

Absence of strict monogamy in the Eurasian jackdaw, *Coloeus monedula*

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Abstract The Eurasian Jackdaw is thought to be archetypically monogamous, but recent tagging research uncovered extra-pair copulations in the species. Here we examined extra-pair paternity (genetic monogamy) in Eurasian jackdaws breeding in the Judean Hills, Israel, at the global edge of the species range, using a set of highly polymorphic molecular microsatellites. We found roughly a sixth of nests sampled showed deviations from monogamy, more than previously found in DNA fingerprinting studies of jackdaws, suggesting a mixed mating strategy in this population. These findings support the trend of extra-pair paternity in avian species, even when social monogamy remains the rule, and highlight the importance of continued study of species throughout their geographical range.

Keywords extra-pair paternity; jackdaw; mating behavior; microsatellites; monogamy

Introduction

Mating behaviors can vary considerably among individuals, populations, and species and have both short and long-term fitness implications (Clutton-Brock & Harvey, 1978; Griffith, Owens, & Thuman, 2002; Westneat & Stewart, 2003). Monogamy was traditionally assumed to be the prevailing breeding strategy in birds (Lack, 1968), but with the onset of advancing molecular technologies, sexual monogamy is now known to be the exception rather than the rule (e.g., Griffith et al., 2002; Westneat & Stewart, 2003). Such findings highlight the disparity between observations of social monogamy and genetic studies (Birkhead & Møller, 1995; Dunn & Lifjeld, 1994) and underscore the importance of reassessing mating behaviors, even in the most archetypically monogamous species. Moreover, populations of species with broad distribution ranges or different species ecologies may exhibit different mating strategies, emphasizing the importance of continually broadening focal ranges of study (e.g., Hoset et al., 2014; Minias, Wojczulanis-Jakubas, Rutkowski, Kaczmarek, & Janiszewski, 2016; Westneat & Sherman, 1997).

The Eurasian jackdaw, *Coloeus monedula*, is a semi-colonial bird famous for its linear social hierarchy and enduring pair-bonds (Cramp, Perrins, & Brooks, 1994; Lorenz, 1952). In 1998, with the increased accessibility of molecular technologies, Liebers and Peters (1998) found a single extra-pair young in a total of 15 nests (6.67% extra-pair paternity, EPP) sampled in eastern Germany using genetic fingerprinting. A similar study in the UK by Henderson et al. (2000) coincided with previous knowledge of jackdaw mating behavior, finding strict genetic monogamy

(0% EPP). More recently, a study in southern Germany using bio-loggers identified substantial deviations from sexual monogamy: two of the four males studied exhibited extra-pair copulations (EPC; 16.67% of copulations, $n = 18$; Gill, 2016). The method of DNA fingerprinting has fallen out of use (Schlötterer, 2004), and EPC may not accurately predict EPP (Dunn & Lifjeld, 1994); thus, we examined genetic mating behaviors in the species using more sensitive molecular methods (Schlötterer, 2004).

Methods

Study species, site, and sampling

The study described here was performed as part of a comprehensive study on social dynamics and movement ecology of Eurasian jackdaws (Chen, 2018) in the Judean Plains (31°39'35"N 34°52'47"E), in central Israel. In this region, at the southern edge of the species' breeding range, jackdaws have adopted ancient man-dug caves as nesting colonies. Historic (Mayrose, Hatzofe, Shifman, & Tzuk-Ramon, 2002) and recent (2013–2016, Chen, 2018) direct counts of group sizes during nesting ($n = 35$), foraging ($n = 32$), and roosting ($n = 7$) led us to estimate the overall population size in the study area as roughly 3,000 individuals; however, jackdaw group sizes fluctuated on a diel cycle by two orders of magnitude between roost sites (1324 ± 368), foraging sites (125 ± 22), and nest sites (53 ± 4).

As part of the comprehensive study, an artificial colony containing 20 nest boxes was erected, and each nest box was monitored with a remotely operated infrared camera. Nine of the fourteen nests included in the EPP study belonged to

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the experimental nesting colony, containing ca. 27 breeding pairs throughout the study period; the other five nests were inside nest boxes scattered at the edges of agricultural plots in the study area (initially intended for barn owls). Pairs typically did not reuse nests from year to year. Overall, jackdaws were captured from 20.5.2012–27.9.2015 inside nest boxes or using a walk-in trap or mist nets. A total of 305 individuals were captured, banded with unique color combinations, measured, and DNA-sampled (blood and/or feathers). Of those, 15 adults ($n_{\text{male}} = 8$, $n_{\text{female}} = 7$) successfully nested in the artificial colony: 14 were trapped inside a nest box (during nestling rearing period) and one pre-banded individual was seen entering a nest box during the breeding season. When possible, genetic samples were collected from all offspring in boxes with breeding attempts, ($n_{\text{nests}} = 14$, $n_{\text{offspring}} = 30$), including dead nestlings found in the nest.

