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ORIGINAL ARTICLE

Home range establishment and the mechanisms of philopatry among female Bornean orangutans (*Pongo pygmaeus wurmbii*) at Tuanan

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Abstract

Female orangutans exhibit natal philopatry, living in stable home ranges that overlap with those of their maternal relatives. Using data collected from 2003 to 2017 at Tuanan in Central Kalimantan, Indonesia, we take a longitudinal approach to better understand the mechanisms of female philopatry and the factors that influence the home range establishment process of young female orangutans (*Pongo pygmaeus wurmbii*). Data on movement and sociality were collected during nest-to-nest focal follows of individual orangutans; four young nulli/primiparous females, their three multiparous mothers, and seven other unrelated adult females living in the same area. Our results show that a young female goes through an 'exploration phase', beginning when she is an independent immature and lasting through her adolescence, characterized by an increase in home range size and distance travelled each day. This exploration is facilitated by high resource availability and association with adult males. A young female maintains a high degree of overlap with her natal range but gradually decrease the degree of overlap with her mother's concurrent range. By the time she is a sexually active adolescent, a young female and her mother share as much overlap as a young female does with other related adult females, although she continues to associate more with her mother than with them, even after the birth of her first offspring. Our findings indicate that the high habitat productivity and high orangutan population density of Tuanan lead to a high degree of life-time site fidelity and overlap among maternal kin.

Significance statement

The mechanisms of philopatry and the process of home range establishment among solitary animals with slow life histories are difficult to study and poorly understood for most species. We investigated this process among female Bornean orangutans, using a unique long-term data set comprising 15 years of social and spatial data. We analysed changes in the ranging and association patterns of young female orangutans as they developed, matured and became mothers. We found that females went through a post-dependence phase of exploration characterized by an increase in range size and day journey length, and then settled into home ranges that overlapped highly with their mothers and other female kin, though they associated preferentially with their mothers. Our results illuminate the extreme long-term site fidelity of these female orangutans and emphasize the ecological and social importance of female philopatry among orangutans.

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Introduction

Natal dispersal patterns are a fundamental aspect of many animal mating systems; in dispersing, an animal is able to avoid inbreeding and limit resource and intrasexual mate competition with kin (Greenwood 1980; Johnson and Gaines 1990). However, the costs of dispersal can be high: moving to unfamiliar areas has been shown to reduce feeding efficiency, increase susceptibility to predators and limit opportunities for cooperation between kin (Bonte et al. 2011). Most mammals have evolved sex-biased dispersal: usually, males disperse before or upon reaching sexual maturity, while females remain philopatric, staying in or near their natal areas (Greenwood 1980). Philopatric animals avoid the costs of dispersal and accrue the social and ecological benefits of staying in a familiar area and group, with known kin, after independence and sexual maturity have been reached.

Among solitary animals, philopatry is defined spatially, as an individual remaining in or near its natal area rather than in its natal group (Waser and Jones 1983). Sex-biased natal philopatry among predominantly solitary mammals has been described across a wide range of taxa, including dusky-footed woodrats (*Neotoma fuscipes*; McEachern et al. 2007; Innes et al. 2012), raccoons (*Procyon lotor*; Ratnayeke et al. 2002), red-necked wallabies (*Macropus rufogriseus*; Johnson 1986), otters (*Lutra lutra*, Quaglietta et al. 2013), black bears (*Ursus americans*; Rogers 1987b; Moyer et al. 2006; Costello et al. 2008; Costello 2010), brown bears (*Ursus arctos*; Støen et al. 2005) and tigers (*Panthera tigris*; Smith 1993; Gour et al. 2013). Even among predominantly solitary animals, philopatry can have social benefits. For example, Coquerel's dwarf lemurs (*Mirza coquereli*; Kappeler et al. 2002) and grey mouse lemurs (*Microcebus murinus*; Lutermann et al. 2006) both exhibit evidence of female philopatry, with female relatives clustering together spatially. Lutermann et al. (2006) suggest that, despite grey mouse lemurs' predominantly solitary nature, females may accrue certain social benefits from this philopatry as well, namely access to shared sleeping sites—important resources for predator avoidance and thermoregulation.

Many studies have investigated the processes and mechanisms of natal dispersal (e.g. Johnson and Gaines 1990; Isbell and van Vuren 1996), but fewer studies have sought to understand the opposite process: that of home range establishment, and the mechanisms of natal philopatry, in solitary species. Waser and Jones (1983) suggest three mechanisms through which philopatric parents can remain solitary despite having philopatric offspring: parents can either share, split or leave their ranges. Sharing one's range requires temporal, rather than spatial, avoidance between parents and offspring, and can occur only in non-territorial species. Splitting occurs when a parent bequeaths a part of its home range to its offspring, who then maintains access to this area to the exclusion of the parent (both or either may incorporate new, adjacent area into their home range). Leaving occurs when a parent bequeaths its entire home range to its offspring and disperses to an adjacent or more distant area. Isbell (2004) emphasizes the role of mothers in determining the post-independence ranging patterns of their daughters; mothers would be expected to share their home ranges with their adult daughters (i.e. female philopatry) where the costs of dispersal would lead to lower reproductive success for dispersing daughters, but only if mothers can maintain their own reproduction even in the presence of their adult daughters, e.g. where mothers are able to expand or shift their own ranges.

The three mechanisms described by Waser and Jones (1983) are not mutually exclusive within species or even individuals. Indeed, among black bears (*Ursus americanus*), Rogers (1987a, b) found evidence of splitting and then leaving by mother bears: female yearlings established small home ranges within their mother's ranges that she avoided. As daughters matured, they expanded their ranges into full territories and mothers shifted their own territories away from their daughters (Rogers 1987a). Similar patterns were observed in a population of Bengal tigers (*Panthera tigris*), where daughters usually established ranges adjacent to their mothers, and in some cases, mothers even shifted their own territories to accommodate their maturing daughters' (Smith 1993). Unfortunately, little is known about the mechanisms of philopatry among other species.

Orangutans (*Pongo* spp.) are non-territorial, semi-solitary, great apes (Mackinnon 1974; Galdikas 1985). They exhibit individual-based fission-fusion social organization, with the only long-term cohesive social units consisting of mothers and their dependent offspring (van Schaik 1999). Within-site behavioural observations have suggested, and within- and between-site genetic studies have more recently confirmed, that orangutans exhibit female philopatry and male-biased dispersal (Mackinnon 1974; Galdikas 1985; Singleton and van Schaik 2002; Knott et al. 2008; Arora et al. 2010, 2012; Morrogh-Bernard et al. 2010; van Noordwijk et al. 2012; Nater et al. 2013). Female orangutans live in small (relative to males) generally stable home ranges that overlap with those of their maternal kin, as well as with those of non-kin (Knott et al. 2008; Morrogh-Bernard 2009; Singleton et al. 2009; van Noordwijk et al. 2012).

Although female orangutans are not territorial, they probably defend core areas in one population (Knott et al. 2008). In general, unrelated females limit their association time together, and are more likely to have agonistic interactions than related females (Knott et al. 2008; van Noordwijk et al. 2012; Marzec et al. 2016). Females preferentially associate with their maternal kin, exhibiting higher social tolerance, and allowing their offspring to engage in social play (Knott et al. 2008; Singleton et al. 2009; van Noordwijk et al. 2012). Thus, despite being predominantly solitary, female orangutans' high lifetime site fidelity and clustering with maternal kin allow them to accrue certain important social benefits associated with philopatry.

Orangutans have exceptionally slow life histories; female age at first reproduction is around 15 years, and they have the longest interbirth interval of any mammal (7.6 years) (van Noordwijk et al. 2018). A young orangutan usually remains in close association with its mother for a few years after the mother's next offspring is born (van Noordwijk et al. 2009). This slow development makes it possible to study in detail the step-by-step socio-spatial dynamics of the process of home range establishment among female orangutans, provided sufficient longitudinal data are collected. Thus, we can ask very specific questions about *how* and *where* a young female establishes her home range.

