INTRODUCTION

Passerines are predominantly characterized by social monogamy (Lack, 1968) with posthatching biparental care (Cockburn, 2006), but there are no strict rules of thumb for living according to a certain kind of mating and parental care system (Bennett & Owens, 2002). Hence, there are species where the above systems vary within populations depending on local environmental or social conditions, as in the evergreen case of dunnocks (Prunella modularis, Davies & Lundberg, 1984) or in penduline tits (Remiz pendulinus, Persson & Öhrström, 1989). In spite of this plasticity, cooperative breeding strategies are apparently quite rare among passerines (Brown, 2014; Ligon, 1999). In these cases, a single brood is cared for by at least two individuals belonging to the same
opportunistic cooperative polygyny or communal laying has been observed in a few species, for example, in pied flycatchers (Ficedula hypoleuca, Lifjeld et al., 1992), common starlings (Sturnus vulgaris, Eens & Pintxen, 1993), black-browed reed warblers (Acrocephalus bistrigiceps, Hamao & Ueda, 1998), whereas a helper-at-the-nest system is conventional in superb fairywrens (Malurus cyaneus, Dunn et al., 1995) and Seychelles warblers (Acrocephalus sechellensis, Richardson et al., 2002). In some of these systems, there may be individuals in a “family unit” that help raise the offspring of others, performing alloparental care.

Breeding and parental roles in one of the most investigated model species in behavioral ecology, the collared flycatcher (Ficedula albicollis), have seemed to be only moderately plastic. We have been studying a population since the early 1980s (see below for details). At our study site, these birds arrive from spring migration in late April. During a breeding season, females lay one clutch with 5–8 eggs incubated exclusively by them, but nestlings are fed by females and males together. In our study population, only 5.7% of males become socially polygynous during their lifetime (Herényi et al., 2014), based on capture data. Due to female aggression (Hegeyi et al., 2007), polyterritoriality typically occurs in polygynous males with a territory distance of 15–300 m. In contrast to the very low rate of social polygyny, experimental mating restriction in combination with sperm counting on the perivitelline layer (Michl et al., 2002) and microsatellite-based paternity analyses (Rosivall et al., 2009) have revealed a high rate of genetic promiscuity due to extrapair (EP) copulations. Under natural conditions, 56% of the broods contained offspring from EP males, and approx. 21% of the nestlings were sired by EP father (Rosivall et al., 2009). Studies of other populations of this species have clearly shown the absence of intraspecific brood parasitism (Krist et al., 2005; Sheldon & Ellerigen, 1996). Löhrl (1957) described that nest adoption by a male could occur at nests which the father had deserted, and he took an anecdotal note that once he observed a nest with one female and two males. In addition to the above patterns, we now provide detailed field and genetic data on the occurrence of one kind of cooperative breeding with three carers (two females and one male) and alloparental care in this species.

2 | MATERIALS AND METHODS

We collected data from a collared flycatcher population breeding in artificial nest box plots located in the Pilis–Visegrádi Mountains (Duna–Ipoly National Park, Hungary, 47°43′ N, 19°01′ E), in 2015 and 2016. The study site is covered by deciduous woodland dominated by oaks and consisted of ca. 750 artificial nest boxes (n = 747 in 2015, n = 707 in 2016), which are used principally by collared flycatchers, great tits, and blue tits (pooling the 2 years, there were 534 collared flycatcher nesting events if including failed ones too). Nest box plots were checked at every 5 days in order to determine laying date, clutch size, and hatching date. During the breeding seasons of 2015 and 2016, in a brood-size manipulation experiment, we created trios (n = 10 in 2015, n = 9 in 2016) of certain nests and partially cross-fostered nestlings between two nests within trios (transferring 2 nestlings from nest A to nest B, and 4 nestlings from B to A; C was nonmanipulated), when the older nestlings of a nest were 2 days old. In our population, clutches generally contain asynchronously hatched nestlings: Usually, at least half of the nestlings hatch on the first day, and the others hatch on the next day. Rarely, 2-day asynchrony may occur between the oldest and the youngest nestlings, but these clutches could not be included into our brood-size manipulation experiment, according to our protocol.