Molecular methods

DNA was extracted from samples using a standard NaOH extraction procedure (Ong & Vellayan, 2008; Zhang, Tiersch, & Cooper, 1994). We then amplified nine microsatellites (PPY004, PPY005, PPY008, PPY013, PPY014, PPY015, ck1B5D, ck4A3G, ck5A4B), previously shown to be highly polymorphic in various populations of this species (Fulgione, Ripa, De Luca, & Milone, 2003; Wenzel, Webster, Segelbacher, Reid, & Piertney, 2011) as well as in our population (Chen, 2018). Thermocycler conditions were as follows: 5 min: 95°C; 20 touchdown cycles of 30 sec: 95°C, 30 sec: 65°C (down to 55°C), and 45 sec: 72°C; 20 cycles of 30 sec: 95°C, 30 sec: 55°C, and 45 sec: 72°C; and 5 min: 72°C. PCR amplification was repeated until each individual had no more than one missing locus (typing rate of 0.983, $n = 45$). Microsatellite characteristics are described in the supplemental material.

Following PCR, genotyping was performed using an ABI PRISM™ 3730xl DNA Analyzer by the Hebrew University Center for Genomic Technologies (Jerusalem, Israel). We called alleles using *GeneMapper 4.0* software and then constructed an allele frequency database using all parental genotypes ($n = 15$) and one offspring per nest for nests in which no parents were trapped ($n = 5$; see Turjeman et al., 2016 for explanation of method). Additionally, genotypes of adults trapped in other nest boxes for which there were no offspring data ($n = 18$) were also included in the allele frequency database to increase robustness. We performed tests of Hardy-Weinberg equilibrium (HWE), inbreeding, and marker suitability. See supplementary table S1 for methods and marker summary statistics.

Relatedness analysis

After confirming marker suitability, we analyzed parentage and sib-ship using the two-program method from Turjeman et al. (2016). Sib-ship analysis has become relatively common in cases where it is difficult to obtain parental DNA, and is thought to perform equally well when markers are

reasonably sensitive (Jones & Wang, 2010; Waits, Luikart, & Taberlet, 2001). Briefly, *ML Relate* (Kalinowski, Wagner, & Taper, 2006) was used for pairwise hypothesis testing of most likely relationships (parent-offspring or full-sib, respectively, vs an alternate relationship), and *Colony2* (v.2.0.6.5; Jones & Wang, 2010), a Bayesian family-wide modeling program, was used to construct maximum likelihood based full-families (either with all relevant siblings or with siblings and parent(s)). For both programs, we selected the option of taking typing errors or null alleles into account when calculating relatedness probabilities (Kalinowski & Taper, 2006; Wang, 2004). Program assignments were compared, and congruent outputs were accepted. Specific *Colony2* parameters are given in the supplementary material.

Results

We successfully extracted DNA from and genotyped all samples collected. Two loci showed evidence of null alleles, which were accounted for when implementing both relatedness methods (above). One of these loci also showed deviations from HWE; however, these may be explained by the presence of null alleles (see supplementary table S1). Accordingly, all analyses were also run without this marker, and outputs supported the results presented herein, though their statistical significance was lower. Minor, statistically significant inbreeding was found (FIS = 0.057; permutation test, $n = 10,000$; p -value = 0.030), but such low FIS likely does not support biologically relevant inbreeding (Wright, 1949, 1965; see supplementary table S1 for measures of expected and observed heterozygosity). Probability of identity and sibling probability of identity were $2.10E-9$ and $5.07E-4$ respectively, suggesting that while including parental genotypes can strengthen findings, markers are suitably sensitive for sibship analyses (0.001–0.0001 suggested for individual-based genetic studies, Waits et al., 2001), and inclusion of nests without parental DNA should not bias results.

We found high agreement between both programs for 13 of the 14 nests tested (Table 1). For 11 of these 13 nests (84.6%), there was no support for EPP. The two remaining nests (15.4%) showed absence of full sibship: one nest (ID 70) had EPP and the other (ID 36) had either EPP or conspecific brood parasitism (CBP). For nest 70, offspring were conclusively found to be half-siblings (one full sibling pair and one half sibling): *Colony2* found absence of full sibship (it could not detect presence of half-siblings as “male and female monogamy” priors were used in this model, so the option of half-sibling vs. no relation was not tested). *ML-Relate* ruled out unrelatedness for this individual with statistical significance, and thus we concluded a half-sibling relationship and EPP. In the other nest (ID 36), while there was statistically significant support for the absence of full sibship for one individual, the programs could not reliably differentiate between half sibling and unrelated relationships (though half sibship had slightly more support).

Table 1. Nest composition and relatedness results from *ML-Relate* and *Colony2*. *ML-Relate* was used to compare pairs of putative relationships (e.g. parent-offspring vs unrelated or full-sib vs half-sib). *Colony2* was used to reconstruct full families including all siblings, and, when relevant, parents. “Monogamous” suggests a family where all offspring are related in a full-sibling manner and/or the social parent(s) are also genetic parent(s). “Non-monogamous” suggests extra-pair paternity (half-sibship) or conspecific brood parasitism (unrelated).

