Facultative heterospecific brood parasitism among the clutches and broods of duck species breeding in South Bohemia, Czech Republic

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Abstract

Heterospecific brood parasitism (HBP) frequently occurs in waterfowl, though much less often than conspecific brood parasitism. In this study, we assess the rate of HBP among clutches and broods of five sympatric breeding duck species: Gadwall *Anas strepera*, Mallard *Anas platyrhynchos*, Red-crested Pochard *Netta rufina*, Common Pochard *Aythya ferina* and Tufted Duck *Aythya fuligula* from nest and brood surveys carried out in the Třeboň Biosphere Reserve and surrounding area (South Bohemia, Czech Republic) in 2006–2015 inclusive. Assessment of 2,323 clutches and 3,056 broods found a higher rate of HBP in clutches than in broods. The rate of HBP in the broods of host birds did not increase with the rate of HBP in host clutches for the five species investigated. The highest proportion of brood parasitism recorded was among Red-crested Pochard. Tufted Duck showed the lowest difference in the HBP rate between clutches and broods; Mallard the highest. From the parasitising female's perspective, the rate of HBP in clutches increased with the rate of HBP in broods for each species investigated. We can conclude that the choice of host affects the success of HBP (*i.e.* the frequency of HBP in clutches *vs.* rate of HBP in broods), and that this can differ between the five species included in the study. Tufted Duck seems to be the most suitable host species as well as the most successful parasite.

Key words: ducks, parasitised broods, parasitised nests.

Facultative brood parasitism is an alternative but not necessarily exclusive reproductive strategy where a parasitising female lays its eggs in another bird's nest then leaves the host to incubate the eggs and raise the hatchlings. This strategy is common in many precocial birds, including waterfowl (Weller 1959; Payne 1977; Yom-Tov 1980; Rohwer & Freeman 1989), probably due to the lower costs of brood care for the parasitised female compared to those accruing to females of altricial species (Davies 2000). There are obvious benefits to the parasitising female that can lead to this behaviour. For instance, female fitness may be enhanced without incurring the energetic

costs of incubation and brood-rearing (Yom-Tov 1980; Sorenson 1998; Andersson & Åhlund 2000), although the increase in clutch size can potentially reduce hatching success (Davies & Baggott 1989; Sayler 1992; Amat 1993; Sorenson 1997; Kear 2005). In spite of this, the strategy is common in ducks (Sayler 1992; Geffen & Yom-Tov 2001), probably because the costs to both the parasitising and the parasitised female is relatively low compared to those in atricial species (Lyon & Eadie 1991; Sorenson 1992; Deeming 2002). Females can lay eggs in the nest of the same species (conspecific brood parasitism – CBP) or, in the nests of other species (heterospecific brood parasitism – HBP), as reviewed by Kear (2005). HBP occurs in all waterfowl groups and in all geographic regions (Yamauchi 1995; Geffen & Yom-Tov 2001; Kear 2005; Krakauer & Kimball 2009). However, in contrast to CBP, HBP is much less frequently observed and studied.

We have been monitoring HBP at a site in the Czech Republic since 1999. Our long-term study follows similar work conducted in the same area during the 1970s (Smrček 1981). In an earlier analysis, Musil & Neužilová (2009) found that HBP occurred in 6.6% of nests monitored in South Bohemia, Czech Republic in 1999–2007. This rate was lower than that recorded across almost the same area in 1975–1980, a period when the breeding population size of most duck species peaked in South Bohemia, and 13.9% of clutches were found to have been parasitised (Smrček 1981).

