

# The social and genetic mating system in flickers linked to partially reversed sex roles

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The type of social and genetic mating system observed in birds is influenced by the need of both sexes to provide parental care. In woodpeckers, unlike most birds, females are partially emancipated as males provide most of the care including nocturnal incubation. We analyzed the mating system of northern flickers *Colaptes auratus* and used microsatellite markers to assess parentage of 326 nestlings from 46 monogamous broods and 41 nestlings from 7 polyandrous broods. No cases of extrapair paternity were found in monogamous broods, but there was one such case in the brood of a secondary male of a polyandrous female. Intraspecific parasitism lead to 17% of broods containing at least one parasitic egg. The identity of the parasitic female was determined in 5 cases to be a close neighbor with a mate and clutch of her own. Between 0% and 5% of females annually were polyandrous with the timing of the 2 nests slightly staggered. Polyandrous females were older than average females in the population, and their primary males were older than secondary males. Polyandrous females raised nearly twice as many (10.8) nestlings compared with monogamous females (5.5). Although most female flickers are strictly socially and genetically monogamous, some can benefit from engaging in the alternate reproductive tactics of polyandry and brood parasitism. Therefore, at least in flickers, such tactics of laying eggs in multiple nests are not the result of poor-quality females “making the best of a bad situation” but are a way to increase reproductive success. **Key words:** extrapair paternity, intraspecific brood parasitism, mating system, polyandry, woodpecker. [*Behav Ecol*]

For animals with parental care, the evolution of mating systems is linked closely to the type and amount of parental care provided by females and males (Black 1996; Ligon 1999). Because the reproductive rate of males is generally more limited by access to mates than is the reproductive rate of females (Hartley and Royle 2007) or simply because male birds or mammals usually have the option to desert the offspring first (Trivers 1972; Székely et al. 1996), females in these groups typically perform most of the parental care while males more often become polygynous (Gowaty 1996; Ligon 1999), contrary to the pattern in fish (reviews in Clutton-Brock 1991). Birds have provided much of the stimulus for studies of mating systems, but because most of the focus has been on taxa with female-biased care (Hartley and Royle 2007), our understanding about the variety of reproductive strategies, especially of females, is still limited. Insight into the evolution of alternate reproductive strategies of females can come from observing species where the typical roles of parents in parental care are reversed (Andersson 2005). Woodpeckers (Picidae) are especially interesting in this context because males do most of the incubation and brooding of young (Winkler et al. 1995; Wiebe 2008) and in at least some species appear to invest more heavily in parental care than females across the reproductive attempt (Wiebe and Elchuk 2003; Wiebe 2005).

Linked to high paternal investment by male woodpeckers appear to be flexible and complex mating systems including cooperative breeding and polygynandry in a few species (Winkler et al. 1995) with competitive egg laying by females (Mumme et al. 1983). Even among those woodpecker species once thought to be socially monogamous, reports of classical

polyandry are accumulating as populations with marked individuals are studied in more detail (Willimont et al. 1991; Kotaka 1998; Wiktander et al. 2000; Wiebe 2002; Pechacek et al. 2005). However, characteristics of females that become polyandrous in a population and the reproductive payoff of polyandry remains the focus of theoretical debate. Pechacek et al. (2006) hypothesized that female three-toed woodpeckers *Picoides tridactylus* became polyandrous out of “desperation” to salvage reproduction when their primary male proved to be of low quality, that is, they were making the “best of a bad job.” Wiebe (2005) hypothesized that polyandry increased reproductive output of female northern flickers *Colaptes auratus* but that it was constrained by a fairly even sex ratio in the population.

