Current Biology

Decoupling of Genetic and Cultural Inheritance in a Wild Mammal

Highlights

- Young banded mongooses inherit their foraging niche from cultural role models

- Cultural inheritance occurs in the first few months of life, but lasts a lifetime

- One-to-one cultural inheritance can maintain behavioral diversity within groups

Authors

Catherine E. Sheppard,
Harry H. Marshall, Richard Inger, ...,
David A. Wells, Robbie A. McDonald,
Michael A. Cant

Correspondence

m.a.cant@exeter.ac.uk

In Brief

Sheppard, Marshall, et al. demonstrate cultural inheritance of adult foraging niche in wild banded mongooses. As theory predicts, one-to-one cultural inheritance in this system maintains behavioral diversity within groups.

CellPress

Decoupling of Genetic and Cultural Inheritance in a Wild Mammal

Catherine E. Sheppard,[1,5] Harry H. Marshall,[1,2,5] Richard Inger,[3] Faye J. Thompson,[1] Emma I.K. Vitikainen,[1,6] Sam Barker,[3] Hazel J. Nichols,[4] David A. Wells,[4] Robbie A. McDonald,[3] and Michael A. Cant[1,7,*]

[1]Centre for Ecology and Conservation, University of Exeter, Penryn Campus, Penryn, Cornwall TR10 9FE, UK
[2]Centre for Research in Ecology, Evolution and Behaviour, University of Roehampton, London SW15 4JD, UK
[3]Environment and Sustainability Institute, University of Exeter, Penryn Campus, Penryn, Cornwall TR10 9FE, UK
[4]School of Natural Sciences and Psychology, Liverpool John Moores University, Liverpool L3 3AF, UK
[5]These authors contributed equally
[6]Present address: Department of Biosciences, University of Helsinki, P.O. Box 65 (Viikinkaari 1), 00014 Helsinki, Finland
[7]Lead Contact
*Correspondence: m.a.cant@exeter.ac.uk
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SUMMARY

Cultural inheritance, the transmission of socially learned information across generations, is a non-genetic, "second inheritance system" capable of shaping phenotypic variation in humans and many non-human animals [1–3]. Studies of wild animals show that conformity [4, 5] and biases toward copying particular individuals [6, 7] can result in the rapid spread of culturally transmitted behavioral traits and a consequent increase in behavioral homogeneity within groups and populations [8, 9]. These findings support classic models of cultural evolution [10, 11], which predict that many-to-one or one-to-many transmission erodes within-group variance in culturally inherited traits. However, classic theory [10, 11] also predicts that within-group heterogeneity is preserved when offspring each learn from an exclusive role model. We tested this prediction in a wild mammal, the banded mongoose (*Mungos mungo*), in which offspring are reared by specific adult carers that are not their parents, providing an opportunity to disentangle genetic and cultural inheritance of behavior. We show using stable isotope analysis that young mongooses inherit their adult foraging niche from cultural role models, not from their genetic parents. As predicted by theory, one-to-one cultural transmission prevented blending inheritance and allowed the stable coexistence of distinct behavioral traditions within the same social groups. Our results confirm that cultural inheritance via role models can promote rather than erode behavioral heterogeneity in natural populations.

RESULTS

At our study site in western Uganda, banded mongooses live in groups of around 20 adults of both sexes, plus offspring [12].

Multiple females in each group reproduce in each breeding attempt, typically giving birth on the same day to a large combined litter that is reared cooperatively by the rest of the group. Pups are kept in an underground den for the first month of life, after which they emerge from the den and forage with the group. From this point until they reach nutritional independence at 3 months old, pups form close caring relationships with adult helpers called "escorts" (Figure 1; see Video S1). Pups are not more closely genetically related to their escorts than they are to random adults in the group [13]. In a previous study, we showed, using a food puzzle, that pups in a close escorting relationship learn specific foraging techniques from their escort via contextual imitation [14]. Cultural inheritance might therefore contribute to observed variation between group members in individual foraging niche and foraging specialization [15]. On any given foraging trip, pups associate with a single escort; however, the fidelity of these escorting relationships varies widely across the care period, even among members of the same communal litter. Some pups associate exclusively with a single escort every day during the period that they learn foraging techniques from adults (one-to-one relationships), whereas others associate with multiple escorts over the care period, and hence are exposed to multiple potential cultural role models (many-to-one relationships; Figure 2).

