

Delayed juvenile dispersal and monogamy, but no cooperative breeding in white-breasted mesites (*Mesitornis variegata*)

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Abstract Although cooperative breeding is known from only about 9 % of bird species, it has received substantial attention because individuals foregoing their own reproduction to help others represent a long-standing evolutionary puzzle. We studied group formation, breeding system, spatial distribution and several life-history traits of white-breasted mesites (*Mesitornis variegata*). Based on field observations across 3 years, we found that white-breasted mesites live in year-round stable pairs, and that groups are formed by juvenile philopatry. As other family-living birds, *M. variegata* exhibit a slow pace-of-life, characterized by high annual adult survival, low productivity, long chick dependence and extended parental care. However, although reproduction is monogamous and juveniles showed interest in their parents' nests, we found no evidence of cooperative breeding. We suggest that slow life-histories, extended parental care and year-round territoriality predispose juvenile mesites to delay dispersal. However, adult intolerance toward older juveniles may prevent them from adopting a cooperative lifestyle. Comparisons with other species of mesite indicate that monogamy and delayed juvenile dispersal are necessary, but not sufficient for the evolution of cooperative breeding in this family of birds, and that particular ecological and social conditions have facilitated the transition from pair-living to a type of group that

may represent a stepping stone in the evolution of cooperative breeding in mesites and other birds.

Keywords Cooperative breeding · Delayed dispersal · Mating system · Mesitornithidae · Social system

Introduction

Cooperative breeding (cooperation of more than two individuals in rearing a single brood of young) is known from only about 9 % of bird species (Cockburn 2006), but it has received substantial theoretical and empirical attention (e.g., Hatchwell 2009; Cornwallis et al. 2010; Jetz and Rubenstein 2011; Leggett et al. 2012) because individuals foregoing their own reproduction to help others represents a long-standing evolutionary puzzle. Cooperative breeding requires the (at least temporary) presence of more than two independent individuals, i.e., the formation of groups. Permanent groups can arise either when several individuals form a group after dispersing from the natal territory, or when offspring do not disperse and form a group with their parents (Cahan et al. 2002). In the first case, groups are mainly formed by unrelated individuals or distant relatives, depending on the species' dispersal patterns and population viscosity (Rollins et al. 2012; Hatchwell 2009), and classical benefits of group-living [e.g., decreased predation risk and increased feeding efficiency (Krause and Ruxton 2002)] have been proposed to explain the origins of group-living. Cooperative breeding in some of these societies is related to direct fitness benefits, mediated by the perceived paternity of the brood (Davies 2000) or future prospects of reproduction (Woolfenden and Fitzpatrick 1978; Pen and Weissing 2000). Species that forage more efficiently in groups, particularly vulnerable to predators, and with low reproductive skew are expected to live in such groups.

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The formation of family groups, on the other hand, has been explained by the cost–benefit balance between philopatric and dispersing juvenile strategies (Kokko and Ekman 2002) and by the species' life-history traits (Ricklefs 1975; Arnold and Owens 1998). Such families are found most commonly in species with slow pace of life (e.g., long-lived, low-productivity, low-population turnover) under social or ecological constraints for dispersal and/or under situations benefiting philopatric strategies (Emlen 1982; Covas and Griesser 2007). Helping behavior during breeding by previous offspring is largely explained by indirect benefits by increasing the reproductive success of relatives (inclusive fitness) in family groups (Mumme 1992) and direct benefits such as an improved ability to rear offspring (Clutton-Brock 2002) or chances to become breeders (Cockburn 1998). The decision to live in family groups is not necessarily followed by the decision to help during breeding, although the combination of these traits is frequently observed in birds (Komdeur and Ekman 2010).

Recent comparative studies including a broad range of bird species (Cornwallis et al. 2010; Jetz and Rubenstein 2011), as well as others restricted to certain families of birds (Rubenstein and Lovette 2007), have been useful in determining proximate mechanisms of cooperative breeding such as monogamy and environmental variability. Therefore, further insights into the evolution of cooperative breeding can be gained by comparing the social systems, life histories and ecology of closely related species with different levels of cooperation.

Mesites are tropical birds found in Madagascar that belong to the endemic family Mesitornithidae. Their phylogenetic relations to other bird families are not very clear, and they have been allied with the Gruiformes (Sibley and Monroe 1990), Turniciformes (Livezey and Zusi 2007) and close to Columbiformes (Hackett et al. 2008) by different studies. This family of birds includes only three species: the brown mesite (*Mesitornis unicolor*), which lives and breeds in pairs in the eastern rain forests (Hawkins and Seddon 2003), the subdesert mesite (*Monias benschi*), which lives in the southern spiny forests in groups of related and unrelated individuals and breeds cooperatively (Seddon et al. 2003, 2005), and the white-breasted mesite (*Mesitornis variegata*), which lives in the dry deciduous forests of western Madagascar. White-breasted mesites are terrestrial, monomorphic and have a mean body mass of 110 g (Ramanitra et al. 2006). They are commonly found in pairs or small groups, assumed to be family units (Hawkins and Seddon 2003). As a result, they have been classified as cooperative breeders (Cockburn 2006), but they have also been characterized as 'at least monogamous' (Hawkins and Seddon 2003). However, the genetic relatedness, age, sex composition and stability of these groups have not been previously studied. Moreover, mesite chicks have been described as precocial (Evans et al. 1996), but food provisioning has been reported in subdesert mesites

(Seddon et al. 2003), which suggests a semi-precocial developmental mode, although it is not known for how long chicks are actually dependent on parental care.