The present study aims to compare recent (2006–2015) data collected on the rate of HBP found in clutches with HBP rates recorded for broods for five sympatric breeding duck species: Gadwall *Anas strepera*, Mallard *Anas platyrhynchos*, Red-crested Pochard *Netta rufina*, Common Pochard *Aythya ferina* and Tufted Duck *Aythya fuligula*. The presence of parasitic nestlings in broods is considered visual evidence of successful HBP. Given that Musil and Neužilová (2009) found inter-specific differences in the probability of HBP being recorded within clutches, we predicted that there would similarly be statistically significant variation between the five species in the rate of HBP recorded in broods, and that the difference in the HBP rate recorded in broods *versus* in HPB clutches (indicative of the success of the HPB strategy and the suitability of the host species for being parasitised) would also vary across the five species being investigated. We hypothesised that the Red-crested Pochard, found in earlier studies to be the species with both the highest rate of HBP in its nests and the most frequent parasite (Musil & Neužilová 2009), would be the most suitable host species as well as the most successful parasite, with the lowest reduction in the proportion of HBP recorded in broods compared to clutches.

Methods

Nest surveys

Nest surveys were made on islands and in the littoral stands of fishponds in the Třeboň Biosphere Reserve and surrounding area in South Bohemia, Czech Republic (48.97–49.26°N, 14.66–14.97°E) from 2006 to 2015 inclusive. Nest survey sites were the same as those covered by subsequent brood

counts (see below). Each pond was visited at 7–14 day intervals from May to July, and each nest was checked at least twice during incubation. The occurrence of HBP was determined by the different colour, size and shape of the eggs (Weller 1959; Amat 1991; Dugger & Blums 2001; Šťastný & Hudec 2016). Heterospecific clutch parasitism was defined as any nest that contained at least one egg of a different species.

Brood counts

Brood counts were carried out on the same wetlands as nest surveys from April to August. For each brood sighted, the species of the adult female, the age of brood (Gollop & Marshall 1954), and the number of ducklings of each species were recorded (*e.g.* Šťastný & Hudec 2016). It was assumed that broods containing ducklings of a different species represented HBP. While such instances could be the result of post-hatch brood amalgamation or accidental mixing, data from monitoring of individually-marked females at our site (*i.e.* marked by nasal saddles) suggest that post-hatch mixing virtually never occurred. No case of post-hatch brood mixing was documented for 189 marked females on the study area between 2006 and 2015, but we recorded 23 broods reared by marked females that contained one or more ducklings of other species. We considered there to be a record of HBP if at least one duckling of a different species was found in the brood of the host female.

Data analysis

Data from the nest surveys and from the brood counts were used to calculate the percentage of incubated clutches and reared broods of a given species that had been parasitised by another species (*i.e.* where the clutch or brood contained at least one egg or duckling of a different duck species). Additionally, the extent to which a given species parasitised other species was calculated as the number of occasions on which the species' eggs were found in a clutch being incubated by a different species divided by the total number of clutches containing the eggs of that species (*i.e.* the sum of the number of parasitised clutches and the number of the species' own clutches), with brood data being treated in the same way.

The difference in the proportion of HBP recorded in clutches and in broods for each species in each year was calculated to assess the success of HPB in relation to both the parasitising and the parasitised species. Multiple linear regression (in Statistica version 13) was then used to analyse the effects of year and species on this difference (arcsine transformed) between clutches and broods in the levels of parasitism recorded.

Results

In total, 2,323 clutches and 3,056 broods were recorded in South Bohemia between 2006 and 2015. Among these, HBP was found in 228 clutches (9.8%) and 133 broods (3.7%). The highest frequency of HBP was found in both the clutches and broods of Red-crested Pochard. The frequency of HBP was higher in clutches than in broods for all species, but the difference was least pronounced in Tufted Duck (Table 1). There was no significant

Table 1. Occurrence of heterospecific brood parasitism among the nests and broods of five species of ducks breeding at a site in South Bohemia, Czech Republic, 2006–2015.