Using stable isotope analysis of facial vibrissa (whisker) samples to measure individual foraging niche [16–18], we tested three predictions deriving from the hypothesis that foraging niche is culturally rather than genetically inherited in this system. First, we predicted that the foraging niche of offspring would more closely resemble that of their escorts, compared to their genetic parents or other adults in the group. Second, we predicted that the influence of an escort on an offspring's foraging niche would develop over the escorting period and persist in adulthood, long enough to influence the next generation. Third, on the basis of cultural evolution theory [10, 11], we predicted that offspring in one-to-one relationships with a single escort would show higher fidelity cultural transmission and hence closer niche similarity to that escort compared to those that associated with multiple escorts (many-to-one relationships).

Across all age groups, individual isotope values were closer to the isotope values of the (adult) individuals that escorted them as

Figure 1. Escorting in Banded Mongooses

From the age of around 30 days until they reach nutritional independence at 90 days, pups are cared for by adults that are no more closely related than random group members. Escorts provision pups, help them to find food, and carry them away from danger. Photo: Dave Seager. See also Video S1.

long after escorted pups became adults themselves. Isotope values of pups sampled at less than 3 months old (mean ± SD age = 37 ± 7 days, n = 11) were not closer to those of their escorts than a random group member (Figure 4A; p = 0.78, n = 11). Since vibrissae take several months to grow [15] (see STAR Methods), vibrissa composition at this age reflects nutrition in utero and/or during lactation. By contrast, the isotope values of independent juvenile individuals sampled at 3–12 months (mean ± SD age = 231 ± 65 days, n = 32) and adult individuals aged over 1 year (mean ± SD

a pup than to those of random (adult) group members that were sampled at the same time (Figure 3; mean observed value = 0.67, null distribution mean = 0.77, p = 0.002; n = 107). Individuals were closer to their escort than a random group member in both $\delta^{13}C$ and $\delta^{15}N$ values when examined separately ($\delta^{13}C$: observed value = 0.48, null distribution mean = 0.54, p = 0.03; $\delta^{15}N$: observed value = 0.40, null distribution mean = 0.46, p = 0.02). Individuals' isotope values were not closer to either parent compared to a random group member (Figure 3; father: p = 0.9, n = 17; mother: p = 0.85, n = 27) and in fact were farther from their fathers' values than from random group members.

Foraging niche similarity between pups and their escorts became evident in samples that grew during the escorting period, and this culturally inherited niche similarity persisted

age = 2.2 ± 1.0 years, n = 64) were significantly closer to their escort than a random group member (Figure 4A; juvenile: mean observed value = 0.94, null distribution mean = 1.13, p = 0.003, n = 32; adult: mean observed value = 0.53, null distribution mean = 0.62, p = 0.02, n = 64). The mean age of former pups sampled as adults (2.2 years) is 66% of expected lifespan of individuals that reach adulthood (3.33 years [19]), and the maximum age of individuals in this sample was 5.6 years, or 168% of expected adult lifespan. Our results thus suggest that the culturally inherited foraging niche acquired in the first 3 months of life persists across the lifespan.