With respect to *how* a young female establishes her range, previous studies have shown that nulliparous female orangutans experience a prolonged phase of adolescent sterility prior to their first pregnancy, during which time they become more gregarious and temporarily expand their home ranges (Galdikas 1995; Singleton and van Schaik 2001). Among female chimpanzees, who are usually not philopatric, male protection of newly immigrated females has been described (Nishida 1989). The 'social passport hypothesis' has been proposed to explain shorter postpartum amenorrhea and an increased number of cycles to conception among younger females, i.e. those females who are usually recently immigrated and unable to compete effectively against older, more established, females: more swellings until conception increases the duration of young females' attractiveness to males (Boesch and Boesch-Achermann 2000; Deschner and Boesch 2007). This extended attractivity ensures the presence and support of males, thus lessening the aggression that young females receive from older, more established females (Deschner and Boesch 2007; Kahlenberg et al. 2008), and could explain why nulliparous females who emigrate from their natal groups have significantly older ages at first reproduction than nulliparous females who remain philopatric (Walker et al. 2018). It could be that the extended phase of adolescent sterility among female orangutans serves a similar function: attracting males and thus limiting the intolerance that these young females receive from adult females while exploring and establishing their own adult home ranges.

With respect to *where* a young female establishes her range, we can extrapolate from cross-sectional studies that suggest or demonstrate female philopatry and high home range overlap between related adult females (Singleton and van Schaik 2002; Knott et al. 2008; Morrogh-Bernard et al. 2010; Arora et al. 2012; van Noordwijk et al. 2012) and assume that young females generally settle into ranges that overlap highly with their female maternal relatives. More specifically, Morrogh-Bernard (2009) proposed the 'Petal Hypothesis' for explaining the spatial patterning of related females' home ranges: daughters settle into ranges that partially overlap those of their mothers, thus forming 'petals' around the mother's range which makes up the 'floral head'. She suggested that habitat resource distribution influences the extent of related females' home range overlap, with more homogenous habitats leading to smaller, less overlapping home ranges (Morrogh-Bernard 2009).

Our study aims to better understand the process of females' home range establishment among a population of Bornean orangutans (*Pongo pygmaeus wurmbii*). Using detailed longitudinal data, we address the questions of *how* and *where* young female orangutans establish their home ranges. Specifically, we investigate *how* a young female establishes her home range by quantifying (1) evidence of an 'exploration phase' among young females based on changes in their daily travel and home range size, (2) changes in young females' association patterns with their mothers, other adult female relatives, and unrelated adult females and (3) changes in young females' association patterns with adult males, as well as potential social and spatial correlates of associations with males pre-parity. We investigate *where* a young female established her home range by quantifying (1) changes in home range overlap and shift between young females and both their mothers' ranges and their natal ranges and (2) changes in the degree of home range overlap between young females and their mothers compared with the degree of home range overlap between young females and other related and unrelated adult females. By combining analyses of how and where a young female establishes her home range, we hope to gain a better understanding of the mechanisms of female philopatry among orangutans.

Methods

Study site and subjects

We conducted this study at the Tuanan Orangutan Research Station (2.151° S; 114.374° E) in the Mawas Reserve, Central Kalimantan, Indonesia, between 2003 and 2017. The study area is composed of approximately 12 km^2 of a gridded trail system through a generally homogenous, formerly selectively logged, peat-swamp forest. Orangutan density in the study area is approximately 4.25–4.5 individuals/km^2, the highest of any naturally occurring Bornean orangutan population (van Schaik et al. 2005).

Our primary study subjects are four nulli/primiparous females. Three of these females have been followed since the study began in 2003, and the fourth, since her birth in 2008. These four daughters are members of the same matriline, which spans 3 generations of maternally related females (Fig. 1a). The females of this matriline all live in overlapping home ranges that are entirely encompassed within the Tuanan study area. In order to remain consistent and clear, we will use the term ‘daughters’ to refer to these females—even after these daughters have become mothers themselves.

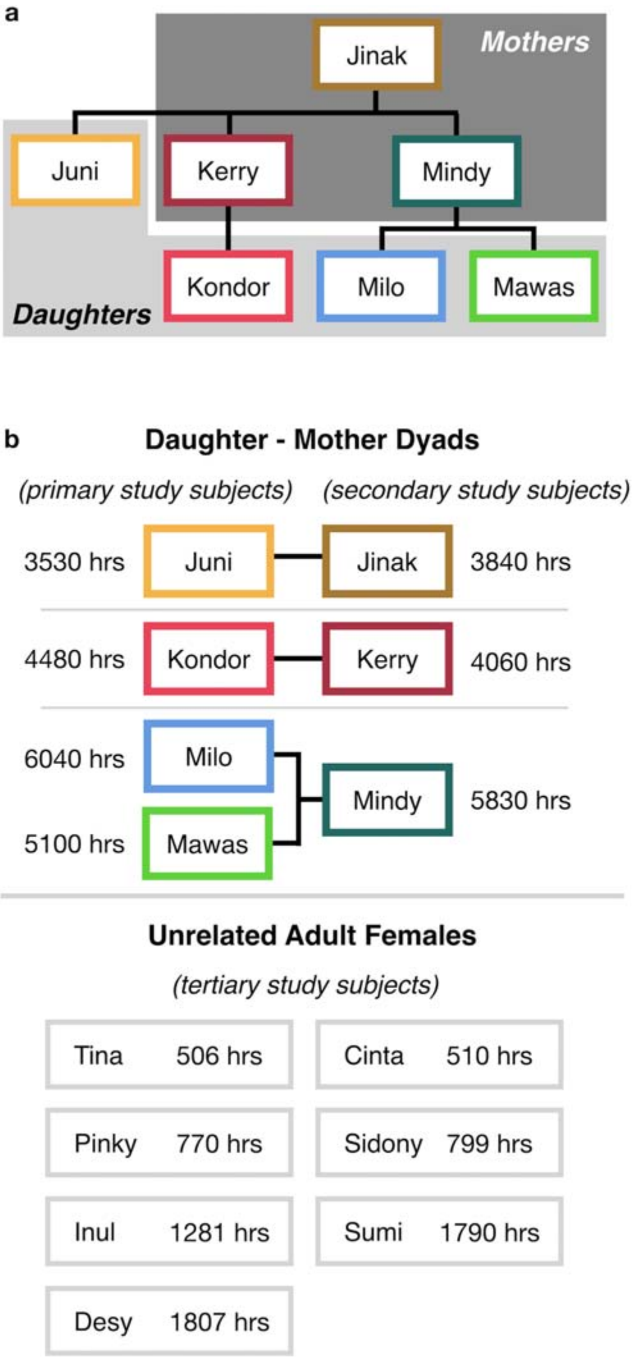


Fig. 1 **a** The pedigree of daughters (primary study subjects) and mothers (secondary study subjects), and **b** the IDs and overall focal observation hours included in this study for all daughters, mothers and unrelated females

Our secondary study subjects include the three multiparous mothers of these daughters. Our tertiary study subjects are seven other local adult females (i.e. parous females) who are not related to the focal females (genetic relatedness established: see Arora et al. 2012; van Noordwijk et al. 2012). From the perspective of each daughter, there are three categories of adult female included in this study: her mother, her adult female relatives (all other parous females of her matriline aside from her mother) and the unrelated females.

Data collection

All data were collected in accordance with standardized protocols (https://www.aim.uzh.ch/de/research/orangutannetwork.html). Orangutans were found opportunistically, and then focal followed from morning nest until night nest for up to 10 days in a row (Altmann 1974). Figure 1b gives the total sample sizes per individual (in hours of focal observation). Our study includes focal association and social interaction data of the four daughters, but only focal location data for the other related and unrelated adult females. It was not possible to record data blind because our study involved focal animals in the field.

Focal behavioural data, including activity and distance to conspecifics, were recorded instantaneously at 2-min intervals. Orangutans were considered “in association” if they were estimated to be within 50 m of each other. The duration of time that focal females spent in association with specific age-sex classes of conspecifics or specific individual orangutans was calculated as the number of minutes (i.e. 2× the number of 2-min instantaneous intervals) spent in association. Daily proportions of time that focal individuals spent in association were calculated as the number of minutes in association with any other conspecifics divided by the total duration of the active period of the focal orangutan (in minutes). Phase-level proportions of time that focal individuals spent in association with specific conspecifics were calculated as the total proportion of the focal’s phase spent in association with each other individual conspecific. We did not count numbers of associations or encounter rates as it is difficult to deduce at exactly what proximity orangutans are aware of their conspecifics, and so counting the number of associations/encounters between, for example, two individuals who move in and out of 50-m proximity, is extremely prone to over-inflation.

