Rare insights into intraspecific brood parasitism and apparent quasi–parasitism in black–capped chickadees

K. A. Otter, B. W. Murray, C. I. Holschuh & K. T. Fort

Abstract

Rare insights into intraspecific brood parasitism and apparent quasi–parasitism in black–capped chickadees.— Genetic analysis of passerine birds often finds evidence of extra–pair copulations within species, but genetic evidence of intraspecific brood parasitism (IBP) and quasi–parasitism (Q–P) are relatively rare. Further, it is even rarer for genetic patterns that might indicate quasi–parasitism (resident male sires offspring through extra–pair copulations, and allows the female to lay these within the male's nest) to be coupled with observational evidence of this behavior. In this paper, we report behavioral observations surrounding the nest of black–capped chicka- dee, one of the few species in which both IBP and Q–P have been detected through a genetic analysis. These were later confirmed to have young genetically mismatched with both attending parents, as well as mismatched with the attending female but sired by the attending male. The behavioral patterns associated with this nest are contrasted with the two previously reported cases of IPB/Q–P in this species, and suggest that rare 'detection' of quasi–parasitism may be explained by converging patterns of extra–pair behavior and the rarer strategy of intraspecific brood parasitism.

Key words: Interspecific brood parasitism, Quasi–parasitism, Black–capped chickadees.

Resumen

Ideas poco frecuentes del parasitismo de puesta intraespecífico y el cuasiparasitismo aparente del carbonero cabecinegro.— El análisis genético de los paseriformes a menudo se tropieza con evidencias de cópulas fuera de pareja ocurridas dentro de la misma especie, sin embargo las evidencias genéticas del parasitismo de puesta intraespecífico (IBP) y el cuasiparasitismo (Q–P) son relativamente raras. Además, es incluso más raro que los patrones genéticos que podrían indicar el cuasiparasitismo (un macho residente engendra hijos mediante una cópula fuera de su pareja, y permite que la hembra ponga los huevos dentro del nido masculino) estén respaldados por evidencias observadas de esta conducta. En este artículo, informamos de las observaciones etológicas que tuvieron lugar en torno a un nido de carbonero cabecinegro, una de las pocas especies en las que se ha detectado tanto el IBP como el Q–P mediante análisis genético. Más adelante se confirmó que los jóvenes no coincidían genéticamente con ambos padres cuidadores, así como tampoco coincidían con la hembra cuidadora, pero si con el macho cuidador. Los patrones conductuales asociados a este nido se comparan con los otros dos casos conocidos con anterioridad de IPB/Q–P en esta especie, y se sugiere que la "detección" poco frecuente del cuasiparasitismo puede explicarse mediante los patrones convergentes de las conductas extra pareja y la estrategia aún más rara del parasitismo de puesta intraespecífico.

Palabras clave: Parasitismo de puesta intraespecífico, Cuasiparasitismo, Carbonero cabecinegro.

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Introduction

Intraspecific brood parasitism (IBP) –eggs/nestlings appearing within a nest though they are not genetically related to either the resident male and female– commonly occurs in some bird taxa that have precocial young, such as ducks and coots. The prevalence of IBP (or 'egg dumps') within these groups increases with nesting densities (Eadie et al., 1998). Conservation programs to increase population sizes, such as in wood ducks (*Aix sponsa*), find that rates of IBP increase if nestboxes are placed either too close together or in too exposed a location, attracting parasitic females and giving them the opportunity for egg dumping (Eadie et al., 1998). As IBP increases, clutch sizes increase, and hatching success of parasitized females declines due to inefficient incubation. Yet IBP is not a byproduct of management but has evolved as a strategy by which some females can increase their reproductive success through parasitizing the efforts of others (Eadie et al., 1998; Slagsvold, 1998)