Finally, the number of escorts to which a pup had access influenced the fidelity of cultural transmission of foraging niche, supporting our third prediction. Individuals that associated with a
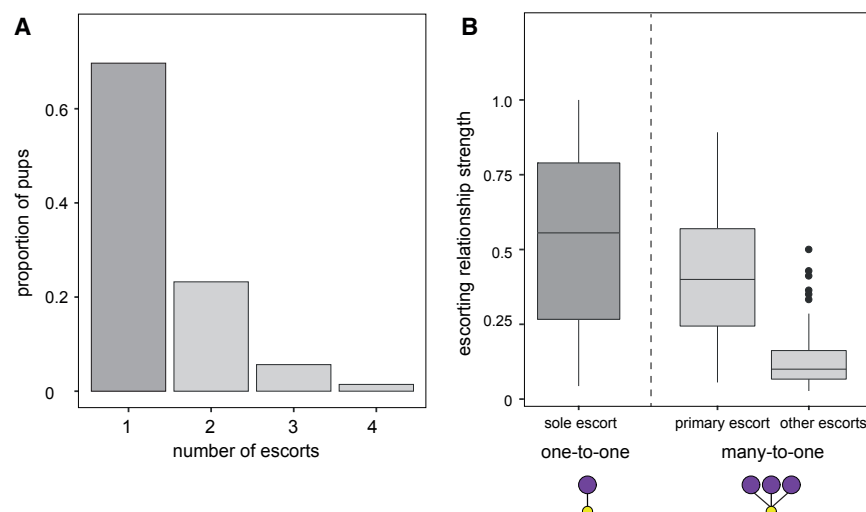

Figure 2. Exclusivity and Strength of Escort-Pup Relationships

(A) Histogram of association patterns between adults and pups. Most pups were cared for by a single escort over the entire 2 month escorting period ("one-to-one" pups). Data are from 1,061 escorting relationships of 762 pups in ten groups. (B) Where pups were cared for by multiple escorts ("many-to-one" pups), they were observed most of the time with a single, "primary" escort; other escorts accounted for a relatively small proportion of the total amount of escorting experienced by a particular pup. Box-and-whisker plots show the median (horizontal midline), interquartile range (boxes) and 1.5 times the interquartile range (whiskers). The points show data that fall outside of this range.
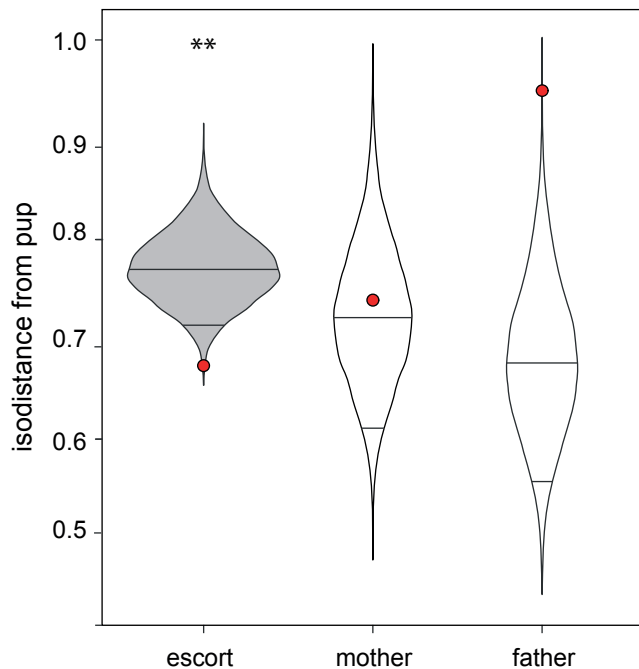
Figure 3. Foraging Niche Is Inherited from Escorts, Not from Genetic Parents