All occurrences of agonistic social interactions between females were recorded continuously throughout all focal daughter follows. Agonistic social interactions included aggression, such as hitting, chasing and biting, as well as clear displacements and instances of avoidance or fleeing. We recorded time, actor(s)/winner(s) and receiver(s)/loser(s) of the agonistic interaction, other orangutans also in association, and a description of each event.

The locations of the focal orangutans were collected at every night nest and throughout the follow at 30-min intervals. During the earlier years of the study, location data were collected by hand-drawn points on printed maps of the study area and trail system, whereas since 2012, waypoints were collected on hand-held GPS units. Garmin MapSource (v6) and ESRI's ArgGIS (v9.3) software were all used to digitize hand drawn maps and to import GPS unit data. Prior to all analyses, we applied a smoothing algorithm to the points in order to minimize GPS and observer movement error. A detailed description of this algorithm is given in Online resource 1, Supplementary method 1.

Furthermore, habitat fruit availability data were collected from approximately 1500 marked trees in delineated plots within the study area. Fruiting data were collected once each month, and the percentage of stems bearing fruit was used as the measure of 'fruit availability' in our analyses (for details of fruit availability data collection methods, see Vogel et al. 2016).

Data analysis

Data sub-setting

For the majority of the analyses, all data were divided into *phases* based on key developmental or reproductive milestones of the *daughters*. Figure 2a describes these phases, gives the phase name abbreviations which are used in this text and outlines the parameters used to delineate each different phase – i.e. which behavioural or reproductive milestone was used to determine the transition date between each phase. Table S1 gives a more detailed overview of the daughters' phases, and the data included in these analyses. Furthermore, for each daughter and for each of her phases, we calculated the *mean fruit availability* as the mean of the fruit availability values for all months whose 15th day fell within that phase.

For one small subsection of the analysis, which focuses on mothers' movement and ranges, mothers' data were divided into *her own (rather than her daughter's) phases*, based on her own reproductive status and the dependence status of each of her offspring. Figure 2b describes these phases, gives the phase name abbreviations which are used in this text, and outlines the parameters used to delineate each different phase, and the sample sizes therein. The mean fruit availability was also calculated for each of the mothers' phases, in the same way as for the daughters (above).

Spatial data calculations

To measure daily travel, we calculated day journey length (DJL) for each of all of the daughters' and the mothers' nest-to-nest focal follows by summing up the cumulative Euclidian step distances between the focal orangutan's morning nest point, consecutive 30-min range points, and the night nest point.

For each daughter and for each mother, we calculated a home range for each of her own phases. Furthermore, for each of all daughters' phases, we also calculated a home range for her mother, and for each other related and unrelated adult female. These home ranges are henceforth referred to as *phase ranges.* Phase ranges were delineated at the 95% isopleth of the kernel density utilization distribution (UD). To calculate the h (smoothing) value, we ran multiple iterations of the kernel density utilization distribution calculations for each phase range using progressively smaller and smaller h-values, and then calculated the 95% isopleth polygons for all of these UDs. We selected the UD with the smallest h-value (i.e. the least amount of smoothing, or estimation error) that still maintained a single polygon at the 95% isopleth (Fieberg and Börger 2012; R code modified after Börger and Cozzi). Only phase ranges which were calculated from at least 500 location points were included in the analysis, as this was the number of points required for a phase range to reach a stable size (more details are given in Online resource 1, Supplementary method 2). We opted to focus our analyses on phase-range outlines, rather than the encompassed utilization distributions. Because our field methods yielded short bouts (1–10 days) of high-resolution location data followed by periods of up to 6 months of 'missing' (i.e. no) data for each female, and because these data were further subdivided by phase, the overall shape and location of these ranges was less subject to the biases of our sampling methods, and therefore more reliable, than the utilization distribution therein.

Phase-range centroid coordinates were calculated as the geometric centre of mass of each range polygon, assuming uniform density. Phase-range overlap values were calculated using the simple measure of the proportion of one animal's range that is overlapped by another animal's range. These calculations gave two directional values: the proportion of individual A's range overlapped by individual B's, and the proportion of individuals B's range overlapped by A's. Depending on the analysis (see below), we used either these singular directional overlap values, or dyadic overlap values. The dyadic overlap between two individuals' concurrent ranges was calculated as the product of these two singular directional overlap values:

$$\mathrm{DyadicOverlap}_{\mathrm{AB}} = \frac{\mathrm{Overlap}_{\mathrm{AB}}}{\mathrm{Area}_{\mathrm{A}}} \times \frac{\mathrm{Overlap}_{\mathrm{AB}}}{\mathrm{Area}_{\mathrm{B}}}$$

where $\mathrm{Overlap}_{\mathrm{AB}}$ is the area of overlap of the phase ranges of individuals A and B, $\mathrm{Area}_{\mathrm{A}}$ is the total range size of individual A and $\mathrm{Area}_{\mathrm{B}}$ is the total range size of individual B. Assuming that both animals used their ranges uniformly, this value gives the probability of both individual A and B being in the overlapping area simultaneously (Hutchinson and Waser 2007).

Statistical analysis

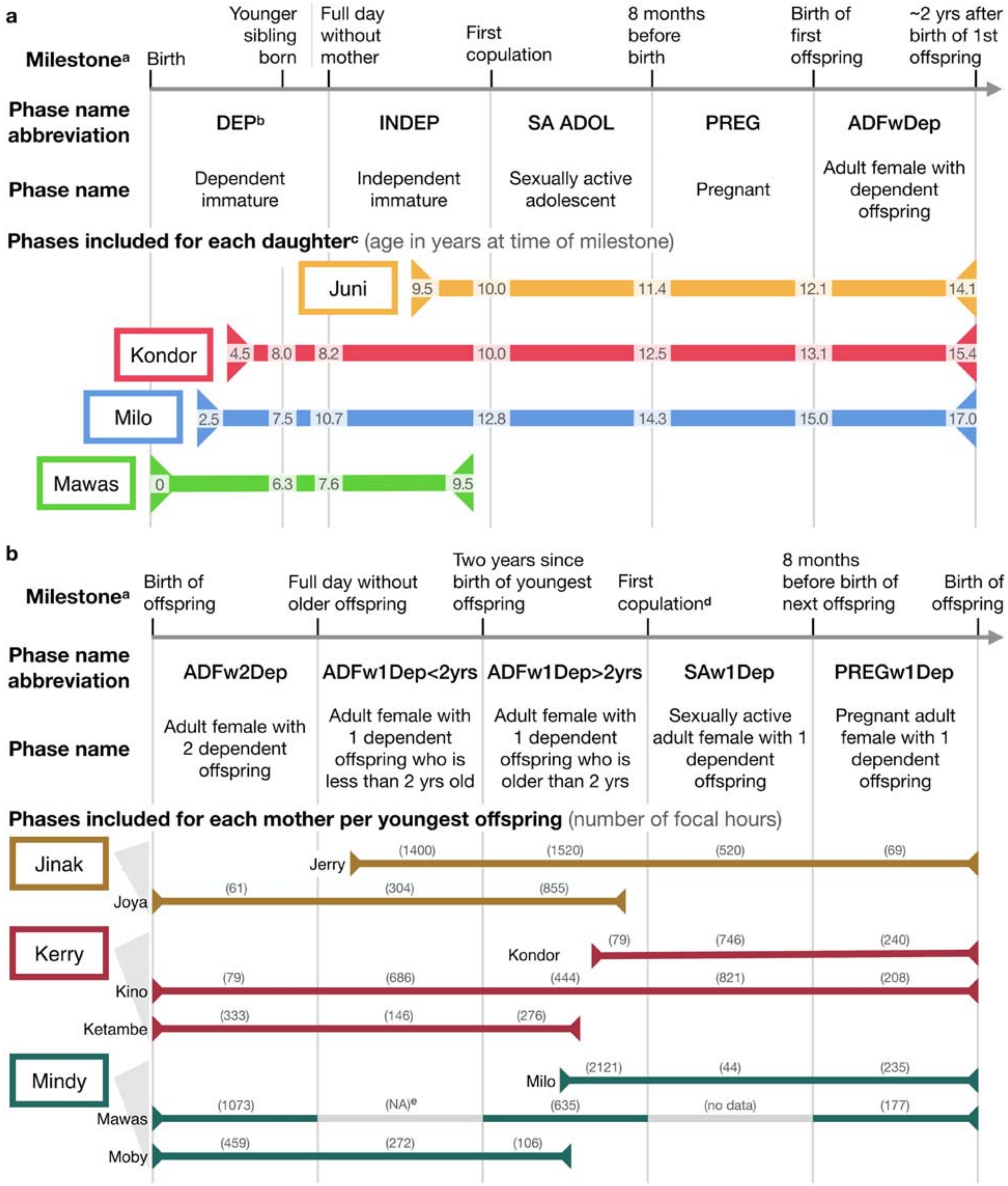
All spatial and statistical analyses were conducted in R version 3.5.1 (R Core Team 2018). Phase-range polygons, areas and overlap, were calculated using the adehabitatHR packages (Calenge 2006). All general linear mixed models (LMMs) were calculated using the lme function from the nlme package (Pinheiro et al. 2018). Generalized linear mixed models (GLMMs) were calculated using the glmmTMB function from the glmmTMB package (Brooks et al. 2017), except for those requiring the inclusion of a temporal autocorrelation variance structure and were therefore calculated using the glmmPQL function from the MASS package (Venables and Ripley 2002). In all applicable models, the focal's *phase* was a categorical variable and included as a fixed effect, with polynomial contrasts set in order to test for patterns of change in the outcome variable over the course of time. Planned contrasts were also set for the *relationship* factor, in all applicable models, specifically: mothers compared with non-relatives, and mothers compared with other relatives. Single-term deletions from each mixed model were performed using the drop1 function in the lme4 package (Bates et al. 2015), in order to obtain the likelihood ratio values for each fixed effect. Table S3 gives details about the specific models used in each analysis, including outcome variables, fixed effects and random effects.