Although females may often have only one social mate, DNA analysis has revolutionized the way biologists interpret social mating systems. For example, although most avian species (ca., 90%) have biparental care and are socially monogamous, nearly 90% of species have extrapair young as a result of the female copulating outside the pair bond (Griffith 2007). A burgeoning literature centers on explaining the adaptive value of extrapair copulations and fertilizations (EPCs/EPFs) for females (reviews in Petrie and Kempenaers 1998; Ligon 1999; Griffith 2007). To date, there is only genetic information on paternity for 3 species of socially monogamous woodpeckers: middle spotted *Picodes medius*, great spotted *Picodes major* (Michalek and Winkler 2001), and three-toed woodpeckers *Picoides tridactylus* (Pechacek et al. 2005). These studies indicate that males rarely, if ever, lose paternity, which is consistent with the hypothesis that males should invest heavily in care only if they fathered the offspring (Davies et al. 1996; Kempenaers and Sheldon 1997).

DNA analysis has also revealed intraspecific brood parasitism (IBP) in about 2.4% of bird species, mainly precocial species (Yom-Tov 2001; Krüger and Brooke 2007). Genetic evidence for IBP in woodpeckers is generally lacking,

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although Pechacek et al. (2005) report one nestling three-toed woodpecker not related to the female, and there is an anecdotal report of an irregular laying sequence in flickers that suggests IBP (Bower and Ingold 2004). The causes and reproductive payoffs for IBP are not well known for most birds although authors have tried to classify hypotheses in general ways. For example, Davies (2000) stresses 3 categories: 1) mixed evolutionarily stable strategy (ESS) (brood rearing vs. brood parasitism as frequency-dependent strategies in the population), 2) conditional ESS (females that cannot secure a nest site make the best of a bad job), and 3) enhancement of fitness by laying additional parasitic eggs after one's own clutch is complete. A recent review by Lyon and Eadie (2008) suggests that such a classification is confounded and recommends a focus on flexible life-history strategies for females and on the prevailing ecological and social conditions that lead to IBP in different contexts.

In this paper, we describe the social mating system in a population of northern flickers and use microsatellite markers to test for alternate female strategies such as EPF and IBP. Using information on reproductive success from the largest data set yet obtained for a "socially monogamous" woodpecker, we explain the context and the fitness benefits of alternate reproductive strategies in females and highlight ecological and physical traits linked to the evolution of such strategies in birds.

## MATERIALS AND METHODS

### Study area and field methods

Northern flickers were studied from 1998 to 2007 in central British Columbia, Canada, near Riske Creek (51°52'N, 122°21'W) on a study area that covers about 100 km<sup>2</sup>. The area contains grassland interspersed with clumps of aspen trees (*Populus tremuloides*), Douglas fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), and wetlands. The area shows a high diversity and density of cavity nesting species, but nest sites do not appear limiting (Aitken et al. 2002). Each year, we monitored the reproduction of between 85 and 150 breeding pairs of flickers from the time they arrived on territories after migration in late April until young fledged in late July. Flickers are normally socially monogamous, but about 5% of females per year may have 2 simultaneous nests with different males (Wiebe 2005). Because visibility on the grassland landscape is good, we are confident that most nest sites in the core of the study site were located and that we could determine the social pairings of most females reliably by observing who incubated at nests. However, we could not detect all nests, especially at the boundary of the study area, so the estimate of 5% polyandry may be biased slightly low. Clutch sizes ranged from 3 to 12, incubation took about 11 days, and nestlings fledged at 25–27 days (Wiebe and Swift 2001; Wiebe 2005). Typically, both parents contribute to incubation, brooding, and provisioning of nestlings at both monogamous and polyandrous nests (Wiebe 2005, 2008).