Violin plots showing the null distributions of the mean distance in bivariate isotopic space ("isodistance") between a focal individual and a random group member (gray and white "violins") compared to the observed mean isodistance (red dots) between a focal individual and the individual that escorted them when they were a pup (n = 107) or genetic parents (mothers, n = 27; fathers, n = 17). Horizontal lines mark the median and 5th percentiles within the distribution. Asterisks denote a significant difference between the observed mean and the null distribution: **p = 0.002.
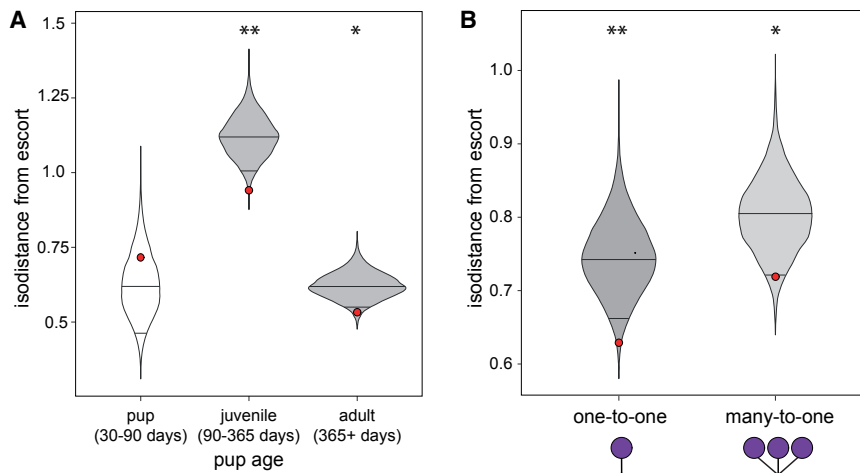
single escort throughout the escorting period (one-to-one pups) had isotope values that were significantly closer to their escort than to random group members (mean observed value = 0.63, null distribution mean = 0.75, p = 0.006, n = 54; Figure 4B). Pups that had multiple escorts (many-to-one pups) also had isotopic niche values that were more similar, on average, to their escorts than to random group members (mean observed value = 0.72, null distribution mean = 0.80, p = 0.041, n = 53; Figure 4B). However, the fidelity of cultural transmission (as measured by the deviation from the null distribution) was much stronger for the one-to-one compared to the many-to-one case. In addition, the amount of time that a pup spent with its escort influenced the fidelity of cultural inheritance, particularly for pups with a single escort. Pups with a "strong" one-to-one relationship with a single escort (where a strong relationship was defined as spending more than half of the escorting period days together) showed closer niche similarity to their escort than pups with a "weak" relationship to one or more escorts ([mean observed value, null distribution mean, p value, n] for strong one-to-one relationships = [0.63, 0.75, 0.03, 35]; weak one-to-one relationships = [0.62, 0.73, 0.07, 12]; strong many-to-one relationships, average isodistance to all escorts = [0.86, 0.93, 0.19, 22]; weak many-to-one relationships, average isodistance to all escorts = [0.62, 0.71, 0.08, 31]).

DISCUSSION

Our results provide strong evidence of cultural inheritance in banded mongooses because the unusual escort system of allo-parental care represents a natural cross-fostering experiment, decoupling genetic and non-genetic influences on behavior. Non-genetic inheritance in this system occurs via imitation of adult preferences for particular foraging techniques (e.g., smashing versus biting of hard-shelled prey items [14]) and, potentially, preferences for foraging in particular areas or substrates (e.g., under bushes or in elephant dung). In birds and fish, cross-fostering and transplantation experiments provide similarly clear evidence that key behavioral traits (e.g., foraging or site preferences) are culturally transmitted over generations in the wild [20–22]. In mammals, cross-fostering is logistically difficult, but cultural inheritance can be inferred from geographic or population variation in behavior that cannot be explained by genetic or environmental differences (e.g., tool use and foraging techniques in apes [2, 23, 24] and dolphins [25, 26]) or the very rapid diffusion of behavioral traits in space and time (e.g., songs in whales [27, 28]). Cooperatively breeding species in which adults care for unrelated offspring [29] or offspring of varying relatedness [30] may offer new opportunities to reveal subtle but potentially pervasive non-genetic forms of inheritance of phenotypic traits in natural populations.