Because delayed juvenile dispersal is most commonly found in tropical species with slow life histories, and since this is partly the path of group formation in the closely related *M. benschi*, white-breasted mesites may be living in families. However, because of their ground-dwelling habits, their relative small-size, and chicks that potentially require little care, family living may not be expected, but other paths to group formation other than delayed dispersal might be possible. We therefore investigated group formation in *M. variegata* by analysing their social organization, i.e., the sex and age composition and genetic structure of social units (Kappeler et al. 2013). We measured group stability, spatial cohesion and several life-history traits to determine whether this tropical species is characterized by a slow pace of life, and whether habitat saturation potentially constrains juvenile dispersal. Finally, we studied the mating system and parental care pattern in this species to establish whether white-breasted mesites breed cooperatively or not.

We predicted that groups are formed by delayed dispersal of juveniles, if this species is characterized by high adult survival and if chicks are dependent for several months. In this case, we also expected stable pair bonds and cooperative breeding when the mating system is mostly monogamous (related helpers have high indirect benefits; Cornwallis et al. 2010). Alternatively, if mesite chicks are relatively precocial, juveniles would disperse early, and groups would not be composed of related individuals. In this case, cooperative breeding would be expected if the mating system is not monogamous, allowing for direct benefits of helpers.

Methods

We studied a population of white-breasted mesites from October 2009 to April 2012 in Kirindy Forest, a forestry concession managed by the Centre National de Formation, d'Etudes et de Recherche en Environnement et Foresterie (CNFEREF) in western Madagascar. The habitat consists of dry deciduous forest characterized by a hot wet season from November to April, corresponding to the breeding season of white-breasted mesites and a cooler dry season from May to October. Several grid systems of narrow foot trails with intersections every 25 to 50 m are present in the area. More detailed information on the study site is provided in Kappeler and Fichtel (2012).

Most of the data were collected in four field seasons: from November 2009 to January 2010, June to September 2010, October 2010 to March 2011 and October 2011 to April 2012, with additional data on group size and composition collected by a local field assistant between these periods, providing about a data point per month for most groups.

Adult and juvenile birds were captured using mist nets. Birds were color-ringed and a 1.8 g radio-transmitter mounted on the tail (BD-2 model, Holohill Systems Ltd) was attached to one individual per group. We took blood or feather samples from all captured individuals for genetic analyses. Resident individuals that could not be captured were photographed and identified based on plumage characteristics (Hawkins 1994). We classified the birds into three age categories: chick (<3 months), juvenile (3–12 months), and adult (>12 months) based on size, and rectrix and tertial shape (Gamero and Lehtikoinen, unpublished data).

Birds were located with the help of radio-transmitters, by searching the study site or by waiting for the birds to descend from their traditional roosting trees before dawn. Due to the terrestrial habits of the species and the habituation to humans by most individuals, birds could generally be followed and observed at close proximity (<7 m) for several hours per day.

Social organization

A group/social unit was defined as a cohesive set of individuals that foraged and roosted together. To determine group stability in size and composition, social units were monitored regularly, and all individuals present were noted. Because secondary dispersal is very rare in white-breasted mesites, adult annual survival was calculated for each year as the proportion of color-ringed individuals resighted the next year (Ebbinge et al. 1991). The spatial position of each group was recorded every 20 min with a portable GPS device (76CSX, Garmin) to determine group home range size, stability and overlap with neighboring groups. We used the bootstrap function of the R package “move” (Kranstauber and Smolla 2013) to create plots of home range size estimates using minimum convex polygons (MCPs) based on different numbers of locations. Visual inspection of plots from eight different groups revealed that asymptotes were achieved after about 53 locations. Therefore, home range sizes were estimated and plotted for social units for which at least 55 geographic locations were available per season (non-breeding: July–August, and breeding: December–February) based on MCPs calculations using Arcview GIS 3.3. For social units with more locations, 55 randomly selected locations were used for the analysis to avoid differences related to differential sampling effort. Because of the secretive behavior of the species and their range outside the path system of our study area, data on home range overlap was only available for seven neighboring groups during the non-breeding season in 2010. We used data from five of these groups and two non-neighboring groups for the analysis of within-group seasonal variation in home range, because these were the only groups for which we had enough spatial data from both breeding and non-breeding seasons.