We conducted video recordings to collect data on nestling feeding rates (number of visits with food delivery per hour) at the nests of the trios when the older chicks in each nest were 10 days old (n = 29 in 2015, n = 26 in 2016). As nestlings were of the same age within a trio, video recordings of nests of a trio were conducted on the same day and hour. We performed the video recordings between 0900 and 1830, mostly during the first half of the day. Earlier it had been described for this study population that no difference exists between morning and afternoon feeding rates of parents (Kiss et al., 2013). We avoided recording in midday hours (1200–1400). Recording length was a few minutes more than 1 hr, and we analyzed 60 min of the footages, without the first few 10–15 min. For detailed methods and results, see Laczi et al., 2017. Additionally, for another experiment, video recordings were conducted (with 2-hr footages) at other nests too with 10-day-old offspring (n = 17 in 2015, n = 19 in 2016, see details in Szász et al., 2019).

Just after recording, we set up a spring trap at each nest box. According to our general protocol, we finish trapping after we catch a female and a male bird (supposing that they are the only parents) or after a maximum of 1.5 hr. We ringed the adult birds if they were not ringed formerly. Blood samples (ca. 10–15 μl) were collected from the wing vein of nestlings and the captured parents for the purpose of paternity analysis. Blood samples were stored in absolute ethanol and kept at −20°C until the analyses. DNA was extracted using an ammonium-acetate method (Nicholls et al., 2000). We assessed maternity and paternity by using ten polymorphic microsatellite loci (FhU2, FhU4, Fhy405, Fhy407, Fhy428, Fhy429, Fhy431, Fhy452, Cu4, Pdou5 (Ellergren, 1992; Primmer et al., 1996; Griffith et al., 1999; Gibbs et al., 1999; Leder et al., 2008)). All PCRs were run using the Type-it microsatellite PCR kit (QIAGEN) and the following thermal profile: 95°C for 5 min, 30 cycles of 95°C for 30 s, 56°C for 30 s, 72°C for 30 s, and a final step of 60°C for 30 min.

PCR products were analyzed on ABI 3130xl Genetic Analyzer (Applied Biosystems, Foster City, USA). We used the internal size standard GeneScan 600 LIZ (Applied Biosystems, Foster City, USA). Fragment lengths were determined using Peak Scanner Software v1.0 (Applied Biosystems, Foster City, USA).

Maternity and paternity testing of the nestlings was performed manually by the exclusion method (Jones & Ardren, 2003). Assuming Mendelian inheritance, offspring were classified as not related to their putative parents if they did not match at one or more loci.
3 | RESULTS

Breeding data indicated that the first egg in the nest box in question was laid on 27 April 2016. On 03 May, we found five eggs, which suggested that the last egg was laid on 01 May as females typically lay one egg on each consecutive day. On 07 May, the nest contained seven eggs. This means that there was a gap of a few days in egg laying, with a restart between 04 and 06 May. On May 20, we found six nestlings: three of them were 1 day old and the others were 2 days old, based on their appearances and body masses. We did not find any further propagule, indicating that one egg or hatching had vanished. This missing offspring could not be sampled for DNA later.

The nest was subject to a cross-fostering experiment, and it was enlarged by three nestlings (from six to nine). Processing the video records, we observed that two females, which were distinguished by their different plumage patterns, and one male (Figure 1.) were visiting the nest regularly. During the 1-hr record we analyzed, we found that female (A) brought prey items 23 times, female (B) 15 times, and the male 28 times. The mean feeding rate of the other males was as follows: 19.31/22.13/32.81 in reduced/control/enlarged broods, for other females, it was 17.50/24.75/34.31, respectively (see Laczi et al., 2017). The two females attending this brood were standing together inside the nest box three times.

