Growing up wild: social learning opportunities during foraging in immature baboons

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Immature individuals may play an important role in group-level information transmission because they learn socially more than adults. However, little is known about social learning during development, particularly in nontool-using species. Our aim was to determine how immatures' social learning opportunities during foraging changed with age and differed between the sexes, and from whom immatures had more opportunities to learn. Behavioural data on 53 immature wild chacma baboons, *Papio ursinus*, were collected across 2 years, recording all behaviours associated with social learning in other species: observing others while foraging, inspecting or eating food dropped by others, sniffing others' mouths, stealing food from others, joining the same location that others are foraging and eating the same food. Results showed that immatures had relatively more opportunities to learn from others before and around the weaning period, but no sex differences were found. Immatures had more opportunities to learn from individuals in proximity when they were young, but their learning opportunities were limited to relatively more specific 'demonstrators' (that is, possible learning partners) when older. In general, immatures had relatively more opportunities to learn from grooming affiliates and individuals of a similar age as themselves. Immature males had less opportunities to learn from grooming partners compared with female peers. Finally, high-ranking immatures had greater opportunities to learn socially compared with low-ranking peers. The relatively greater social learning opportunities of immatures around weaning could improve their independent foraging competence before being weaned. In addition, tolerance, through shared proximity and grooming, may be important in determining from whom immatures have greater opportunities to learn. Baboons live in a matrilineal society with a high degree of nepotism; thus, the greater opportunities of immatures to learn from tolerant individuals may translate into a higher within-matriline versus across-matriline information spread, which could limit group-level information transmission.

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Social learning is widespread in the animal kingdom (Allen, 2019). It is defined as acquiring information from other individuals or their artefacts (Laland, 2004) and potentially applying and exploiting such social information (Carter et al., 2016). Gaining information from others is advantageous because it can require less energy (exploration time and effort) and have lower costs (e.g. eating a toxic food) than acquiring it personally (Laland, 2004). The transmission of social information has been a major research focus in animal behaviour because of its role on the formation of culture, that is, socially learned behaviours shared by most members of a group and maintained through time (Allen, 2019; Laland & Janik, 2006). Understanding the constraints on social information transmission may be important because cultural differences can produce variation in fitness (Marcoux et al., 2007; McComb et al., 2001), with potential implications for population conservation (Brakes et al., 2021).

Immature individuals could play a fundamental role in group-level information transmission because they tend to learn socially more than adults (Mesoudi et al., 2016; Whiten & van de Waal, 2018). In experiments conducted in captivity and in the

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wild, juveniles learn socially more than adults across animal taxa, such as smooth-coated otters, *Lutrogale perspicillata* (Ladds et al., 2017), Australian skinks, *Eulamprus quoyii* (Noble et al., 2014), and chacma baboons (Carter et al., 2014). This difference may be due to the lack of experience of immatures with the environment, leading them to have a different balance of costs and benefits of asocial and social learning compared with adults. Given their lack of experience, the costs of asocial learning could be higher for immatures than for adults, thereby increasing the benefits of learning from more experienced individuals (Laland, 2004). For example, learning about predators from conspecific adults improves the survival of juvenile Siberian jays, *Perisoreus infaustus* (Griesser & Suzuki, 2017), and black-tailed prairie dogs, *Cynomys ludovicianus* (Shier & Owings, 2007).

Considering that immatures are well tolerated by other group members, they have wide opportunities to learn socially (meerkats, *Suricata suricatta*: Thornton, 2008; tufted capuchins, *Sapajus apella*: Ottoni & Izar, 2008; and bottlenose dolphins, *Tursiops truncatus*: Mann et al., 2007). Most studies focused on the acquisition of foraging skills because the first challenges faced by young immatures are learning where to find food, what food they can eat and how to process it (Rapaport & Brown, 2008; Thornton & Clutton-Brock, 2011). Apart from foraging skills, immatures learn in other domains, such as nest building (e.g. Bornean orangutans, *Pongo pygmaeus*, and Sumatran orangutans, *P. abelii*: Schuppli, Meulman, Forss, Aprilinayati, van Noordwijk, & van Schaik, 2016), vocal communication (e.g. spider monkeys, *Ateles geoffroyi*: Briseno-Jaramillo et al., 2018; meerkats: Hollén & Manser, 2006) and migratory routes (e.g. whooping cranes, *Grus americana*: Mueller et al., 2013).

Although most studies in the wild are observational and, thus, cannot quantify the role of social versus individual learning (but see Hobaiter et al., 2014), studies conducted in the wild report behaviours that may be indicative of social information acquisition (e.g. proportional to foraging competence), application (e.g. increasing individual exploration) and exploitation (e.g. affecting foraging choices; Schuppli, Meulman, et al., 2016; Thornton & Hodge, 2009). Experimental work has further confirmed that individuals exposed to social information are more likely to adopt novel foraging skills (Thornton, 2008; Troisi et al., 2021). These 'social learning behaviours' include observing others while foraging; inspecting or eating food gathered by others; sniffing others' mouths, potentially obtaining olfactory information on the food eaten; joining the same location that others are foraging and eating the same food type (species) and item (part of a plant, that is, coforaging; Rapaport & Brown, 2008; Thornton & Clutton-Brock, 2011). These behaviours may entail social learning of long-lasting skills (e.g. where to find food, what to eat and how to process it) and the acquisition of ephemeral social information (e.g. ephemeral patch location and patch quality; Bonnie & Earley, 2007; Rieucau & Giraldeau, 2011). Most of these social learning occurrences may involve 'simple' processes, such as local or stimulus enhancement (that is, the attraction towards the location or part of an object used by another individual). In addition, social learning behaviours may encompass different steps of social information use (Carter et al., 2016), ranging from information acquisition (observing others, inspecting food and sniffing mouths) to information exploitation (feeding on food gathered by others and coforaging). Finally, for social species, particularly those with extended juvenescence (Jones, 2011; Street et al., 2017), immatures' knowledge and skill acquisition involves a combination of social and individual (asocial) learning, as individuals gather information and improve their skills through practice and physical maturation (e.g. motor development and dental eruption; Bray et al., 2018; Landová et al., 2017).

Immatures' propensity to learn from others may vary by age and sex. In most cases, immatures must be nutritionally self-sufficient by weaning because postweaning provisioning is rare (Carvajal & Schuppli, 2022). For omnivorous species, the dietary knowledge to be learned may be vast (Whiten & van de Waal, 2018): for example, yellow baboons, *Papio cynocephalus*, can consume more than 250 types of food (Alberts, 2019). Nevertheless, adult-level dietary breadth and efficiency for most foods is reached by weaning (Bray et al., 2018; Schuppli, Forss, Meulman, Zweifel, Lee, Rukmana, Vogel, van Noordwijk, & van Schaik, 2016). Accordingly, social learning of foraging skills is more common in infants than in juveniles (orangutans: Mikeliban et al., 2021; tufted capuchins: Gunst, Boinski, & Fragaszy, 2010; and meerkats: Thornton & Hodge, 2009). During juvenescence, learning from others may continue at relatively high levels up to sexual maturity to include rare foods in the diet and refine certain foraging skills, such as extractive foraging in banded mongooses, *Mungos mungo* (Müller & Cant, 2010), predation in many mammalian predators (Thornton & Clutton-Brock, 2011) and tool use in bottlenose dolphins (Sargeant & Mann, 2009). Variation in social learning may also occur depending on the sex of immatures. In particular, juvenile females may have greater social learning opportunities compared with male peers because they are better integrated in the group's social network (e.g. killer whales, *Orcinus orca*: Weiss et al., 2021; female-philopatric primates: Amici et al., 2019; Lonsdorf, 2017), which could translate to enhanced social learning (van Boekholt et al., 2021; meerkats: Hollén & Manser, 2006).

Apart from the individual characteristics that can affect juveniles' tendencies to acquire social information, immatures may also learn from different demonstrators depending on their age and sex. The demonstrators from whom immatures learn may differ on the basis of their spatial associations within their social group or other characteristics. Young immatures could be constrained in their choice of demonstrators by the proximity of close kin, who provide care and protection (Bateson, 1994; Lehmann et al., 2006). Consequently, immatures learn first from related individuals who are more frequently in spatial proximity, primarily the mother, and shift towards other group members later during development (vervet monkeys, *Chlorocebus pygerythrus*: Grampp et al., 2019; orangutans: Schuppli, Meulman, et al., 2016; and bottlenose dolphins: Mann et al., 2007), when they expand their social network beyond the maternal one (Roatti et al., 2023; Tsai & Mann, 2013). Independently from spatial proximity, other characteristics that could affect the suitability of individuals as a demonstrator may include age, sex, affiliation and social rank (Lonsdorf & Bonnie, 2010). Older, more experienced individuals and the philopatric sex may be chosen because of their local knowledge (white-faced capuchins, *Cebus capuchinus*: Barrett et al., 2017; vervet monkeys: van de Waal et al., 2010; and bottlenose dolphins: Mann et al., 2007). Social affiliates, including close kin, and low-ranking individuals may be targeted because their tolerance allows for close proximity and, thus, better learning opportunities (chimpanzees, *Pan troglodytes*: Watson et al., 2017; ravens, *Corvus corax*: Kulahci et al., 2016; and chacma baboons: Marshall et al., 2015). Conversely, high-ranking individuals may be preferred as demonstrators because they can access high-quality food patches (vervet monkeys: Canteloup et al., 2020; chimpanzees: Kendal et al., 2015; and chacma baboons: Huchard et al., 2013).

Immatures' social learning has been relatively understudied in nontool-using species probably because of the difficulty of assessing information acquisition in the absence of material artefacts (Schuppli & van Schaik, 2019; Whiten & van de Waal, 2018). However, the growing knowledge on behaviours quantitatively

associated with learning from others (Schuppli, Meulman, et al., 2016) may allow the exploration of social learning in species with no material culture (Grampp et al., 2019; Thornton & Hodge, 2009). Considering that the social learning behaviours recorded were not directly linked to social information acquisition in this study, the occurrence of these behaviours was referred to as 'social learning opportunities'.

In this study, we aimed to understand (1) how social learning opportunities during foraging change throughout development in a nontool-using species, the chacma baboon and (2) from whom immature baboons have greater opportunities to learn while they forage. A longitudinal approach was adopted in this study, which allows the detection of developmental trends and selective social attention at different age stages (Lonsdorf & Bonnie, 2010; Mesoudi et al., 2016). Baboons are ideal models to study social learning opportunities because they live in large social groups (Cheney & Seyfarth, 2007; van Boekholt et al., 2021), and their ability to learn socially has been confirmed by experimental studies (Carter & Cowlishaw, 2021; Carter et al., 2014, 2016). Baboons' multimale and multifemale social groups are organized into matrilines, that is, social units formed by a mother and her offspring (van de Waal et al., 2012). Females are philopatric, whereas males disperse after sexual maturity (Cheney & Seyfarth, 2007). Given the broad and opportunistic diet of baboons, learning from others may be fundamental to advance immatures' acquisition of an adult-level foraging competence (Alberts, 2019). Furthermore, identifying constraints on immature baboons' social learning opportunities may contribute to understanding why baboons and similar group-living, social-learning species show limited evidence of culture compared with other nonhuman primates (hereafter referred to as primates; Sapolsky, 2006) despite their propensity to learn socially (Carter et al., 2014, 2016).

Building on the current literature, two hypotheses on social learning opportunities during development in baboons were tested. The first hypothesis (H1) stated that immatures' opportunities to learn socially change with age and differ by sex. We had two predictions for H1. Considering that young immatures need to acquire the necessary dietary knowledge to reach foraging independence (Carvajal & Schuppli, 2022) and that they are well tolerated by other group members (Rapaport & Brown, 2008), we predicted that (P1a) social learning opportunities would increase during infancy and decrease during juvenile years. We also predicted that (P1b) this decrease would be greater in males than in females because of their lower sociability compared with female peers (Lonsdorf, 2017). The second hypothesis (H2) stated that immatures' social learning opportunities would involve different demonstrators depending on their own age and on the demonstrators' characteristics. We had three predictions for H2. We predicted that (P2a) immatures' learning opportunities from individuals in proximity would decrease with age because these are restricted to relatively more specific demonstrators when immatures are older (Grampp et al., 2019); (P2b) immatures' opportunities to learn from older individuals and the philopatric sex (females in baboons) would be relatively greater because immatures prefer demonstrators who are knowledgeable of local resources (Barrett et al., 2017; van de Waal et al., 2010); (P2c) in chacma baboons' despotic society (King et al., 2008), immatures' opportunities to learn from demonstrators tolerant of immatures' proximity, such as close kin, grooming affiliates and low- or similarly ranked individuals (Lonsdorf & Bonnie, 2010), would be relatively greater (King et al., 2009).

METHODS

Study Site and Species

This research was carried out at the Tsaobis Baboon Project, a long-term, individual-based study of a wild chacma baboon population (TBP, 2019). Tsaobis is a semidesertic area located on the edge of the Namib desert, in central Namibia (22°22′ S, 15°44′ E). The main features of the area are the ephemeral Swakop river and its tributaries, bordered by dense patches of woodland and surrounded by rocky hills with scarce vegetation (Cowlishaw & Davies, 1997).

The study population was formed of two troops (J and L) that range across the Tsaobis Nature Park and the surrounding farmland. The troops were habituated to the presence of observers on foot, and the majority of the individuals were recognizable through a unique combination of ear marks. Adult females give birth to an infant approximately every 2 years (Dezeure, Baniel, Carter, Cowlishaw, Godelle, & Huchard, 2021), and infants of both sexes are weaned around 12−18 months of age at Tsaobis (Carboni et al., 2022; Huchard et al., 2013). For the purposes of this study, individuals aged ≤5 years were considered immatures, and those aged ≤12 months were considered infants (Roatti et al., 2023). Females undergo menarche around 5 years of age, and they give birth to their first infant around 6 years old; males develop secondary sexual characteristics around 6 years of age, reaching full adult development after approximately 8 years old, when they typically emigrate (Alberts & Altmann, 1995; Altmann et al., 1981; Cheney et al., 2004).

Data Collection and Manipulation

Behavioural observations

Observations were conducted on the two study troops during two field seasons in 2021 (approximately 6 months) and 2022 (approximately 3 months), totalling 9 months of data collection over the 2 years (Roatti et al., 2025). Baboons were followed daily from dawn to dusk while collecting observational data using CyberTracker (Liebenberg, 2022). A total of 59 and 64 individuals were included in troop J and 72 and 79 individuals in troop L in 2021 and 2022, respectively (Supplementary material, section 1). The proportion of recognizable individuals accounted for 1.0 in 2021 and 0.98 in 2022 (across both troops).