Breeding behavior

We recorded the identity and the order in which birds were involved in nesting site inspections (climbing or flying to bushes giving a bubbling call, often carrying a twig). We recorded nest-building behavior by noting the number of times each bird brought nest material, and the time it spent building the nest. Active nests were found by regularly monitoring nests found under construction or by following adults going back to incubate at the nest. We recorded the clutch size of each nest, and we took a blood sample from the brachial vein and weighed each chick on the nest shortly after hatching. Chicks were not individually marked at the nest because of their small tarsi size. When remains of depredated or abandoned eggs were found, we took a sample of the embryonic tissue for genetic analyses.

We monitored 21 nests until they failed or chicks left, using a custom-made video surveillance system consisting of a motion detector camera connected to a digital recorder in a waterproof box (Neumann, Ettlingen, Germany), powered by a car battery (see Pyritz et al. 2013). We set the system to record from 5:00 to 19:00 (local time, corresponding to daylight hours) at 1 frame/s in the absence of movement at the nest and at 25 frame/s when a movement was detected to reduce the size of the digital recordings. The camera was situated 1.5 to 3 m from the nest as soon as possible after the nest was found. We used times when the nests were unattended to install the cameras and to check the nests to minimize disturbance. All birds returned to incubate shortly after the setup and measurements were finished. The identity of caring individuals, the time spent incubating and the rate at which they fed the chicks were determined by analysing the footage from each nest, which could be downloaded with a portable monitor, a remote control and a hard disk. The digital recorder and battery were placed at 10–20 m from the nest, allowing for regular checks of the system, change of battery and download of the recordings without disturbing the incubating birds.

Because the bird incubating at 19:00 h was always the same bird incubating the next morning at 5:00 h, and this species is not active at night, we assumed that night incubation was uninterrupted and entirely done by this individual, following Seddon et al. (2003). Therefore, we provide values for full day (0:00–24:00 h) and daytime incubation (5:00–19:00 h) below.

Parental care share was calculated based on four data sets: inspecting nest sites (151 inspections from 17 pairs), nest building (13.9 h of observations from eight breeding pairs), incubation (173 complete days of video recordings on 21 nests from 12 different pairs), and chick care and parental aggression (371 h of observations of 15 pairs with offspring, including video recordings from hatchlings at the nest). Offspring age was certain for 19 out of 26 broods. For the remaining seven broods, which were found when juveniles were older than 4 months, we assumed they had hatched in March, because white-breasted mesites are seasonal breeders, and in our study population, 75 % of the surviving offspring hatched that month.

Genetic analyses

We used the same protocols and 9 of the 10 microsatellite markers described in Gamero et al. (2013) to genotype 75 individuals using DNA extracted from feathers, blood and tissue. We excluded one of the loci from the analysis because it deviated significantly from Hardy–Weinberg equilibrium (Gamero et al. 2013) due to a high frequency of null alleles (>0.30). We determined the sex of all birds using the P2/P8 primers described in Griffiths et al. (1998). PCR products obtained from the sex determination test were sized on a 3130XL Genetic Analyzer (Applied Biosystems/Hitachi) due to the small size difference (10 bp) between them. This test produced two products of 385 and 395 bp for females, and one product of 385 bp for males of *M. variegata*.

Parentage and relatedness analysis

We used COLONY V2 (Jones and Wang 2010) to assign paternity of juveniles and chicks and to assign pairs of full and half siblings. We implemented the full likelihood method, a polygamous mating system without inbreeding [recommended when analysing parentage of offspring from several breeding seasons (Jones and Wang 2010)], and a genotyping error rate of 0.01. We assumed that the percentage of candidate fathers and mothers sampled in our population corresponded to the percentage of adult males (90 %) and females (65 %) sampled, respectively. We included as candidate parents all individuals hatched the previous year or before, regardless of whether they were resighted in the area. We accepted the most likely parentage assignments with a probability of more than 0.80. All second most likely parentage assignments had very low probabilities, ranging from 0.002 to

0.14. We accepted full-sibling and half-sibling clusters with a probability higher than 0.80.

We used COANCESTRY V1 (Wang 2011) to calculate the pairwise relatedness coefficients of Queller and Goodnight (1989) between all individuals.

