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Divorce and extrapair mating in female black-capped chickadees (*Parus atricapillus*): separate strategies with a common target

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Abstract Patterns of divorce and extrapair mating can provide insights into the targets of female choice in free-living birds. In resident, site-faithful species with continuous partnerships, the better options and the incompatibility hypotheses provide the most likely explanations for divorce. Extrapair mating can be explained by a number of hypotheses often making similar predictions. For example, the good genes and future partnerships hypotheses predict similar patterns if males with good genes also make the best future partners. By considering both divorce and extrapair mating, it may be possible to distinguish between these comparable hypotheses. We examined natural patterns of divorce and extrapair mating in a long-term study of black-capped chickadees (*Parus atricapillus*). Out of 144 partnerships over 8 years, we observed 11 divorces and 38 faithful pairs between seasons. Females usually divorced between their first and second breeding seasons for males of higher social rank than their previous partners, had similar reproductive success prior to divorce as females who retained their previous partners, and did not divorce on the basis of previous reproductive success. These results confirm earlier experimental evidence that females divorce for better options. Females who divorced were significantly more likely to have had mixed-paternity broods prior to divorce than females who stayed with their previous partners. There was no evidence that females divorced in favour of previous extrapair partners. These results support the good genes hypothesis for extrapair mating, suggesting that female chickadees use divorce and multiple mating as separate strategies sharing a common target.

Keywords Divorce · Extrapair mating · Better options · Good genes · Black-capped chickadees

Introduction

After extrapair paternity, divorce has recently attracted perhaps the greatest amount of attention in both theoretical and empirical studies of partnerships in birds (Black 1996). Divorce is intimately related to mate choice and provides one of the best examples of the value of using game theoretical models in the study of sexual selection (Ens et al. 1996; McNamara et al. 1999). Here we examine the relationship of extrapair paternity to patterns of divorce in a long-term study of black-capped chickadees (*Parus atricapillus*), for which studies have already been conducted on individual reproductive success (Otter et al. 1999), extrapair mating (Otter et al. 1998), and willingness to divorce under experimental conditions (Otter and Ratcliffe 1996; S.M. Ramsay, unpublished data).

Black-capped chickadees are socially monogamous songbirds that are year-round residents throughout their range and typically nest only once per year (Godfrey 1986). Outside the breeding season, chickadees live in dominance-structured flocks composed of 4–12 individuals (Smith 1991). Flocks are composed of pairs that bred in the area in the previous season and young-of-the-year that have immigrated into the flock. Within flocks, males are usually dominant to females and older birds are dominant to younger birds. During winter, high-rank individuals have priority access to food and roosting sites. For females, high rank means that individuals experience less aggression from flockmates than would be expected from their overall position within the flock hierarchy (Lemmon et al. 1997). Partnerships in chicka-

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dees are maintained year round, and new recruits usually establish partnerships by early winter (Smith 1991).

During the breeding season, high social rank confers reproductive benefits on females through enhanced fecundity and fledging success (Otter et al. 1999) and on males through female-solicited extrapair mating (Smith 1991; Otter et al. 1998). Given the opportunity through either natural mortality or experimental removal, females will divorce low-rank males for higher-rank partners (Smith 1991; Otter and Ratcliffe 1996; S.M. Ramsay, unpublished data). To date, no one has examined the combination of extrapair paternity and divorce as part of the overall mating strategies of female chickadees.

Cezilly and Nager (1995) found a positive association between extrapair mating and divorce in a series of independent linear contrasts and paired comparisons across species. Their results point to the intimate link between the two behaviours. There are two possible interpretations for their results. First, extrapair mating may allow females to assess and form alliances with future social partners (Wagner 1992). Alternatively, extrapair mating and divorce may be two elements of a common strategy to obtain good genes but which are not necessarily linked. Because divorce and extrapair mating can be viewed as dynamic games, the players are likely to change between breeding bouts, reducing the possibility of divorcing in favour of previous extrapair partners. To untangle these two hypotheses, we need to consider the reasons for divorce.

Choudhury (1995) identified a number of hypotheses to explain the occurrence of divorce, and each may be related to the life history characteristics of particular species. Of these hypotheses, the better options and incompatibility hypotheses are relevant to resident, site-faithful birds with continuous partnerships like chickadees.