IBP as a reproductive strategy, however, appears to be rarer among socially monogamous passerines with atricial young (Slagsvold, 1998). Despite numerous studies in the past decade, mixed parentage in most passerines results from extra–pair copulations (young sired by the resident female and an extra–pair male) rather than from brood parasitism by conspecific parents not associated with the nest (IBP), or through quasi–parasitism (young sired by the resident male and an extra–pair female and subsequently laid in the male's nest) (Griffith et al., 2004). Where IBP has been noted, these strategies may be adopted by females whose ability to nest independently is either limited or uncertain (a bet–hedging strategy to increase the chances of leaving some offspring; Otter et al., 1998; Hughes et al., 2003; Blackmore & Hinsohn, 2008). Alternately, IBP may be a mixed, sequential strategy, such as occurs in Starlings (*Sturnus vulgaris*) where unmated, recently–arriving females parasitize conspecifics during the period in which they themselves are settling, and then lay their own clutches normally once they have acquired a nest site (Sandell & Diemer, 1999). In this manner, the female supplements the fecundity of her own nests by adding offspring in other nests, ecologically equivalent to the gains made by males pursuing extra–pair copulations. Finally, IBP may be both a strategic and opportunistic behaviour, such as when females in colonial species in close proximity of each others' nests occasionally egg–dump to take advantage of both mixed strategies and bet–hedging strategies (Alves & Bryant, 1998).

Quasi–parasitism is an even rarer strategy than IBP among socially–monogamous passerines (Griffiths et al., 2004). In the few studies where it has been noted, it is difficult to distinguish whether the pattern of mixed parentage is the result of a quasi–parasitic strategy –males seeking EPCs, and then allowing the females to lay their sired egg within the male's nest– or whether quasi–parasitism is the occasional result of converging patterns of EPCs and IBPs within a population. If females seek EPCs with males with specific attributes as extra–pair partners, and the same social pairs are the occasional targets of females engaging in IBP, then occasionally the parentage of nests may reflect patterns that appear to invoke explanations of quasi–parasitism (Griffiths et al., 2004). True quasi–parasitism, though, suggests intentionality on the part of the male to allow laying access to the nest by the secondary female, and thus is partially a male behavioural strategy. Young in the nest mismatched to the resident female, but not the resident male (apparent quasi–parasitism), that result from female–initiated patterns of EPC and IBP may not, however, involve the resident male intentionally granting laying access to the nest. Detailed behavioural observations are required to distinguish between these, but which are typically lacking due to the surreptitious nature of many of the strategies under discussion.

In this paper, we report on the behaviour observed at a nest of black–capped chickadees *Poecile atricapillus* (one of the few species in which genetic patterns of quasi–parasitism have been reported (Otter et al., 1998)) in which IBP was suspected, and later genetically confirmed. These observations, coupled with observations from our previous studies, provide potential insight into the rare occurrence of maternally–mismatched young within chickadee nests, and suggest quasi–parasitic parentage patterns may result from overlapping strategies of EPC and IBP in female chickadees. We then discuss the potential implications for land management scenarios that may increase the particular circumstances that appear to promote these alternate strategies in chickadees, and perhaps other species.

Methods

Banding

Birds were captured in winter flocks during January through February 2000 at temporary feeders with either potters traps or mistnets. Upon capture, each bird was fitted with a CWS numbered legband and a unique combination of three additional colored legbands to facilitate individual identification. A 75 μL blood sample was extracted at the time of winter capture for the majority of birds. For others, banding and blood samples were collected from adults by catching them at nests in June 2000 as they fed nestlings.

Nest monitoring

Individually–marked birds were tracked every three to four days throughout late April, May and June 2000 to document the breakup of winter flocks and individual territorial establishment (defined as the exclusive defense of habitat used for nesting and foraging). Territory boundaries were delineated by mapping the locations of song contests and fights between neighboring males following the period of flock–breakup, which occurs within our population around mid–April.