Statistical analyses

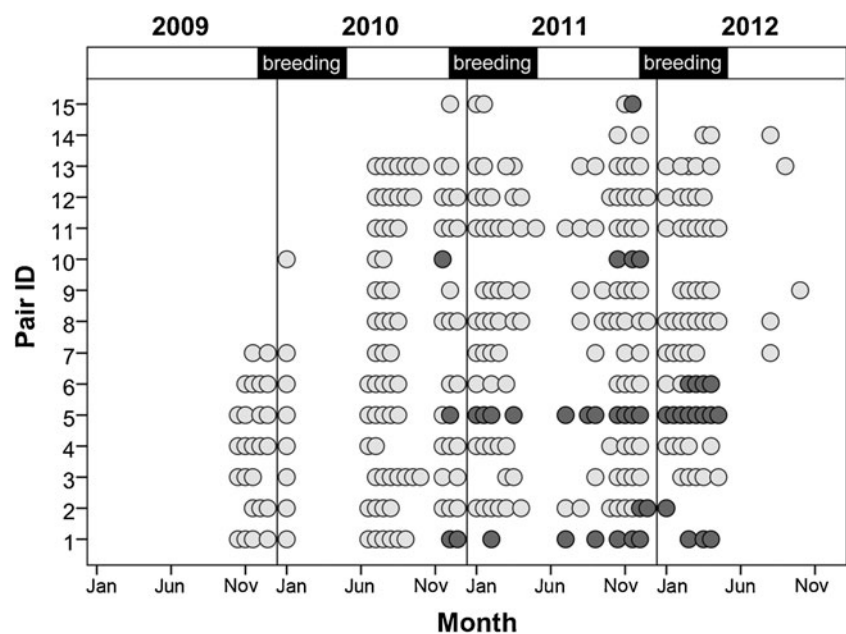
All statistical tests were conducted with IBM SPSS Statistics 20. All values are given as mean \pm SD, obtained from averaged values per social unit or individual. Likewise, statistical tests were performed on averaged values per social unit or individual to avoid pseudo-replication. We tested the distribution of the variables with a Shapiro–Wilk test and used parametric or nonparametric statistics accordingly. We used Wilcoxon signed rank tests to compare sex differences in parental care share and seasonal differences in group size, and a paired sample *t*-test for seasonal differences in home range size within social units.

Results

Social organization

Social units consisted of an adult male, an adult female and 0 to 2 juveniles. Group size was significantly higher during the non-breeding season (2.8 ± 0.4 individuals) than during the breeding season (2.1 ± 0.2 individuals; $Z = 3.541$; $P < 0.001$; $N = 18$). Adult birds had a mean annual survival of 0.87 ± 0.05 and were, in general, stable members of one group during the study period (Fig. 1). We detected six changes in adult composition in 15 social units that were followed for 1 year ($N = 2$), 2 years ($N = 6$) or 3 years ($N = 7$). Four out of six

Fig. 1 Pair stability in white-breasted mesites over a 3-year study period. Each dot represents at least one observation per fortnight and pair. Different shading refers to an adult change (see Results)



seemed to be a consequence of the death of one partner since these individuals were never resighted in the area. The remaining two cases were females that deserted their mate for a neighboring male that had just lost its partner. Juvenile composition changed annually, with no juvenile staying in the same social unit for more than 13 months.

Parentage was tested for 15 juveniles belonging to 11 groups (Table 1). For all juveniles for which the adult male of the group was sampled ($N=14$), this adult male was assigned as the genetic father. Maternity assignments of the 13 juveniles for which the adult female of the group was

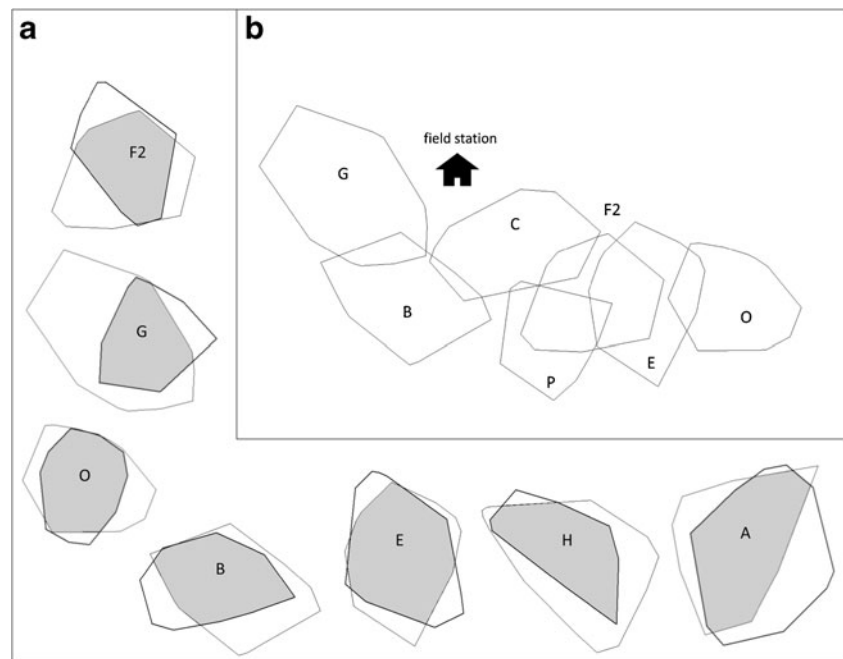
sampled revealed that only seven could be assigned to the putative mother, while the rest ($N=6$) could not be assigned to any other female sampled in the study area. Relatedness coefficients between each of these six offspring and the adult female of the group was -0.167 ± 0.13 (range: -0.357 to -0.024), indicating that these females were unrelated to the juveniles of the group. All paternity assignments were at >0.95 probability, except for offspring B4b, for which the probability was 0.92. All maternity assignments were at >0.95 probability, except for offspring F86, for which the probability was 0.81.