The genetic analysis of the six offspring that remained and the captured adults suggests that the captured female was related to none of the nestlings. On each locus, we could identify two alleles, either of which was present in every offspring. The most likely scenario is therefore that all nestlings shared the same mother (which we did not catch), even though we cannot completely exclude the existence of multiple mothers. The captured male sired only one progeny, and, assuming one mother, the other nestlings were sired by at least two other males. The captured female and male were unrelated or very distantly related to each other. The alleles of captured female, male, and offspring together with the assumed alleles of the putative mother are indicated in Table 1. Figure 2 shows a graphical representation of this unusual family setup.

4 | DISCUSSION

In our case study, we detected cooperative parental care with two females and one male in the collared flycatcher, a species previously described as showing social monogamy (or polyterritorial polygyny) and biparental care. Neither of the two females nor the male that appeared on the video record seemed to be a prospector, because all of them showed active parental behavior in terms of providing nourishment and taking out nestling feces several times, and none of these are attributes of prospective behavior in this species (Doligez et al., 2004). Feeding rate of the male was similar to the mean feeding rate of the other males that raised enlarged broods. In contrast, neither of the females showed the expected elevated feeding intensity. However, the two females together fed at a total rate (38) similar to the mean feeding rate of socially monogamous females of enlarged broods. It is clear that in spite of the presence of two females’ assistance, the male’s feeding intensity did not reduce, as well as from this triparental care the nestlings did not gain extra advantages at least with regard to their mean body mass at 12 days of age, close to fledging (12.4 g; in other enlarged broods: 12.7 g, Laczi et al., 2017).

The original nest contained eggs that had been laid in two separate turns. Based on this and the behavioral observations, one would conceive that the parenting mothers shared the genetic maternity too. If we take a look at the microsatellite patterns, we can draw quite a different conclusion, namely that there was probably only one genetic mother. This is also supported by the highly synchronous hatching (at most 1-day difference between the older and the

**FIGURE 1** Cooperative parental care at a collared flycatcher nest. Each of the parents delivered food for the nestlings and took out the nestling-feces
# Genetic profiles of the captured female, male, the nestlings, and the potential profile of the putative mother at ten microsatellite loci

## Table 1

| Microsatellite | Captured female | Captured male | Nestling 1 | Nestling 2 | Nestling 3 | Nestling 4 | Nestling 5 | Nestling 6 | Putative mother |
|---------------|-----------------|---------------|------------|------------|------------|------------|------------|------------|----------------|
| FN1           | 139 149 167     | 139 149 167   | 139 149    | 139 149 167| 139 149    | 139 149    | 139 149    | 139 149    | 139 149       |
| FN2           | a 149 b 220     | a 149 b 220   | a 149      | a 149 b 220| a 149 b    | a 149 b    | a 149 b    | a 149 b    | a 149 b       |
| FN3           | 167 220 222     | 167 220 222   | 167 222    | 167 220 222| 167 220    | 167 220    | 167 220    | 167 220    | 167 220       |
| FN4           | 220 222 224     | 220 222 224   | 224 222    | 220 222 224| 220 222    | 220 222    | 220 222    | 220 222    | 220 222       |
| FN5           | 222 224 226     | 222 224 226   | 226 224    | 222 224 226| 222 224    | 222 224    | 222 224    | 222 224    | 222 224       |
| FN6           | 224 226 228     | 224 226 228   | 228 226    | 224 226 228| 224 226    | 224 226    | 224 226    | 224 226    | 224 226       |
| FN7           | 226 228 230     | 226 228 230   | 230 228    | 226 228 230| 226 228    | 226 228    | 226 228    | 226 228    | 226 228       |
| FN8           | 228 230 232     | 228 230 232   | 232 230    | 228 230 232| 228 230    | 228 230    | 228 230    | 228 230    | 228 230       |
| FN9           | 230 232 234     | 230 232 234   | 234 232    | 230 232 234| 230 232    | 230 232    | 230 232    | 230 232    | 230 232       |
| FN10          | 232 234 236     | 232 234 236   | 236 234    | 232 234 236| 232 234    | 232 234    | 232 234    | 232 234    | 232 234       |

Note: The alleles were identified by capillary gel electrophoresis. Only one nestling was sired by the captured male (nesting 1). Alleles that could be transmitted by the male are indicated in bold. A13 loci are marked with asterisks for the putative mother.