Sample collection

In the study nest, the attending male and female and the nine chicks were all captured, banded and blood sampled in 2000. The secondary pair associated with this nest consisted of a banded female captured and blood sampled in 2000, and an unbanded male with whom she associated. This male was not captured in 2000, but may have been among the returning adult birds captured in winter 2001, so all males from the subsequent winter were screened for paternity in analysis. Blood samples were collected from 59 additional territorial males that were captured and banded in 2000 through 2002. Approximately 90% of the adult territorial male birds in our study area were sampled over these three years. Whole blood was stored in 95% ethanol and DNA was extracted following a standard phenol/chloroform isolation procedure (Sambrook & Russell, 2001)

Microsatellite typing

Microsatellite alleles were typed at three highly informative loci, Pocc6 (Bensch et al., 1997), Pdou5 (Griffith et al., 1999) and PAT–MP243 (Otter et al., 1998). One µL of DNA was added to 14 µL of master mix containing the following: 1X PCR buffer, 1.67–3.67 mM $MgCl_2$ (3.67 mM for Pocc6 and 1.67 mM for Pdou5 and PAT–MP243), 100 µM of each dNTP, 0.5 µM of each primer, 0.5 mg/mL BSA, and 0.5 units of *Taq* DNA polymerase (Invitrogen, Carlsbad, CA). Amplifications were carried out on a DYAD or PTC–100 thermal cycler (MJ Research Inc., Waltham, MA). The thermal cycle for PAT–MP243 and Pdou5 loci was 94°C for 4 minutes, followed by 5 cycles of 94°C for 1 minute, 57°C for 1 minute (decreased by 2°C per cycle), and 72°C for 1.5 minutes; and 33 cycles of 94°C for 30 seconds, 59°C for 30 seconds, and 72°C for 1.5 minutes, and a final extension phase of 72°C for 4 minutes. The thermal cycle for Pocc6 samples was 94°C for 3 minutes, followed by 40 cycles of 94°C for 30 seconds, 56°C for 30 seconds, and 72°C for 30 seconds, and a final extension phase of 72°C for 4 minutes. Products of the separate amplification reactions were pooled. Alleles were sized using the CEQ8000 Genetic Analysis system (Beckman Coulter Inc., Fullerton, CA) and viewed using the Fragment Analysis Module (400 bp size standard; cubic model; PA ver.1 dye mobility calibration).

To ensure accuracy of scoring all nestlings, putative mothers and immediate resident males were typed at least three times. The remaining males were typed multiple times as needed to obtain genotype information for all loci examined.

Paternity analysis

Maternal identification was established based on non–exclusion. As the maternity of all nestlings was consistent with one of the two females associated with the nest, a paternity analysis on each chick was performed using the program CERVUS, version 3.0 (Kalinowski et al., 2007) assuming known maternity.

The set of 60 resident males was used to assess the loci for Hardy–Weinberg equilibrium and to estimate allele frequency data upon which to build likelihood estimates and run paternity simulations for significance testing. Simulation parameters were 10,000 offspring, 60 candidate fathers, 85% of the candidate fathers sampled, all 3 loci completely typed, 1% of loci mistyped and a 1% error rate. An 85% chance of sampling the candidate father was used, based on the average number of males within the neighborhood of the nest that were blood–sampled and geneotyped in the analysis. The delta LOD score was used to assess confidence in the assigned male using relaxed (80%) and strict (95%) criteria.

Results

Observational data

Following flock–breakup for the rest of the population in late April 2000, we observed two males and two female chickadees traveling together and collectively defending a single breeding territory. These birds constituted what appeared to be a non–disbanded wintering flock made up of a dominant male (YA/RB) and female (UB) along with a subordinate male (UB) and female (BA/MG). The dominant male and subordinate female were banded prior to the breeding season (in January and February), but the dominant female and subordinate male were unbanded at the beginning of the spring. These two birds were still distinguishable due to their clear associations within this territorial flock, and the fact that all but one neighboring male in the area was color–banded in 2000 (this lone unbanded neighbor was mated to a banded female, allowing for identification through pair–wise association). The relative dominance status of the four birds was determined by repeated observations of interactions during tracking periods, with the unbanded female supplanting the banded female, and the banded male supplanting the unbanded male. Chickadee pairs can be distinguished even within flocks, as mated pairs usually travel in closer proximity to each other during foraging than non–mated pairs (Smith, 1991). Using these criteria, we determined that the dominant banded male and dominant unbanded female constituted one 'pair', and the subordinate unbanded male and subordinate banded female appeared to constitute the other 'pair' within this tetrad.