Table 1 Parentage assignments for 43 white-breasted mesite offspring (28 chicks sampled at the nest and 15 juveniles of 5–13 months of age) based on nine microsatellites (Gamero et al. 2013)

Offspring ID	Brood ID	Brood size	Group ID	Year	Sampled adults	Assigned mother	Assigned father
Chicks							
<i>B21, B22</i>	1	2	B	2011	All	Adult female	Adult male
B25	2	2	C	2011	All	Adult female	Adult male
B38, B40	3	2	C	2012	All	Adult female	Adult male
B16, B17	4	2	E	2011	All	Adult female	Adult male
B56, B58	5	2	E	2012	All	Adult female	Adult male
B20, B27	6	2	F	2011	All	Adult female	Adult male
B36	7	2	F2	2012	All	Adult female	Adult male
B63, B67	8	2	G1	2012	All	Adult female	Adult male
B49, B53	9	2	H	2012	All	Adult female	Adult male
B18, B19	10	2	I2	2011	All	Adult female	Adult male
B61	11	2	I2	2012	All	Adult female	Adult male
<i>B47</i>	12	2	H1	2012	Adult male	–	Adult male
B51	12	2	H1	2012	Adult male	–	–
B23, B24	13	2	O	2011	Adult male	–	Adult male
B43, B44	14	2	O	2012	Adult male	–	Adult male
F70, F71	15	2	P	2011	Adult male	–	Adult male
B54	16	1	P	2012	Adult male	–	Adult male
Juveniles							
	Social unit ID	Group size					
B2	1	3	F	2009	All	Adult female	Adult male
<i>B4b, F9</i>	2	4	C	2009	All	–	Adult male
F17	3	3	H	2009	All	Adult female	Adult male
F25	4	4	B	2009	All	Adult female	Adult male
F40, F41	5	4	M	2010	All	–	Adult male
F46	6	3	G	2010	All	Adult female	Adult male
F51	7	3	F2	2010	All	–	Adult male
F100	8	3	F	2012	All	Adult female	Adult male
F101	9	3	B	2012	All	Adult female	Adult male
<i>F86</i>	10	3	G1	2012	All	Adult female	Adult male
B6	11	4	J	2009	Adult female	–	–
F52	12	3	O	2010	Adult male	–	Adult male
4a	13	3	A	2009	Adult male	–	Adult male

Offspring IDs in *italics* correspond to assignments with a probability lower than 0.95

Fig. 2 Minimum convex polygons (MCP) calculated from 55 locations for each white-breasted mesite social unit representing **a** within group home range variation between the breeding (*thick lines*) and non-breeding periods (*narrow lines*) and **b** between group overlap during the non-breeding season



Home ranges were fairly stable throughout the year, since analysis of size and overlap within social units in different seasons revealed a 55.8 ± 11.5 % home range overlap and no significant size differences (non-breeding: 9.41 ± 1.71 ha; breeding: 7.34 ± 2.50 ha; $t = 1.945$; $P = 0.100$, $N = 7$; Fig. 2a). Home ranges also overlapped among neighbors during the non-breeding season (Fig. 2b).

Breeding variables

White-breasted mesites laid 1 or 2 eggs per clutch (1.92 ± 0.18 ; $N = 39$ nests from 16 breeding pairs) and pairs produced up to three clutches per breeding season. Successful nests were active for 28–30 days (egg laying period: 2–3 days, incubation: 25 days and brooding chicks at the nest: 1–2 days). Hatchling weight was 9.34 ± 0.70 g, based on 23 chicks from 10 pairs.

Parental care share

Nest building

Males exhibited more inspecting of nesting sites than females ($Z = -2.596$; $P = 0.009$) and juveniles (the latter including only the seven social units with juveniles, Table 2). The individual initiating this behavior was in 83 % of the cases the adult male of the group, while adult females and juveniles initiated 16 % and 1 % of inspections, respectively. Adult males brought nest material at higher rates than adult females ($Z = -2.521$; $P = 0.012$), but both sexes spent the same amount of time building the nest ($Z = 0.169$; $P = 0.866$). We recorded only one juvenile male bringing nest material on two occasions.

Incubation

Nests were incubated 94.8 ± 2.3 % of the time (full day). Interruptions in the incubation had a mean duration of $34.9 \pm$

Table 2 Summary of the parental care share (mean \pm SD) from adult males, females and juvenile white-breasted mesites

Parental investment	Adult male	Adult female	Juveniles	Pairs (N)	Groups (N)	Sex bias
Inspecting nesting sites (% participation)	84.1 ± 26.2	40.4 ± 36.6	11.1 ± 21.7	17	7	Male
Nest building rate (visits/min)	0.23 ± 0.10	0.13 ± 0.05	Rarely	8	2	Male
Nest building bouts (min)	2.92 ± 1.68	3.64 ± 2.78	Rarely	7	2	–
Full day incubation (h)	15.94 ± 0.49	6.79 ± 0.61	0.0	12	3	Male
Daytime incubation (h)	5.94 ± 0.49	6.79 ± 0.61	0.0	12	3	Female
Feeding chicks (food items/h chick)	1.27 ± 1.41	1.00 ± 1.11	–	15	0	–

Sex bias is noted when one sex invested significantly more, based on within-pair comparisons excluding juveniles [Wilcoxon tests; $P < 0.05$; $N =$ Pairs (N)]. Groups (N) correspond to the subset of pairs [Pairs (N)] that were associated with at least one juvenile