The better options hypothesis predicts that individuals divorce to improve their own mating situation, irrespective of previous breeding experience and the motives of the previous partner to maintain or abandon the partnership (Choudhury 1995; Ens et al. 1996). Better options predicts that there are a few high-quality individuals who are good partners for any given individual of the opposite sex. The differences in quality between individuals may be related to any of a number of factors including control of territorial resources, parental ability, or heritable attributes. Under this hypothesis, we predict that females will divorce for higher-rank males than their previous partner. Divorces should occur early in life, and will be unrelated to previous breeding success but should, rather, be related to the potential for improvement (Choudhury 1995). Indeed, reproductive success may be lower in the first breeding attempt following divorce and rebound in successive attempts (McNamara et al. 1999).

The incompatibility hypothesis suggests that individuals divorce to obtain a partner with whom they are better suited. Typically, this hypothesis is considered from the point of view of complementary parental care skills (Ens et al. 1996). The most common examples cited for this kind of compatibility come from pelagic seabirds where coordination of foraging and brooding are essential for nesting success (Williams 1996; Wooler and Bradley 1996; Bried et al. 1999). This factor is also important in passerines like chickadees where males provision females during incubation and provide the bulk of feedings to nestlings; coordination of provisioning with incubation or brooding effort is important to the fitness of each parent (Smith 1991; Otter et al. 1999). Compatibility could also be considered from a genetic perspective where, for example, individuals may be incompatible as partners because they are closely related (Ens et al. 1996). Under this hypothesis, divorces will be unrelated to the social rank of the new partner. Because the compatibility of a partner may only become apparent following breeding, we predict that divorces will occur at any age, and any given female may divorce more than once in her life. We also predict that divorce will be more likely to occur following a breeding failure, and reproductive success will improve following mate change (Choudhury 1995).

An additional hypothesis of mate choice is also relevant to patterns of social fidelity. The familiarity hypothesis suggests that an individual’s best choice is a partner with whom it has prior experience (Ens et al. 1996). Thus, maintaining a previous partnership may be more beneficial than change. Under this hypothesis, we predict divorces to be rare, and unrelated to social rank when they occur. Females will decide to stay with their previous partners regardless of previous breeding success, but reproductive success should improve over subsequent breeding seasons.

If females seek extrapair matings for future mate choice, we predict that the target of divorce will be their previous extrapair partners, regardless of the reasons for divorce. Because of the possibility of mate mortality, under this hypothesis, we predict that females who retain their previous partners will also use extrapair mating. On the other hand, if females use extrapair mating for current genetic benefits, then we predict that females who divorce will have extrapair young in their broods prior to divorce, but they will not necessarily divorce for their previous extrapair partner. By comparison, we predict few or no mixed-paternity broods among females who retain their partners between years.

Our objective in this study was to examine the natural patterns of divorce and partner retention in our study population over eight breeding seasons. We looked at patterns in relationship to age, social rank and reproductive success. We also examined the patterns of divorce and partner retention in relationship to extrapair mating.

Methods

The data for this study come from a long-term database drawn from a population of black-capped chickadees at Queen’s University Biological Station, Chaffey’s Lock, Ontario, Canada (44°34′ N 76°19′ W). The methods for dominance assessment, partnership assessment, assessment of reproductive success, and extrapair paternity are described in detail elsewhere (Otter and Ratcliffe 1996; Otter et al. 1998, 1999); in our analyses we have been able to assign extrapair paternity in 90% of broods with mixed parentage (Otter et al. 1998; S.M. Ramsay and D.J. Mennill, unpublished data). We examined mate fidelity between years in our study population from 1992 to 1999. In each year, we marked individuals with unique combinations of Canadian Wildlife Service number bands and two or three plastic colour bands. Thus, we were able to monitor the identity of partners and reproductive success of all individuals in our population from their first appearance until their presumed deaths.

We considered pairs to have been faithful (“stays”) when both members of the pair nested together in two or more breeding attempts. We considered a divorce to have occurred when one individual was paired with an individual other than its partner in the previous breeding season while its previous partner was still alive. Using this definition, there are three patterns for divorce: one individual can desert its partner for another, one individual can usurp the partner of another, and one individual can form a preemptive partnership with another individual before its previous partner returns (Ens et al. 1996). Since chickadees are non-migrant and maintain year-round partnerships, we expect to find only the first two types of divorce.