Our study focused on 53 immature study subjects (J: 24; L: 29), born from 38 mothers (0−58 months of age; median = 30 ± 33 months). Among these, 37 immatures (J: 15; L: 22) were followed throughout the study period (in both years). In 2021, the sample included all the individuals aged ≤4 years at the start of the field season plus those born during the field season (34 females and 19 males), of which 23 were infants and 30 were juveniles when they entered the study. The same individuals were observed in 2022, except for 16 individuals who were no longer immature (eight), who had died (four) or were not recognizable when they became independent from their mother (four). The 2022 sample comprised 23 females and 14 males, who were all juveniles, but one of them was infant at the start of the field season.

To test our predictions, four different kinds of behavioural data were collected (Altmann, 1974): focal observations on the social behaviours of immatures, ad libitum grooming and dominance interactions on all troop members, proximity scans on all troop members and long-term data on age, sex and maternal relatedness on all troop members. Interaction records included the identity of the social partners and their directionality (given or received).

Focal observations consisted of 20 min observations on a specific focal individual included in the immature study subject sample. To avoid bias towards the time of the day, observations per individual were distributed evenly in four daily blocks of ~3 h each: (1) from dawn until 1000 hours, (2) from 1000 to 1300 hours, (3) from 1300 to 1600 hours and (4) from 1600 h until dusk. In addition, to increase data independence, each individual was observed as a focal only up to twice per day in two different and nonconsecutive time blocks (Supplementary material, section 2). Ad libitum grooming and dominance interactions on all troop members were collected while moving through the troops as part of other data collection protocols. This approach minimized the bias towards recording interactions on the individuals who were easier to find (Carter et al., 2016). Proximity scans on all troop members involved recording the neighbours within 10 m of 'target' individuals chosen from a randomized list of all troop members to ensure sampling independence. Individuals who did not have a neighbour within 10 m were recorded as alone. Target individuals and their neighbours were not resampled within an hour if appearing again in a list. During long resting periods when group membership did not change, observations were ceased until the group moved (and thus individuals mixed again). Young infants were included in the list when they could move independently from their mothers since before that point they share their mothers' networks (Carter et al., 2016). Details on how these data contributed to the behavioural variables tested are indicated below (Supplementary material, section 3).

We adopted a longitudinal approach with repeated measures of individuals within our sample. We divided the data into three time periods of approximately 3 months each: two in 2021 (first and second half of the 6-month field season) and one in 2022. These time windows were selected because they fitted our data resolution and could capture developmental changes. Data of individuals who were present for less than a month in each time period were removed because these data may not be representative of the whole time period (Farine & Whitehead, 2015). These individuals were either born towards the end of a time period (seven), died (three) or emigrated (one) at the beginning of a time period (social network and focal data), or they were no longer followed among immatures (one) because they became adult at the beginning of a time period (focal data). One adult male emigrated between the study troops in 2022, and he was present for about half of the time in each of the two troops. The focal individuals included in a time period had >7 h of observation in that time period.

Social learning behaviours

During focal observations, the frequency of six behaviours indicative of social learning was collected during foraging (that is, feeding or searching for food; Fig. 1), as described in other primate species: 'observe feed', defined as peering for ≥ 3 s at another individual while the latter is foraging (Biro et al., 2003; Schuppli, Meulman, et al., 2016); 'inspect food', defined as manipulating the food accessed by another individual without eating it (Rapaport & Brown, 2008; Schiel & Huber, 2006); 'feed scraps', defined as feeding on the scraps dropped by another individual (Ottoni et al., 2005; Tan et al., 2018); 'sniff mouth', defined as smelling the mouth of another individual (Alberts, 2019; Gunst, Leca, Boinski, & Fragaszy, 2010); 'steal food', defined as grabbing a generally difficult to gain food item in possession of another individual (Brown et al., 2004; Mikeliban et al., 2021); 'coforaging', defined as joining another individual in the same location and foraging on the same food type (species) and item (part of a plant, e.g. pod or berry) as the other individual, within 1 m of the latter (Jaeggi et al., 2010; O'Mara & Hickey, 2012; see the Electronic Supplementary Material for a video on social learning behaviours by A. C.).

The first five social learning behaviours (all but coforaging) were defined as directed (by the immature focal individual) towards one specific individual within a short distance (approximately 0-3 m). Coforaging could be directed towards more than one individual because several individuals could be within 1 m of each other in a patch. The relatively shorter distance threshold of 1 m was selected for coforaging to assess immature's choice of a specific place to forage based on the demonstrator's behaviour and not to simply reflect the preference in association partners (Huchard et al., 2013; King et al., 2009).

For most social learning behaviours (all but 'observe feed'), the demonstrators could be present during the interaction, or they could have just left (within approximately 10 s, seen by the immature before leaving). Considering that chacma baboons live in a highly hierarchical society (King et al., 2008), recording these 'delayed' learning opportunities allowed us to account for instances in which an immature would not approach a more dominant individual or a demonstrator left because a more dominant immature approached.

The social learning behaviours of immatures were divided into two categories based on the type of behaviour: (1) coforaging and (2) other social learning behaviours, including the other five learning behaviours (see above). Coforaging was more frequent than all the other learning behaviours combined (proportion of coforaging = 0.6; other social learning behaviours = 0.4), allowing for separate analyses. To increase data independence, in each of these two categories, observations of the same dyad within the same 30 s were removed. To test our predictions (see below), a binary variable (0 = absent; 1 = present) describing the presence of coforaging and the other learning behaviours given by each immature individual in each focal observation was created. In addition, in each time period, the proportion of coforaging and the other learning behaviours directed to each demonstrator chosen by each immature individual was calculated.

Social networks

Social networks based on proximity and grooming interactions may provide different information (Castles et al., 2014), and both networks play a role in quantifying the association between the immature study subjects and other troop members. Social networks were measured at the immature and troop level. Social networks at the immature level were used to derive proximity and grooming association values between each immature study subject and each other troop member through ego-networks (that is, the vectors that correspond to the square matrix row of each immature individual; Hobson et al., 2013; Turner et al., 2018). Immatures' proximity and grooming ego-networks were produced for each time period within each troop. Both networks were weighted (that is, the values indicate the presence and strength of a social connection; Croft et al., 2011), and the grooming network was directed. For the immatures' proximity ego-networks, the scan samples performed every 5 min during the continuous focal observations were used. During focal scans, the identities of all the neighbours within 5 m of a focal individual and the activity of the focal individual (that is, forage, groom, nurse, play, rest and travel) were recorded. To ensure data independence, one scan was randomly sampled per focal observation. Then, foraging ego-networks were built from scans when the focal individual was foraging. A simple ratio index (SRI, that is, the proportion of time two individuals associated) was used to calculate dyadic weighted connections through the package 'asnipe' (Farine, 2013) and the function 'get_network'. This index is recommended only when individuals can be detected and identified correctly (Hoppitt & Farine, 2018) as is the case at Tsaobis where group membership is stable, and visibility is usually excellent due to low vegetation

Figure 1. Social learning behaviours of wild immature chacma baboons, including (a–e) 'observe feed', (f) 'inspect food', (g–i) 'sniff mouth' and (i–l) 'coforaging'. Photo: E. Fernández-Fueyo (b, d, f, g, i) and V. Roatti (a, c, e, h, j–l).

cover. For the immatures' grooming ego-networks, the frequency of immatures' grooming interactions were recorded during focal observations and ad libitum. To avoid pseudoreplication, a grooming dyad was not recorded more than once within the same half an hour (Carter et al., 2016). Then, the proportion of the total counts of grooming given and received by a focal individual with each other troop member was calculated.

Social networks at the troop level were used to derive individuals' proximity degree, that is, the number of social partners in the proximity network (Sosa et al., 2021). Troop proximity networks were produced from the proximity scan data collected

on all troop members. Network graphs were created from proximity SRI (see above) using the package 'igraph' (Csardi & Nepusz, 2006) and the function 'graph_adjacency'. Then, individuals' degree was derived using the 'degree' function from 'igraph'. To make values comparable across networks of different sizes, they were standardized within each time period by mean-centring them around zero with a SD of one through the function 'scale' (Wey et al., 2008).

Dominance ranks

Dominance behaviours comprised displacements, supplants, threats, chases and attacks (Huchard & Cowlishaw, 2011). These behaviours were recorded during focal observations and ad libitum. However, only one dominance interaction was collected to avoid pseudoreplication, although this interaction involved several dominance behaviours in sequence (Huchard & Cowlishaw, 2011). Dominance ranks were determined for each troop member in each time period using the 'I & SI' method (Schmid & De Vries, 2013). This method is suitable for linear dominance hierarchies (de Vries, 1995; Sánchez-Tójar et al., 2018) and is consistent with other

studies on this population (Huchard & Cowlishaw, 2011). Dominance matrices were tested for triangle transitivity, which is a measure of linearity for large social groups, using the package 'compete' (Curley, 2023) and the function 'ttri' (1000 permutations; Shizuka & McDonald, 2012). The resulting matrices were strongly linear. Ordinal ranks were computed using the function 'isi13' from 'compete' (500 iterations; Sánchez-Tójar et al., 2018; Vilette et al., 2020). Infants ($\leq$12 months old) were involved in very few or no dominance interactions; thus, they were excluded from the rank calculation and assigned one ordinal rank below their mothers' (Lee & Cowlishaw, 2017). Absolute ranks were standardized by controlling for group size using the formula $1 - [(1 - r) / (1 - n)]$, where r is an individual's absolute rank, and n is the group size. Relative ranks range from '0' (lowest) to '1' (highest; Baniel et al., 2018).

Individual data

Age, sex and maternal kinship were determined for all troop members using long-term data. Baboons' ages (in months) were calculated from known and estimated dates of birth. The first case

Table 1
Models' summary

Hypothesis	Predictions	Type	Model dependent variable	Fixed predictors	Fixed controls	Random factors	Sample size/ No. observations	Support
H1: Immatures' social learning opportunities change with age and differ by sex.	P1a: Social learning opportunities will increase during infancy and decrease during juvenile years; P1b: This decrease will be greater in males than in females.	GLMM binomial (link 'logit').	1: Presence/ absence of immatures' coforaging given in each focal observation.	P1a: Immatures' age, age^2; P1b: Age:sex, age^2:sex, sex.	Immatures' rank; time period, troop, observation length.	Immatures' identities nested in the mothers' identities.	53 immatures born from 38 mothers; 4511 observations.	P1a: Yes; P1b: No (immatures' age^2:sex not significant).
			2: Presence/ absence of immatures' other learning behaviours given in each focal observation.					P1a: Partial (immatures' age^2 not significant); P1b: No (immatures' age^2:sex not significant).
H2: Immatures' learning opportunities from different individuals depend on their own age and on the demonstrators' characteristics.	P2a: Learning opportunities from demonstrators in proximity will decrease with immatures' age; P2b: Immatures will prefer demonstrators knowledgeable on local resources (older individuals and philopatric females); P2c: Immatures will prefer tolerant demonstrators (grooming affiliates, low- or similarly ranked individuals).	GLMM binomial (link 'logit') with weights (counts).	3: Proportions of immatures' coforaging given to each demonstrator in each time period.	P2a: Immatures' age, immature –demonstrator dyads' proximity foraging, age: dyads' proximity foraging; P2b: Demonstrators' age and sex; P2c: Dyads' grooming allocation, rank difference.	Immatures' rank, total grooming amount, degree proximity; demonstrators' availability (age); time period, troop.	Immatures' identities nested in the mothers' identities; demonstrators' identities.	52 immatures born from 37 mothers; 142 demonstrators; 1508 observations.	P2a: Yes; P2b: Partial (no effect of demonstrators' sex); P2c: Partial (no effect of dyads' rank difference).
			4: Proportions of immatures' other learning behaviours given to each demonstrator in each time period.				53 immatures born from 38 mothers; 137 demonstrators; 991 observations.	P2a: Yes; P2b: No (no effect of demonstrators' age and sex); P2c: Partial (no effect of dyads' rank difference).

The summary of the models (1–4) used to test the predictions of hypotheses H1 and H2 includes the type of test used, dependent variable, models' fixed factors (predictors and controls) and random factors, sample size and number of observations. The last column indicates whether each prediction was supported and, if not or only partially, how. H1 models (1 and 2) were run as full models, whereas the variables of H2 models (3 and 4) were selected using an information-theoretic approach.

was applied to births occurring during fieldwork. In the second case, when births occurred in between field seasons, the dates of birth were estimated on the basis of (1) the observation of infants' coloration (Dezeure, Dagorrette, Baniel, Carter, Cowlishaw, Marshall, Martina, Raby, & Huchard, 2021), (2) possible infants' conception dates from consortship records (that is, mate-guarding events at the peak of a female's fertility; Alberts & Fitzpatrick, 2012) after which a female did not menstruate and assuming a pregnancy duration of 6 months (Altmann et al., 1978), or (3) for individuals not observed as infants (eight), dentition (molar emergence and wear; Huchard et al., 2009). For all individuals, age was calculated as the number of months at the date midpoint (median) of each time period. Sex and the identity of an infant's mother were assigned when an infant was first identified through direct observation (nursing). Maternal relatedness for each dyad was represented by a three-level coefficient: '0' for nonrelatives, '0.5' for mother−offspring dyads and '0.25' for half siblings (Grampp et al., 2019). Other levels of maternal relatedness were not considered in this study because the grandmothers' identities were not available for a part of the individuals.