To investigate *how* a young female establishes her home range, we first analysed changes in daughters' and mothers' daily travel, specifically their DJLs, and phase-range sizes. Thus, two parallel analyses were conducted, one for daughters (i.e. nulli/primiparous females) and one for mothers (i.e. multiparous females), in order to establish what aspects of movement and range size changes could be attributed simply to reproductive phase, and what aspects were specific to young females' development. (Note that for all subsequent analyses, we used only data subdivided by daughters' phases.)

Next, we analysed changes in the amount of time that daughters spent in association with their mothers through the daughters' phases. We then investigated overall changes in association time that daughters spent with their mothers and with other related and unrelated adult females over time, by calculating the proportion of time that each daughter spent in association with each other local adult female during each phase. Thus, for each focal daughter, for each of her phases, the total proportion of time spent in association with her mother, and with each other adult female in the area (including relatives and non-relatives) was calculated. Only association values for females with whom the focal daughter had non-zero phase-range overlap during at least one phase (or—in cases where there was not enough focal data of the other female for her ranges to be calculated—non-zero proportion of time spent in association during at least one phase), were included in the analysis (i.e. adult females with whom the daughter never had any range overlap nor association were not included). In order to establish the phase at which the amount of time that daughters spent in association with their mothers no longer differed with the amount of time that daughters spent in association with other adult females (if at all), we ran four post hoc tests (one for each phase except PREG, for which the sample size was too small).

Lastly, to investigate the effect of association with males on daughters' phase-range development, we first looked at basic overall association time with flanged and unflanged males (these are different sexually mature male morphs; e.g. Utami Atmoko and van Hooff 2004; Dunkel et al. 2013) across the phases, including post hoc per-phase tests designed to establish exactly how the time that daughters spent associating with flanged and unflanged males changed over the phases. We then looked at the effects of associating with males on daughters' association time with other adult females during the INDEP, SA ADOL and PREG phases. Next, to specifically investigate the effects of male association on agonistic interactions between nulliparous females and other adult females, we calculated the rates of agonistic interactions involving daughters per hour of observation when she was in association and not in association with an adult male. Because agonistic interactions were rare, we pooled all social interaction data from the INDEP, SA ADOL, and PREG phases (i.e. from independence to first parturition) and only included the three daughters for whom we had data for all of three of these phases. Interactions were divided into those *directed towards the daughters by adult females*, and those *directed towards adult females by the daughters*. We compared the rates of both kinds of agonistic interactions when the daughter was in association with a male vs. when she was not in association with a male. Lastly, to specifically investigate the effect of association with males on spatial exploration, we focussed on the three daughters who had already completed the SA ADOL phase. For each of these three daughters, we overlaid all of her location points from the SA ADOL phase over her INDEP range to see where she associated with males while sexually active, relative to her past range, and we tested whether being in association with a male was a predictor of whether a sexually active adolescent female was inside or outside her INDEP phase range.

To investigate *where* a young female establishes her home range, we quantified their shifting of ranges through daughters' development in two ways—in both cases, using the daughters' DEP phase ranges to represent the 'natal ranges': (1) we compared both daughters' and mothers' phase-range overlap of daughters' post-



[a] New phase begins on day that milestone is first observed

[b] For daughters' day journey length and association with males analyses, only data after the mother's next offspring (i.e. the daughter's younger sibling) was born is included in the DEP phase

[c] Numbers on each bar represent the (estimated) ages of the daughter at time of milestone. Details about the dates, ages, durations, and sample sizes of daughters' phases are in Table S1

[d] First time that the mother is observed copulating with an adult male and within 1 year she is either pregnant, or she is observed copulating again (i.e. single isolated copulations, long before she actually becomes pregnant again, and without any subsequent copulations observed within 1 year, are ignored)

[e] Milo (older sibling) was not independent until Mawas was over 2 years old

Fig. 2 An overview of the phases into which the data were split: **a** phases of the four daughters, which were used for all analyses and,by which all other females' data were divided, and **b** phases of the three mothers, which were used only for the analysis of mothers' daily travel and phase-range size dependence phases to the daughters' natal range, and (2) we compared both daughters' and mothers' phase-range centroid positions of daughters' post-dependence phases to the centroid of the daughters' natal ranges. We also investigated changes in the relative positions of mother and daughter phase ranges through daughters' phases in two ways: (1) we analysed changes in the degree of daughter-mother phase-range overlap, and (2) we measured the Euclidian distance between the centroids of daughters and their mothers through each of their phases.

Furthermore, we investigated changes in phase-range overlap between daughters and mothers compared with the overlap between daughters and other related and unrelated adult females in the area. Only ranges based on at least 500 location points, and ranges of females with whom the focal daughter