We determined reproductive success by clutch size and considered a nest to have fledged successfully if at least one nestling survived to leave the nest. We assessed paternity using a combination of single- and multi-locus molecular techniques (see Otter et al. 1999 for full details). We examined whether broods contained extrapair young in the year prior to both divorces and stays. For all cases of extrapair paternity and divorce, we determined whether the extrapair male in the first year was also the new social partner in the second year.

Between 1995 and 1998, we conducted a number of experimental removals in this study population to document rank-related patterns of divorce and female-female competition. None of the divorces that occurred in those experimental removals are reported here; we have restricted our analyses to divorces that occurred naturally. Because divorce is a dynamic game whose players vary from year to year, each breeding bout is essentially an independent event even though some individuals may be involved in multiple bouts. Since none of our hypotheses predicts consistent behaviour by individuals between breeding events, we have considered all breeding data for every individual in our analyses.

Results

Over the 8 years of our study, we monitored 144 partnerships with a return rate of 49.4% for males and 38.2% for females; 20% of males and 17.8% of females lived through three or more breeding seasons. Of the partnerships we monitored, there were 49 cases where both members of a pair returned for a subsequent breeding season. Of these 49 cases, we found 38 cases (77.6%) of pairs that remained faithful between years, and 11 cases (22.4%) of divorce between years. Of the 11 divorces we observed, 10 were cases where females deserted their previous partners between years. The 11th divorce was a situation where one female whose partner died between breeding seasons was partnered in the subsequent year on the territory of another male whose previous partner was still alive. We were not present to observe the process of this divorce; thus, we cannot discern whether it was a case of a female usurping a male from another female or the male deserting one female for another. Because the weight of evidence suggests that divorce in this species is a female strategy, and the fact that the female moved to the male’s territory, we describe this case as a usurpation, without ruling out the possibility of male complicity in the process (Ens et al. 1996).

Table 1 Partnership decisions by year of occurrence, and paternity in the season leading to the decision. First refers to divorces that occurred between the first and second breeding season. Later refers to second or later breeding seasons. Full-paternity broods are those sired entirely by the social partner of the female. Mixed-paternity broods are those that contain extrapair young

Decision	Breeding season		Paternity	
	First	Later	Full	Mixed
Stay	18	20	17	3
Divorce	9	1	2	4
Likelihood ratio	6.72**	5.74*		

*$P<0.025$; **$P<0.01$

There were three additional desertions that occurred during the breeding season before the females had breeding experience with the partner they divorced. In two of the three cases, the female had begun cavity excavation with her first partner and experienced a cavity failure (one through flooding, and one through collapse of the tree limb containing the cavity); in the third case, the divorcing female was in early stages of excavation. All three cases coincided with the death of a neighbouring female. In two of the three cases, the second male was higher ranked than the female’s first partner; in the third case, we had no information on the relative ranks of the two males involved. Since these divorces occurred before the females had a full nesting bout with the males they deserted, we can only consider these cases with respect to the relative social rank of the males.

The proportion of partnerships ending in divorce was greater between a female’s first and second breeding seasons compared with later breeding seasons (Table 1; likelihood ratio=6.72, df=1, P=0.009). Whether a female stayed or divorced was not related to either previous clutch size (stay=6.53±0.35 vs divorce=6.17±0.62, one-tailed t=0.50, df=23, P=0.62) or previous fledging success (stay: 20/27 nests successfully fledged vs divorce: 7/8 nests successfully fledged; likelihood ratio=0.70, df=1, P=0.40). We had before and after clutch size data for only three divorcing females: two of these had reduced clutch size following divorce and one had an increased clutch size. We had before and after fledging success data for six divorcing females: three of five that had been successful in the year prior to divorce were also successful following divorce. The one nest that was unsuccessful in the first year was also unsuccessful following divorce. Clutch sizes did not increase from first to second seasons for staying females (mean change=0.2, one-tailed paired t=0.61, df=9, P=0.28). There was no inter-year pattern of fledging success for staying females: 4 improved in the second year, 8 did worse, and 9 did not change (one-tailed sign test, P=0.92).