Between 23 April 2000 and 19 May 2000, when the dominant female began incubating at the sole nest in the territory, this tetrad of birds was consistently seen in the same actively–defended territory on seven separate occasions. Apart from the distinction of being a tetrad, the birds acted as typical territorial breeding black–capped chickadees. The dominant male actively engaged in territorial contests with the six neighboring males that bordered this territory, often with the subordinate male from the tetrad taking a minor reinforcing role. However, this does not appear to have constituted a case of 'tolerating floaters' as

the subordinate male and female actively engaged with the dominant pair in the excavation of at least three separate nest cavities (witnessed 23, 30 April and 3, 4 May). At each of the three nest sites, all four birds were seen simultaneously excavating in alternating fashion typical of black–capped chickadees, where each individual waited on a nearby branch while another bird was in the nest, entering only when the excavating bird had exited to dispose of the excavated wood.

Just prior to egg laying, female chickadees begin producing a distinctive food–solicitation call, the *broken dee* (see Ficken et al., 1978 for description). As the two females in the tetrad began producing this call (14 May), the subordinate male disappeared from the territory. The dominant male was witnessed giving courtship feedings to both the dominant and subordinate female during the *broken dee* calling period (14 May). However, once incubation of the nest began (19 May), the subordinate banded female was never seen entering the cavity to incubate, and disappeared from the territory early in this period (additional nest observations on 23, 25, 29 May and 1, 5 June). For the remainder of the breeding season, only the unbanded dominant female and the dominant male were seen attending the nest and feeding the nestlings. The subordinate female was seen foraging alone on a neighboring territory on the 23 May, but the banded female associated with this territory was already incubating and her banded mate was witnessed feeding her at their cavity within the same hour as the subordinate female was seen.

During banding of nestlings (10 June), the dominant female was captured at the nest and banded (MA/GO). A blood sample was extracted at this time for parentage analysis. Within this nest, nine nestlings were sampled and two unhatched eggs observed; this clutch size of 11 was over double that of the average clutch size for this population (mean 5.0 ± 1.6 SD based on 16 other nests that fledge in 2000 where clutch size could be determined).

Allele frequency data

All three loci were found to be highly informative markers for paternity analysis (table 1). Due to the large number of alleles at the Pat–MP243 and Pocc–6 loci, many genotypes had sample sizes less than 5, and analysis of Hardy–Weinberg equilibrium could not be performed. Observed and expected heterozygosity values for these loci are similar. Analysis of the Pdou–5 locus shows no significant difference from Hardy–Weinberg expectations. The average polymorphism information content for these loci is very high and the combined non–exclusion probability of a second parent, with the first known is below 0.05 (0.016).

Paternity analysis

Of the nine offspring, four were genetically consistent with maternity of the dominant female (MA/GO) and five for the subordinate female (BA/MG). In the paternity analysis, the identity of the female was assumed as known. For eight of the offspring, the banded, dominant male (YA/RB) associated with this nest was identified as the most likely father (four at 95%, two at 80% confidence, and the remaining two at just under 80% confidence). Other candidate males were identified for offspring who had 80% confidence or below; however, only the assumed father was common to all candidate lists, and was classified as the most likely father in all cases. Further, many of the other candidate males did not have territories neighboring the focal nest.

One nestling with subordinate female maternity was not the offspring of the assumed father (a case of IBP). In this case two candidate males were identified but one of these was banded in distant territories while the most likely father (80% confidence) was the resident male of a territory adjacent to the nest (BA/GY). This male was a subordinate male within his own flock, and subordinate to YA/RB, but his territorial status would suggest he was dominant to the unbanded, subordinate male of the tetrad (relative age and territorial status would infer this relationship –Smith, 1991).

