



# Reply to Jan T. Lifjeld et al.: Female agency and fitness benefits of mixed-paternity broods remain

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In their commentary on Krams et al. (1), Lifjeld and Slagsvold (2) argue that there may be two reasons for observing mixed paternity in broods of pied flycatchers (*Ficedula hypoleuca*): 1) females mate with males other than their social mate or 2) females switch from being secondary mates of polyterritorial males to pairing with another male within the 2 to 3 d of their fertile period. The first instance will fall within the concept of extra-pair mating, while the latter may be categorized as sequential monogamy. We argue that this strict categorization of dynamic mating behaviors may restrict our understanding, emphasizing male-male competition at the expense of adaptive female behavior. In fact, theory predicts that paternity in a neighboring nest incentivizes males to defend against nest predators (3), as demonstrated in our experiments (1), and that females benefit irrespective of the sequence of pair bonding and copulatory events.

The distance between nest-box triplets in our experiment was relatively short, 125 m on average. Nests defended by polyterritorial males are typically much further apart [as also stated by Lifjeld and Slagsvold (2)]. Males may benefit from defending a second territory at some distance, as this may reduce the risk of instigating conflicts with their primary female. We did not observe territorial behavior at more than one nest within our nest-box triplets and therefore consider it unlikely for these males to have a secondary female nearby.

Lifjeld and Slagsvold (2) suggest that if mixed paternity is caused by females being “taken over by another male” then females have little or no agency as matters are settled in male mating competition and territorial disputes. They claim that investment in secondary females is no news—although socially polygamous males generally invest little in distant secondary nests after the female starts incubating (4). This may hence be short of an optimal situation for females. A secondary female may

therefore benefit from soliciting help and accepting mating and territorial intrusion from a second male.

When the choice to pair with a dominant male is not available to a female, pairing with a less-profitable male in the vicinity of a dominant territory holder may be beneficial. In the lazuli buntings (*Passerina amoena*), territorial adult males socially engineer their local neighborhood (5). They show low aggression toward dull colored males but do not allow bright males nearby. For a dull male, this comes at a cost of the dominant male siring extra-pair offspring in his nest, but this can still be a beneficial strategy (5). Choosing a nest site close to an established territorial male may represent an even greater benefit to females.

Although circumstances vary, females may obtain direct benefits from several males via strategic nesting site placement and mating decisions, thus alleviating fitness detriments from suboptimal pairing. Whether females do so through extra-pair copulation or sequential monogamy does not invalidate their agency, nor does it change the fitness benefits received.

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