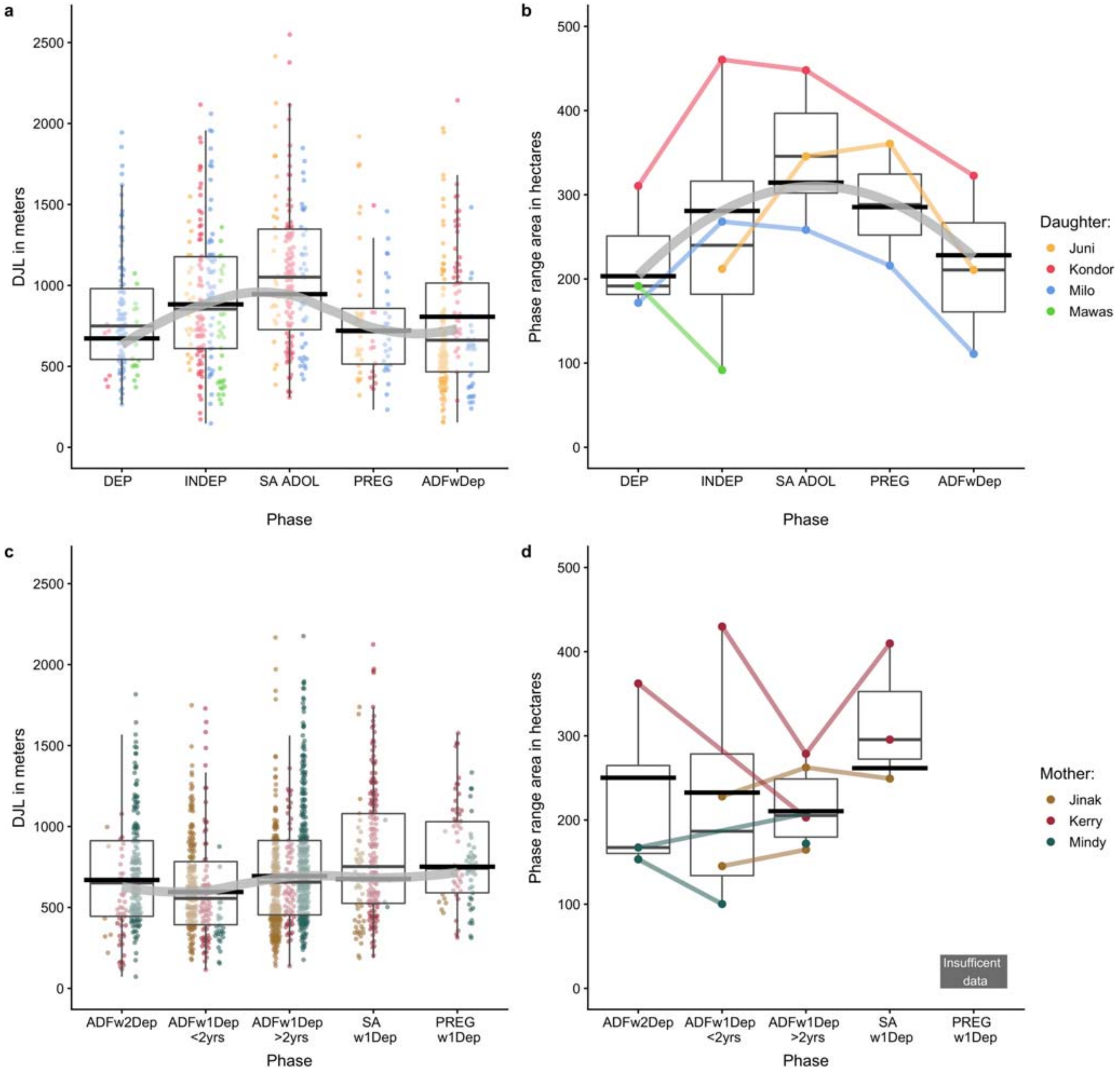


Fig. 3 Daughters' **a** day journey length (DJL) and **b** phase-range size results, and mother's **c** DJL and **d** phase-range size results; points are raw data, the boxes show the median and interquartile ranges, the whiskers extend to the maximum and minimum data points that are within 1.5 times the interquartile range from the upper and lower quartiles, thick black horizontal lines represent mean model predictions when controlling for other factors and the thick transparent grey lines represent the significant polynomial patterns seen across phases. Note that in the plot of mothers' phase-range sizes (**d**), each line connecting point represents that mothers' phase-range sizes with a particular youngest dependent offspring. For abbreviations of phases, see Fig. 2

had non-zero proportion overlap during at least one phase, were included in the analysis. In order to establish the phase at which dyadic overlap between daughters and mothers no longer differed with dyadic overlap between daughters and other adult females (if at all), we ran four post hoc tests (one for each phase except PREG, for which the sample size was too small).

Data availability

The datasets generated and/or analysed during the current study are available from the corresponding author on reasonable request.

Results

Daily travel and phase-range size

The mean DJL of daughters was 882 m (range = 147 to 2550 m, SD = 425.2, $n = 688$). Daughters had significantly longer DJLs (square root transformed to ensure normality of the residuals) on days when they spent a lower proportion of time alone ($X^2(1) = 9.33$, $p < 0.005$; $b \pm \mathrm{SE} = -2.34 \pm 0.744$, $t = -3.14$, $p < 0.005$), a higher proportion of time on the ground ($X^2(1) = 5.88$, $p < 0.05$; $b \pm$ SE $= 10.70 \pm 4.417$, $t = 2.42$, $p < 0.05$), and when fruit availability was higher ($X^2(1) = 68.87$, $p < 0.0001$; $b \pm \mathrm{SE} = 0.86 \pm 0.101$, $t = 8.52$, $p < 0.0001$). Phase had a significant quartic effect on DJL ($X^2(4) = 40.93$, $p < 0.0001$; $b \pm \mathrm{SE} = 1.51 \pm 0.591$, $t = 2.56$, $p < 0.05$) (Fig. 3a). The mean (across individuals) model predictions per phase—when holding other fixed effects constant at their means—indicated that DJLs increased from DEP to INDEP, then increased again from INDEP to SA ADOL and then decreased to PREG and increased again to ADFwDep (see Fig. 2a for phase abbreviations).

The mean DJL of mothers was 726 m (range = 72 to 2176 m, SD = 361.4, $n = 1294$). Mothers had significantly longer DJLs (square root transformed to ensure normality of the residuals) on days when they spent a lower proportion of time alone ($X^2(1) = 53.25$, $p < 0.0001$; $b \pm \mathrm{SE} = -3.91 \pm 0.527$, $t = -7.41$, $p < 0.0001$) and when fruit availability was higher ($X^2(1) = 117.65$, $p < 0.0001$; $b \pm \mathrm{SE} = 0.665 \pm 0.060$, $t = 11.13$, $p < 0.0001$), while the proportion of time that they spent on the ground did not have a significant effect on DJL ($X^2(1) = 2.89$, $p = 0.09$; $b \pm \mathrm{SE} = 7.54 \pm 4.437$, $t = 1.698$, $p = 0.09$). Phase had a significant quartic effect on DJL ($X^2(4) = 21.43$, $p < 0.0005$; $b \pm \mathrm{SE} = 1.16 \pm 0.399$, $t = 2.91$, $p < 0.005$) (Fig. 3c). The mean (across individuals) model predictions per phase—when holding other fixed effects constant at their means—indicated that DJLs decreased from ADFw2Dep to ADF1Dep < 2 years, and then increased to ADF1Dep > 2 years, stayed almost constant to SAw1Dep, and then peaked slightly during PREGw1Dep. Comparing PREGw1Dep with ADFw2Dep (i.e. looping back from pre-birth to post-birth), there was a decrease in DJL (see Fig. 2b for phase abbreviations).

The mean phase-range size of daughters was 265 ha (range = 92 to 460 ha, SD = 109.8, $n = 15$). Daughters tended to have larger phase ranges when mean fruit availability was higher ($X^2(1) = 6.12$, $p < 0.05$; $b \pm \mathrm{SE} = 29.86 \pm 13.944$, $t = 2.14$, $p = 0.08$), and the effect of phase also approached significance ($X^2(4) = 9.41$, $p = 0.05$). Phase had a quadratic effect on range size ($b \pm \mathrm{SE} = -88.72 \pm 31.528$, $t = -2.81$, $p < 0.05$) (Fig. 3b). The mean (across individuals) model predictions per phase—when holding mean fruit availability constant—indicated that range size increased from DEP to INDEP, peaked during SA ADOL, and then decreased again during PREG and during ADFwDep.

The mean phase-range size for mothers was 239 ha (range = 100 to 430 ha, SD = 96.3, $n = 16$). Mothers' range size was not significantly predicted by phase ($X^2(1) = 1.733$, $p = 0.63$) or mean fruit availability ($X^2(1) = 0.383$, $p = 0.54$). Although the mean phase-range size during sexual activity was higher than during the other phases, the mean model prediction—controlling for mean fruit availability—was not significantly higher (Fig. 3d).

These results indicate that there was a difference between the patterns of change in DJL and phase-range size between nulli/primiparous females (daughters) and multiparous females (mothers). Most notably, while daughters' DJL peaked during sexual activity, mothers' DJL peaked during pregnancy, immediately prior to the birth of their next offspring. Furthermore, unlike daughters, mothers did not show any significant changes in phase-range size through their reproductive phases—i.e. there was no expansion of their range size during sexual activity nor a subsequent contraction in range size after the birth of their offspring.