Species	Clutches		Broods	
	No. incubated	% parasitised (*n*)	No. reared	% parasitised (*n*)
Mallard	711	9.7% (69)	922	2.3% (21)
Gadwall	274	13.5% (37)	687	2.3% (16)
Red-crested Pochard	30	40.0% (12)	133	8.3% (11)
Common Pochard	583	8.4% (49)	702	2.7% (19)
Tufted Duck	725	8.4% (61)	612	7.5% (46)
Total	2,323	9.8% (228)	3,056	3.7% (113)

Table 2. Parasitism rates expressed as the percentage of duck nests or broods found to have been parasitised by a given species in South Bohemia, Czech Republic. The values show the number of occasions when eggs or ducklings were found in a clutch or brood incubated/reared by a different species in relation to the total number of clutches or broods with at least one egg or duckling of that species (*i.e.* parasitised nests plus the species own clutches or broods). * = sum of the species' own clutches and the number of clutches where it was found to have parasitised another species. ** = sum of the species' own broods and the number of broods where it was found to have parasitised another species.

Species	Clutches		Broods	
	No. containing at least one egg of this species*	% cases where these were parasitising another species (*n*)	No. containing at least one duckling of this species**	% cases where these were parasitising another species (*n*)
Mallard	728	2.3% (17)	932	1.1% (10)
Gadwall	284	3.5% (10)	695	1.2% (8)
Red-crested Pochard	55	45.5% (25)	172	22.7% (39)
Common Pochard	641	9.0% (58)	742	5.5% (41)
Tufted Duck	759	4.5% (34)	635	3.3% (21)
Total	2,467	5.8% (144)	3,175	3.7% (119)

correlation between frequency of HBP recorded in the clutches and broods of the five species considered (Spearman rank correlation: $r_s = 0.44$, $n = 5$, $P = 0.46$, n.s.).

Red-crested Pochard was more likely than the other species considered to exhibit parasitism; 25 (45.5%) of 55 clutches and 39 (22.7%) of 172 broods with at least one Red-crested Pochard egg or duckling were cases of HBP (Table 2). Conversely, only 4.5% of 759 clutches and 3.3% of 635 broods that included Tufted Duck eggs or ducklings were being reared by another species (Table 2). The proportion of parasitism by a given species in clutches and in broods was highly correlated (Spearman rank correlation: $r_s = 1.00$, $n = 5$, $P \leq 0.02$; Fig. 1). Although this relationship was driven mainly by Red-crested Pochard, which appeared to have a relatively high parasitising rate at both the clutch and brood-rearing stage, this correlation remained significant on excluding Red-crested Pochard from the analysis (Spearman rank correlation: $r_s = 1.00$, $n = 4$, $P \leq 0.05$; Fig. 1).

The degree of reduction in the rate of HBP in broods compared to clutches varied significantly between species (Fig. 2, Table 3). This change was markedly lower in Tufted Duck than in the other species, both for the probability of the birds being parasitised by another duck species and for the probability of Tufted Duck parasitising