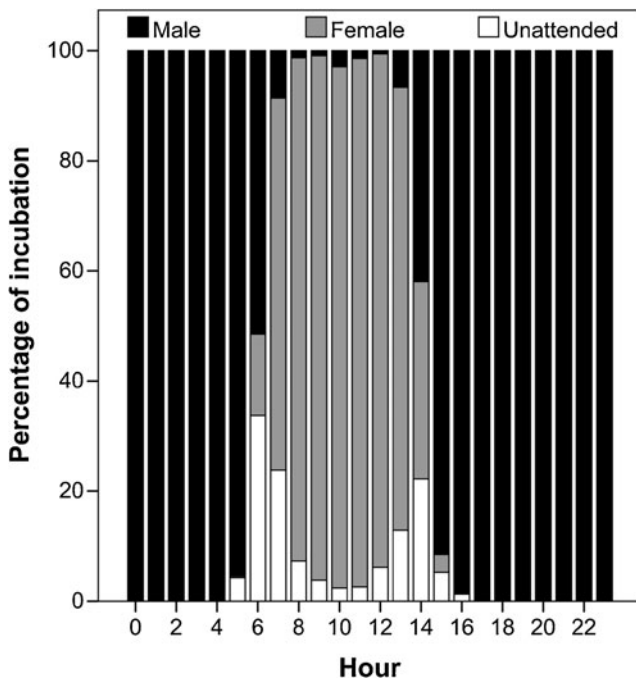


Fig. 3 Incubation pattern for white-breasted mesites representing the percentage of incubation done by males (*black*), females (*grey*) and left unattended (*white*) for each hour of the day based on mean values per breeding pair ($N=21$ nests from 12 pairs; daylight period 5:00–19:00)

20.0 min and were mainly related to a change in the incubating bird ($87.7 \pm 16.2\%$) and rarely to a break within an incubation bout ($12.3 \pm 16.2\%$). Full-day incubation was done only by adult individuals and was male-biased ($Z=-3.059$, $P=0.002$), but daytime incubation was female-biased ($Z=2.197$; $P=0.028$, Table 2). The incubation pattern consisted generally of two bouts (Fig. 3): females incubated only during daylight (from about 6:00–7:00 h until about 13:00–14:30 h), and males started incubating in the early afternoon (13:30–15:00 h) until the next morning (5:00–6:00 h).

Offspring food provisioning and aggression

Chicks have the eyes open, are mobile and able to walk shortly after hatching. They leave the nest within 12–36 h after hatching and follow their parents. Food provisioning is done at high rates for 2 months (4.3 ± 3.1 food items per chick and hour; $N=10$ social units), after which adults rarely feed them (0.1 ± 0.1 food items per chick and hour; $N=13$ social units; Fig. 4). Adult males and females provide food at similar rates ($Z=-1.274$; $P=0.203$; Table 2), and no juvenile was recorded in the groups during the chick provisioning time. Adults were observed chasing juveniles that were older than 7 months at low rates (0.1 ± 0.2 chases per chick and hour; $N=10$ social units), but never younger than that age (Fig. 4).

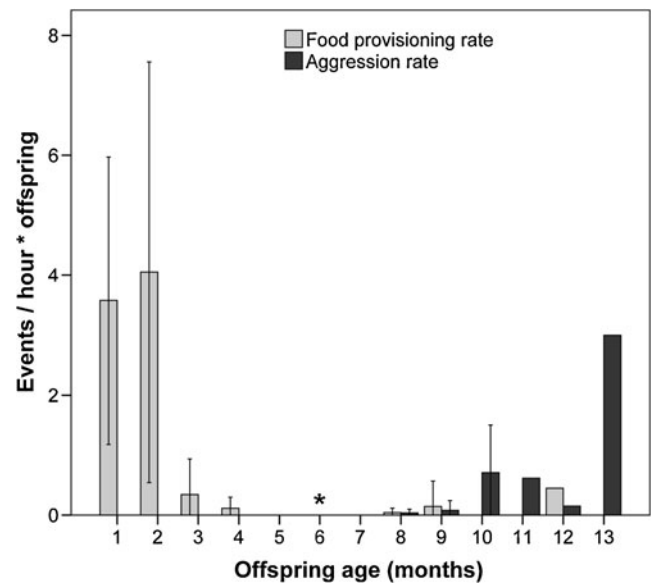


Fig. 4 Mean \pm SD of adult food provisioning and aggression rate to offspring in respect to their age, based on 26 broods/social units from 15 pairs. * No observation available at this age

Mating system

All copulations observed ($N=16$) involved social breeding partners. We had samples from all the social fathers and of 73 % of the social mothers of the 28 chicks sampled at the nest and tested for parentage (Table 1). Paternity could be assigned for 27 chicks, and social and genetic fathers corresponded in all cases. The paternity of the remaining chick could not be assigned and was assumed to be an extra-pair sired chick. Maternity could be assigned only for the chicks for which the sample of the caring female was available. In all these cases (19 chicks), social mothers were assigned as genetic mothers. All paternity assignments were at 0.95 probability, except for offspring B21 and B47, for which the probabilities were 0.93 and 0.86, respectively. All maternity assignments were at 0.95 probability. Summary of full- and half-sibling relationships including all offspring (chicks and juveniles) is provided in Table 3. Mean exclusion probabilities of the full-sibling clusters were 0.98 (range: 0.81–1.0).