Association with adult females

The proportion of time that daughters spent in association with mothers during each phase ranged from 0 to 0.994 (mean = 0.32, SD = 0.399, $n = 16$). The proportion of time that daughters spent in association with their mothers was significantly predicted by phase ($X^2(4) = 33.19$, $p < 0.0001$) but not by mean fruit availability ($X^2(1) = 0.067$, $p = 0.80$). Their proportion of time in association decreased quadratically over the phases ($b \pm \mathrm{SE} = 0.36 \pm 0.095$, $t = -3.81$, $p < 0.01$), with the highest association occurring during the DEP phase, followed by a 57% decrease into the INDEP phase, then another 57% decrease into the SA ADOL phase, and a further decrease down to a predicted value of no association during PREG, and a slight increase during the ADFwDep phase (Fig. 4a).

The proportion of time that daughters spent in association with other local adult females ranged from 0 to 0.994 (mean =

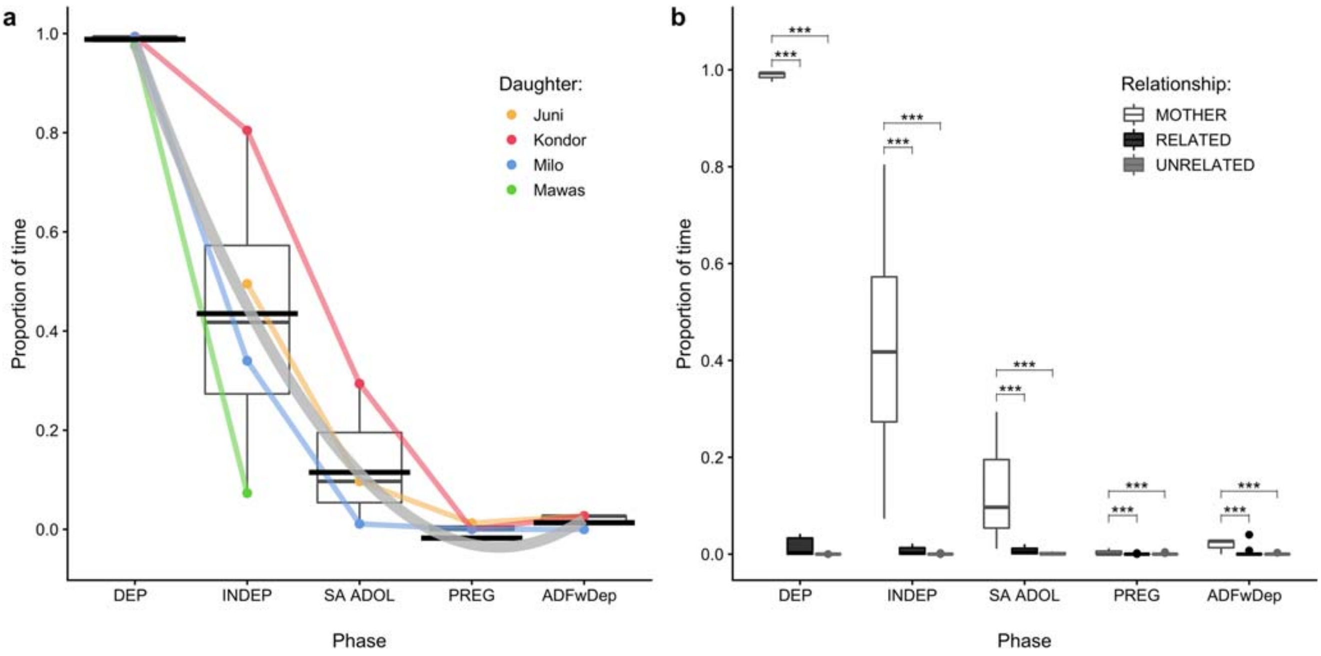


Fig. 4 **a** Daughters' association time with their mothers, and **b** daughters' association time with each other adult female; in (**a**) and (**b**), the boxes show the median and interquartile ranges, the whiskers extend to the maximum and minimum data points that are within 1.5 times the interquartile range from the upper and lower quartiles; in (**a**), points joined by coloured lines are raw data, thick black horizontal lines represent mean model predictions when controlling for other factors and the thick transparent grey lines represent the significant polynomial pattern seen across phases; in (**b**), significance stars refer to post hoc per-phase tests of mothers compared with related females and mothers compared with unrelated females, and points denote outliers. For abbreviations of phases, see Fig. 2

0.043, SD = 0.172, *n* = 129). The proportion of time that daughters spent with their mothers is summarized above, while the proportion of time that they spent in association with relatives varied between 0 and 0.042 (mean = 0.007, SD = 0.012, *n* = 53), and that with non-relatives varied between 0 and 0.006 (mean = 0.0005, SD = 0.001, *n* = 60).

Daughters' time spent in association with other adult females was significantly predicted by an interaction between their relationships with the other adult female and her phase ($X^2(8) = 248.24$, $p < 0.0001$) but not by mean fruit availability ($X^2(1) = 0.069$, $p = 0.79$). Post hoc per-phase generalized linear mixed models show that daughters spent significantly more time, through all phases, in association with their mothers than with other related adult females and more time with their mothers than with unrelated adult females (Fig. 4b; Table S4). Post hoc per-phase models also indicated that mean fruit availability may have had a positive effect on daughters' association with other adult females during the INDEP and ADFwDep phases.

Association with males

The proportion of time during each phase daughters spent in association with adult males (flanged or unflanged) varied between 0 and 0.267 (mean = 0.059, SD = 0.090, *n* = 16). The proportion of time that daughters spent in association with adult males has a clear peak during SA ADOL, when they spent approximately 45% of their time in association with an adult male. Daughters' proportion of time spent with adult males was significantly predicted by an interaction between adult male morph and her phase ($X^2(4) = 89.45$, $p < 0.0001$) but not by mean fruit availability ($X^2(1) = 0.135$, $p = 0.71$). Post hoc per-phase Poisson GLMMs show that daughters spent significantly more time with unflanged males than with flanged males during all phases, except for PREG when there was no difference (Fig. 5; Table S5). The strongest difference was during INDEP and SA ADOL, when daughters spent almost ten times more time with unflanged males than with flanged males.

From INDEP to PREG, the proportion of the day that a daughter spent in association with other adult females (including her mother) was not predicted by whether or not she was in association with an adult male (flanged or unflanged) that day ($X^2(1) = 0.009$, $p = 0.92$). In other words, daughters were equally likely to associate with other adult females whether or not they were in association with an adult male as well.

During these same phases, daughters were aggressed by other adult females at a mean rate of 0.077 times (SD = 0.049) per focal observation hour during which they were in association with another adult female. Table 1 gives an overview of the rates of agonism received from, and directed towards, other adult females for each focal daughter. Two daughters received the highest rates of aggression from other unrelated adult females, while one daughter received the highest rate of aggression from related adult females. All daughters received aggression from their mothers, though

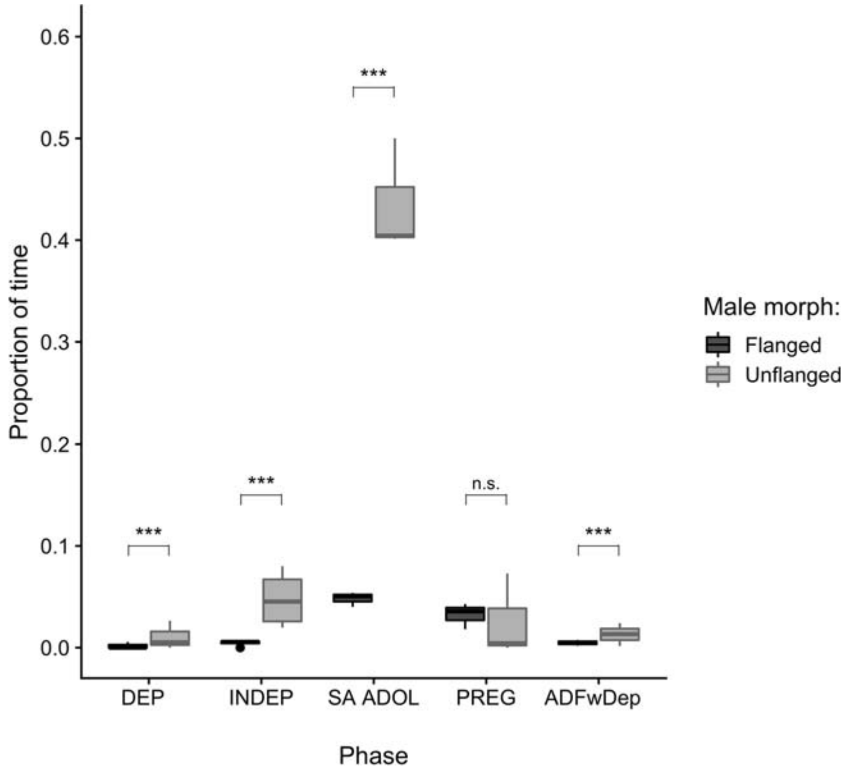


Fig. 5 Daughters' proportion of time spent in association with each morph of adult male; the boxes show the median and interquartile ranges, and the whiskers extend to the maximum and minimum data points that are within 1.5 times the interquartile range from the upper and lower quartiles; significance stars refer to post hoc per-phase tests of time spent with unflanged males compared with flanged males. For abbreviations of phases, see Fig. 2