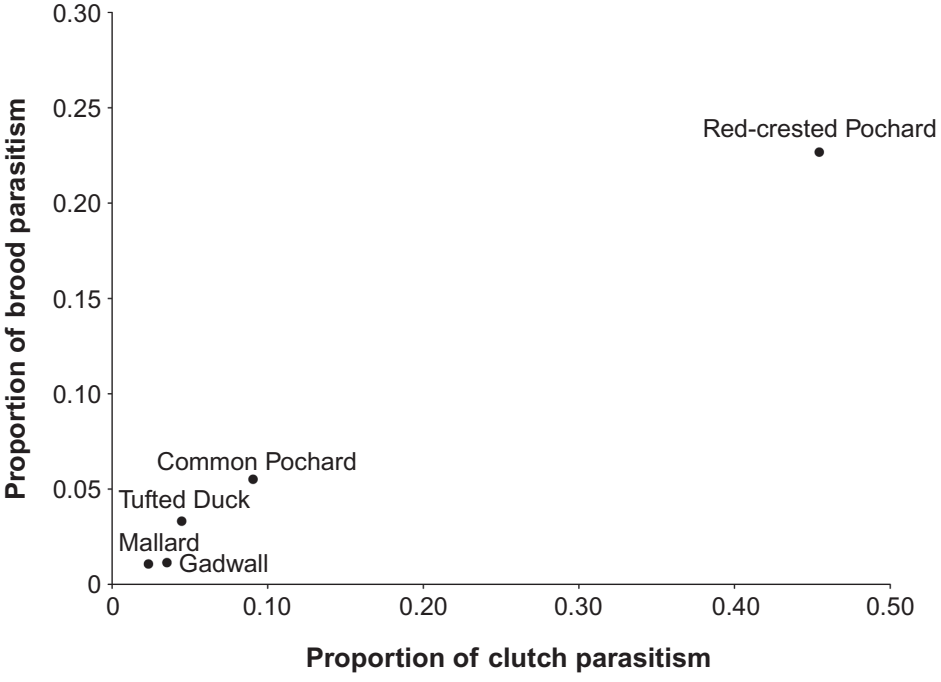

Figure 1. Relationship between the proportions of parasitism by a given species in clutches and in broods.

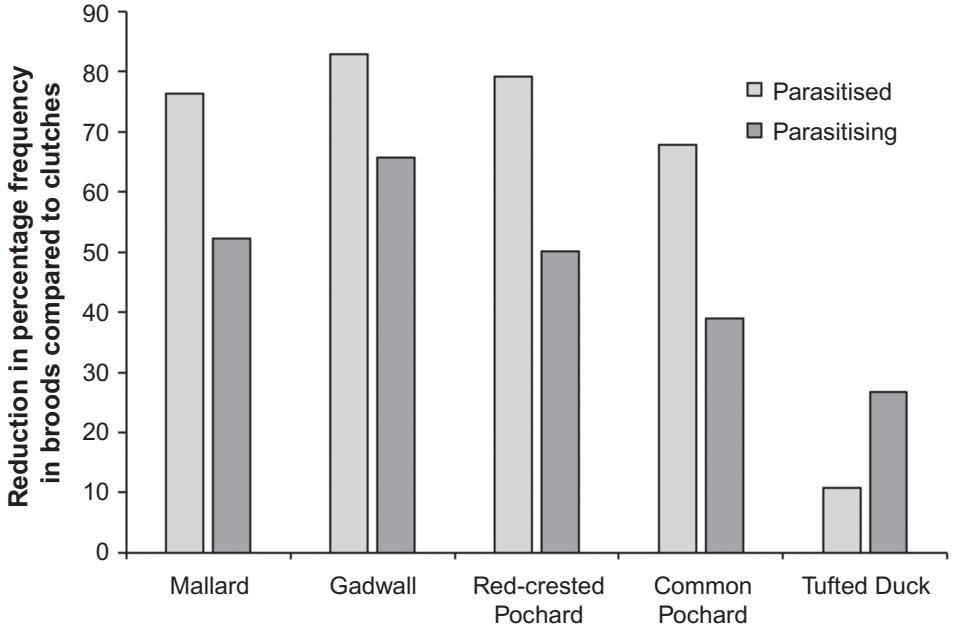

Figure 2. Reduction in the frequency (% occurrence) of heterospecific brood parasitism recorded during the breeding season (*i.e.* the decrease in HBP between clutches and broods), both when parasitising other species and on being parasitised by another species.

others (Fig. 2). There was no evidence to suggest that the HBP rate varied significantly between years during the 2006–2015 study (Table 3).

Discussion

In general, the level of breeding parasitism was found to be higher in clutches than in broods, probably because of disadvantages to the parasitic eggs and ducklings experienced during incubation and early brood rearing. Previous studies have found that, compared to non-parasitic eggs, parasitic eggs suffer more from possible nest desertion of large clutches, egg breakage, false timing of egg-laying, differential post-hatch survival and associated lower survival of large broods, and incomplete imprinting (Andersson & Eriksson 1982; Geffen & Yom-Tov 2001; Birkhead & Brillard 2007). The species in the present study appear to differ in the extent to which they are used as hosts and also in the success of the HBP ducklings in their host broods. Tufted Duck seem to be the species for which parasitic females benefit most during incubation and early brood rearing, with 8.4% of HBP in clutches compared to 7.5% of HBP in broods. Conversely, the proportion of parasite ducklings in Mallard, Gadwall and Red-crested Pochard broods compared to their occurrence in nests of dabbling duck species was very low.