Discussion

Group formation

White-breasted mesites live in stable pairs and groups, the latter of which are formed by delayed dispersal of recent offspring that stay in the natal territory for up to 13 months. They show a typical pattern of a 'slow pace-of-life' species: high adult survival, small clutch sizes and a maximum of 2 juveniles per year.

Table 3 Full-sibling and half-sibling clusters for 43 white-breasted mesite offspring (28 chicks and 15 juveniles)

Full-sibling cluster	Pair	Full-siblings IDs	Full-siblings mother	Full-siblings father	Half-siblings IDs
1	A	4a	Unassigned	Male_1	–
2	B	<i>B21, B22, F25, F101</i>	Female_1	Male_2	–
3	C	B25, B38, B40	Female_2	Male_3	<i>B4b, F9</i>
4	C1	<i>B4b, F9</i>	Unassigned	Male_3	B25, B38, B40
5	E	B16, B17, B56, B58	Female_3	Male_4	–
6	F	B20, B27, B2, F100	Female_4	Male_5	–
7	F2	F51	Unassigned	Male_6	B36
8	F2	B36	Female_5	Male_6	F51
9	G	F46	Female_6	Male_7	B63, B67, F86
10	G1	<i>B63, B67, F86</i>	Female_7	Male_7	F46
11	H	B49, B53, F17	Female_8	Male_8	<i>B47</i>
12	H1	B47	Unassigned	Male_8	<i>B49, B53, F17</i>
13	H1	B51	Unassigned	Unassigned	–
14	I2	B18, B19, B61	Female_9	Male_9	–
15	J	B6	Female_10	Unassigned	–
16	M	F40, F41	Unassigned	Male_10	–
17	O	F52, B23, B24, B43, B44	Unassigned	Male_11	–
18	P	F70, F71, B54	Unassigned	Male_12	–

IDs in *italics* denote cluster probabilities lower than 0.95

Juvenile dispersal can be constrained by the unavailability of good territories (Komdeur 1992) and mates (Hatchwell and Komdeur 2000) and is thought to be a result of a low-population turnover found in species with high adult survival (Arnold and Owens 1998). In white-breasted mesites, social units do not generally tolerate neighbors and adults show territorial defence against other groups regardless of the season (Hawkins 1994). However, they seem unable to maintain stable borders and exclusive territories as home ranges overlapped among neighbors and borders changed across seasons.

The inability to defend territories while being aggressive to neighbors could suggest that the study area was saturated with groups, which may be a result of the high adult annual survival (Arnold and Owens 1998). However, although habitat saturation constrains independent breeding of juveniles, it is not sufficient to explain why juveniles stay in the natal area, as habitats without breeding vacancies are also found in species that do not delay juvenile dispersal. The decision to stay at home instead of dispersing and becoming a floater seems to be related to an intrinsic benefit of the natal territory, such as extended parental care, which can increase survival and life time reproductive success of juveniles that stay longer (Stacey and Ligon 1991; Ekman et al. 2000; Tarwater and Brawn 2010a). In this species of mesite, adults showed extended parental care as they also irregularly fed chicks older than 2 months (the age at which they seem to become nutritionally independent), at very low rates until they were 12 months of age.

According to the classification of different chick developmental modes by Stark and Ricklefs (1998), mesite chicks can be classified as semi-precocial. In many semi-precocial species, such as members of the Laridae and Alcidae (Stark and Ricklefs 1998), it is obvious why mobile chicks cannot get access to food by themselves, as food sources are distant (Ricklefs 1979) and require the ability to fly and fish. However, in the case of mesites, chicks leave the nest within 1–2 days after hatching and follow their parents while they feed on terrestrial arthropods, but do not try to get food by themselves until they are about 3 weeks old. Because *M. variegata* find arthropods by flicking leaves over (Hawkins 1994), small-sized chicks may not be able to access this food resource until a more advanced age. Alternatively, mesite chicks may need a long time to acquire the foraging skills necessary for independent survival, as found in other species delaying dispersal (Heinsohn 1991). Accordingly, food provisioning time in this semi-precocial species lasts about as long as in tropical altricial birds (Schaefer et al. 2004; Tarwater and Brawn 2010b), which tend to feed the chicks after the postfledging period longer than temperate species (Russell et al. 2004).