Data Analyses

Statistical models

Data analyses were performed using R 4.0.3 (R Core Team, 2022) with α set at 0.05 (Chowdhury & Turin, 2020; Tredennick et al., 2021). To test our predictions, generalized linear mixed-effect models (GLMMs) with the function 'glmer' from the package 'lme4' were used (Bates et al., 2015). A total of four binomial 'logit' models were built (see below and Table 1, including the sample size and number of observations for each model), which are recommended to fit dependent variables with ≤ 2 categories that are binary (H1) or proportions derived from counts (H2; Douma & Weedon, 2019). R^2 values (coefficient of determination) were obtained from the package 'MuMIn' (Bartoń, 2022) and the function 'r.squaredGLMM'. Before running the models, we checked for independent variables' linear correlations by computing their Pearson's correlation coefficients (r; Thomas et al., 2015). Variables with $r \geq 0.5$ were not included in the same model (Dormann et al., 2013; Suzuki et al., 2008; Supplementary material, section 4). In addition, multicollinearity was assessed after running the models using variance inflation factors (VIFs) with the package 'car' (Fox et al., 2023) and the function 'vif'. In all cases, VIFs were <3, indicating low collinearity (Dormann et al., 2013). Under or overdispersion values were verified using the package 'DHARMa' (Hartig, 2022) and the function 'testDispersion'. In all cases, significant dispersion values ranged from 0.7 to 2, indicating a normal degree of variation for a binomial distribution (Thomas et al., 2015). The overall model fit was also checked plotting simulated residuals with the function 'simulateResiduals' from 'DHARMa'. When singular fits were obtained, the problematic random factors were initially identified using the function 'rePCA' from 'lme4', and then the results were confirmed by rerunning the models without those random factors (Burrow & Maerz, 2021; Oberpriller et al., 2022). For each model variable, the odds ratios (OR) and the 97.5% CIs were obtained. OR represents the strength of the association between an exposure (independent variable) and an outcome (dependent variable). When OR = 1 or CIs cross one, no relationship is found between the exposure and the outcome (no change); when OR are <1 or >1 (and CIs do not cross one), the exposure is associated with lower or higher odds of the outcome, respectively (George et al., 2020; Szumilas, 2010). The percentage change in OR per unit variation in an independent variable was expressed as (OR − 1) × 100. In the presence of an interaction, the main effects were interpreted as conditional effects (Bauer & Curran, 2005; Brambor et al., 2006).

In all models, we controlled for the following independent variables: considering that dominance rank may affect the opportunities to acquire social information (King et al., 2009; Marshall et al., 2012), immatures' rank was included as a fixed factor. To control for differences in food availability between years and seasons, as well as for differences between the two troops, the (categorical) time period ('1' winter 2021; '2' summer 2021; '3' winter 2022) and troop ('J' and 'L') were included as fixed factors (<5 levels; Harrison et al., 2018). Our data have repeated measures from the same individuals through time; thus, the immatures' identity and the identity of their mothers were included as random factors. Immatures' identities were nested within their mothers' identities because maternal behaviour could affect the offspring's sociality (Maestripieri, 2018). Other independent variables specific to each hypothesis were added to test the outlined predictions. Model selection varied between H1 and H2 depending on the aim of each hypothesis' test (see below).

Testing H1: Age and sex changes in learning opportunities

Two models were built to test our predictions for hypothesis H1. The dependent variables included the binary outcome (0/1) of the presence of either (model 1) coforaging or (model 2) other social learning behaviours given by each immature in each focal observation. Considering that most observations had either no social learning behaviours or one behaviour, we opted for a binary dependent variable instead of a count (Supplementary material, section 5). Both models had the same independent variables as fixed factors. To test for P1a, that is, social learning opportunities increase during infancy and decrease during juvenile years, immatures' linear age (continuous) and quadratic age (to model a nonlinear relationship with learning presence) were included as predictors using orthogonal second-degree polynomials (Thomas et al., 2015). To test for P1b, that is, the decrease in social learning opportunities with age will be greater in males than in females, the interactions between age (linear and quadratic) and sex (the latter was also added as a main factor) were added as predictors. Apart from the abovementioned control variables, we controlled for observation length as a continuous fixed factor.

For H1, we were interested in the effects of specific variables on social learning opportunities (that is, age, sex and their interaction, based on our predictions; rank, for its importance to baboon society). Thus, 'full models' were presented: the models did not undertake any a posteriori simplification procedure (Chowdhury & Turin, 2020; Tredennick et al., 2021). The predicted values were derived using the package 'ggeffects' (Lüdecke, 2018) and the function 'ggpredict'. The differences in OR from one age (t_0) to another (t_1) were expressed as increase/decrease percentages using the formula $[(OR t_1 − OR t_0 / OR t_0)] \times 100$. Two age periods were selected on the basis of the literature: (1) 1 year old, when infant baboons are weaned or almost weaned (Huchard et al., 2013) but still spent most of the time with the mother (Altmann, 1980; Roatti et al., 2023), and (2) 4 years old, when immatures should be fully foraging competent and have formed their own social relationships (Johnson & Bock, 2004; Roatti et al., 2023). CIs were derived using the function 'confint.merMod' from 'lme4' with the 'Wald' method.

Testing H2: Demonstrators' choice

To test our predictions for hypothesis H2, another two models were built. The dependent variables were (model 3) the proportion of the number of coforaging events directed by each immature to each demonstrator in each time period over an immature's total coforaging and (model 4) the proportion of the number of other social learning behaviours directed by each immature to each demonstrator in each time period over an immature's total

number of these learning behaviours. The total counts associated with these proportions were included as weights (Thomas et al., 2015). Both models had the same independent variables as fixed factors. To test for P2a, that is, learning opportunities from individuals in proximity decreases with immatures' age, the interaction between immatures' age and the proximity foraging ego-network value (SRI) correspondent to the immature−demonstrator dyad (which were also included as a main continuous factors) were included as predictors. To test for P2b, that is, immatures prefer demonstrators who are knowledgeable on local resources, such as older individuals and the philopatric sex (females), the demonstrators' age (continuous) and sex were included as predictors. To test for P2c, that is, immatures prefer tolerant demonstrators, such as close kin, grooming affiliates and low- or similarly ranked individuals, a dyad's grooming (total) ego-network value (grooming allocation) and their relative rank difference (ΔRR = immature's rank − demonstrator's rank) were included as predictors. The latter served to check whether the rank of the demonstrator tends to be relatively lower (ΔRR positive) and for immature−demonstrator rank similarity (ΔRR close to zero). For the last prediction (P2c), maternal relatedness was not included because it was strongly and positively correlated with the proportion of grooming total (Supplementary material, section 4), in accordance with the preference of matriline members to groom together (Charpentier et al., 2012; Kulik et al., 2015). Therefore, we prioritized testing for learning from grooming affiliates, who include maternal kin and other closely bonded individuals. However, to control for the importance of within-matriline bonds, the number of matriline members (that is, the mother and maternal siblings) per time period was included as a continuous fixed factor. In addition, we controlled for the following variables as continuous fixed factors: immatures' total amount (count) of grooming given and received in each time period (because the overall grooming effort could influence the dyadic grooming allocation), immatures' proximity degree in each time period (because the number of proximity social partners may affect the dyadic network association) and the proportion of individuals of a certain age in each troop/time period to control for demonstrator availability. Finally, the demonstrators' identity was included as a random factor to control for repeated learning from the same individuals. Considering that immatures' sex was correlated with the total amount of grooming (Supplementary material, section 4), it was not included in the models. Thus, we ran the models with a full dataset (both sexes, see below) and for females and males separately to determine potential sex differences. The results of the sex-separated models were qualitatively similar to those of the combined-sexes models (Supplementary material, section 6). Whether our results on coforaging were affected by circularity was further verified because coforaging is defined as foraging within 1 m of another individual, and our coforaging model included a dyad's foraging proximity among the predictors. We ran another model substituting foraging proximity with the proximity outside of a foraging context (that is, during grooming, playing, resting and travelling). The results of this alternative model and the main coforaging model were qualitatively similar, indicating that circularity was not a concern (Supplementary material, section 8).

For H2, we were interested in finding the 'best model' explaining the distribution of immatures' social learning opportunities towards different individuals. Considering the great number of factors potentially involved in explaining immatures' choice of demonstrators, we needed to select which variables to include in the final models. Thus, we adopted an information-theoretic approach (Chowdhury & Turin, 2020; Tredennick et al., 2021) based on the Akaike's information criterion (AIC; Anderson et al.,

2000). To compare the effects of different predictors, we first standardized the models' independent variables with a mean of zero and SD of 0.5 using the package 'arm' (Gelman & Su, 2022) and the function 'standardize'. Then, we used the function 'dredge' from 'MuMIn' to calculate the AICc values (corrected for small sample size) and weights (that is, models' relative likelihood) for a set of candidate models (Symonds & Moussalli, 2011; Thomas et al., 2015). To compare the biologically plausible models (Burnham et al., 2011), we constrained the model set to include fixed variables (that is, present in all models) and subset models that included controls for specific variables. The fixed variables were immatures' age (to control for the decrease in social learning with age), a dyad's proximity during foraging (SRI; to test for the effect of demonstrators' characteristics independently from association patterns), immatures' proximity degree (the number of partners being a control for dyads' SRI) and their number of matriline members (to control for the effect of these bonds on social learning), time period and troop. We additionally subset models that included either one of immatures' rank or a dyad's rank difference. The two variables could not be present together because they were correlated with each other (Supplementary material, section 4), but one of the two needed to be present to control for the effect of immatures' rank on learning opportunities (Marshall et al., 2012). Finally, we constrained the proportion of individuals of a certain age and immatures' total grooming amount (controls) to be present together with demonstrators' age and a dyad's grooming proportion, respectively (Supplementary material, section 7). Then, we selected and averaged the best models, with ΔAICc < 7 (including those with a sum of weights of <0.95), using the functions 'get.models' and 'model.avg' from 'MuMIn' (Burnham et al., 2011). We interpreted the results derived from the full average (that is, an estimate of zero is added in models where a variable is absent) to determine which factors have the strongest effect on the proportion of social learning (Grueber et al., 2011). CIs were calculated using the function 'confint.default'. We assessed the relative importance of each independent variable (RVI) by summing its best models' Akaike weights. RVI equals to 1 indicates that the variable is present in all the best models, which explains a large part of the variance in the dependent variable (Grampp et al., 2019).

Ethical Note

This study was strictly observational and dependent on behavioural data collected noninvasively on animals well habituated to human observers. Our research procedures were evaluated and approved by the Ethics Committee of the Zoological Society of London and the Ministry of Environment and Tourism, Namibia (MET Research/Collecting Permits: RPIV00392018). Our study was conducted in accordance with the ASAB/ABS Guidelines for the Treatment of Animals in Behavioural Research and Teaching.

RESULTS

Results H1: Age and Sex Changes in Learning Opportunities

To address our first hypothesis, we tested how immatures' social learning opportunities changed with (P1a) age and (P1b) sex (Table 2; model 1, coforaging; model 2, other learning behaviours; see Tables S13 and S14 in supplementary material, section 8, for the full tables, including control variables). Our first prediction for H1, P1a, was partially confirmed: coforaging significantly increased up to weaning age and then decreased during juvenescence (Fig. 2a); by contrast, the other social learning behaviours significantly and linearly decreased with age, but the quadratic age effect was not significant (Fig. 2b). Between 1 and 4 years old, the

Table 2
Models' results for hypotheses H1 (full models) and H2 (averaged models)

Model	Variable	Estimate	SE	z value	P	OR	LCI	UCI	Percentage change
1	**Age immature**	**−11.3419**	**4.7092**	**−2.4085**	**0.016**	**0.00**	**0.00**	**0.46**	**−100.00**
	Age:Sex	1.1684	7.4901	0.1560	0.876	3.22	0.00	6.29E + 07	221.69
	Age² immature	**−18.6803**	**3.9576**	**−4.7201**	**<0.001**	**0.00**	**0.00**	**0.00**	**−100.00**
	Age²:Sex	6.3010	6.2056	1.0154	0.310	545.09	0.00	5.99E + 08	5.44E + 04
	Rank immature	**0.7648**	**0.2262**	**3.3805**	**<0.001**	**2.15**	**1.29**	**3.57**	**114.85**
	Sex immature	0.0116	0.1176	0.0987	0.921	1.01	0.78	1.32	1.17
2	**Age immature**	**−16.1940**	**3.7098**	**−4.3652**	**<0.001**	**0.00**	**0.00**	**0.00**	**−100.00**
	Age:Sex	−11.8188	6.0851	−1.9422	0.052	0.00	0.00	6.17	−100.00
	Age² immature	−3.9443	3.4911	−1.1298	0.259	0.02	0.00	48.46	−98.06
	Age²:Sex	1.6544	5.7195	0.2893	0.772	5.23	0.00	1.93E + 06	423.00
	Rank immature	0.1907	0.1877	1.0159	0.310	1.21	0.79	1.84	21.01
	Sex immature	−0.0601	0.0932	−0.6456	0.519	0.94	0.76	1.16	−5.84
3	**Age demonstrator**	**−0.1238**	**0.0642**	**1.9275**	**0.054**	**0.88**	**0.79**	**0.96**	**−11.65**
	Age immature	**0.5975**	**0.0652**	**9.1520**	**<0.001**	**1.82**	**1.60**	**2.07**	**81.75**
	Age:Proximity	**−0.5542**	**0.1050**	**5.2755**	**<0.001**	**0.57**	**0.47**	**0.71**	**−42.55**
	Groom. Allocation	**0.5049**	**0.0417**	**12.1068**	**<0.001**	**1.66**	**1.53**	**1.80**	**65.68**
	Prox. Foraging	**0.4776**	**0.0634**	**7.5235**	**<0.001**	**1.61**	**1.42**	**1.83**	**61.22**
	Rank immature	**−0.2752**	**0.0661**	**4.1609**	**<0.001**	**0.76**	**0.67**	**0.86**	**−24.06**
	Sex demonstrator	0.0191	0.0400	0.4759	0.634	1.02	0.95	1.16	1.92
4	Age demonstrator	−0.0059	0.0294	0.1992	0.842	0.99	0.84	1.10	−0.58
	Age immature	**0.7488**	**0.0852**	**8.7773**	**<0.001**	**2.11**	**1.79**	**2.50**	**111.45**
	Age:Proximity	**−0.5329**	**0.1539**	**3.4580**	**<0.001**	**0.59**	**0.43**	**0.79**	**−41.31**
	Groom. Allocation	**0.6557**	**0.0519**	**12.6292**	**<0.001**	**1.93**	**1.74**	**2.13**	**92.64**
	Prox. Foraging	0.1608	0.1067	1.5049	0.132	1.17	0.95	1.45	17.44
	Rank difference	−0.0329	0.0580	0.5669	0.571	0.97	0.82	1.07	−3.24
	Rank immature	−0.0220	0.0527	0.4171	0.677	0.98	0.83	1.09	−2.18
	Sex demonstrator	0.0145	0.0489	0.2962	0.767	1.01	0.90	1.23	1.46

The variables of interest shown (depending on the model) include immatures' linear (H1 and H2) and quadratic (H1) age; immatures' sex (male) and age−sex interactions (':', H1); immatures' rank (H1 and H2); demonstrators' age and sex (male, H2); a (immature−demonstrator) dyad's grooming (Groom.) allocation; proximity (Prox.) in the foraging network and rank difference (H2). The estimate, SE, z value, P value, the odds ratios (OR), the lower (LCI) and upper (UCI) 97.5% CIs and the percentage change in the odds of coforaging (models 1 and 3) and performing other social learning behaviours (models 2 and 4) at the increase of one unit (models 1 and 2) or SD (models 3 and 4) in the independent variable are shown for each variable/model. The variables that have an effect on the response are shown in boldface.

odds of coforaging decreased by 41.8% and 35.6% in females and males, respectively; the odds of performing other learning behaviours decreased by 41.6% and 58.6% in females and males, respectively. Our second prediction, P1b, was not supported: the interactions between age (linear and quadratic) and sex were not significant in either model. Immature's rank, which had a significant effect only in the coforaging model, was the variable affecting immatures' odds of coforaging the most, whereas age had the strongest influence on immatures' odds of performing other learning behaviours (Supplementary material, section 9). In particular, high-ranking immatures were relatively more likely to coforage with others (Fig. 2c): With the increase of one rank position, the odds of coforaging increased by 114.9%. The raw data plot of a single social learning behaviour (Fig. 2d) shows that 'sniff mouth' had a similar developmental pattern as coforaging, increasing up to weaning age before decreasing, whereas all other behaviours declined throughout immatures' growth. During and after weaning, the most common behaviour was coforaging, followed by 'observe feed' and 'sniff mouth' at much lower but roughly equal frequencies.