In line with theoretical predictions [10, 11], the influence of escorts in shaping the foraging niche of developing pups depended on the number of cultural role models to which pups were exposed. Niche similarity between escort and pup was particularly strong in cases where the pup was escorted exclusively by the same adult day after day (one-to-one pups), compared to cases where pups associated with multiple escorts (or where they spent much of their time unescorted). Despite the observation that pups with multiple escorts spent most of their time with a single primary escort (Figure 2), their exposure to other escorts diluted the culturally transmitted niche similarity to this primary escort, as expected if pups exhibit blending cultural inheritance when they are exposed to multiple role models. Our results thus support models of cultural evolution of quantitative traits which predict that variation in the number of "cultural parents" [11] or the degree of social "compartmentalization" [10] constrains cultural blending inheritance and determines, at least in part, whether cultural transmission erodes or maintains heterogeneity in social groups.

Although classic models of cultural inheritance examine the consequences of different transmission modes (e.g., one-to-one, many-to-one, or many-to-many) for phenotypic variation, there has been little exploration of the ecological and social conditions for which different modes of transmission might be favored by natural selection. At first sight, one-to-one transmission has several potential disadvantages for the spread of fitness-enhancing cultural traits: offspring might miss out on beneficial innovations and skills that are available to other offspring in the same litter or might fail to exploit all of the resource types available to the group. One-to-one inheritance also weakens between group cultural selection for group-beneficial traits [31]. In some circumstances, however, natural selection may favor genetically or culturally determined modes of cultural transmission that maintain within-group variation [32]. In banded mongooses, individuals respond to within-group foraging competition by adopting more specialized, less overlapping

Figure 4. Durability and Fidelity of Cultural Inheritance

(A) Isodistance to escort when the focal individual was sampled as a pup (30–90 days; n = 11), juvenile (90–365 days; n = 32), and adult (>365 days; n = 64). Since whiskers take several months to grow [15], samples from pups reflect nutrition in utero and during lactation; samples from juveniles include the escorting period. **p = 0.003, *p = 0.02.

(B) Isodistance to escort in cases where pups had a single escort (one-to-one pups; n = 54) versus multiple escorts (many-to-one pups; n = 53). **p = 0.006, *p = 0.041.

individual foraging niches [15]. Our results suggest that one-to-one cultural transmission may enhance niche partitioning among competing litter- or group-mates, alleviating competition for shared resources. The unusual escort system might therefore be linked to another unusual feature of this system, extreme birth synchrony and intense reproductive competition in communal litters [33]. At a group level, heterogeneous groups may be less susceptible to Allee effects that are pervasive in cooperative breeders [34] and more resilient to environmental changes [35]. Thus, both genetic natural selection and cultural group selection could favor the evolution of cultural mechanisms that contribute to persistent phenotypic variation in natural animal populations.

To summarize, our results demonstrate cultural inheritance of foraging niche across generations in a wild mammal and support the theorized effect of variation in intergenerational association patterns on within-group variation in culturally inherited traits. A historical focus on animal cultures and traditions as group-level phenomena may have underestimated the potential for cultural evolution to contribute to persistent behavioral diversity in natural animal populations.

STAR★METHODS

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SUPPLEMENTAL INFORMATION

Supplemental Information includes one video and can be found with this article online at https://doi.org/10.1016/j.cub.2018.05.001.

AUTHOR CONTRIBUTIONS

Conceptualization, M.A.C., H.H.M., C.E.S., R.I., and R.A.M.; Methodology, C.E.S., H.H.M., and R.I.; Formal Analysis: C.E.S. and H.H.M.; Investigation, C.E.S., H.H.M., F.J.T., E.I.K.V., H.J.N., D.A.W., S.B., and M.A.C; Writing – Original Draft, M.A.C., C.E.S., and H.H.M.; Writing – Review & Editing, M.A.C., H.H.M., F.J.T., E.I.K.V., H.J.N., R.I., and R.A.M.; Funding Acquisition, M.A.C.; Resources, R.A.M., S.B., R.I., and H.J.N.; Supervision, M.A.C., H.H.M., and R.A.M.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Figshare Data Repository (https://figshare.com)	This paper	https://doi.org/10.6084/m9.figshare.6204812
Experimental Models: Organisms/Strains		
Mungos mungo	Mweya, Queen Elizabeth National Park, Uganda	N/A

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Michael Cant (m.a.cant@exeter.ac.uk).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Ethical Note
All research procedures received prior approval from Uganda Wildlife Authority and Uganda National Council for Science and Technology, and adhered to the ASAB/ABS Guidelines for the Treatment of Animals in Behavioral Research and Teaching. All research was approved by the Ethical Review Committee of the University of Exeter.