Females showed a marginally significant trend towards divorce for males of higher social rank than their previous mates (8 higher vs 2 lower, 3 unknown; one-tailed sign test, *P*=0.055). The one female who usurped ended up mated with a high-rank male. The usurper was dominant to the female she displaced in the season when the divorce occurred. In all but three cases, females divorced for males who were in their second or later breeding seasons. Two of the females who divorced for a male in his first breeding season subsequently paired with third males when their second partners failed to return for a second season. The third female deserted her second partner for a new male in her third breeding season.

We observed 7 broods with extrapair paternity in the 26 broods where we had parentage data: in all 7 cases we were able to assign paternity to the extrapair male. Females were significantly more likely to have extrapair young in the year prior to a divorce than in the year prior to a stay (Table 1; likelihood ratio=5.74, *df*=1, *P*=0.017). Six of the seven extrapair males survived to subsequent breeding seasons; the lone male who did not survive fathered young in the brood of a female who subsequently divorced. In only one case out of the remaining three divorces was the extrapair male the female's subsequent social partner; one male returned with his previous partner and the other paired with a third female. The three cases of mixed paternity prior to stays involved two females (one in two seasons) whose extrapair partners and the high-rank males from neighbouring flocks retained their mates between years.

In eight cases, females returned for an additional breeding season following the year of divorce. In only two of these cases did the female remain paired with her new mate. The mates of the remaining females died between breeding attempts; thus we cannot determine whether they would have remained faithful.

The single case of usurpation occurred between 1997 and 1998 and involved a female (OG/MS) who first bred in 1995, and had a mixed-paternity brood that year. She deserted her first partner around the time of flock breakup in 1996 for a dominant flockmate (S-/BG) when his partner died. OG/MS and S-/BG bred successfully in 1996 with no extrapair young in their brood. During the winter of 1997, S-/BG broke a leg which never healed such that it could be used for perching or manipulating food items; nevertheless, OG/MS continued her partnership with him. Their nest in 1997 was depredated during the nestling stage. During the autumn of 1997, S-/BG died. In 1998, OG/MS mated with RB/MS, the new alpha male who had been subordinate to S-/BG in 1997. The pair successfully raised a brood of six young. The previous partner of RB/MS mated with a new male who was subordinate to RB/MS.

Discussion

The most common mating decision for females in our population was to stay with previous partners. The fact that there was no pattern of improving clutch size or fledging success with stays suggests that familiarity is a default mode of choice. These results suggest that staying does not guarantee increased fecundity or fledging success for a female but it may spare her the cost of searching for a new partner or competing with another female to usurp her partner. However, we must consider the fact that our analyses are confined to the subset of our entire breeding population where survivorship was high. These may be the highest-quality individuals in the population and the scope for variation in reproductive success may be low, giving a false impression of no benefit of familiarity.

Desertions were the most common form of divorce in our population. The pattern of extrapair paternity in the year leading to the decision to stay or divorce, the number of breeding attempts prior to divorce, and the general pattern of divorce in favour of higher-rank males all support the better options hypothesis. The lack of difference in clutch size and fledging success between stays and divorces in the year leading to the decision, and the mixed results before and after divorce confirm that the decision to stay or desert is not related to incompatibility, a pattern also recorded for the closely related willow tit (*P. montanus*; Orell et al. 1994). Furthermore, the evidence from our three within-season divorces demonstrates that females will divorce a male in the absence of any prior breeding experience with him. This is further supported by evidence from experimental removals in the same study population (Otter and Ratcliffe 1996; S.M. Ramsay, unpublished data).

The incompatibility hypothesis predicts that divorce is unrelated to individual quality, but rather to the combined attributes of the pair. As such, there would be no one best partner for a group of females. Half of our breeding population in any given year was composed of new males, providing ample divorce options for females who had low fecundity or nest failure in a previous season. Instead of seeing high rates of change, we saw females remaining with their previous partners unless they had an opportunity to pair with an older, and preferably a higher-rank male. This observation lends further support to the idea of benefits from familiarity when the opportunities to divorce for better options are limited.