Results H2: Demonstrators' Choice

To address our second hypothesis, we tested whether immatures preferred to learn from (P2a) individuals in proximity at different ages, (P2b) older and philopatric (female) individuals, (P2c) grooming affiliates and low- or similarly ranked individuals (Table 2; model 3, coforaging; model 4, other learning behaviours; see Table S15 in supplementary material, section 8, for the full tables, including control variables). The best models comprised all the predictors (that is, all fixed factors that were not already

constrained to appear in all candidate models) except for the rank difference between the immature and the demonstrator, which was included in the best models for the other social learning behaviours but not in the best models for coforaging. Among the unconstrained variables, the interaction between immatures' age and a (immature−demonstrator) dyad's proximity during foraging and a dyad's grooming allocation were present in all of the best models (RVI = 1), for coforaging and the other learning behaviours, whereas the immatures' rank was present in all of the best coforaging (but not the other learning behaviours) models (Table 3).

The results of the (final) averaged models yielded variable support to our predictions (Fig. 3). First, our P2a prediction was confirmed: the odds of coforaging with and performing other learning behaviours towards individuals in proximity decreased by 42.5% and 41.3%, respectively, with each increase in one SD in immatures' age (approximately 16 months). In addition, immatures' age had the strongest effect on the odds of learning from a particular demonstrator in both models. For one SD increase in immatures' age, the odds of coforaging with and performing other learning behaviours towards a certain demonstrator increased by 81.8% and 111.5%, respectively. A dyad's proximity during foraging had an effect on the immatures' odds of coforaging but not on the odds of performing other learning behaviours (CIs crossing 1). For one SD increase in the proximity index (approximately 0.1) between an immature and a demonstrator, the odds of coforaging increased by 61.2%. Second, our P2b prediction was partially supported: a demonstrator's sex did not affect the immatures' odds of coforaging or the odds of performing other learning behaviours; a demonstrator's age, which was included in most of the best coforaging models (RVI = 0.9), only affected the immatures' odds
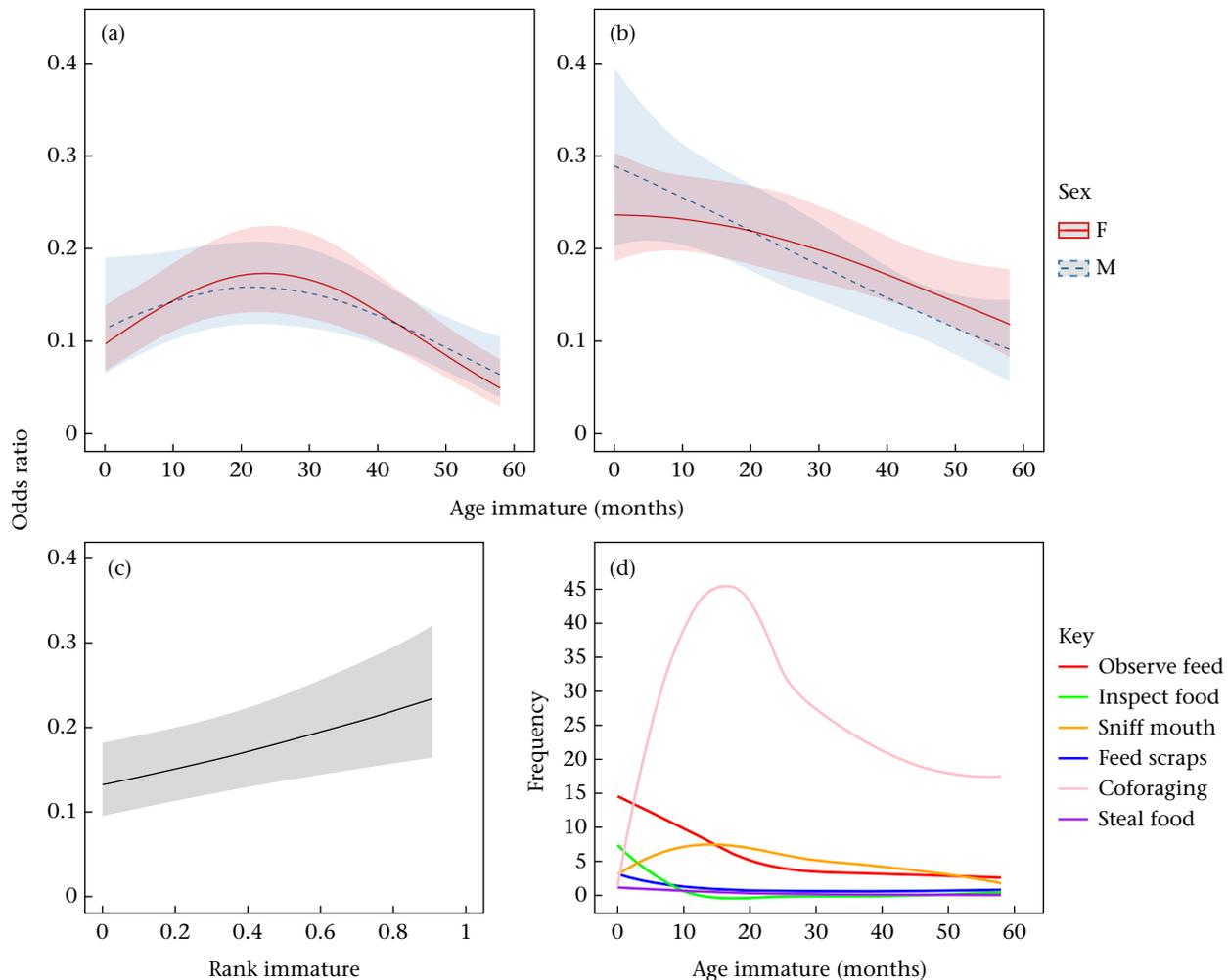
Figure 2. Significant results of hypothesis H1 models for (a, c) coforaging and (b) other social learning behaviours. The results include immatures' age changes in the odds of (a) coforaging and (b) performing other social learning behaviours for females (F) and males (M); (c) changes in the odds of coforaging with immatures' rank. Higher odds ratios indicate a relatively higher likelihood of an event (*y*-axis variable) to occur. Ribbons represent 97.5% CIs. The last section (d) shows the age changes in learning behaviours (arranged on the basis of their appearance on the *y*-axis) from raw data (behaviours summed across focal individuals in each time period). The weaning period is between 12 and 18 months of age.

Table 3
Relative importance of model variables

Model	Variable	RVI
3	Age demonstrator	0.89
	Age immature	**1.00**
	Age:Proximity	**1.00**
	Groom. Allocation	**1.00**
	Prox. foraging	**1.00**
	Rank immature	**1.00**
	Sex demonstrator	0.37
4	Age demonstrator	0.13
	Age immature	**1.00**
	Age:Proximity	**1.00**
	Groom. Allocation	**1.00**
	Prox. foraging	**1.00**
	Rank difference	0.54
	Rank immature	0.46
	Sex demonstrator	0.30

The relative importance of the variables of interest (RVI), including immatures' age and rank; demonstrators' age and sex (male); a (immature−demonstrator) dyad's grooming (Groom.) allocation; proximity (Prox.) in the foraging network and rank difference, of hypothesis H2 averaged models (model 3: coforaging; model 4: other social learning behaviours) is presented. The variables present in all best models (RVI = 1) are shown in boldface.

of coforaging, with an opposite trend compared with what we predicted. Indeed, the odds of coforaging with a certain demonstrator decreased by 11.7% with an increase in one SD (approximately 50 months) in demonstrators' age. Third, our P2c prediction was partially supported. As predicted, a dyad's grooming allocation had an effect on both models: the odds of coforaging and performing other learning behaviours increased by 65.7% and 92.6%, respectively, with a one SD increase (approximately 0.1) in grooming allocation. However, a dyad's rank difference had no effect in either model, which does not support the second part of our P2c prediction. Finally, high-ranking immatures were relatively less likely to learn from a specific demonstrator, but rank had an effect only for the coforaging model: the odds of coforaging with a certain demonstrator decreased by 24.1% with an increase in one SD (approximately 0.2) in immature's rank.

DISCUSSION

In this study, we explored social learning opportunities during foraging in wild immature chacma baboons. We found that weaning-age immatures had more opportunities to learn from others than older ones. In chacma baboons' despotic society, social
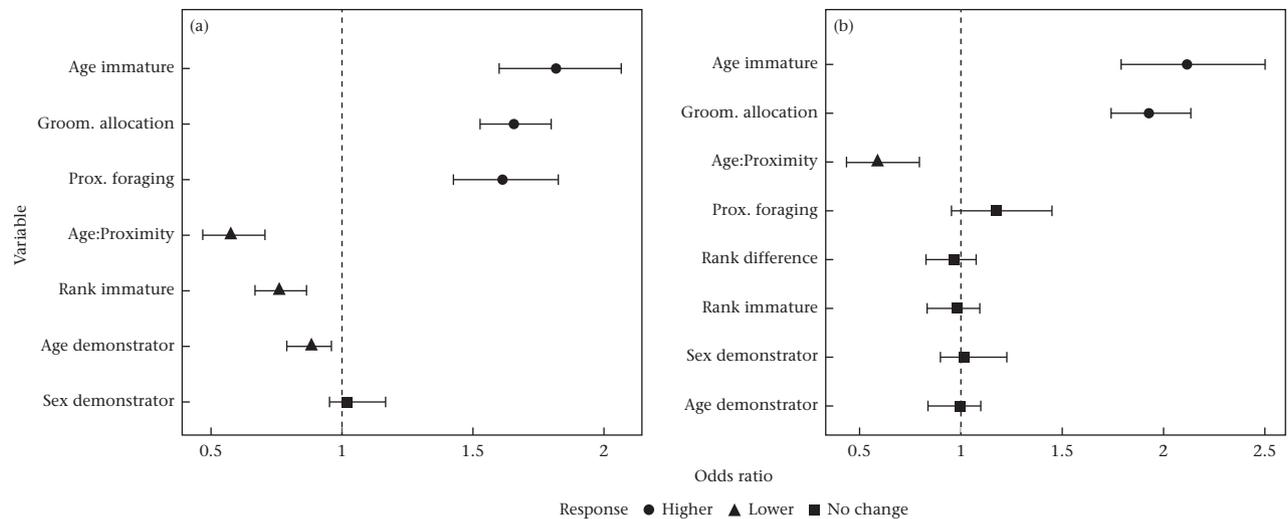
Figure 3. Results of hypothesis H2 averaged models for (a) coforaging and (b) other social learning behaviours. The variables of interest (arranged on the basis of the effect size) include immatures' age and rank; demonstrators' age and sex (male); a (immature−demonstrator) dyad's grooming (Groom.) allocation; proximity (Prox.) in the foraging network and rank difference. The points of the independent variables represent odds ratios, and the whiskers indicate 97.5% CIs. The points have different shapes depending on whether their CIs overlap with 1 (the odds of learning from a certain demonstrator, that is, the response, do not change when the independent variable increases), they are <1 (the response decreases when the independent variable increases) or they are >1 (the response increases when the independent variable increases).

affiliation, through spatial proximity and grooming, played an important role in determining immatures' social learning opportunities. Targeting tolerant individuals limited the learning opportunities of low-ranking immatures more than those of high-ranking ones. Here, we discussed our results and commented on the potential implications of the observed patterns on social information transmission at the group level.

Age Changes in Immatures' Social Learning Opportunities

We found that the social learning opportunities of immature baboons heightened around the weaning period but decreased during the juvenile years. Our results are consistent with the current literature describing social learning changes during infancy and juvenescence, thereby supporting the hypothesis that young immatures learn from others more than older ones to reach foraging independence when they cease to be nursed (Bray et al., 2018; Carvajal & Schuppli, 2022). Infant baboons start to feed on solid food when they are around 3 months old (Altmann, 1980) and are weaned between 12 and 18 months at Tsaobis (Carboni et al., 2022; Huchard et al., 2013). Accordingly, the odds of coforaging, which involved the ingestion of solid food, were relatively low for young infants, but they increased throughout infancy until weaning age before declining. By contrast, the odds of performing other social learning behaviours, which mainly represented opportunities to collect foraging-related information, were relatively high from a young age, and they decreased steadily throughout the immature period. Alternatively, or complementary, explanations to our results may involve immatures' social connectedness and social tolerance from other group members rather than social learning. We discussed our results in light of these two possible explanations (that is, social learning and other social aspects). Nevertheless, the weaning-centred timing of baboons' learning behaviours indicates that the need of immatures to learn from others at this transitional time in their lives may not be excluded as an explanation of the observed patterns (Carvajal & Schuppli, 2022). Indeed, these behaviours were linked to social learning in numerous studies (Schuppli & van Schaik, 2019; Whiten & van de Waal, 2018).