Early in spring, potential nest cavities on active flicker territories were checked with a mirror and flashlight until eggs were found and then a small, replaceable "door" was cut into the tree trunk to give access to eggs and nestlings and to allow us to band adults. This procedure did not cause abandonment, and trees with doors have been reused for many consecutive years (Fisher and Wiebe 2006a). Annually, more than 95% of known breeding adults on the study area were trapped at the nest either by stuffing the nest hole during incubation or by pulling a net over the cavity entrance during brood rearing. Birds were weighed, measured, and aged (up to 4 years, according to molt patterns described in Pyle et al. 1997), and each received a unique color band combination. For a multi-

variate measure of body size (Rising and Somers 1989), we used the score on the first axis of a principal component analysis (PCA1) based on 6 measures: lengths of the wing, bill, tail, tarsus, ninth primary, and bill depth. Separate PCA analyses were done for each sex because of slight sexual size dimorphism. For an index of body condition that controlled for structural body size, we used the residuals of a regression of PCA1 and body mass. After hatch, nests were visited at least 3 times during the nestling period to document nestling mortality. The number of nestlings on the last visit, when nestlings were around 21 days old, was considered to be "fledging success" unless dead nestlings were found subsequently when nest cavities were measured at the end of the summer. Distance between nests was determined with GPS.

Flickers have an annual adult mortality rate approaching 60% and a "fast" life history, so turnover in the population is rapid (Fisher and Wiebe 2006b; Wiebe 2006a).

Therefore, individual females were not represented twice in reproductive data collected on polyandry and IBP. Average reproductive parameters calculated from the population over 9 years do, however, include a fraction of duplicate observations of females.

### Blood sampling and parentage analysis

Breeding densities of flickers vary somewhat across our large study area. Blood was sampled from some isolated breeding pairs, but sampling was focused on locations with several near neighbors (breeding within about 200 m) to increase the chance of detecting EPFs or IBP. Therefore, sampling does not reflect precisely the breeding densities at the larger landscape scale, but results should generally reflect a typical range of densities in the population. DNA was extracted from a 50-μL blood sample taken from the brachial vein of adults or nestlings and stored in buffer solution (Longmire et al. 1988) until analysis in the laboratory. We attempted to sample entire families, but occasionally a nestling died before sampling at about 8 days old.

In 2001 and 2002, blood samples from 15 flicker families were analyzed by GenServe Laboratories (Saskatchewan Research Council, Saskatoon, Canada) using 3 microsatellite markers (WL3E29, WL3109, and WM6A09) originally sequenced from yellow warblers *Dendroica petechia*. Offspring mismatching the putative father or mother was assigned using the maximum likelihood procedure in Cervus v 2.0 computer program (Marshall et al. 1998) where the confidence level of assignment was set at 96%. Later, 14 new microsatellite markers for flickers were developed (see Kuhn et al. 2008), and a further 33 flicker families that were sampled in 2006 and 2007 were then analyzed at the Max Planck Institute for Ornithology (Seewiesen, Germany). Parentage analysis was based on 12 markers (Cau1-12; Kuhn et al. 2008), with a minimum of 6 typed markers for each offspring.

We used Cervus v 3.0 (Kalinowski et al. 2007) with the following parameters: error rate set at 0.03%, 100% of loci typed, proportion of candidate mothers sampled: 0.95, and proportion of candidate fathers sampled: 0.80. The analyses were done in 3 steps: 1) maternity analysis with all known females as potential mothers. For 19 offspring, 2 females (of which one was the social mother) showed no mismatch. In all these cases, the social female was assigned the genetic mother, even when Cervus suggested the other female as the most likely parent ( $N = 2$  cases); 2) paternity analysis with the mother identified in step 1 as the known parent and with all known males as potential fathers; and 3) parentage analyses with all known males and females as potential parents (search for parent pair). The outcome of the third procedure matched the outcome of steps (1) and (2) in all cases. Offspring were

only assigned if they showed 0–1 mismatch with the candidate parent and the assignment could be done with high confidence (95%). Only one offspring showed one mismatch with an assigned male. Other statistical analyses were performed by SPSS (2004), and all tests were 2 tailed.

