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SHORT COMMUNICATION

Genetic relatedness in Monk Parakeet breeding trios

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Abstract Monk Parakeets (*Myiopsitta monachus*) are cooperative breeders, which means that one adult helps the breeding pair (trios). We found a breeding trio composed of two males and one female in a single breeding chamber of a two-chamber compound nest. Males were full siblings. The female was the half sibling of both males. The female and one male were genetic parents of all nestlings. The sampled parakeet population showed a higher than expected level of inbreeding. The Monk Parakeet provides an interesting model for understanding of the role and benefits of helping and extra parental behavior in cooperative breeding birds.

Keywords Argentina · Communal breeding · Helpers at the nest · Inbreeding · Invasive species · Extra pair paternity

Zusammenfassung

Genetische Verwandtschaft bei Mönchssittich-Bruttrios

Beim kooperativ brütenden Mönchssittich (*Myiopsitta monachus*) bildet ein adulter Bruthelfer mit dem Brutpaar ein Trio. Wir entdeckten ein aus zwei Männchen und einem Weibchen bestehendes brütendes Trio in einer einzelnen Brutkammer eines zweikammerigen Gemeinschaftsnestes. Die Männchen waren Vollgeschwister. Das Weibchen war ein Halbgeschwister beider Männchen. Das Weibchen und ein Männchen waren die genetischen Eltern aller Nestlinge. Die untersuchte Sittichpopulation wies einen höheren Inzuchtgrad als erwartet auf. Der Mönchssittich stellt ein interessantes Modell zum Verständnis der Rolle und der Vorteile von Bruthilfe und außerelterlichen Verhaltens bei kooperativ brütenden Vögeln dar.

Introduction

Cooperative breeding is a social system characterized by alloparental care: offspring receive care not only from their parents, but also from additional group members, often called helpers. The key concept behind cooperative breeding is the forfeiting of an individual's reproductive fitness to aid the reproductive success of others. This behaviour has posed a major problem for evolutionary biologists, and despite decades of research many questions remain unresolved (Hatchwell 2009).

The Monk Parakeet (*Myiopsitta monachus*) is a colonial breeder that builds compound stick nests with multiple individual chambers (Spreyer and Bucher 1998). In an overview of the Monk Parakeet biology, Bucher et al.

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(1991) proposed that Monk Parakeets show characteristics typical of cooperative breeders, including delayed breeding, reduced dispersal, and possibly direct helping by allofeeding.

Delayed breeding and dispersal were later confirmed by Martin and Bucher (1993) and Bucher and Aramburu (2014). Regarding helping, cases of a third adult parakeet helping the breeding pair in the wild were first reported by Eberhard (1998). Of the three cases described by Eberhard, two included one female and two males, and the remaining was composed of two females and one male. Eberhard (1998) concluded that further information about the frequency of breeding trios, and their genetic relationships would be important in testing that the Monk Parakeet mating system includes helping features. To answer this key question, we present information on the degree of genetic relatedness among trio members and their nestlings and the level of inbreeding in the Monk Parakeet populations.

Materials and methods

Genetic analyses were based on a sample of 42 adults and 154 nestlings from 28 compound nests with 37 nest chambers, collected in two nearby localities in the province of Córdoba (Argentina): Marull (31°40′S, 62°49′W) and Miramar (32°55′S, 62°40′W). Samples were collected on a single date for each site. Parakeets were captured following the same procedure described previously in Martin and Bucher (1993). Genomic DNA was extracted from blood samples and analyzed as in Martinez et al. (2013). Seven loci of microsatellites were used for relatedness and parentage analyses. Basic genetic parameters were calculated with Arlequin 3.5 (Excoffier and Lischer 2010).

Relatedness values among individuals was estimated using programs called Storm (Frasier 2008) and ML-Relate (Kalinowski et al. 2006), and kinship among individuals using ML-Relate relationships. Full-sibs and parentage of nestlings were identified in Colony 2.0.1.1 (Jones and Wang 2010) (see Martinez et al. 2013). We estimated indices of inbreeding, homozygosity by loci (HL) (Aparicio et al. 2006) and internal relatedness (IR) (Amos et al. 2001) in nestlings ($N = 154$) using Storm. Following the results from Martinez et al. (2013), individuals were classified in four categories according to the breeding relationship detected in each nest (monogamy, extra-pair paternity (EPP), monogamy-brood parasitism, and EPP-brood parasitism). HL and IR across breeding relationship categories were compared using parametric and non-parametric tests (one-way ANOVA and Kruskal–Wallis tests, respectively). Expected distribution of HL and IR values of simulated offspring under random mating were generated in Storm using the genotypes of adult individuals, from which p values for the observed values of inbreeding in the nestling data set were obtained.

Results

We found one trio and four nestlings in a single chamber of a two-chamber compound nest (see Martinez et al. 2013 for details). The trio was composed of two males (W215 and W216) and one female (W217). All of them were adults. The two adult males of the trio were full siblings ($r = 0.67$ and ML-$r = 0.57$). The female was the half sibling of both males, although relatedness was higher with the breeding male, W215. The genetic relatedness values between W215 and W217 were: $r = 0.11$ and ML-$r = 0.27$, whereas between W216 and W217 $r = 0.05$ and ML-$r = 0.13$.

One of the males (W215) and the female (W217) were the genetic parents of the four nestlings, according to COLONY, with high probability ($p = 1$). Nestlings were full siblings (COLONY's probability: $p = 1$; mean $r = 0.554$ and mean ML-$r = 0.493$).