In our sample, coforaging and sniffing others' mouths increased until weaning and decreased gradually during juvenescence. Coforaging was the most common learning behaviour, followed by sniffing others' mouths. The link between coforaging and social information use (e.g. about patch location and patch quality) has been supported by a wide range of empirical studies (Rieucau & Giraldeau, 2011), including on this population (King et al., 2009; Lee & Cowlishaw, 2017), where the use of social information when coforaging was confirmed experimentally (Carter et al., 2016; Lee & Cowlishaw, 2017). In addition, coforaging may aid the acquisition of a demonstrator's (e.g. the mother) diet, independently from encountering a similar food availability (Bornean orangutans: Jaeggi et al., 2010; ring-tailed lemurs, *Lemur catta*: O'Mara & Hickey, 2012). Sniffing others' mouths is common in baboons (Alberts, 2019; Cheney & Seyfarth, 2007), and this behaviour may drive immatures' foraging choices. For example, dogs, *Canis familiaris* (Lupfer-Johnson & Ross, 2007), and brown rats, *Rattus norvegicus* (Galef & Wigmore, 1983), interacting with another individual who had previously been fed preferred to eat the food with the same flavour as the one eaten by the first individual.

Immature baboons' observation of others during foraging, the inspection of food items accessed by others and feeding on food gained by others decreased gradually during development. The observation of others during foraging, which can occur while infants are still carried by their mothers, was higher than coforaging until approximately 3 months of age, when baboons start to feed on solid food (Altmann, 1980). Instead, the inspection of food items accessed by others and feeding on food gained by others, in the form of feeding on scraps or tolerated stealing (Brown et al., 2004), were relatively uncommon in our study. The observation of others has been related to how much immatures need to learn: observation increases with food processing complexity but decreases with an item's frequency in the diet and immatures' increasing foraging competence, thereby increasing access to the same kind of items or locations, independently from their availability in the environment (eastern chimpanzees, *P. t. schweinfurthii*: Lamon et al., 2018; orangutans: Schuppli, Meulman, et al., 2016; and marsh harriers, *Circus aeruginosus*: Kitowski, 2009). Inspecting food manipulated by others rapidly decreased in our study when infant baboons started coforaging. Given that baboons do not use

tools for foraging and difficult-to-access foods may be rare in their diet (Cheney & Seyfarth, 2007) compared with species that regularly process embedded food items (nut-cracking in capuchins: Ottoni & Izar, 2008; and western chimpanzees, *P. t. verus*: Biro et al., 2003), infant baboons may be more likely to feed on a food item than inspect it. For the same reasons, immature baboons fed on foods already acquired by others only for a small variety of food types probably because of difficulty in gaining those food types on their own (Supplementary material, section 10). These 'food transfers' have been related to the need of immatures to learn rather than their nutritional requirements because they occur mainly when the food is difficult to access, independently from its quality, decrease with the increase of foraging competence (eastern chimpanzees: Mikeliban et al., 2021; orangutans: Jaeggi et al., 2008) and may affect immatures' independent foraging choices (golden lion tamarins, *Leontopithecus rosalia*: Troisi et al., 2021; meerkats: Thornton, 2008).

The age changes in baboons' social learning behaviours indicate that immatures' social learning opportunities remained high after weaning before they gradually decreased. Immature baboons' learning from others may continue beyond the weaning period to acquire the species' full dietary repertoire (Carvajal & Schuppli, 2022) and refine their knowledge of the characteristics indicating profitable foraging patches (marsh harriers: Kitowski, 2009; chacma baboons: Johnson & Bock, 2004). In particular, although juvenile baboons may have acquired knowledge about the most common food items before being weaned, because of their broad and flexible diet, they may encounter rare or seasonal foods for the first time only during juvenescence (Alberts, 2019). In addition, our study population's overall range covers an area of approximately 20 km^2, with seasonal and year-to-year changes in area use from both troops. Therefore, immatures may still learn about the location of profitable foraging patches throughout juvenescence. The relatively lower social learning levels during juvenescence may foreshadow adults' lower reliance on social information during foraging compared with immatures, although the use of social cues to gauge food availability and quality remains an active strategy throughout the lifespan (Danchin et al., 2004; Thornton & Clutton-Brock, 2011).

Alternatively, or complimentary, an explanation for the weaning-age–centred patterns of social learning behaviours observed in this population could be that, at weaning age, individuals experience social conditions that facilitate learning from others (van Boekholt et al., 2021). Therefore, weaning-age immatures may perform more social learning behaviours not because they are actively acquiring, applying and exploiting social information but because they 'can' perform these behaviours based on their young age. Compared with older juveniles, infants and young juveniles have more proximity associates (Roatti et al., 2023; Turner et al., 2025; Vilette et al., 2022) and, hence, more individuals to whom they direct learning behaviours. However, social connectedness did not appear to drive the age changes in immatures' social learning behaviours (Supplementary material, section 11), which could indicate that younger immatures perform more social learning behaviours than older ones because of their greater need to learn. This finding was also supported by our results on the effects of immatures' sex and dominance rank. In addition, considering that younger immatures are granted a higher social tolerance from other group members (Pereira, 1988b; Tarnaud & Yamagiwa, 2008), their opportunities to perform some social learning behaviours may be higher than those of older juveniles. For example, social tolerance may play an important role in determining immature baboons' coforaging opportunities because coforaging requires direct competition for or sharing of a resource, thereby reducing demonstrators' feeding efficiency (Lee & Cowlishaw, 2017; Marshall et al., 2015). Consequently, grooming affiliation with a demonstrator and a younger demonstrator age (promoting tolerance) could be more important in explaining immatures' coforaging choices, rather than to whom they direct other social learning behaviours, which mostly do not involve direct resource competition. However, grooming affiliation with a demonstrator and a younger demonstrator age were similarly important in determining immatures' demonstrator preferences both for coforaging and for the other learning behaviours. This finding may indicate that familiarity with a demonstrator, whether they are grooming partners or individuals of similar age (potentially play partners), may promote social learning in a way that is not exclusively dependent from social tolerance (Laland, 2004). For example, deer mice, *Peromyscus maniculatus*, who previously observed conspecifics adopting defensive responses to biting flies, showed increased self-burying, during exposure to inactive biting flies (mouth removed), when the 'demonstrators' observed were familiar individuals compared with unfamiliar ones (Kavaliers et al., 2005).

Immatures' Choice of Demonstrators

Three main factors affected immature baboons' demonstrator preferences: immatures' age, social affiliation with a demonstrator and demonstrators' age. First, as predicted, learning opportunities from individuals in proximity decreased with age, independently from the number of partners with whom immatures associated; as they aged, immatures' learning opportunities shifted from a wide range of individuals to specific demonstrators. Second, as predicted, immature baboons had relatively more opportunities to learn from individuals who were closer in their proximity and grooming networks. Third, contrary to our prediction, immatures chose young over older, hypothetically more experienced, demonstrators.

Infants and young juveniles tend to be constrained by the proximity of caring figures for nurture and agonistic support when their dominance rank is not yet established (Bateson, 1994; Holekamp & Smale, 1991). Therefore, infants and young juveniles may learn from anyone in proximity, which will usually be individuals from their mother's network (vervet monkeys: Grampp et al., 2019; long-tailed macaques, *M. fascicularis*: Tan et al., 2018), such as maternal kin (Holekamp et al., 1997; Silk et al., 2010). The tolerance of close kin may allow youngsters to exploit foraging resources that they could not access on their own (Chapais & Belisle, 2001; Silk, 2009). For example, juvenile baboons associating with their mother and father feed on relatively higher quality patches and foods (olive baboons, *P. anubis*: Lynch et al., 2020; chacma baboons: Huchard et al., 2013). Conversely, older juveniles may actively look for specific demonstrators apart from their regular foraging associates (vervet monkeys: Grampp et al., 2019; bottlenose dolphins: Mann et al., 2007). Because, compared with younger immatures, older juveniles tend to be less bonded to maternal kin (Gibson & Mann, 2008; Roatti et al., 2023), and their proximity may be less tolerated by others (Pereira, 1988a; 1988b), their learning opportunities may be limited to fewer tolerant demonstrators (Lonsdorf & Bonnie, 2010).

Grooming affiliation was more important than spatial proximity in determining immatures' choice of demonstrators across age stages. Immature baboons had relatively more opportunities to learn from their grooming partners, irrespective of how much grooming they gave and received. Considering that grooming can be traded for tolerance by primates living in despotic societies (Borgeaud & Bshary, 2015; Marshall et al., 2012), sharing strong grooming bonds may enable immatures to access better learning and foraging opportunities independently from their kinship and

dominance relationships (long-tailed macaques: Tan et al., 2018; tufted capuchins: Coelho et al., 2015). The adult chacma baboons from our study population coforage with close grooming partners, regardless of kin bonds (King et al., 2009, 2011); and grooming affiliation reduces the agonism received by low-ranking baboons during foraging (Marshall et al., 2015). Concurrently, some grooming tolerance may derive from nepotism (Chapais & Belisle, 2001; Silk, 2009) because, in matrilineal societies, close maternal relatives preferentially groom together (Charpentier et al., 2012; Kulik et al., 2015). Immatures' grooming allocations were positively correlated with maternal relatedness (Spearman rank correlation: $r_s = 0.4$, $N = 2780$, $P < 0.001$). These results are consistent with the hypothesis that social tolerance enhances social information transmission (Bonnie & de Waal, 2006; Pasquaretta et al., 2014), which was also supported by our findings on demonstrators' age.

Immature baboons had relatively more opportunities to learn from other immatures and young sub/adults, independently from their shared proximity and grooming associations. Considering that the distribution of the immature–demonstrator age differences peaked around zero, with most values within a 60-month age difference (Supplementary material, section 6), the preferred demonstrators included the younger age classes independently from their availability in the troop. We expected that, when gathering social information, immatures would choose older demonstrators, who are knowledgeable about the local food resources (Lonsdorf & Bonnie, 2010). However, considering that baboons do not need extensive experience in food processing skills (Cheney & Seyfarth, 2007), immatures may not target older demonstrators as in species that regularly extract embedded foods (long-tailed macaques: Tan et al., 2018; tufted capuchins: Coelho et al., 2015). Instead, immatures could choose demonstrators of their age because they are among their play partners (Cheney, 1978; Owens, 1975) and are, thus, more tolerant towards them (Shimada & Sueur, 2017). Social play, which, in primates, decreases with age as grooming increases during the immature years, may have the same social bonding function as grooming for juveniles (Shimada & Sueur, 2014, 2017), especially for males (Amici et al., 2019; Lonsdorf, 2017).

Effects of Immatures' Sex and Dominance Rank

The sex and dominance rank of immature baboons affected their social learning opportunities and their choice of demonstrators. Although all similarly aged immatures may have an equal need to learn (Carvajal & Schuppli, 2022), sex and rank differences may translate into greater or fewer social learning opportunities. However, our results indicate that male and low-ranking immatures at least partially overcome their phenotypical constraints by being relatively more active in looking for suitable demonstrators, as they have similar social learning opportunities as their female and high-ranking peers. First, considering that baboon females and males are weaned at similar ages at Tsaobis (Carboni et al., 2022), both sexes may need to collect foraging information at the same pace to reach independence (Carvajal & Schuppli, 2022). Although infants of both sexes have a similar social centrality, in female-philopatric species, juvenile males become relatively less integrated in the grooming network and less bonded to their matriline with age (Roatti et al., 2023; Vilette et al., 2022). This change could limit males' choice of tolerant demonstrators from grooming affiliates and maternal kin in proximity, thereby reducing their overall social learning opportunities (Hollén & Manser, 2006). Compared with females, the amount of grooming males shared with an individual was less important in determining their social learning opportunities, and the decrease in learning opportunities from individuals in proximity with age

was more prominent. Nevertheless, the absence of significant sex differences in immatures' social learning opportunities in both models indicates that immature males compensate by looking for different kinds of tolerant demonstrators. In particular, considering that juvenile males engage in more social play than female peers (Amici et al., 2019; Lonsdorf, 2017), they may learn relatively more from play partners, who could constitute a source of affiliates comparable to grooming partners (Shimada & Sueur, 2014, 2017).

Considering the strict hierarchical society of chacma baboons (King et al., 2008; Silk et al., 2017), dominant immatures may have better social learning opportunities because of their greater competitive abilities: they can receive greater agonistic support (Holekamp et al., 1997; Pereira, 1989), which could work as a deterrent against them being attacked (Horrocks & Hunte, 1983; Prud'Homme & Chapais, 1993). Dominant immatures coforaged with others more than low-ranking peers, and, independently from their age and their number of proximity associates, high-ranking immatures had relatively more coforaging partners. The advantage of having a high rank was evident only for coforaging. Unlike the other social learning behaviours, coforaging involves the depletion of another individual's patch, leading to agonistic competition (Lee & Cowlishaw, 2017; Marshall et al., 2012). Given their 'protected' social status, high-ranking immatures may be able to coforage relatively more opportunistically from any available demonstrator (Chapais, 1988; Markham et al., 2015). Conversely, low-ranking peers could benefit relatively more from selecting closely bonded demonstrators, from whom they are less likely to receive agonism during foraging (Borgeaud & Bshary, 2015; Marshall et al., 2015). In a low-competition scenario (other learning behaviours), low-ranking immatures could have had similar social learning opportunities as high-ranking peers by actively searching for more tolerant demonstrators, but this strategy may have been insufficient to offset for their lower social status in a high-competition scenario (coforaging). Similarly, low-ranking chacma baboons in this population maintained stable foraging levels in low- but not in high-competition artificial foraging patches despite their tendency to coforage with grooming affiliates in both cases (Marshall et al., 2015).

Our results could have implications on group-level social information transmission and on the formation of culture in wild social groups. As mentioned, the high propensity of immatures to learn from others could play a fundamental role in the spread of group-level information (Mesoudi et al., 2016). When a behaviour is acquired by most members of a social group and is maintained through time, creating a within-group behavioural conformity, it forms a local culture (Laland & Janik, 2006). However, the presence of social clusters can limit the spread of social information to the whole group. For example, in vervet monkeys, immatures pay more attention to matriline members than to individuals outside their matriline (Grampp et al., 2019; van de Waal et al., 2014). Consequently, behaviours conform at the matriline level rather than at the group level, leading to the formation of 'matrilineal cultures' as opposed to group cultures (van de Waal et al., 2012). In this baboon population, proximity and grooming associations play the most important role in determining immatures' social learning opportunities, indicating that matriline members, who associate and affiliate together (Holekamp et al., 1997; Silk et al., 2010), could be important sources of social information. Therefore, the strong nepotistic biases (Silk et al., 2010) of chacma baboons may limit the transmission of group-level social information and the formation of culture, which is traditionally defined as a group-level phenomenon (Pasquaretta et al., 2014; van de Waal et al., 2012).