## RESULTS

### IBP and extrapair paternity

Altogether, 46 socially monogamous families with their 326 nestlings were tested. In 38 (83%) of these families, all nestlings were related to both social parents. The other 8 (17% of families) contained offspring related to neither parent. These nests with IBP had 1–3 parasitic nestlings per brood (average 1.8), which translated to about 5% of nestlings in the population being raised by foster parents. The 7 of 46 families that were sampled in isolated locations had no parasitic eggs, whereas IBP was observed in 3 different clusters of breeding flickers on the study area at densities ranging from 11 to 35 pairs per km<sup>2</sup>. One of the 7 (14%) polyandrous broods also contained an IBP egg, a frequency similar to that found in the monogamous broods.

In 5 of the 9 cases of IBP in the monogamous and polyandrous pairs, the identity of the parasitic female could be determined. In all cases, she was a neighbor on an adjacent territory with a nest of her own, and the male that sired the parasitic offspring was her social mate, that is, there was no “quasi-parasitism” (Krüger and Brooke 2007) with the male of the parasitized nest siring the parasitic offspring. The timing of laying in the 2 nests showed that parasitic females completed their own clutch first, laying 1 egg per day, and then added eggs to their neighbors’ nests, and in at least 3 cases, it was apparent that more than one parasitic female was responsible for laying in a nest. Those parasitic females that we could identify all went on to successfully raise on average 6.9 (range: 5–8) offspring in their own nest, so there is no evidence that IBP occurred as a result of a failed nesting attempt or a poor-quality mate. One female that parasitized her neighbor’s nest was also polyandrous, meaning that she simultaneously had offspring in 3 different nests being reared by 3 different males.

### Social polyandry

The incidence of social polyandry varied from 0% to 5% of females annually, and we had detailed information on the timing of laying and reproductive performance in 13 cases. Polyandrous females were significantly older than monogamous females in the population (mean  $\pm$  standard deviation [SD]: polyandrous:  $3.1 \pm 1.6$  years, monogamous:  $1.8 \pm 1.0$ ;  $t$ -test:  $t_{782} = 4.27$ ,  $P < 0.001$ ). “Primary” males (those with first clutches) were older ( $3.4 \pm 1.8$  years) than secondary males ( $2.1 \pm 1.2$  years; paired  $t$ -test:  $t_{12} = 1.97$ ,  $P = 0.042$ ). Primary males did not differ in body size (PCA score for primary males =  $87.1 \pm 0.95$  SD, secondary =  $87.0 \pm 0.84$ ;  $t_{12} = 0.66$ ,  $P = 0.52$ ) or in condition from secondary males (primary male’s weight residual =  $-10.0 \pm 7.1$  SD, secondary =  $-17.9 \pm 12.3$ ;  $t_6 = 0.09$ ,  $P = 0.93$ ). In 2 cases, the secondary males had first been paired with their own female, but she abandoned after the nest was usurped by European starlings *Sturnus vulgaris*. In the other cases, we noted that the secondary male was calling and drumming alone on his territory for several days (i.e., displaying to attract a partner), and so we assume that he did not have a mate before he paired to an already-mated female.

Primary and secondary males in polyandrous trios always defended their own nest cavities, which were on average

$380 \pm 321$  m SD apart (range 41–1110 m). In 10 cases (77%), the 2 males were neighbors, whereas in the other 3 cases, 1–3 other breeding pairs were situated between the 2 nests of the polyandrous female. Breeding activities with her 2 males overlapped: the average number of days between the first egg in each clutch was  $17.4 \pm 6.2$  SD,  $n = 12$ , and 4–22 days separated the laying of the last egg in the first clutch and the first egg in the second clutch.