these rates were relatively low. Rates are calculated as the number of events per focal observation hour during which the daughter was in party with an individual of that relationship class (mother, related, unrelated) of adult female. With respect to their association with males, daughters were aggressed by other adult females a mean of 0.025 times (SD = 0.015) per observation hour when they were not in association with an adult male, and 0.007 (SD = 0.0009) when they were in association with a male. Two out of three daughters received substantially lower rates of agonistic interactions from other adult females when in association with males (Fig. 6a). For the third, Milo, there was basically no difference, but she already received extremely low rates of agonistic interactions when not with an adult male. The only daughter who ever won or directed an agonistic interaction at other adult females, Juni, did so towards unrelated adult females only, and she won a higher rate of agonistic interactions when in association with an adult male (Fig. 6b).

During her SA ADOL phase, association with a male was not a significant predictor of whether a daughter was inside or outside her previous phase's (INDEP) range ($b \pm SE = 0.206 \pm 0.149$, $t = 1.381$, $p = 0.17$). In other words, sexually active daughters were equally likely to be with a male inside and outside new and familiar areas.

Phase-range overlap and shift

Both mothers and daughters of each dyad maintained a substantial degree of overlap with the daughter's natal range throughout the four post-dependence phases (mean = 0.69, range = 0.53 to 0.90, SD = 0.098, $n = 15$). There were no significant changes in overlap through the phases ($X^2(3) = 0.269$, $p = 0.97$), and mothers and daughters did not significantly differ in their degree of overlap with the natal range ($X^2(1) = 0.063$, $p = 0.80$) (Fig. S4a).

Table 1 Rates of agonism (events per hour when focal daughter was in association with each class of adult female), including aggression such as chasing, hitting, biting, pushing and direct displacements such as supplantation, avoiding and fleeing

Daughter	Rate of agonism received from …				Rate of agonism directed towards …			
	Mother	Related ADF	Unrelated ADF	Overall	Mother	Related ADF	Unrelated ADF	Overall
Juni	0.122	0.125	*0.417*	0.134	0.000	0.000	*0.625*	0.011
Kondor	0.040	*0.329*	0.223	0.056	0.000	0.000	0.000	0.000
Milo	0.041	0.025	*0.115*	0.043	0.000	0.000	0.000	0.000

Values set in italics indicate the highest rate of agonism received/given for each daughter

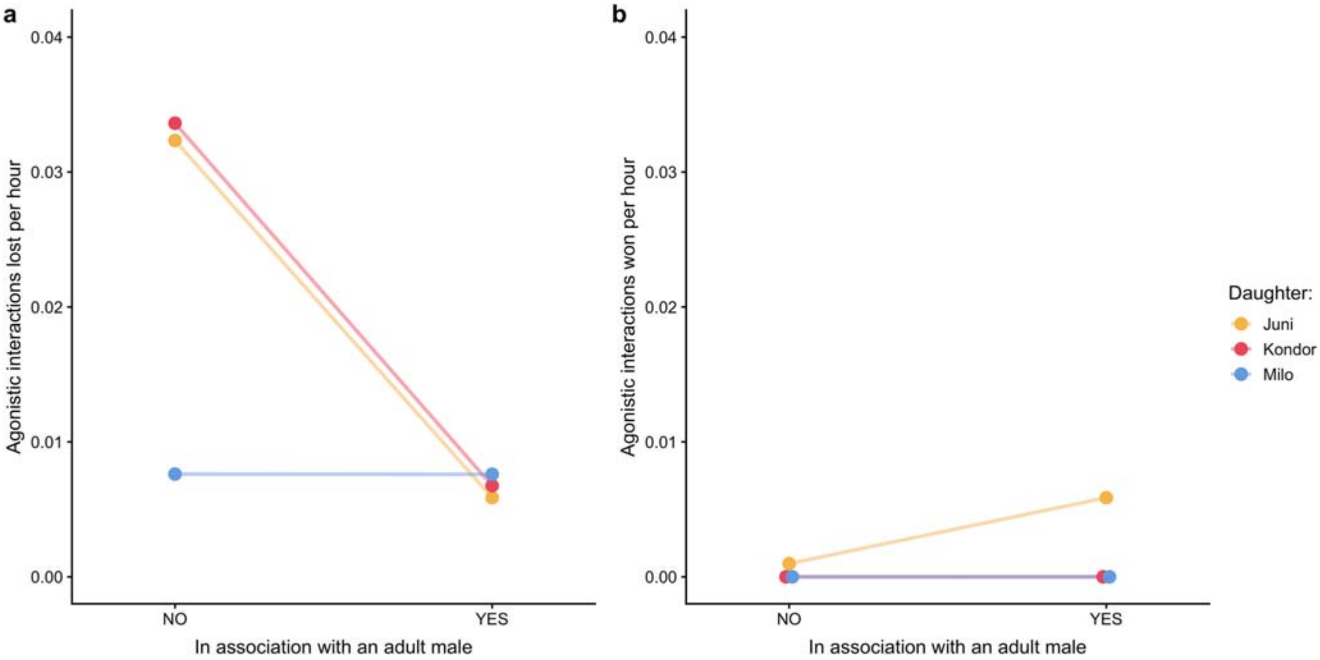


Fig. 6 The rate (events per hour) of agonistic interactions that daughters **a** received from, and **b**)directed towards, other adult females when in association and when not in association with an adult male

After daughters' DEP phases, both mothers and daughters shifted the centroids of their ranges away from the centroid of the daughter's natal range (mothers: mean = 374 m, range = 170 to 594 m, SD = 139, $n = 7$; daughters: mean = 255 m, range = 94 to 330 m, SD = 81, $n = 8$). The effect of phase on shift distance approached significance as a linear effect ($X^2(3) = 6.99$, $p = 0.07$; $b \pm \mathrm{SE} = 95.96 \pm 44.59$, $t = 2.15$, $p = 0.06$), driven by the significant effect of class: mothers shifted the centroid of their ranges significantly farther from the natal range than daughters ($X^2(1) = 6.84$, $p < 0.01$; $b \pm \mathrm{SE} = 111.88 \pm 45.19$, $t = 2.48$, $p < 0.05$) (Fig. S4b).

Dyadic overlap between mothers and daughters varied between 0.13 and 0.98 (mean = 0.56, SD = 0.29, $n = 14$). Dyadic overlap was significantly predicted by phase ($X^2(4) = 40.69$, $p < 0.0001$) and mean fruit availability ($X^2(1) = 5.318$, $p < 0.05$). Mean fruit availability had a significant positive effect on dyadic overlap value ($b \pm \mathrm{SE} = 0.18 \pm 0.080$, $Z = 2.23$, $p < 0.05$). Dyadic overlap decreased quadratically over the phases ($b \pm \mathrm{SE} = 1.44 \pm 0.189$, $Z = 7.63$, $p < 0.0001$), with the highest overlap occurring during the DEP phase (mean = 0.96, $n = 3$), and decreasing until it levelled off during the PREG (mean = 0.28, $n = 1$) and ADFwDep (mean = 0.29, $n = 3$) phases (Fig. 7a).