Author Contributions

Vittoria Roatti: Writing − original draft, Visualization, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Axelle Delaunay:** Writing − review & editing, Funding acquisition, Data curation. **Guy Cowlishaw:** Writing − review & editing, Project administration, Funding acquisition. **Elise Huchard:** Writing − review & editing, Project administration, Funding acquisition. **Alecia Carter:** Writing − review & editing, Supervision, Project administration, Funding acquisition, Formal analysis, Conceptualization.

Data Availability

The data and R scripts used for this study's analyses are deposited on Zenodo https://doi.org/10.5281/zenodo.17004462. See Roatti et al. (2025).

Declaration of Interest

The authors declare that they have no conflict of interests.

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Supplementary Material

Supplementary material associated with this article is available at https://doi.org/10.1016/j.anbehav.2025.123463.

References

Alberts, S. C. (2019). Social influences on survival and reproduction: Insights from a long-term study of wild baboons. *Journal of Animal Ecology, 88*(1), 47−66. https://doi.org/10.1111/1365-2656.12887

Alberts, S. C., & Altmann, J. (1995). Preparation and activation: Determinants of age at reproductive maturity in male baboons. *Behavioral Ecology and Sociobiology, 36*(6), 397−406. https://doi.org/10.1007/BF00177335

Alberts, S. C., & Fitzpatrick, C. L. (2012). Paternal care and the evolution of exaggerated sexual swellings in primates. *Behavioral Ecology, 23*(4), 699−706. https://doi.org/10.1093/beheco/ars052

Allen, J. A. (2019). Community through culture: From insects to whales - How social learning and culture manifest across diverse animal communities. *BioEssays, 41*(1900060), 1−8. https://doi.org/10.1002/bies.201900060

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour, 49*(3/4), 227−267.

Altmann, J. (1980). *Baboon mothers and infants* (2001st ed.). The University of Chicago Press.

Altmann, J., Altmann, S. A., & Hausfater, G. (1978). Primate infant's effects on mother's future reproduction. *Science, 201*(4360), 1028−1030. https://doi.org/10.1126/science.98844

Altmann, J., Altmann, S., & Hausfater, G. (1981). Physical maturation and age estimates of yellow baboons, *Papio cynocephalus*, in Amboseli National Park, Kenya. *American Journal of Primatology, 1*(4), 389−399. https://doi.org/10.1002/ajp.1350010404

Amici, F., Kulik, L., Langos, D., & Widdig, A. (2019). Growing into adulthood—A review on sex differences in the development of sociality across macaques. *Behavioral Ecology and Sociobiology, 73*(2), 18. https://doi.org/10.1007/s00265-018-2623-2

Anderson, D. R., Burnham, K. P., & Thompson, W. L. (2000). Null hypothesis testing: Problems, prevalence, and an alternative. *Journal of Wildlife Management, 64*(4), 912. https://doi.org/10.2307/3803199

Baniel, A., Cowlishaw, G., & Huchard, E. (2018). Context dependence of female reproductive competition in wild chacma baboons. *Animal Behaviour, 139*, 37−49. https://doi.org/10.1016/j.anbehav.2018.03.001

Barrett, B. J., McElreath, R. L., & Perry, S. E. (2017). Pay-off-biased social learning underlies the diffusion of novel extractive foraging traditions in a wild primate. *Proceedings of the Royal Society B: Biological Sciences, 284*(1856). https://doi.org/10.1098/rspb.2017.0358

Bartoń, K. (2022). *MuMIn: Multi-model inference.* https://CRAN.R-project.org/package=MuMIn [Computer software].

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software, 67*(1), 1−48. https://doi.org/10.18637/jss.v067.i01

Bateson, P. (1994). The dynamics of parent-offspring relationships in mammals. *Trends in Ecology & Evolution, 9*(10), 399−403. https://doi.org/10.1016/0169-5347(94)90066-3

Bauer, D. J., & Curran, P. J. (2005). Probing interactions in fixed and multilevel regression: Inferential and graphical techniques. *Multivariate Behavioral Research, 40*(3), 373−400. https://doi.org/10.1207/s15327906mbr4003_5

Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C., & Matsuzawa, T. (2003). Cultural innovation and transmission of tool use in wild chimpanzees: Evidence from field experiments. *Animal Cognition, 6*(4), 213−223. https://doi.org/10.1007/s10071-003-0183-x

Bonnie, K. E., & de Waal, F. B. M. (2006). Affiliation promotes the transmission of a social custom: Handclasp grooming among captive chimpanzees. *Primates, 47*(1), 27−34. https://doi.org/10.1007/s10329-005-0141-0

Bonnie, K. E., & Earley, R. L. (2007). Expanding the scope for social information use. *Animal Behaviour, 74*(2), 171−181. https://doi.org/10.1016/j.anbehav.2006.12.009

Borgeaud, C., & Bshary, R. (2015). Wild vervet monkeys trade tolerance and specific coalitionary support for grooming in experimentally induced conflicts. *Current Biology, 25*(22), 3011−3016. https://doi.org/10.1016/j.cub.2015.10.016

Brakes, P., Carroll, E. L., Dall, S. R. X., Keith, S. A., McGregor, P. K., Mesnick, S. L., Noad, M. J., Rendell, L., Robbins, M. M., Rutz, C., Thornton, A., Whiten, A., Whiting, M. J., Aplin, L. M., Bearhop, S., Ciucci, P., Fishlock, V., Ford, J. K. B., Notarbartolo di Sciara, G., … Garland, E. C. (2021). A deepening understanding of animal culture suggests lessons for conservation. *Proceedings of the Royal Society B: Biological Sciences, 288*(1949), Article 20202718. https://doi.org/10.1098/rspb.2020.2718

Brambor, T., Clark, W. R., & Golder, M. (2006). Understanding interaction models: Improving empirical analyses. *Political Analysis, 14*(1), 63−82. https://doi.org/10.1093/pan/mpi014

Bray, J., Emery Thompson, M., Muller, M. N., Wrangham, R. W., & Machanda, Z. P. (2018). The development of feeding behavior in wild chimpanzees (*Pan troglodytes schweinfurthii*). *American Journal of Physical Anthropology, 165*(1), 34−46. https://doi.org/10.1002/ajpa.23325

Briseno-Jaramillo, M., Ramos-Fernández, G., Palacios-Romo, T. M., Sosa-López, J. R., & Lemasson, A. (2018). Age and social affinity effects on contact call interactions in free-ranging spider monkeys. *Behavioral Ecology and Sociobiology, 72*(12), 192. https://doi.org/10.1007/s00265-018-2615-2

Brown, G. R., Almond, R. E. A., & Bergen, Y. van (2004). Begging, stealing, and offering: Food transfer in nonhuman primates. *Advances in the Study of Behavior, 34*, 265−295. https://doi.org/10.1016/S0065-3454(04)34007-6

Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. *Behavioral Ecology and Sociobiology, 65*(1), 23−35. https://doi.org/10.1007/s00265-010-1029-6

Burrow, A. K., & Maerz, J. C. (2021). Experimental confirmation of effects of leaf litter type and light on tadpole performance for two priority amphibians. *Ecosphere, 12*(9), Article e03729. https://doi.org/10.1002/ecs2.3729

Canteloup, C., Hoppitt, W., & van de Waal, E. (2020). Wild primates copy higher-ranked individuals in a social transmission experiment. *Nature Communications, 11*(1), 459. https://doi.org/10.1038/s41467-019-14209-8

Carboni, S., Dezeure, J., Cowlishaw, G., Huchard, E., & Marshall, H. H. (2022). Stable isotopes reveal the effects of maternal rank and infant age on weaning dynamics in wild chacma baboons. *Animal Behaviour, 193*, 21–32. https://doi.org/10.1016/j.anbehav.2022.08.010

Carter, A. J., & Cowlishaw, G. (2021). Cultural behaviours can be experimentally induced in wild baboons despite constraints on social information transmission. *bioRxiv.* https://doi.org/10.1101/2021.07.12.452028

Carter, A. J., Marshall, H. H., Heinsohn, R., & Cowlishaw, G. (2014). Personality predicts the propensity for social learning in a wild primate. *PeerJ, 2*(e283), 1–22. https://doi.org/10.7717/peerj.283

Carter, A. J., Torrents Ticó, M., & Cowlishaw, G. (2016). Sequential phenotypic constraints on social information use in wild baboons. *eLife, 5*(e13125), 1–21. https://doi.org/10.7554/eLife.13125

Carvajal, L., & Schuppli, C. (2022). Learning and skill development in wild primates: Toward a better understanding of cognitive evolution. *Current Opinion in Behavioral Sciences, 46*, Article 101155. https://doi.org/10.1016/j.cobeha.2022.101155

Castles, M., Heinsohn, R., Marshall, H. H., Lee, A. E. G., Cowlishaw, G., & Carter, A. J. (2014). Social networks created with different techniques are not comparable. *Animal Behaviour, 96*, 59–67. https://doi.org/10.1016/j.anbehav.2014.07.023

Chapais, B. (1988). Experimental matrilineal inheritance of rank in female Japanese macaques. *Animal Behaviour, 36*(4), 1025–1037. https://doi.org/10.1016/S0003-3472(88)80062-9

Chapais, B., & Belisle, P. (2001). Tolerated co-feeding in relation to degree of kinship in Japanese macaques. *Behaviour, 138*(4), 487–509. https://doi.org/10.1163/156853901750382124

Charpentier, M. J. E., Huchard, E., Widdig, A., Gimenez, O., Sallé, B., Kappeler, P., & Renoult, J. P. (2012). Distribution of affiliative behavior across kin classes and their fitness consequences in mandrills. *Ethology, 118*(12), 1198–1207. https://doi.org/10.1111/eth.12026

Cheney, D. L. (1978). The play partners of immature baboons. *Animal Behaviour, 26*, 1038–1050. https://doi.org/10.1016/0003-3472(78)90093-3

Cheney, D. L., & Seyfarth, R. M. (2007). *Baboon metaphysics, the evolution of a social mind*. The University of Chicago Press.

Cheney, D. L., Seyfarth, R. M., Fischer, J., Beehner, J., Bergman, T., Johnson, S. E., Kitchen, D. M., Palombit, R. A., Rendall, D., & Silk, J. B. (2004). Factors affecting reproduction and mortality among baboons in the Okavango Delta, Botswana. *International Journal of Primatology, 25*(2), 401–428. https://doi.org/10.1023/B:IJOP.0000019159.75573.13

Chowdhury, M. Z. I., & Turin, T. C. (2020). Variable selection strategies and its importance in clinical prediction modelling. *Family Medicine and Community Health, 8*(1), Article e000262. https://doi.org/10.1136/fmch-2019-000262

Coelho, C. G., Falótico, T., Izar, P., Mannu, M., de Resende, B. D., Siqueira, J. O., & Ottoni, E. B. (2015). Social learning strategies for nut-cracking by tufted capuchin monkeys (*Sapajus* spp.). *Animal Cognition, 18*(4), 911–919. https://doi.org/10.1007/s10071-015-0861-5

Cowlishaw, G., & Davies, J. G. (1997). Flora of the Pro-Namib Desert Swakop River Catchment, Namibia: Community classification and implications for desert vegetation sampling. *Journal of Arid Environments, 36*(2), 271–290. https://doi.org/10.1006/jare.1996.0203

Croft, D. P., Madden, J. R., Franks, D. W., & James, R. (2011). Hypothesis testing in animal social networks. *Trends in Ecology & Evolution, 26*(10), 502–507. https://doi.org/10.1016/j.tree.2011.05.012

Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal, Complex Systems*, 1695. https://igraph.org.

Curley, J. P. (2023). *Compete: Analyzing social hierarchies*. https://github.com/jalapic/compete [Computer software].

Danchin, É., Giraldeau, L.-A., Valone, T. J., & Wagner, R. H. (2004). Public information: From nosy neighbors to cultural evolution. *Science, 305*(5683), 487–491. https://doi.org/10.1126/science.1098254

de Vries, H. (1995). An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Animal Behaviour, 50*(5), 1375–1389. https://doi.org/10.1016/0003-3472(95)80053-0

Dezeure, J., Baniel, A., Carter, A., Cowlishaw, G., Godelle, B., & Huchard, E. (2021a). Birth timing generates reproductive trade-offs in a non-seasonal breeding primate. *Proceedings of the Royal Society B: Biological Sciences, 288*(1950). https://doi.org/10.1098/rspb.2021.0286. rspb.2021.0286, 20210286.

Dezeure, J., Dagorrette, J., Baniel, A., Carter, A. J., Cowlishaw, G., Marshall, H. H., Martina, C., Raby, C. L., & Huchard, E. (2021b). Developmental transitions in body color in chacma baboon infants: Implications to estimate age and developmental pace. *American Journal of Physical Anthropology, 174*(1), 89–102. https://doi.org/10.1002/ajpa.24118

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography, 36*(1), 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Douma, J. C., & Weedon, J. T. (2019). Analysing continuous proportions in ecology and evolution: A practical introduction to beta and Dirichlet regression.

Methods in Ecology and Evolution, 10(9), 1412–1430. https://doi.org/10.1111/2041-210X.13234

Farine, D. R. (2013). Animal social network inference and permutations for ecologists in R using *asnipe*. *Methods in Ecology and Evolution, 4*(12), 1187–1194. https://doi.org/10.1111/2041-210X.12121

Farine, D. R., & Whitehead, H. (2015). Constructing, conducting and interpreting animal social network analysis. *Journal of Animal Ecology, 84*(5), 1144–1163. https://doi.org/10.1111/1365-2656.12418

Fox, J., Weisberg, S., & Price, B. (2023). *Car: Companion to applied regression*. https://CRAN.R-project.org/package=car [Computer software].

Galef, B. G., & Wigmore, S. W. (1983). Transfer of information concerning distant foods: A laboratory investigation of the 'information-centre' hypothesis. *Animal Behaviour, 31*(3), 748–758. https://doi.org/10.1016/S0003-3472(83)80232-2

Gelman, A., & Su, Y.-S. (2022). *Arm: Data analysis using regression and multilevel/hierarchical models*. https://CRAN.R-project.org/package=arm [Computer software].