The 13 polyandrous females laid on average  $15.0 \pm 1.5$  SD eggs in their 2 nests (range 13–18), compared with an average clutch size of  $7.9 \pm 1.4$  SD for a monogamous female ( $n = 1017$ ) in the population. Only 1 of the 26 nests of these polyandrous females failed completely because it was depredated (a nest of a primary male). This meant that each polyandrous female fledged on average  $10.8 \pm 1.6$  SD nestlings, which was almost double the  $5.5 \pm 2.2$  fledged by monogamous females in the long-term data over 9 years for the population ( $t$ -test:  $t_{787} = 7.95$ ,  $P < 0.001$ ). DNA analysis of 7 polyandrous families containing 41 nestlings showed that the social father was also the genetic father of all offspring except for one nestling in the nest of a secondary male that was sired by the female’s other social mate, the primary male. In other words, 4.5% of 22 nestlings in secondary broods were sired by the primary rather than the secondary male. This particular case of extrapair paternity occurred when only 4 days separated the laying of the 2 clutches. A summary of the number of fledglings and relative effort for each sex within 3 reproductive strategies is shown in Table 1.

## DISCUSSION

Most flickers in our population were socially monogamous yet some features of the social and genetic mating system were consistent with the general idea that emancipation of females from nest building, nest guarding, and incubation facilitates alternate reproductive behaviors (Andersson 2005). Mating systems of flickers seem to stand out from those of most birds in 3 ways: 1) complete genetic monogamy among the socially monogamous pairs, 2) presence of IBP, and 3) facultative polyandry.

**Table 1**  
Reproductive payoffs for female and male northern flickers according to 3 reproductive strategies

Strategy	Nestlings per male	Nestlings per female	Male’s effort per nestling	Female’s effort per nestling
Monogamy	5.5	5.5	1 <sup>a</sup>	1 <sup>a</sup>
Polyandry	5.7 (primary) 4.6 (secondary)	10.8	1.5 <sup>b</sup>	0.5
IBP + own nest	7.3 <sup>c</sup>	7.3	0.75 <sup>d</sup>	0.75

Values in the first 2 columns are calculated average numbers of fledglings from the population at Riske Creek, British Columbia (data from 1998 to 2007). The negligible loss of paternity for secondary males (see text) is ignored here.

<sup>a</sup> For simplicity, assumes equal effort of males and females for monogamous pairs which is true during nestling provisioning but actually weighted toward males if nest excavation and incubation are included in the care.

<sup>b</sup> Females work as if they were monogamous but for twice as many nestlings, whereas males take up the extra work.

<sup>c</sup> Assuming an average of 1.8 nestlings raised in the parasitized nest + 5.5 nestlings in own nest.

<sup>d</sup> The number of nestlings is increased by about 25% without any increase in parental care.

### Genetic monogamy and paternal care

Most bird species show some extrapair paternity (EPP; Griffith 2007), but we failed to detect any in socially monogamous flicker broods despite a large sample size of 326 nestlings. Neither have we observed any anecdotal cases of attempted EPC in the field. This lack of EPP appears to be consistent among all woodpeckers studied to date, including the 2 cooperatively breeding species (Haig et al. 1994; Dickenson et al. 1995) and also the 3 socially monogamous species (Michalek and Winkler 2001; Pechacek et al. 2005). One possibility is that the genetic advantages proposed for EPC in other species (review in Griffith 2007) are simply not important among woodpeckers. However, reviews of EPP in birds have highlighted a link between genetic monogamy and high levels of paternal care (Gowaty 1996; Møller 2000; Whittingham and Dunn 2001; Arnold and Owens 2002), and so woodpeckers, with high absolute and relative investment by males (Winkler et al. 1995; Wiebe 2005), certainly follow this pattern.

There are 2 main hypotheses for why male care is associated with a lack of EPP (Table 2). Time constraints prohibiting contact with multiple females (Owens 2002) are an unlikely explanation for flickers, however, because males do not defend feeding territories (Elchuk and Wiebe 2003a). Home ranges of radio-tagged males and females could overlap those of 3–5 neighboring pairs, and foraging could occur in small, conspecific, and mixed-sex flocks without aggression (Elchuk and Wiebe 2003b). Nest densities were also relatively high, as was breeding synchrony on the study area, with about 150–200 flicker pairs laying eggs within about 2 weeks (Wiebe 2005). Therefore, many males in the population have the opportunity to interact with multiple fertile females during the laying and incubation periods. It is unknown, but probably unlikely, that males could retaliate against females (see Table 1) because there seems to be no mate guarding (Wiebe and Moore 2008). Instead, one partner usually remains at the nest cavity to guard it from competitors while the mate forages at some distance.