Breeding system

The breeding system of white-breasted mesites is characterized by monogamy and bi-parental care. Parental care is male-biased during the prehatching period and lacks sex bias during the posthatching period, in contrast to the female-only incubation reported previously (Evans et al. 1996). Importantly, we found

no evidence of cooperative breeding. Juveniles only rarely participated in early stage breeding activities (e.g., inspecting nest sites and anecdotally in nest building); they were never observed incubating and were never present during the chick provisioning phase. Based on direct observations and paternity analysis of 28 chicks, the reproductive system of *M. variegata* can be classified as monogamous. The only chick that was not sired by a social father was from a newly formed pair, halfway through the breeding period after the disappearance of the previous breeding female. All pairs had invested in at least one breeding attempt by then, and it was possible that the new female had previously been paired with another male.

Comparative studies in insects (Hughes et al. 2008), birds (Cornwallis et al. 2010) and mammals (Lukas and Clutton-Brock 2012) revealed that female monogamy promotes cooperative breeding in family-living species, as it results in an increase in within-group relatedness, and thus enhanced inclusive fitness benefits for non-reproducing helpers. Monogamy may thus be necessary for, or at least, an important factor facilitating evolutionary transitions to cooperative breeding.

The presence of some families in which the breeding female was not related to the juveniles of the group suggests that these females had replaced the previous breeding females. Because in this monogamous species direct reproductive benefits are not likely for juveniles from the previous year, this decrease in within-group relatedness and reduced inclusive fitness benefits for potential helpers may explain the lack of cooperative breeding in these cases, similarly to promiscuous family-living birds (Cornwallis et al. 2010).

In most mesite groups, however, the juveniles were the recent offspring of both breeding adults, providing juveniles with potential high inclusive fitness of helping in their parents' next breeding attempt. Indeed some juveniles seemed interested in their parents' nests; however, adults were not very tolerant toward older juveniles, particularly after the start of the breeding season. It seems then that the nature of social relationships may be more important than kin selection in explaining the absence of cooperative breeding in white-breasted mesites. That may explain both the extent to which juveniles can stay in the natal territory (Tarwater and Brawn 2010a) and the bi-parental care found in this species. Aggression toward juveniles near the nesting sites is also indicated as the mechanism preventing cooperative breeding in the family living Siberian Jay (*Perisoreus infaustus*; Ekman et al. 1994). Therefore, the breeding system of *M. variegata* could be considered as somewhere along the transition from a bi-parental to a cooperative breeding system.

Adult aggression toward older juveniles may also imply that the benefits for parents to retain juveniles from the previous year decrease with offspring age and that juvenile delayed dispersal is costly for their parents, particularly when it coincides with the next breeding attempt. This is supported by the observation that even though some pairs laid up to three

clutches per season, re-nesting was only observed after a nest failure, and no pair that had a brood of young, even consisting of fairly nutritionally independent juveniles (2–3 months of age) was observed to do so.

Comparison of mesite social systems

Because life-history traits of closely related species are relatively similar (Pienaar et al. 2013), and mesite species have similarly small clutch sizes and low productivity (Hawkins and Seddon 2003; Seddon et al. 2003), slow life histories may be the general pattern in mesites. Slow life histories have been suggested to select for family living in birds (Covas and Griesser 2007) and, consequently, may predispose mesites to delayed juvenile dispersal. The differences in the social systems between mesite species may subsequently arise because of adaptation to local ecological conditions as each species is confined to a different forest type. For example, the pair-living brown mesite found in the eastern mountainous rain forests make seasonal altitudinal migrations which result in nonstable, small territories (Evans et al. 1996). In this case, juvenile dispersal may be less constrained than in the two other species exhibiting juvenile philopatry (Seddon et al. 2005) and stable, packed territories (Seddon et al. 2003) and/or the benefits for juveniles staying in the natal area may be lower for brown mesites, which do not defend territories year-round (Hawkins and Seddon 2003). Likewise, juvenile delayed dispersal found in some populations of carrion crows (*Corvus corone*) seems to be related to year-round territoriality of their parents (Baglione et al. 2005).

The larger groups characteristic of subdesert mesites may form because of higher predation risk in the much more open habitats this species inhabits (Hawkins and Seddon 2003). Additionally, higher prevalence of multi-male groups in *M. benschi* may be a consequence of a male-biased adult sex ratio (Seddon et al. 2003), which can lower male reproductive opportunities.

The pattern of adults providing care is also found in the cooperative breeding subdesert mesite, in which parental care is shared between male and female adult birds of the group, with individuals younger than a year old rarely contributing to it (Seddon et al. 2003). Thus, the occurrence of cooperative breeding in the generally monogamous subdesert mesites (Seddon et al. 2005) may be facilitated by higher social tolerance toward philopatric individuals than in white-breasted mesites, allowing juveniles to stay longer and to help. However, other direct and long-term fitness benefits of group-living, such as extra-group paternity and higher survival were also suggested to play a role in the emergence of helping behavior, particularly in males (Seddon et al. 2005).

In summary, we suggest that a combination of slow life-history and adaptations to local ecological and social conditions may explain the similitudes and differences in patterns of group formation and breeding systems among the three species of

mesite. Despite a strong phylogenetic signal of cooperative breeding in birds (Ligon and Burt 2004), particular ecological and social conditions seem to play an important role in the evolution of this breeding system at lower taxonomic levels.

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Conflict of interest None.

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