One of the identified costs of divorce is searching for a new mate of suitable quality (Choudhury 1995; Ens et al. 1996; McNamara et al. 1999). Flocking outside the breeding season will reduce this cost for female chickadees. Flocks act as information centres where females can gain continuous information on who is partnered with whom, who has recently died, and the relative quality of potential partners (Dhondt et al. 1996). Following the breakup of winter flocks, males honestly advertise their quality and partnership status during the dawn chorus (Otter and Ratcliffe 1993; Otter et al. 1997), allowing females to continue assessment from the breakup of winter flocks until they have completed egg-laying. Thus, female chickadees do not have to engage in costly searching to decide if divorce is a worthwhile option.

If search costs are low, the main costs of divorce in chickadees must be those associated with intrasexual competition. There is intense competition among female chickadees when two claim partnership with a single male (Otter and Ratcliffe 1996; S.M. Ramsay, unpublished data). Encounters between disputing females quickly escalate into fights and have the potential to result in serious injury for the combatants. Once this cost is removed, females will switch partners as long as they have not already initiated egg-laying (Otter and Ratcliffe 1996; S.M. Ramsay, unpublished data). Thus, divorce in this species seems to be limited by opportunity rather than by a lack of motivation to change partners.

Divorce in our population appears to be an opportunistic strategy, yet extrapair mating occurs in approximately 30% of broods (Otter et al. 1998). For a long time, the thinking on sexual selection theory predicted strong selection against multiple mating by females (Bateman 1948; Trivers 1972), yet we see female-solicited extrapair mating in this and a number of other species (Møller and Ninni 1998). Extrapair mating, therefore, must have greater benefits to females than those associated with future mate choice. The evidence we have assembled from our population suggests that extrapair mating is a female tactic to obtain good genes for their offspring.

It is also possible that divorce and extrapair mating in chickadees could help a female to gain some form of material benefits, but we think this is unlikely for the following reasons. Detailed observations in our population show that female chickadees do not receive any food, parental care or nest defence as a result of extrapair mating (Otter et al. 1998), and if this were the motivation for seeking extrapair copulations then we would not predict a rank-related pattern of extrapair mating. There is evidence to suggest that high-rank individuals have an advantage in territory aquisition when there are surplus breeders (Desrochers et al. 1988; Smith 1991); however, in our study the females that divorced were already established on breeding territories. Moreover, there is little evidence of rank-related variation in territory size or characteristics in this species (Smith 1991; Ramsay et al. 1999). Finally, levels of paternal care are unrelated to male rank (Otter et al. 1999), giving a female no benefit through enhanced input to her young.

The results in this and previous studies (Smith 1991; Otter and Ratcliffe 1996) show a preference in female chickadees to form partnerships with high-rank males, but because of constraints imposed by other females, individuals may be forced to choose a lower-rank partner rather than forego breeding altogether. Over 60% of females in our population breed in only a single season, thus a missed breeding opportunity might represent loss of an entire lifetime's reproductive success. Choosing to settle with a lower-rank male, however, need not be a final decision. Extrapair mating allows females to gain the genetic benefits of a high-rank partner for part or, rarely, all of some broods. Should a female survive to a second breeding season, the opportunity to divorce further enhances her prospects by allowing her to gain the direct benefits of high-rank partnership as well as genetic benefits. The two behaviours, extrapair mating and divorce, are related by the common thread of choice for high-rank males, and may reflect constraints imposed on some females to form social partnerships with suboptimal males. Indeed, we observed that the females who divorced between breeding seasons were significantly more likely to have mixed-paternity broods prior to divorcing. Extrapair paternity and divorce are distinct in that extrapair paternity is not a form of mate sampling (Cezilly and Nager 1995): females did not show a tendency to divorce for their previous extrapair partners.

We have evidence from mating strategies that females are choosing good genes in their social and extrapair mates. We have yet to identify the actual genetic benefits provided by high-rank males. Because of chickadee dispersal patterns (Weise and Meyer 1979), devising methods to assess the heritability of rank will be difficult. There is evidence for both sexes that rank influences survival and territory acquisition when there is a surplus of breeders (Desrochers et al. 1988; Smith 1991), thus any genetic variation associated with low rank will show variable representation in a population depending on the number of individuals competing for limited breeding space. More research is be needed to address these issues.

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