Among the four identified parents within this nest (YA/RB, MA/GO, BA/MG and the neighbor BA/GY), only BA/GY returned in 2001 to breed. As dispersal between breeding seasons is very low in black–capped chickadees (Smith, 1991), failure to return to the breeding population in subsequent years is typically an indicator of failure to survive the winter.

Discussion

If assessed strictly on genetic classification of nestlings, without insight into the behavioural patterns surrounding this particular nest, we would have identified this as a case of both quasi– and Intraspecific brood parasitism; five of the young in the nest were sired by a female not incubating the nest (IBP) and of these, four young were sired by the resident attending male (quasi–parasitism). Further, the identified parasitic female was known to be subordinate to the attending pair in the preceding winter flock, and the sole other identified father of the one pure IBP nestling was a male subordinate to the attending male. This pattern closely matches the one other documented case of genetically–identified quasi–parasitism in black–capped chickadees (Otter et al., 1998), where the eggs of a subordinate female were found in the nest of a dominant pair from the same flock. A number of those eggs were sired by the dominant male through extra–pair copulations (as these were truly separate breeding pairs), as well as by the parasitic female's social mate —himself subordinate to the dominant male in whose nest his mate had dumped her eggs. In this nest, we had not been able to clarify whether mis–matched maternity may have been the result of a rapid nest switch. However, in that same study a second nest with pure IBP was also found among chickadees in which rapid nest switching could be ruled out.

In all three nests (this study and those in Otter et al., 1998), however, the pattern of mis–matched

Table 1. Summary statistics of allele frequency analysis of 60 resident males. For each locus the sample size (N), number of alleles detected (k), observed (H_{obs})) and expected (H_{exp}) heterozygosity, polymorphism information content (PIC) and the probability of excluding father when the mother is known (NE–pat) is shown: * Product of individual loci.

*Tabla 1. Resumen estadístico del análisis de frecuencia alélica de 60 machos residentes. Para cada locus se incluye el tamaño de la muestra (N), el número de alelos detectados (k), la heterozigosidad observada (H_{obs}) y esperada (H_{exp}), el contenido de información del polimorfismo (PIC) y la probabilidad de excluir al padre cuando se conoce la madre (NE–pat): * Producto de locus individuales.*

Locus	N	k	H_{obs}	H_{exp}	PIC	NE–pat
Pat–MP243	60	23	0.950	0.900	0.884	0.211
Pocc–6	60	18	0.950	0.921	0.907	0.175
Pdou–5	60	6	0.750	0.786	0.748	0.424
Average (product*)	60	15.67	0.883	0.869	0.846	0.016*

maternity, regardless of the siring male, is consistent. The eggs mismatched to the attending female came from a subordinate female that occupied the same winter flock, and that subordinate female was unsuccessful in nesting in the year that dumping occurred. In this regard, IBP in chickadees may be a rare strategy following the 'bet–hedging' pattern suggested by Hughes et al. (2003) when population densities are relatively high and rates of nest failure are fairly high. The latter is certainly the pattern that occurs in black–capped chickadees, where nesting success is rank–dependent . Subordinate pairs are more likely to suffer nest loss than are dominant pairs (Otter et al., 1999), an effect that is amplified in marginal habitats (Fort & Otter, 2004; Otter et al., 2007). If subordinate females have low potential to successfully rear a brood to fledging, it may be strategic for them to lay eggs in the nests of known dominant neighbours, as dominant birds are more likely to successful fledge young. Where this has potential conservation implications is when land–use practices affect the perceived quality of the habitats to the birds –within our region, birds that nest in young forests that are regenerating from recent logging experience low success rates, especially among subordinate pairs (such as early–seral forests; Otter et al., 2007). Such scenarios could lead to increased use of intraspecific brood parasitism as a strategy by subordinate females to ensure reproductive success.