George, A., Stead, T. S., & Ganti, L. (2020). What's the risk: Differentiating risk ratios, odds ratios, and hazard ratios? *Cureus*. https://doi.org/10.7759/cureus.10047

Gibson, Q. A., & Mann, J. (2008). The size, composition and function of wild bottlenose dolphin (*Tursiops* sp.) mother–calf groups in Shark Bay, Australia. *Animal Behaviour, 76*(2), 389–405. https://doi.org/10.1016/j.anbehav.2008.01.022

Grampp, M., Sueur, C., van de Waal, E., & Botting, J. (2019). Social attention biases in juvenile wild vervet monkeys: Implications for socialisation and social learning processes. *Primates, 60*(3), 261–275. https://doi.org/10.1007/s10329-019-00721-4

Griesser, M., & Suzuki, T. N. (2017). Naïve juveniles are more likely to become breeders after witnessing predator mobbing. *American Naturalist, 189*(1), 58–66. https://doi.org/10.1086/689477

Grueber, C. E., Nakagawa, S., Laws, R. J., & Jamieson, I. G. (2011). Multimodel inference in ecology and evolution: Challenges and solutions: Multimodel inference. *Journal of Evolutionary Biology, 24*(4), 699–711. https://doi.org/10.1111/j.1420-9101.2010.02210.x

Gunst, N., Boinski, S., & Fragaszy, D. M. (2010a). Development of skilled detection and extraction of embedded prey by wild brown capuchin monkeys (*Cebus apella apella*). *Journal of Comparative Psychology, 124*(2), 194–204. https://doi.org/10.1037/a0017723

Gunst, N., Leca, J.-B., Boinski, S., & Fragaszy, D. (2010b). The ontogeny of handling hard-to-process food in wild brown capuchins (*Cebus apella apella*): Evidence from foraging on the fruit of *Maximiliana maripa*. *American Journal of Primatology, 72*(11), 960–973. https://doi.org/10.1002/ajp.20856

Harrison, X. A., Donaldson, L., Correa-Cano, M. E., Evans, J., Fisher, D. N., Goodwin, C. E. D., Robinson, B. S., Hodgson, D. J., & Inger, R. (2018). A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ, 6*(e4794), 1–32. https://doi.org/10.7717/peerj.4794

Hartig, F. (2022). *DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models*. http://florianhartig.github.io/DHARMa/ [Computer software].

Hobaiter, C., Poisot, T., Zuberbühler, K., Hoppitt, W., & Gruber, T. (2014). Social network analysis shows direct evidence for social transmission of tool use in wild chimpanzees. *PLoS Biology, 12*(9), Article e1001960. https://doi.org/10.1371/journal.pbio.1001960

Hobson, E. A., Avery, M. L., & Wright, T. F. (2013). An analytical framework for quantifying and testing patterns of temporal dynamics in social networks. *Animal Behaviour, 85*(1), 83–96. https://doi.org/10.1016/j.anbehav.2012.10.010

Holekamp, K. E., Cooper, S. M., Katona, C. I., Berry, N. A., Frank, L. G., & Smale, L. (1997). Patterns of association among female spotted hyenas (*Crocuta crocuta*). *Journal of Mammalogy, 78*(1), 55–64. https://doi.org/10.2307/1382638

Holekamp, K. E., & Smale, L. (1991). Dominance acquisition during mammalian social development: The "inheritance" of maternal rank. *American Zoologist, 31*(2), 306–317. https://doi.org/10.1093/icb/31.2.306

Hollén, L. I., & Manser, M. B. (2006). Ontogeny of alarm call responses in meerkats, *Suricata suricatta*: The roles of age, sex and nearby conspecifics. *Animal Behaviour, 72*(6), 1345–1353. https://doi.org/10.1016/j.anbehav.2006.03.020

Hoppitt, W. J. E., & Farine, D. R. (2018). Association indices for quantifying social relationships: How to deal with missing observations of individuals or groups. *Animal Behaviour, 136*, 227–238. https://doi.org/10.1016/j.anbehav.2017.08.029

Horrocks, J., & Hunte, W. (1983). Maternal rank and offspring rank in vervet monkeys: An appraisal of the mechanisms of rank acquisition. *Animal Behaviour, 31*(3), 772–782. https://doi.org/10.1016/S0003-3472(83)80234-6

Huchard, E., Benavides, J. A., Setchell, J. M., Charpentier, M. J. E., Alvergne, A., King, A. J., Knapp, L. A., Cowlishaw, G., & Raymond, M. (2009). Studying shape in sexual signals: The case of primate sexual swellings. *Behavioral Ecology and Sociobiology, 63*(8), 1231–1242. https://doi.org/10.1007/s00265-009-0748-z

Huchard, E., Charpentier, M. J., Marshall, H., King, A. J., Knapp, L. A., & Cowlishaw, G. (2013). Paternal effects on access to resources in a promiscuous primate society. *Behavioral Ecology, 24*(1), 229–236. https://doi.org/10.1093/beheco/ars158

Huchard, E., & Cowlishaw, G. (2011). Female–female aggression around mating: An extra cost of sociality in a multimale primate society. *Behavioral Ecology, 22*(5), 1003–1011. https://doi.org/10.1093/beheco/arr083

Jaeggi, A. V., Dunkel, L. P., Van Noordwijk, M. A., Wich, S. A., Sura, A. A. L., & Van Schaik, C. P. (2010). Social learning of diet and foraging skills by wild immature Bornean orangutans: Implications for culture. *American Journal of Primatology, 72*(1), 62–71. https://doi.org/10.1002/ajp.20752

Jaeggi, A. V., van Noordwijk, M. A., & van Schaik, C. P. (2008). Begging for information: Mother−offspring food sharing among wild Bornean orangutans. *American Journal of Primatology, 70*(6), 533−541. https://doi.org/10.1002/ajp.20525

Johnson, S. E., & Bock, J. (2004). Trade-offs in skill acquisition and time allocation among juvenile chacma baboons. *Human Nature, 15*(1), 45−62. https://doi.org/10.1007/s12110-004-1003-y

Jones, J. H. (2011). Primates and the evolution of long, slow life histories. *Current Biology, 21*(18), R708−R717. https://doi.org/10.1016/j.cub.2011.08.025

Kavaliers, M., Colwell, D. D., & Choleris, E. (2005). Kinship, familiarity and social status modulate social learning about micropredators (biting flies) in deer mice. *Behavioral Ecology and Sociobiology, 58*(1), 60−71. https://doi.org/10.1007/s00265-004-0896-0

Kendal, R., Hopper, L. M., Whiten, A., Brosnan, S. F., Susan, P., Schapiro, S. J., & Hoppitt, W. (2015). Chimpanzees copy dominant and knowledgeable individuals: Implications for cultural diversity. *Evolution and Human Behavior, 36*(1), 65−72. https://doi.org/10.1016/j.evolhumbehav.2014.09.002.Chimpanzees

King, A. J., Clark, F. E., & Cowlishaw, G. (2011). The dining etiquette of desert baboons: The roles of social bonds, kinship, and dominance in co-feeding networks. *American Journal of Primatology, 73*(8), 768−774. https://doi.org/10.1002/ajp.20918

King, A. J., Douglas, C. M. S., Huchard, E., Isaac, N. J. B., & Cowlishaw, G. (2008). Dominance and affiliation mediate despotism in a social primate. *Current Biology, 18*(23), 1833−1838. https://doi.org/10.1016/j.cub.2008.10.048

King, A. J., Isaac, N. J. B., & Cowlishaw, G. (2009). Ecological, social, and reproductive factors shape producer−scrounger dynamics in baboons. *Behavioral Ecology, 20*(5), 1039−1049. https://doi.org/10.1093/beheco/arp095

Kitowski, I. (2009). Social learning of hunting skills in juvenile marsh harriers *Circus aeruginosus*. *Journal of Ethology, 27*(3), 327−332. https://doi.org/10.1007/s10164-008-0123-y

Kulahci, I. G., Rubenstein, D. I., Bugnyar, T., Hoppitt, W., Mikus, N., & Schwab, C. (2016). Social networks predict selective observation and information spread in ravens. *Royal Society Open Science, 3*(7), Article 160256. https://doi.org/10.1098/rsos.160256

Kulik, L., Amici, F., Langos, D., & Widdig, A. (2015). Sex differences in the development of social relationships in rhesus macaques (*Macaca mulatta*). *International Journal of Primatology, 36*(2), 353−376. https://doi.org/10.1007/s10764-015-9826-4

Lüdecke, D. (2018). ggeffects: Tidy data frames of marginal effects from regression models. *Journal of Open Source Software, 3*(26), 772. https://doi.org/10.21105/joss.00772

Ladds, Z., Hoppitt, W., & Boogert, N. J. (2017). Social learning in otters. *Royal Society Open Science, 4*(8), Article 170489. https://doi.org/10.1098/rsos.170489

Laland, K. N. (2004). Social learning strategies. *Animal Learning & Behavior, 32*(1), 4−14. https://doi.org/10.3758/bf03196002

Laland, K. N., & Janik, V. M. (2006). The animal cultures debate. *Trends in Ecology & Evolution, 21*(10), 542−547. https://doi.org/10.1016/j.tree.2006.06.005

Lamon, N., Neumann, C., & Zuberbühler, K. (2018). Development of object manipulation in wild chimpanzees. *Animal Behaviour, 135*, 121−130. https://doi.org/10.1016/j.anbehav.2017.11.003

Landová, E., Hotová Svádová, K., Fuchs, R., Štys, P., & Exnerová, A. (2017). The effect of social learning on avoidance of aposematic prey in juvenile great tits (*Parus major*). *Animal Cognition, 20*(5), 855−866. https://doi.org/10.1007/s10071-017-1106-6

Lee, A. E. G., & Cowlishaw, G. (2017). Switching spatial scale reveals dominance-dependent social foraging tactics in a wild primate. *PeerJ, 5*, Article e3462. https://doi.org/10.7717/peerj.3462

Lehmann, J., Fickenscher, G., & Boesch, C. (2006). Kin biased investment in wild chimpanzees. *Behaviour, 143*(8), 931−955. https://doi.org/10.1163/156853906778623635

Liebenberg, L. (2022). *CyberTracker conservation*. https://cybertracker.org/ [Computer software].

Lonsdorf, E. V. (2017). Sex differences in primate behavioral development. *Journal of Neuroscience Research, 95*(1−2), 213−221. https://doi.org/10.1002/jnr.23862

Lonsdorf, E. V., & Bonnie, K. E. (2010). Opportunities and constraints when studying social learning: Developmental approaches and social factors. *Learning & Behavior, 38*(3), 195−205. https://doi.org/10.3758/LB.38.3.195

Lupfer-Johnson, G., & Ross, J. (2007). Dogs acquire food preferences from interacting with recently fed conspecifics. *Behavioural Processes, 74*(1), 104−106. https://doi.org/10.1016/j.beproc.2006.09.006

Lynch, E. C., Johnson, C. A., Lynch, R. F., Rothman, J. M., Di Fiore, A., & Palombit, R. A. (2020). Mothers and fathers improve immature baboon foraging success. *Behaviour, 157*(5), 387−414. https://doi.org/10.1163/1568539X-bja10006

Müller, C. A., & Cant, M. A. (2010). Imitation and traditions in wild banded mongooses. *Current Biology, 20*(13), 1171−1175. https://doi.org/10.1016/j.cub.2010.04.037

Maestripieri, D. (2018). Maternal influences on primate social development. *Behavioral Ecology and Sociobiology, 72*(8), 130. https://doi.org/10.1007/s00265-018-2547-x

Mann, J., Sargeant, B. L., & Minor, M. (2007). Calf inspections of fish catches in bottlenose dolphins (*Tursiops* sp.): Opportunities for oblique social learning? *Marine Mammal Science, 23*(1), 197−202. https://doi.org/10.1111/j.1748-7692.2006.00087.x

Marcoux, M., Rendell, L., & Whitehead, H. (2007). Indications of fitness differences among vocal clans of sperm whales. *Behavioral Ecology and Sociobiology, 61*(7), 1093−1098. https://doi.org/10.1007/s00265-006-0342-6

Markham, A. C., Lonsdorf, E. V., Pusey, A. E., & Murray, C. M. (2015). Maternal rank influences the outcome of aggressive interactions between immature chimpanzees. *Animal Behaviour, 100*, 192−198. https://doi.org/10.1016/j.anbehav.2014.12.003

Marshall, H. H., Carter, A. J., Ashford, A., Rowcliffe, J. M., & Cowlishaw, G. (2015). Social effects on foraging behavior and success depend on local environmental conditions. *Ecology and Evolution, 5*(2), 475−492. https://doi.org/10.1002/ece3.1377

Marshall, H. H., Carter, A. J., Coulson, T., Rowcliffe, J. M., & Cowlishaw, G. (2012). Exploring foraging decisions in a social primate using discrete-choice models. *American Naturalist, 180*(4), 481−495. https://doi.org/10.1086/667587

McComb, K., Moss, C., Durant, S. M., Baker, L., & Sayialel, S. (2001). Matriarchs as repositories of social knowledge in African elephants. *Science, 292*(5516), 491−494. https://doi.org/10.1126/science.1057895

Mesoudi, A., Chang, L., Dall, S. R. X., & Thornton, A. (2016). The evolution of individual and cultural variation in social learning. *Trends in Ecology & Evolution, 31*(3), 215−225. https://doi.org/10.1016/j.tree.2015.12.012

Mikeliban, M., Kunz, B., Rahmaeti, T., Uomini, N., & Schuppli, C. (2021). Orangutan mothers adjust their behaviour during food solicitations in a way that likely facilitates feeding skill acquisition in their offspring. *Scientific Reports, 11*(1), Article 23679. https://doi.org/10.1038/s41598-021-02901-z

Mueller, T., O'Hara, R. B., Converse, S. J., Urbanek, R. P., & Fagan, W. F. (2013). Social learning of migratory performance. *Science, 341*(6149), 999−1002. https://doi.org/10.1126/science.1237139

Noble, D. W. A., Byrne, R. W., & Whiting, M. J. (2014). Age-dependent social learning in a lizard. *Biology Letters, 10*(7), Article 20140430. https://doi.org/10.1098/rsbl.2014.0430

O'Mara, M. T., & Hickey, C. M. (2012). Social influences on the development of ringtailed lemur feeding ecology. *Animal Behaviour, 84*(6), 1547−1555. https://doi.org/10.1016/j.anbehav.2012.09.032

Oberpriller, J., De Souza Leite, M., & Pichler, M. (2022). Fixed or random? On the reliability of mixed-effects models for a small number of levels in grouping variables. *Ecology and Evolution, 12*(7), Article e9062. https://doi.org/10.1002/ece3.9062