### Intraspecific brood parasitism

IBP is known in only 2.4% of avian species (Krüger and Brooke 2007) and has been documented once in three-toed woodpeckers (Pechacek et al. 2005) but not in the few other woodpeckers that have been studied (Haydock et al. 2001; Michalek and Winkler 2001). Flickers showed a relatively high prevalence of nests with parasitic eggs for an altricial species (up to 17% of broods), although prevalences up to about 35% occur in some well-studied precocial species such as goldeneyes and moorhens (Eadie and Fryxell 1992; McRae 1997). Aspects of the life history of flickers and some ecological correlates of breeding may aid parasitic egg laying. Although they are not colonial, flickers can nest in high densities with sometimes only 30–50 m separating nest sites (Wiebe KL, personal observation), and the excavations are obvious so that females can easily locate neighboring nests (e.g., Yom-Tov

2001). Although flickers are altricial, not precocial as are most other species that practice IBP (Rohwer and Freeman 1989), they do have large clutches (Wiebe et al. 2006) and the timing of laying in the population is fairly synchronous, both conditions which favor IBP. Flickers also have among the smallest and energetically cheapest eggs relative to body size of any bird (Wiebe 2006b), and a famous anecdote mentions the ability of a female to lay 71 eggs in 73 days when eggs were removed daily from her nest (Wiebe and Moore 2008). The ability to lay many eggs rapidly is probably an important step in the evolution of alternate reproductive strategies such as brood parasitism and polyandry (Hamilton and Orians 1965; Arnold and Owens 2002; Andersson 2005).

In the framework of hypotheses for IBP outlined by Lyon and Eadie (2008), it is important to determine the context, especially whether or not parasites have their own nest, in order to understand the mechanisms and adaptive significance. Our sampling was not complete enough to identify all the parasitic females, but even in the most conservative interpretation, the majority of flicker parasites had their own nests and mates. The fast life history of flickers, the prevalence of yearling breeders, and lack of evidence for a non-breeding floater population (Wiebe 2005) also suggest that females do not use IBP to save energy in the current breeding attempt in order to increase future fecundity. These observations rule out a best of a bad job strategy, that is, lack of nest sites, mates, or energy resources, at least as a sole explanation for IBP in flickers. Rather, laying parasitic eggs appears to be a strategy for females to simply increase the number of offspring above the number they rear themselves. Our data suggest that females first completed a clutch with their own mate and then went on to lay parasitic eggs in the nests of neighbors. In other birds, whether the female lays parasitic eggs before or after her own clutch can vary according to the ecological context of the individual (Sorenson 1993).

Some details about the mechanisms and fitness benefits of IBP remain to be elucidated in flickers. Future studies could take an optimal clutch size approach and address the marginal fitness gains from laying more eggs in one's own nest versus another's nest (Lyon 1998). The extent to which parasitic egg laying is fine-tuned to the reproductive stage of the host also needs further investigation. Some flicker nests with nestlings a week or more old also contained unhatched eggs with small, yet alive, embryos (personal observation). Presumably, these were parasitic eggs that were laid after incubation had already begun in the host clutch suggesting that parasitic egg laying was not always especially fine-tuned (see Lyon 2003).