Study population
The research was conducted on a population of wild banded mongooses living on and around Mweya peninsula, western Uganda (0°12′S, 29°54′E) which has been studied continuously since 1995 [12]. This study utilized samples and life history data spanning 22 years from October 1995 to February 2017. All individuals in the population are identifiable through use of unique shave patterns on their backs and pit tags (TAG-P-122IJ, Wyre Micro Design, UK) inserted under the skin of their nape. Two members of each group are fitted with a radiocollar (Sirtrack, Havelock North, New Zealand) which allows them to be located on a daily basis. On first capture a 2 mm skin sample was collected from the end of the tail using sterile scissors for genetic analyses. Further details of the study species and site can be found in [12].

METHOD DETAILS

Sample collection and stable isotope analysis
Stable isotope analysis is based on the premise that the stable isotope ratios of a consumer's tissue reflects that of its dietary sources during the time the tissue was synthesized [17, 18]. We used vibrissae samples from individual mongooses to measure the ratios of ^{13}C and ^{15}N stable isotope, which vary with habitat and trophic level respectively, representing foraging location and trophic position [36].

Vibrissae were collected from individual banded mongooses under general anesthetic between October 2013 and September 2015. Individuals were captured using box traps (Tomahawk Live Trap Co., Tomahawk, WI, USA) and anaesthetized using isoflurane (see [37] for details of trapping procedure). Vibrissae were sampled from the same side of each mongoose's snout to ensure fresh vibrissa growth was sampled at each trapping. Vibrissa samples from individual banded mongooses (4-5 per sample to obtain enough material for stable isotope analysis) were scraped to remove debris and cut into smaller fragments using a scalpel and forceps. Samples were then weighed to around 0.8mg (mean ± sd: 0.80mg ± 0.28; n = 107) and sealed in small tin capsules in preparation for stable isotope analysis. Analyses of carbon and nitrogen isotope ratios ($\delta^{13}C$/ $\delta^{15}N$) were carried out using a Sercon Integra integrated elemental analyzer and mass spectrometer (CF-IRMS; Cheshire, UK). Expressed as δ values, $\delta^{13}C$ and $\delta^{15}N$ isotope ratios are reported in parts per mil (‰), with reference to international reference materials (IAEA, Vienna) and scaled to V-PDB and air, respectively.

To determine the growth rate of vibrissae we provisioned six adults with Rhodamine-B infused carnivore kibble and collected their vibrissae one month later (see also [15]). This data suggested that the mean time to regrow an entire adult vibrissa was 6.3 months (lower-upper s.e. = 5.3-7.8). Hence we infer that samples from pups in the escorting period (aged 30 to 60 days) primarily reflect nutrition in utero and during lactation (age −60 to 30 days); samples from juveniles aged 90 to 365 days include the entire escorting period and the first month or two of independent foraging; samples over 365 days reflect the foraging niche of individuals aged ∼6 months to 5 years old (since the samples are taken at age 1 to 5.6 years; see Quantification and Statistical Analysis below).

QUANTIFICATION AND STATISTICAL ANALYSIS

Escorting behavior and genetic analyses

Escorting behavior is observed in communal litters each day after emergence through to nutritional independence (See Video S1). Escorting behavior is conspicuous and adult individuals are recorded as an escort in a particular group visit if they associated closely with a focal pup (observed within 0.3 m of the focal pup for over half of the 20-minute observation session [38]). Our study utilizes escorting behavioral data from 134 communal litters from 10 social groups. We calculated escorting relationship strength as the proportion of group visits during the escorting period that a particular adult was recorded as a pup's escort. Pup parentage was assigned using genetic data from 2mm skin samples taken at first capture. DNA was extracted from these samples and was genotyped using a panel of 43 microsatellite loci (see details of DNA analysis and parentage assignment in [39]).