With regard to the male, it has been shown in another collared flycatcher population that socially monogamous males adjust their provisioning rates according to their assumed share of paternity (Sheldon & Ellegren, 1998). We cannot completely exclude that the usually representative 1-hr sampling of parental care may have accidentally fallen on an unusual period at this particular nest. However, if the recorded care pattern is representative, we would speculate based on the feeding rate of the captured male that it was the genetic father of the majority of the original nestlings. By contrast, DNA analyses have shown us that most of the offspring were not sired by the captured male. In socially monogamous bird species, males that engage in extrapair copulations usually do not care for their offspring sired in other than their social mate’s nest (Birkhead & Møller, 1992). In addition, when we estimated the height of the forehead patch of the male on the video record (using box entrance diameter as reference by Scanning Probe Image Processor, Image Metrology, Inc.), it was almost identical to the measured forehead patch size of the captured male (9.0 and 9.1 mm, respectively). Thus, we supposed that the captured male was identical to the one observed on the video record. If so, based on the genetic data, he must have been cuckolded by other males. In a socially monogamous system with extrapairs, it is not a curiosity if a male raises a nest with only one or even no own progeny (Gibbs et al., 1990; Kempenaers et al., 2001).
rearrange the general mating and parental care scenario among a subset of individuals within a population. For example, in the socially monogamous blue tit (*Cyanistes caeruleus*), unbalanced sex ratio of reproductive birds, for example, the death of a neighboring parental male, may give rise to replacement polygyny (Kempenaers, 1994). In the same species, failed breeding could cause the type of nest adoption (Santema & Kempenaers, 2021) which has also been described in the collared flycatcher (*Löhrl*, 1957) (see Introduction). Mating and parental care relationships can be flexibly fine-tuned in accordance with availability of either sex not only in birds, but also in mammals, as described, for example, in the wild boar (*Sus scrofa*), where hunting on males reduced the degree of polygyny (Poteaux et al., 2009).

Our observations convey a warning message for investigations of reproductive behavioral patterns. After capturing a female and a male of a species that is expected to be socially monogamous and biparental, it may not be justified to automatically suppose that they are the mates of each other, and they are the parents or the only parents. As another study on the pied flycatcher suggested, applying various methods together (i.e., genetic and behavioral) may be required to dig out the actual truth in some uncertain cases (Grinkov et al., 2018), thereby avoiding the misinterpretation caused by using one method only. Hence, a holistic approach can be highly beneficial when estimating actual mating preferences and realized reproductive success.

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**CONFLICT OF INTEREST**

The authors declare no competing interest.

**AUTHOR CONTRIBUTIONS**

Miklós Laczi: Conceptualization (lead); data curation (lead); investigation (equal); visualization (lead); writing—original draft (lead); writing—review and editing (lead). Renáta Kopena: Conceptualization (equal); formal analysis (equal); investigation (equal); visualization (equal); writing—review and editing (equal). Fanni Sarkadi: Conceptualization (equal); formal analysis (equal); investigation (equal); visualization (equal); writing—review and editing (equal). Dóra Kötél: Data curation (equal); investigation (equal); visualization (equal); writing—review and editing (equal). János Török: Conceptualization (equal); supervision (equal); visualization (equal); writing—review and editing (equal). Balázs Rosivall: Conceptualization (equal); formal analysis (equal); funding acquisition (equal); resources (equal); visualization (equal); writing—review and editing (equal). Gergely Hegyi: Conceptualization (equal); funding acquisition (lead); investigation (equal); project administration (equal); resources (equal); supervision (equal); visualization (equal); writing—review and editing (equal).
DATA AVAILABILITY STATEMENT

All data are included in the publication.

ORCID

Miklós Laczi https://orcid.org/0000-0001-9235-2553
Fanni Sarkadi https://orcid.org/0000-0001-8732-972X
Gergely Hegyi https://orcid.org/0000-0002-4906-3550

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