect the use of egg morphology for detection of CBP (**Chapter 3**).

In the barn swallow was found 22 % of nests were parasitized (**Chapter 2**). The rate of CBP increased with the breeding synchrony. About ~2 % of parasitic young were sired by nest attending male (QP). Host females had on average about one nestling less than females that were not parasitized. On the other hand, parasitic females and males that sired QP young had about one nestling more than other individuals from the population that did not participate in parasitism (**Chapter 2**).

Aims of the study

- 1) Describe the frequency of CBP in two study species (the common pochard and the barn swallow) and describe the frequency of QP in barn swallow with use of molecular methods
- 2) Find if given aspects affected the frequency of CBP:
 - a. in the common pochard: a timing of breeding.
 - b. in the barn swallow: a timing of breeding, a breeding synchrony, solitary or colonial nesting.
- 3) Describe the difference between a clutch size of host and parasitic female bird in both study species.
- 4) Describe the reproductive tactics of the common pochard and variance in their reproductive effort
- 5) Test if Eadie's method is reliable for detection of parasitized nests and parasitic eggs and found if relatedness can affect this method.

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Chapter 1

Conspecific brood parasitism and host clutch size in Common Pochards *Aythya farina*

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Chapter 2

Brood parasitism and quasi-parasitism in the European barn swallow *Hirundo rustica rustica*

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Chapter 3

Egg morphology fails to identify nests parasitized by conspecifics in common pochard: a test based on protein fingerprinting and including female relatedness

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Chapter 4

Protein fingerprinting revealed high flexibility in brood parasitism strategies among females of the Common Pochard (*Aythya ferina*)

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Appendix 1

Phenotypic differentiation is associated with divergent sexual selection among closely related barn swallow populations.

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Appendix 2

Temporal Stability and the Effect of Transgenerational Transfer on Fecal Microbiota Structure in a Long Distance Migratory Bird.

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