Prediction 1: The foraging niche of offspring will more closely resemble that of their escorts, compared to their genetic parents or other adults in the group

We obtained 107 isotope measures from individual banded mongooses aged from 29 days to 5.6 years old. These were matched with a corresponding measure collected within one month from the individual that escorted the focal individual when he/she was a pup. To test whether there was non-genetic social transmission of foraging niche between escorts and pups, we used a randomized permutation procedure to compare the distances between individuals and their escorts in bivariate isotopic space (hereafter referred to as 'isodistance') with their isodistance from a random group member. Random group members were chosen from individuals who met the following criteria: i) a vibrissa sample was available from them within one month of the focal individual's sample, ii) they were not the escort, mother or father of the focal individual and iii) they were an adult group member (> 1 year old) on the day the focal individual was sampled. In each permutation, a random group member that matched these criteria was assigned to each of the 107 focal individual samples, and a mean isodistance calculated from across these random pairings. We repeated this procedure for 10,000 permutations to create a null distribution of mean isodistances. We then compared the mean observed focal individual-to-escort isodistances to this null distribution and calculated a one-tailed p value testing our *a priori* prediction that individual-to-escort isodistances would be smaller than individual-to-random group member isodistances [40] (our main results are qualitatively unchanged if we assume a two-tailed test). To assess whether any effect on isodistances we found was driven by either $\delta^{13}C$ or $\delta^{15}N$ values, we repeated this process comparing individual-escort and individual-random group member differences in $\delta^{13}C$ and $\delta^{15}N$ separately.

To test whether there was parental transmission of foraging niche, we repeated the above randomization process compared individual-mother and individual-father isodistances with null distributions. Individuals whose father was part of a different social group at the time of sampling were excluded. All mothers in the sample were in the same social group as their offspring at the time of sampling. The resultant datasets were composed of 24 (17 individuals and 9 mothers from four social groups) and 19 (13 individuals and eight fathers from five social groups) paired individual isotope samples, respectively.

Prediction 2: Culturally inherited differences in foraging niche will develop during the escorting period and persist into adulthood

We repeated the above randomization analysis for individual-escort paired samples collected when the individual was a pup (< 90 days; n = 11; mean ± s.d. age = 37 ± 7 days), subadult (≥ 90 days to a year; n = 32; mean ± s.d. age = 231 ± 65 days) and adult (≥ 1 year; n = 64; mean ± s.d. age = 2.2 ± 1.0 years). This allowed us to investigate the ontogeny of foraging niche and whether individuals continue to use similar niches to their escort after they reach nutritional independence (at age 3 months) and adulthood (at age one year [12]).

Prediction 3: Exposure to multiple role models will dilute the fidelity with which foraging niche is culturally inherited

We used our randomization procedure to compare isodistance between pups with single (one-to-one) versus multiple (many-to-one) escorts. For cases involving multiple escorts, each focal individual-to-escort isodistance was represented once in calculating the mean. In addition, we analyzed whether the strength of the relationship between pups and escorts in one-to-one and many-to-one relationships influences fidelity of transmission of foraging niche. We classed a relationship between a pup and escort as 'strong' if they spent over half of the escorting period together. Against the null distribution for each of the following categories, we compared the mean isodistance of pups to escorts in (i) strong one-to-one relationships; (ii) weak one-to-one relationships; (iii) strong many-to-one relationships (where for each escortee we took an average of the isodistance to all of its escorts); (iv) weak many-to-one relationships (again averaging the isodistance to all the escorts of each escortee).

DATA AND SOFTWARE AVAILABILITY

Data used in all the analyses are available via the Figshare Data Repository (https://doi.org/10.6084/m9.figshare.6204812).