Nest ID	Year	Parental Sample	No. Offspring	<i>ML-Relate</i>	<i>Colony2</i>	Agreement
4	2014	both	1	monogamous	monogamous	yes
4	2015	both	4	_*	_**	-
5	2015	both	3	monogamous	monogamous	yes
7	2015	both	1	monogamous	monogamous	yes
10	2015	paternal	2	monogamous	monogamous	yes
11	2014	both	1	monogamous	monogamous	yes
11	2015	both	1	monogamous	monogamous	yes
15	2014	paternal	1	monogamous	monogamous	yes
18	2015	maternal	3	monogamous	monogamous	yes
26	2012	-	3	monogamous	monogamous	yes
37	2012	-	3***	not monogamous	not monogamous	yes
68	2012	-	2	monogamous	monogamous	yes
70	2012	-	3	not monogamous	not monogamous	yes
A	2012	-	2	monogamous	monogamous	yes

* *ML-Relate* showed internal conflict between parentage analysis and sibship analysis. ** *Colony2* showed internal conflict finding only a very low probability of full-sibship for some of the sibling-sibling relationships. *** Two nestlings could not be sampled, but because even in the partial sampling, we found deviations from monogamy, we include this nest in our study (no risk of type II error).

For the last nest (ID 4, year 2015), programs did not converge. This nest had statistically significant deviations from monogamy in *ML-Relate*, with all four offspring belonging to the same mother but the father siring only two nestlings; sib-ship analyses supported this finding. Conversely, *Colony2* classified the nest as a monogamous family. Because of these confounding assignments, we could not reach a conclusion regarding mating behavior in this case.

Discussion

Examination of Eurasian jackdaw breeding behavior using microsatellite markers exposed EPP concordant with the presence of EPCs found by a recent study (Gill, 2016). Our sample size is similar to those of previous EPP studies (Henderson et al., 2000; Liebers & Peters, 1998), and detection of deviations from monogamy, even with a small sample size, suggests that these events are not rare. The Israeli breeding population studied herein is located at the southern periphery of the species' global range and has undergone rapid expansion over the past few decades (Shirihai, 1996), whereas the populations studied previously are long-established ones located more centrally in the species' range (Henderson et al., 2000; Liebers & Peters, 1998). Thus, while EPP may have been under-detected due to methodological short-comings, EPP may also be a strategy only employed more recently or by a portion of Eurasian jackdaw populations.

It is not surprising that the jackdaw, like many other socially monogamous species, deviates from strict monogamy as the behavior can have fitness benefits (Griffith et al., 2002; Westneat & Stewart, 2003). Furthermore, EPP does not preclude social monogamy or the benefits associated with long-term social pair bonds (Dubois & Cézilly, 2002; Griffith et al., 2002; Kvarnemo, 2018) because extra-pair

copulations are often hidden from the social mate (Dunn & Lifjeld, 1994).

Because the jackdaw is a colonial breeder (Cramp et al., 1994; Lorenz, 1952), proximity to other breeding birds may also provide ample opportunities for extra-pair copulations (e.g., de Castro e Souza, Del Lama, & Miño, 2013; Martínez, de Aranzamendi, Masello, & Bucher, 2013; Miño et al., 2011; Miño, Sawyer, Benjamin, & Del Lama, 2009). Further, high nest-site density, like in our study, may be positively correlated with EPP (Griffith et al., 2002; Westneat & Sherman, 1997; Westneat & Stewart, 2003; but see Minias et al., 2016; Turjeman et al., 2016). As jackdaw colony density varies throughout the breeding range, differential rates of EPP may be expected.

Our study adds support that this species is not genetically monogamous and can help to elucidate the extent of EPP across the species' range. Many factors can affect EPP rates including sample size, range coverage, and methods (molecular and computational), underlying the importance of continued study of both model and non-model species. Furthermore, quickly expanding species, like the Eurasian jackdaw, with small founder populations at the fronts of expansion, may employ different mating strategies than more central or well-established populations; founder populations have low genetic variation and are thought to exhibit reduced EPP compared to those that can benefit from a more varied gene pool and the possibility of improving offspring genetic quality (Griffith, 2000; Petrie & Lipsitch, 1994). This may suggest that re-examination of this behavior in established breeding populations could uncover even higher incidence rates. To elicit how various factors affect jackdaw breeding behavior, we suggest that EPP warrants long-term investigation, both in long-established central-range populations and recently-established peripheral ones. Such a longitudinal study can help to tease apart confounding drivers of EPP.

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Permits

All applicable institutional and/or national guidelines for the care and use of animals were followed: Permits were acquired for all sampling and sampling was performed in accordance with the ethical guidelines as approved by the Israel Nature and National Parks Protection Authority (permits: 2012/38421, 2013/39191, 2014/40624).

Conflicts of interests

The authors declare that they have no competing interests.

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