This, however, does not account for two of the three nests reported between this study and Otter et al. (1998) having offspring that mis–matched the attending female, but not the attending male of the focal nest. Such genetic patterns could lead one to conclude that quasi–parasitism was an active, if rare, strategy in black–capped chickadees. Griffith et al. (2004) point out that quasi–parasitism in its truest sense is at least partially a male strategy; the male engages in extra–pair copulations and then *allows* the extra–pair female to lay these eggs within the nest he attends with his social mate. We do not feel that this to be a likely scenario in explaining the patterns of nesting observed in chickadees. First, quasi–parasitism would assume a similar surreptitious nature to that associated with extra–pair copulations. It is not in the male's interest to advertise to his social mate that a number of the young within their nest are not her genetic offspring, lest she diminish parental care. Neither does it necessarily benefit the male to have the extra young of a second female within his brood without securing the parental care from both females. Studies involving experimental increases of clutch sizes clearly indicate that condition and survival of the attending parents are compromised with the increased parental effort involved in feeding large broods (*e.g.* Gustaffson et al., 1995; Yamaguchi, 1997). It is perhaps not a coincidence that the male and female attending the nest in this study, whose brood size was substantively higher than the average for this population, did not return to breed in 2001; by comparison, the neighboring male that sired the single purely–IBP nestling, but did not attend the nest, did survive. However, if this does not constitute true quasi–parasitism in a strategic sense, why does the genetic pattern of this nest –and that reported in Otter et al. (1998)– suggest this pattern? Griffith et al. (2004) have likely identified the explanation: where females within a species seek males with certain attributes for extra–pair copulations, and the nests of the same pairs are also the targets for intraspecific brood parasitism, occasionally the genetic patterns of these nests will collide to suggest quasi–parasitism.

This is the likely scenario to explain these rare occurrences in black–capped chickadees. Female chickadees are the sex that actively seeks extra–pair copulations (Smith, 1988), and their selection of males

is not arbitrary. Females prefer extra–pair sires that are socially dominant to the soliciting female's mate (Smith, 1988; Otter et al., 1994, 1998; Mennill et al., 2004). The only three known cases of nests containing young genetically–mismatched from the attending female were also deposited by subordinate females into the nests of higher–ranking flockmates. This may be strategic due to the differential survival of nests of dominant pairs (Otter et al., 1999; Fort & Otter, 2004). Extra–pair copulations in black–capped chickadees are relatively common, occurring in about 30% of nests (Otter et al., 1998; Mennill et al., 2004), and they typically involve the same males (higher–ranked flockmates) that were found to be the target nests of parasitic females in this and Otter et al. (1998) study. Therefore, it is probabilistic that parasitic females may have engaged in EPCs with the attending male prior to parasitizing the nest. Although the currently–reported case is unusual in the failure of the flock to disband and the early–season breeding affiliation of the resident male with both females, other cases of apparent quasi–parasitism may easily be explained by overlapping, but independent, female strategies that simply have a common target male phenotype. This is already known to be the case for the female strategies of divorce and EPCs in Black–capped Chickadees (Ramsay et al., 2000).

Why, then, is IBP so rare in chickadees? More than a decade of analysis of paternity on an Ontario, Canada population (115 nests combined between Otter et al., 1998; Mennill et al., 2004) found only the two cases of mismatched–maternity. This may arise from the costs of intraspecific nest parasitism evolving when conspecifics have non–asymmetry in nestling size between within–pair and parasitic young (Slagsvold, 1998). Such a scenario merely increases broodsize, stretching parental provisioning efforts and decreasing both the resources to and condition of the individual nestlings. Young from such enlarged broods are likely to have decreased survival, which would tend to diminish the evolutionary potential to pass on parasitic genes. Simultaneously, non–discriminating parents who accept enlarged broods would suffer higher mortality, strongly selecting for behaviors such as abandonment. This has been suggested as an explanation as to why intraspecific brood parasitism is more common in species with precocial young, where increased brood size does not necessarily have the same debilitating effect on parents or offspring survival (Slagsvold, 1998). Of concern, then, is habitat changes that decrease chances for subordinate females to breed (Otter et al., 2007) as this could lead to increased IBP, and in turn result in higher mortality among targeted dominant pairs that suffer from increased parental care costs.

Acknowledgements

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