Regarding inbreeding in the population, HL and IR values were similar across the four categories of breeding behavior (monogamy, EPP, monogamy with brood parasitism, and EPP-brood parasitism) as follows: parametric HL: $F = 0.09$, $df = 3$, $p = 0.963$; IR: $F = 0.177$, $df = 3$, $p = 0.91$) (Fig. 1). Similarly, non-parametric tests (HL: $H = 0.557$, $p = 0.906$; IR: $H = 0.272$, $p = 0.965$) did not detect significant differences in inbreeding coefficients across these categories. The observed values of inbreeding were higher and significant ($p < 0.0001$) than the expected values under random mating.

Discussion

Our observations in Córdoba confirm the widespread occurrence of trios in the Monk Parakeet population, previously mentioned by Eberhard (1998) in Entre Rios province, at about 650 km from our study site. In addition, we also found that an unknown proportion of breeding trios show a high degree of genetic relatedness between its members.

Cases of high genetic relatedness between helpers and the breeding pair as found in our study are frequent among communal breeders (Brown and Brown 1996). The fact that Monk Parakeet helpers are adult individuals suggests an active choice for associating with kin.

Occurrence of adult helpers in trios instead of juveniles of the year, as frequently seen in other communal breeders, may be explained by (a) the Monk Parakeet single and highly synchronous breeding season (Spreyer and Bucher

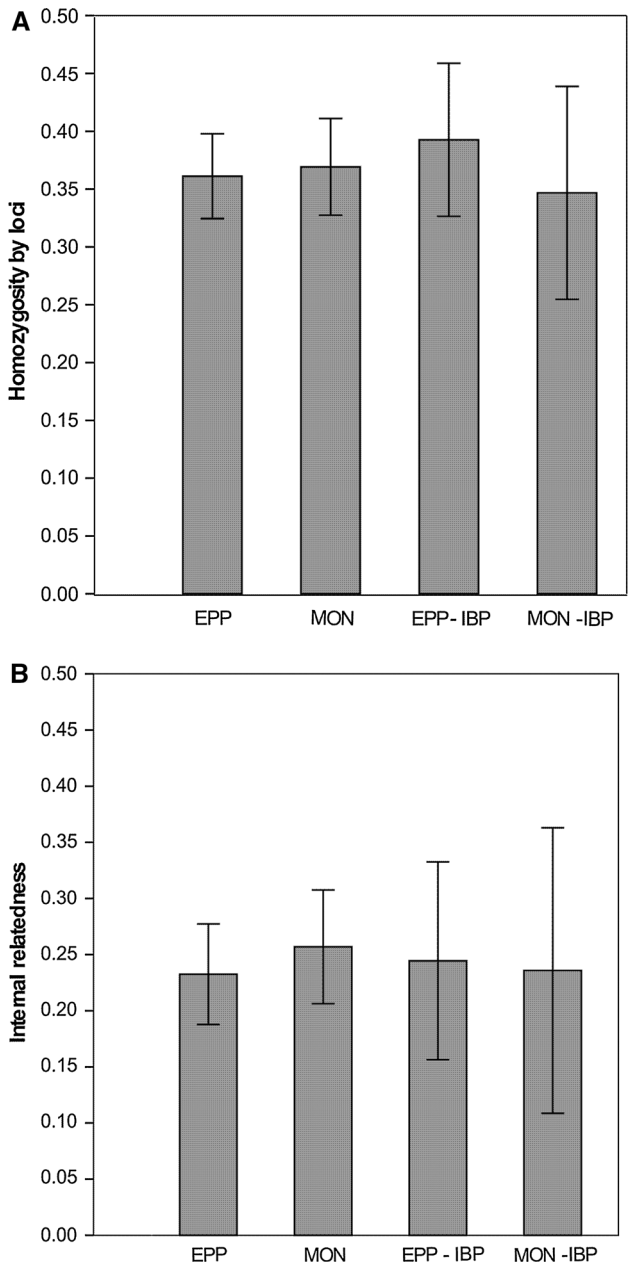

Fig. 1 Levels of homozygosity by loci (**a**) and internal relatedness (**b**) in the Monk Parakeet across the four categories of breeding behavior: *EPP* extra-pair paternity; MON, monogamy; *EPP-IBP* extra-pair paternity and intraspecific brood parasitism; and *MON-IBP* monogamy and intraspecific brood parasitism

1998) which does not allow enough time for young birds becoming helpers during the same year, as seen for example with the social weaver (*Philetairus socius*) (Covas et al. 2006); and (b) because all nestlings leave the area before the next breeding season (Martin and Bucher 1993).

In addition, the high genetic relatedness found in the studied breeding pair suggests the existence of inbreeding in the population, which is frequent among communal breeders, since reduced dispersal leads towards high within-group kin structure and absence of unrelated breeding partners. These processes result in constraints on social mate choice that can lead to pairing with genetically similar mates (Koenig and Haydock 2004). In such cases, it has been suggested that females may seek extra-pair copulations (EPC) as an adaptive strategy to avoid the negative effects of inbreeding (Blomqvist et al. 2002, but see also Szulkin et al. 2013). Coincidently, EPC has been demonstrated in the Monk Parakeet (Martinez et al. 2013). In conclusion, our results indicate that the Monk Parakeet provides an interesting model for the understanding of the role and benefits of non-reproductive helpers and EPP as an adaptive response in communal breeding birds, and particularly in terms of its unique nest breeding behavior among parrots.

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