Ottoni, E. B., de Resende, B. D., & Izar, P. (2005). Watching the best nutcrackers: What capuchin monkeys (*Cebus apella*) know about others' tool-using skills. *Animal Cognition, 8*(4), 215−219. https://doi.org/10.1007/s10071-004-0245-8

Ottoni, E. B., & Izar, P. (2008). Capuchin monkey tool use: Overview and implications. *Evolutionary Anthropology: Issues, News, and Reviews, 17*(4), 171−178. https://doi.org/10.1002/evan.20185

Owens, N. W. (1975). Social play behaviour in free-living baboons, *Papio anubis*. *Animal Behaviour, 23*, 387−408. https://doi.org/10.1016/0003-3472(75)90087-1

Pasquaretta, C., Levé, M., Claidiere, N., van de Waal, E., Whiten, A., MacIntosh, A. J. J., Pelé, M., Bergstrom, M. L., Borgeaud, C., Brosnan, S. F., Crofoot, M. C., Fedigan, L. M., Fichtel, C., Hopper, L. M., Mareno, M. C., Petit, O., Schnoell, A. V., di Sorrentino, E. P., Thierry, B., … Sueur, C. (2014). Social networks in primates: Smart and tolerant species have more efficient networks. *Scientific Reports, 4*, 1−8. https://doi.org/10.1038/srep07600

Pereira, M. E. (1988a). Agonistic interactions of juvenile savanna baboons: I. Fundamental features. *Ethology, 79*(3), 195−217. https://doi.org/10.1111/j.1439-0310.1988.tb00711.x

Pereira, M. E. (1988b). Effects of age and sex on intra-group spacing behaviour in juvenile savannah baboons, *Papio cynocephalus cynocephalus*. *Animal Behaviour, 36*(1), 184−204. https://doi.org/10.1016/S0003-3472(88)80262-8

Pereira, M. E. (1989). Agonistic interactions of juvenile savanna baboons: II. Agonistic support and rank acquisition. *Ethology, 80*(1−4), 152−171. https://doi.org/10.1111/j.1439-0310.1989.tb00736.x

Prud'Homme, J., & Chapais, B. (1993). Aggressive interventions and matrilineal dominance relations in semifree-ranging barbary macaques (*Macaca sylvanus*). *Primates, 34*(3), 271−283. https://doi.org/10.1007/BF02382621

R Core Team. (2022). *R: A language and environment for statistical computing*. Vienna, Austria. R Foundation for Statistical Computing. https://www.r-project.org/ ([Computer software]).

Rapaport, L. G., & Brown, G. R. (2008). Social influences on foraging behavior in young nonhuman primates: Learning what, where, and how to eat. *Evolutionary Anthropology: Issues, News, and Reviews, 17*(4), 189−201. https://doi.org/10.1002/evan.20180

Rieucau, G., & Giraldeau, L.-A. (2011). Exploring the costs and benefits of social information use: An appraisal of current experimental evidence. *Philosophical Transactions of the Royal Society B: Biological Sciences, 366*(1567), 949−957. https://doi.org/10.1098/rstb.2010.0325

Roatti, V., Cowlishaw, G., Huchard, E., & Carter, A. (2023). Social network inheritance and differentiation in wild baboons. *Royal Society Open Science, 10*(5), 1−26. https://doi.org/10.1098/rsos.230219

Roatti, V., Delaunay, A., Cowlishaw, G., Huchard, E., & Carter, A. (2025). Dataset 'Growing up wild: Social learning opportunities during foraging in immature baboons'. *Animal Behaviour*. https://doi.org/10.5281/zenodo.17004462 [Data set].

Sánchez-Tójar, A., Schroeder, J., & Farine, D. R. (2018). A practical guide for inferring reliable dominance hierarchies and estimating their uncertainty. *Journal of Animal Ecology, 87*(3), 594−608. https://doi.org/10.1111/1365-2656.12776

Sapolsky, R. M. (2006). Social cultures among nonhuman primates. *Current Anthropology, 47*(4), 641−656. https://doi.org/10.1086/504162

Sargeant, B. L., & Mann, J. (2009). Developmental evidence for foraging traditions in wild bottlenose dolphins. *Animal Behaviour, 78*(3), 715−721. https://doi.org/10.1016/j.anbehav.2009.05.037

Schiel, N., & Huber, L. (2006). Social influences on the development of foraging behavior in free-living common marmosets (*Callithrix jacchus*). *American Journal of Primatology, 7*(68), 1150–1160. https://doi.org/10.1002/ajp

Schmid, V. S., & De Vries, H. (2013). Finding a dominance order most consistent with a linear hierarchy: An improved algorithm for the I&SI method. *Animal Behaviour, 86*(5), 1097–1105. https://doi.org/10.1016/j.anbehav.2013.08.019

Schuppli, C., Forss, S. I. F., Meulman, E. J. M., Zweifel, N., Lee, K. C., Rukmana, E., Vogel, E. R., van Noordwijk, M. A., & van Schaik, C. P. (2016a). Development of foraging skills in two orangutan populations: Needing to learn or needing to grow? *Frontiers in Zoology, 13*(1), 43. https://doi.org/10.1186/s12983-016-0178-5

Schuppli, C., Meulman, E. J. M., Forss, S. I. F., Aprilinayati, F., van Noordwijk, M. A., & van Schaik, C. P. (2016b). Observational social learning and socially induced practice of routine skills in immature wild orang-utans. *Animal Behaviour, 119*, 87–98. https://doi.org/10.1016/j.anbehav.2016.06.014

Schuppli, C., & van Schaik, C. P. (2019). Animal cultures: How we've only seen the tip of the iceberg. *Evolutionary Human Sciences, 1*(e2), 1–13. https://doi.org/10.1017/ehs.2019.1

Shier, D. M., & Owings, D. H. (2007). Effects of social learning on predator training and postrelease survival in juvenile black-tailed prairie dogs, *Cynomys ludovicianus*. *Animal Behaviour, 73*(4), 567–577. https://doi.org/10.1016/j.anbehav.2006.09.009

Shimada, M., & Sueur, C. (2014). The importance of social play network for infant or juvenile wild chimpanzees at Mahale Mountains National Park, Tanzania: Social play networks in wild chimpanzees. *American Journal of Primatology, 76*(11), 1025–1036. https://doi.org/10.1002/ajp.22289

Shimada, M., & Sueur, C. (2017). Social play among juvenile wild Japanese macaques (*Macaca fuscata*) strengthens their social bonds. *American Journal of Primatology, 80*(1), Article e22728. https://doi.org/10.1002/ajp.22728

Shizuka, D., & McDonald, D. B. (2012). A social network perspective on measurements of dominance hierarchies. *Animal Behaviour, 83*(4), 925–934. https://doi.org/10.1016/j.anbehav.2012.01.011

Silk, J. B. (2009). Nepotistic cooperation in non-human primate groups. *Philosophical Transactions of the Royal Society B: Biological Sciences, 364*(1533), 3243–3254. https://doi.org/10.1098/rstb.2009.0118

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M., & Cheney, D. L. (2010). Female chacma baboons form strong, equitable, and enduring social bonds. *Behavioral Ecology and Sociobiology, 64*(11), 1733–1747. https://doi.org/10.1007/s00265-010-0986-0

Silk, J. B., Roberts, E. R., Barrett, B. J., Patterson, S. K., & Strum, S. C. (2017). Female–male relationships influence the form of female–female relationships in olive baboons, *Papio anubis*. *Animal Behaviour, 131*, 89–98. https://doi.org/10.1016/j.anbehav.2017.07.015

Sosa, S., Sueur, C., & Puga-Gonzalez, I. (2021). Network measures in animal social network analysis: Their strengths, limits, interpretations and uses. *Methods in Ecology and Evolution, 12*(1), 10–21. https://doi.org/10.1111/2041-210X.13366

Street, S. E., Navarrete, A. F., Reader, S. M., & Laland, K. N. (2017). Coevolution of cultural intelligence, extended life history, sociality, and brain size in primates. *Proceedings of the National Academy of Sciences, 114*(30), 7908–7914. https://doi.org/10.1073/pnas.1620734114

Suzuki, N., Olson, D. H., & Reilly, E. C. (2008). Developing landscape habitat models for rare amphibians with small geographic ranges: A case study of Siskiyou Mountains salamanders in the western USA. *Biodiversity & Conservation, 17*(9), 2197–2218. https://doi.org/10.1007/s10531-007-9281-4

Symonds, M. R. E., & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology, 65*(1), 13–21. https://doi.org/10.1007/s00265-010-1037-6

Szumilas, M. (2010). Explaining odds ratios. *Journal of the Canadian Academy of Child and Adolescent Psychiatry, 19*(3), 227–229.

Tan, A. W. Y., Hemelrijk, C. K., Malaivijitnond, S., & Gumert, M. D. (2018). Young macaques (*Macaca fascicularis*) preferentially bias attention towards closer, older, and better tool users. *Animal Cognition, 21*(4), 551–563. https://doi.org/10.1007/s10071-018-1188-9

Tarnaud, L., & Yamagiwa, J. (2008). Age-dependent patterns of intensive observation on elders by free-ranging juvenile Japanese macaques (*Macaca fuscata yakui*) within foraging context on Yakushima. *American Journal of Primatology, 70*(12), 1103–1113. https://doi.org/10.1002/ajp.20603

TBP. (2019). *Tsaobis baboon project*. Tsaobisbaboonproject.org . (Accessed 30 December 2023).

Thomas, R., Lello, J., Medeiros, R., Polard, A., Robinson, P., Seward, A., Smith, V., & Vaughan, I. (2015). *Data analysis with R statistical software: A guidebook for scientists*. Eco-explore, 2017th ed., Vol. 2.

Thornton, A. (2008). Social learning about novel foods in young meerkats. *Animal Behaviour, 76*(4), 1411–1421. https://doi.org/10.1016/j.anbehav.2008.07.007

Thornton, A., & Clutton-Brock, T. (2011). Social learning and the development of individual and group behaviour in mammal societies. *Philosophical Transactions of the Royal Society B: Biological Sciences, 366*(1567), 978–987. https://doi.org/10.1098/rstb.2010.0312

Thornton, A., & Hodge, S. J. (2009). The development of foraging microhabitat preferences in meerkats. *Behavioral Ecology, 20*(1), 103–110. https://doi.org/10.1093/beheco/arn120

Tredennick, A. T., Hooker, G., Ellner, S. P., & Adler, P. B. (2021). A practical guide to selecting models for exploration, inference, and prediction in ecology. *Ecology, 102*(6). https://doi.org/10.1002/ecy.3336

Troisi, C. A., Hoppitt, W. J. E., Ruiz-Miranda, C. R., & Laland, K. N. (2021). The role of food transfers in wild golden lion tamarins (*Leontopithecus rosalia*): Support for the informational and nutritional hypothesis. *Primates, 62*(1), 207–221. https://doi.org/10.1007/s10329-020-00835-0

Tsai, Y.-J. J., & Mann, J. (2013). Dispersal, philopatry, and the role of fission-fusion dynamics in bottlenose dolphins. *Marine Mammal Science, 29*(2), 261–279. https://doi.org/10.1111/j.1748-7692.2011.00559.x

Turner, J. W., Bills, P. S., & Holekamp, K. E. (2018). Ontogenetic change in determinants of social network position in the spotted hyena. *Behavioral Ecology and Sociobiology, 72*(1). https://doi.org/10.1007/s00265-017-2426-x

Turner, Z., Neumann, C., Saccà, T., & Forss, S. (2025). Nutritional needs and social bonds: How early-life dependencies shape meerkat sociality. *EcoEvoRxiv*. https://doi.org/10.32942/X2663P

van Boekholt, B., van de Waal, E., & Sterck, E. H. M. (2021). Organized to learn: The influence of social structure on social learning opportunities in a group. *iScience, 24*(2), Article 102117. https://doi.org/10.1016/j.isci.2021.102117

van de Waal, E., Bshary, R., & Whiten, A. (2014). Wild vervet monkey infants acquire the food-processing variants of their mothers. *Animal Behaviour, 90*, 41–45. https://doi.org/10.1016/j.anbehav.2014.01.015

van de Waal, E., Krützen, M., Hula, J., Goudet, J., & Bshary, R. (2012). Similarity in food cleaning techniques within matrilines in wild vervet monkeys. *PLoS One, 7*(4), Article e35694. https://doi.org/10.1371/journal.pone.0035694

van de Waal, E., Renevey, N., Favre, C. M., & Bshary, R. (2010). Selective attention to philopatric models causes directed social learning in wild vervet monkeys. *Proceedings of the Royal Society B: Biological Sciences, 277*(1691), 2105–2111. https://doi.org/10.1098/rspb.2009.2260

Vilette, C., Bonnell, T. R., Dostie, M. J., Henzi, S. P., & Barrett, L. (2022). Network formation during social integration in juvenile vervet monkeys. *Animal Behaviour, 194*, 205–223. https://doi.org/10.1016/j.anbehav.2022.10.006

Vilette, C., Bonnell, T., Henzi, P., & Barrett, L. (2020). Comparing dominance hierarchy methods using a data-splitting approach with real-world data. *Behavioral Ecology, 31*(6), 1379–1390. https://doi.org/10.1093/beheco/araa095

Watson, S. K., Reamer, L. A., Mareno, M. C., Vale, G., Harrison, R. A., Lambeth, S. P., Schapiro, S. J., & Whiten, A. (2017). Socially transmitted diffusion of a novel behavior from subordinate chimpanzees. *American Journal of Primatology, 79*(6), Article e22642. https://doi.org/10.1002/ajp.22642

Weiss, M. N., Franks, D. W., Giles, D. A., Youngstrom, S., Wasser, S. K., Balcomb, K. C., Ellifrit, D. K., Domenici, P., Cant, M. A., Ellis, S., Nielsen, M. L. K., Grimes, C., & Croft, D. P. (2021). Age and sex influence social interactions, but not associations, within a killer whale pod. *Proceedings of the Royal Society B: Biological Sciences, 288*(1953), Article 20210617. https://doi.org/10.1098/rspb.2021.0617

Wey, T., Blumstein, D. T., Shen, W., & Jordán, F. (2008). Social network analysis of animal behaviour: A promising tool for the study of sociality. *Animal Behaviour, 75*(2), 333–344. https://doi.org/10.1016/j.anbehav.2007.06.020

Whiten, A., & van de Waal, E. (2018). The pervasive role of social learning in primate lifetime development. *Behavioral Ecology and Sociobiology, 72*(5), 80. https://doi.org/10.1007/s00265-018-2489-3