Table 3. Effects of species and year on the difference (reduction) in the frequency of heterospecific brood parasitism (HBP) recorded in broods compared with the frequency of HBP recorded in clutches in South Bohemia, Czech Republic (GLM analysis). (a) = probability of given species being parasitised by another species; (b) = probability a given species parasitising another species (measured as the number of occasions on which the eggs/ducklings of a given species were found in the clutch/brood of a different species, in relation to the total number of all clutches/broods containing eggs/duckling of the given species); n.s. = not significant.

(a) Probability of being parasitised by other duck species

Effect	Estimate	*F*	d.f.	*P*
Intercept	1.716	15.52	1	0.001
Species	1.346	3.04	4	0.036
Year	0.923	0.93	9	n.s.

(b) Probability of parasitising other duck species

Effect	Estimate	*F*	d.f.	*P*
Intercept	3.892	50.157	1	0.001
Species	1.510	4.864	4	0.005
Year	1.298	1.860	9	n.s.

Of the five duck species considered, Red-crested Pochard most frequently parasitised other species, and was also the species most frequent parasitised. The higher rate of breeding parasitism in Red-crested Pochard than in other European duck species has been recorded in several other studies across its breeding range, with HBP noted both in clutches (Amat 1987, 1991, 1993; Fouzari *et al.* 2015) and in broods (Keller 2014). The findings are also in accordance with a comparison of the rate of breeding parasitism recorded in clutches for the same duck species in the same study area over two earlier time periods (1975–1980 and 1999–2007; see Musil & Neužilová 2009). However, the assumption that species parasitising at a higher rate of HBP and presumably benefiting from this alternative reproductive strategy (Lyon & Eadie 1991; Sorenson 1992) have higher success (*e.g.* measured as having a similar HBP ratio at

the brood-rearing stage as at the egg-laying stage) was not confirmed. The level of nest parasitism recorded in clutches of Tufted Duck and Common Pochard in the study area agrees with that reported by others (Mednis 1968; Bezzel 1969; Mlíkovský & Buřič 1983). There is still very little data on parasitism rates recorded for the broods of other European duck species, however, for comparison with the results presented here.

The occurrence of brood parasitism is determined by the costs and benefits of the parasitic behaviour for a parasitic female (Sorenson 1992). Some females lay parasitic eggs before they start their own nests, potentially enhancing their reproductive success in this way (Åhlund & Andersson 2001). The main benefit of parasitism in these cases is the ability to reproduce without caring for the eggs and hatchlings, ultimately increasing female productivity. When parasitic eggs are laid by females during the build-up to the main breeding season, before establishing their own nest site, we can therefore expect that these females are in good condition (Owen & Black 1990; Kear 2005). Females may also lay parasitic eggs to invest and obtain reproductive success when they have failed to compete successfully for nest sites, however, or when they lost their own nest due to predation or bad weather conditions (*i.e.* they make the "best of bad job": Payne 1977; Yom-Tov 1980; Davies 2000); such females may be in poorer condition. These patterns could explain the high success of HBP among Tufted Duck, which showed only little difference between the rate of HBP in clutches and in broods. Because this duck species breeds relatively late in comparison with the other duck species (Neužilová & Musil 2010; Šťastný & Hudec 2016), only early-breeding females can parasitise or conversely could be parasitised by other species. Generally, in the case of early breeders, they are assumed to be in better condition and a higher success of HBP among these individuals could be expected (Owen & Black 1990; Bowler 2005).

Based on the findings of this study, we conclude that the choice of the host female's nest could affect the subsequent success of HBP, which can be measured as the occurrence of ducklings in parasitised broods.

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Photograph: Tufted Duck and Red-crested Pochard ducklings just hatched in a single clutch in South Bohemia, Czech Republic, by Petr Musil.