### Social polyandry

A third remarkable aspect of the breeding system of flickers is classical polyandry, which is found in only about 2% of avian species (Hartley and Royle 2007). Up to 5% of flickers were polyandrous compared with the 7.6% of three-toed

**Table 2**

**Summary of hypotheses for why parental care by males is associated with a lack of extrapair paternity**

Hypothesis	Source	Idea	Applies to flickers?
Trade-off	Ketterson and Nolan (1994)	Time constraints imposed by parental care limit search for more mates	No
		Prolactin (parental care hormone) limits testosterone (advertisement and mate searching)	Unknown
Female constraint	Gowaty (1996)	Males retaliate with reduced care if females seek EPCs	Monitoring by males seems unlikely

woodpeckers (Pechacek et al. 2006) and 8.5% of lesser spotted woodpeckers (Wiktander et al. 2000). Polyandry in flickers seemed to be opportunistic because it occurred when a male either lost a mate early in the season or failed to attract one in the first place. Trios usually involved nearest neighbors, but one female flicker traveled 1.1 km between her 2 males, which is similar to a distance of 1.23 km reported for a polyandrous three-toed woodpecker (Pechacek et al. 2006). However, because neither sex defends feeding territories, polyandrous flickers were not "polyterritorial" in the sense that polygynous male passerines may be (Slagsvold and Lifjeld 1988). Furthermore, females were never observed calling or defending 2 nest cavities in spring with the apparent intention of defending 2 mates. Rather, they responded to the calls and displays of unpaired males.

The reproductive payoffs to polyandrous females were considerable (rearing nearly twice as many offspring as monogamous females), but it appeared that the secondary males only engaged in polyandry to "make the best of a bad job." This is in contrast to the findings of Pechacek et al. (2006) who suggested that females tried to salvage a failed or failing reproductive attempt. We found that polyandrous females were, on average, older and more experienced breeders than monogamous females, and because pairing is assortative by age (Wiebe KL, unpublished data), their primary males also tended to match them in age and experience. In contrast, secondary males were more often yearling breeders, which may explain their difficulty in retaining or attracting a monogamous partner.

Secondary males should only be willing to engage in polyandry if they are certain of paternity. In flickers, this was generally true as they usually fathered all but one of the nestlings they reared. In polyandrous shorebirds, sperm from the first male stored in the reproductive tract may fertilize eggs in clutches of secondary males (Oring et al. 1992; Dale et al. 1999). Such a risk may explain why the nest of the secondary male flicker was usually delayed by over a week so that the laying (fertile) periods of the female did not overlap between partners. Notably, it was a situation in which only 4 days separated the laying of 2 clutches where the sole case of extrapair paternity occurred in flickers. Similarly, the rare cases of paternity loss in male three-toed woodpeckers were also associated with polyandrous trios (Pechacek et al. 2005). Thus, a small risk of paternity loss in flickers may result from residual sperm in the female's reproductive tract, but field observations are needed to elucidate all interactions and timing of copulations within polyandrous trios.

Quantitative data on the division of parental effort in polyandrous trios are still scant, but it is clear that females contributed to incubation at both nests because hatching is severely compromised if there is no contribution by a female (Wiebe 2005). Nevertheless, females incubated less at the nest of the secondary male (Wiebe 2008). Polyandrous females also provisioned nestlings at both nests although they only divided their effort and did not increase their total provisioning rate (flickers: Wiebe 2005; three-toed woodpeckers: Pechacek et al. 2006). Nests of polyandrous flicker females therefore seem to have high success because males completely compensate for the reduced contribution of females (Wiebe 2005).

Polyandry is the most profitable strategy for females but the least profitable for males (Table 1), similar to the well-known situation in dunlocks *Prunella modularis* with a flexible breeding system (Davies and Houston 1986). Although primary flicker males are almost certainly aware of their secondary neighbors, they do not retaliate by reducing care to their own broods. In contrast to polyandry, IBP is equally beneficial for both sexes of a pair. The relatively high frequency of IBP should lead to selection for intense nest guarding to prevent parasitism of one's own nest. In turn, this constrains mate

guarding by males. It thus remains puzzling why female flickers appear not to engage in EPCs although they have ample opportunity.

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