Distances between daughters' and their mothers' phase-range centroids varied between 3 and 911 m (mean = 282 m, SD = 263, $n = 14$). Distance was significantly predicted by phase ($X^2(4) = 15.32$, $p < 0.005$) but not by mean fruit availability ($X^2(1) = 0.789$, $p = 0.37$). Distance increased linearly over the phases ($b \pm \mathrm{SE} = 404.86 \pm 106.20$, $t = 3.812$, $p < 0.05$), with the least distance occurring during the DEP phase (mean = 10 m, $n = 3$), and the largest distance during the ADFwDep phase (mean = 596 m, $n = 3$) (Fig. 7b).

The dyadic overlap between daughters and other individual local adult females ranged from 0 to 0.981 (mean = 0.24, SD = 0.23, $n = 79$). The dyadic overlap between daughters and mothers was summarized above, while the dyadic overlap between daughters and their adult female relatives ranged from 0.01 to 0.48 (mean = 0.23, SD = 0.12, $n = 43$), and dyadic overlap with non-relatives ranged from 0 to 0.40 (mean = 0.059, SD = 0.10, $n = 22$). Figure S5 shows maps of all daughters' and surrounding adult females' ranges per phase.

Daughters' dyadic overlap with other adult females was significantly predicted by an interaction between their relationships with the other adult female and her phase ($X^2(8) = 53.78$, $p < 0.0001$), as well as by the mean fruit availability during that phase ($X^2(1) = 5.50$, $p < 0.05$). Post hoc per-phase linear mixed models show that (1) daughters had significantly higher overlap with their mothers than with unrelated females through all phases, and (2) daughter had significantly higher overlap with their mothers than with related females during the DEP and INDEP phases, but from the SA ADOL on the daughters' overlap with their mothers began to approach that with other adult females, and by their ADFwDep phase, daughters overlap with their mothers was no longer significantly different from that with other related adult females (Fig. 7c; Table S6). Mean fruit availability was positively correlated with dyadic overlap between daughters and other adult females in the overall model ($b \pm \mathrm{SE} = 0.028 \pm 0.012$, $t = 2.35$, $p < 0.05$), but this significant effect was lost in the post hoc per-phase models.

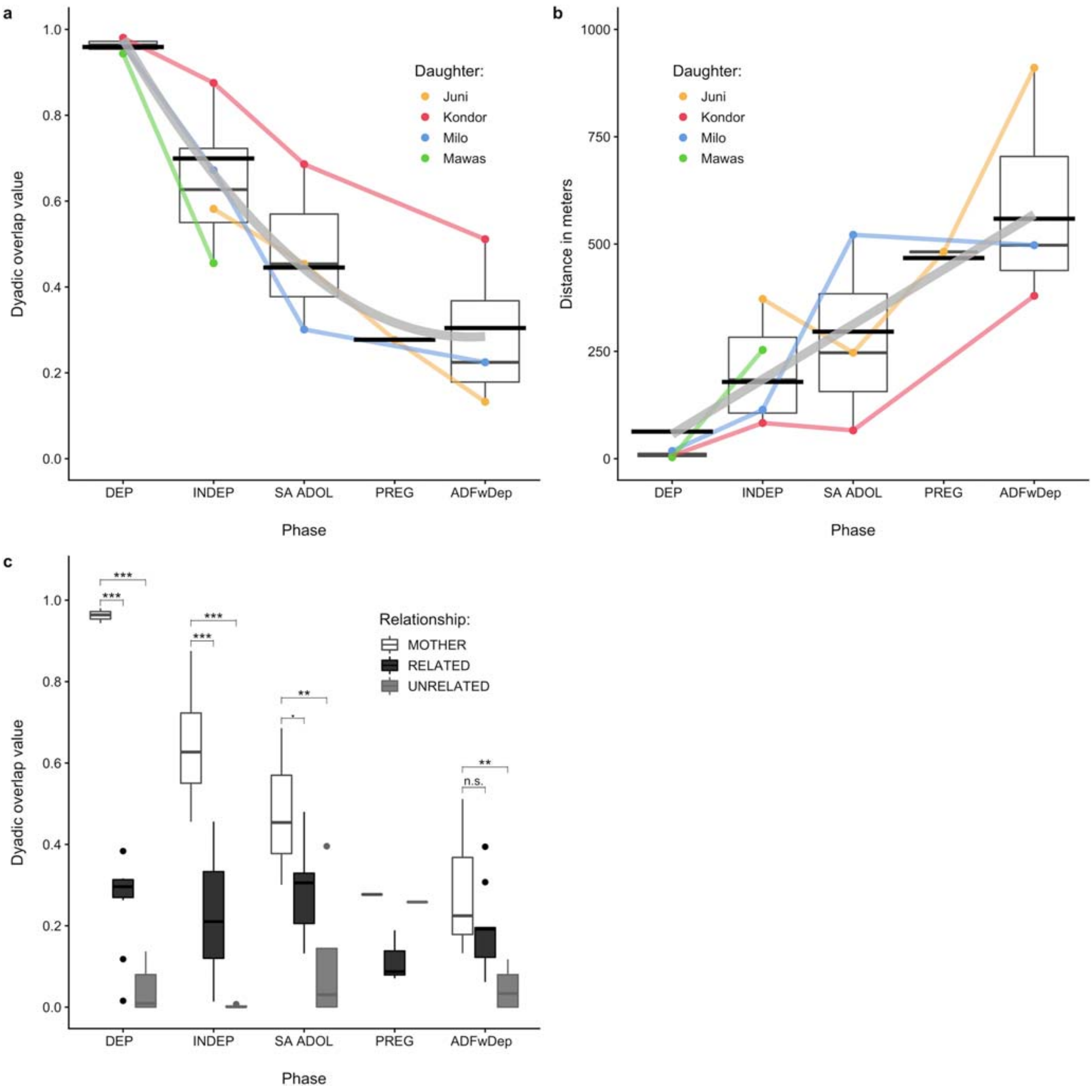


Fig. 7 **a** Daughters' dyadic overlap with their mothers, **b** distance between daughters' and mothers' range centroids and **c** daughters' dyadic overlap with each other adult female; in all three plots, the boxes show the median and interquartile ranges, the whiskers extend to the maximum and minimum data points that are within 1.5 times the interquartile range from the upper and lower quartiles; in (**a**) and (**b**), points joined by coloured lines are raw data, thick black horizontal lines represent mean model predictions when controlling for other factors and the thick transparent grey lines represent the significant polynomial pattern seen across phases; in (**c**), significance stars refer to post hoc per-phase tests of mothers compared with related females and mothers compared with unrelated females, and points denote outliers. For abbreviations of phases, see Fig. 2

Discussion

We conducted a detailed longitudinal study of female movement and association patterns before and after their first parturition in order to gain a better understanding of the process of home range establishment among wild female Bornean orangutans at Tuanan. We found that after the birth of her younger sibling, while she is an independent immature (INDEP), a young female begins to widely explore her surroundings, increasing the size of her home range and the length of her daily paths, suggesting that this is a time of increased spatial exploration. This exploration continues through her adolescence (SA ADOL), a time during which female orangutans are sexually active but not yet able to conceive. During this time, she associates more with unflanged than with flanged males. She may receive fewer agonistic interactions from other adult females when in the presences of an adult male, but she does not specifically use this 'protection' to move through previously unfamiliar areas. A young female and her mother maintain a high degree of overlap with her natal range, but gradually decrease their degree of overlap with each other, as they shift their ranges away from each other's. By the time she is a sexually active adolescent (SA ADOL), a young female and her mother share as much overlap as she does with other related adult females, although she continues to associate more with her mother than with other related adult females, and still does so after the birth of her first offspring. After the birth of her first offspring (ADFwDep), a young female ends up living in a range that has a high degree of overlap with her original natal range and also includes some new surrounding area. Mothers of these daughters also maintain a high degree of overlap with their daughters' natal range, however the center of their ranges shift farther from the daughter's natal range, indicating that they are also incorporating some new areas into their ranges.

Mechanisms of home range establishment

Our results showed that range size and DJL both peaked during adolescent sexual activity, suggesting that young females go through an 'exploration phase' during which they move widely, outside their natal ranges. This is consistent with previous studies that have noted sexually active females' increased home range sizes and day journey lengths, and/or the frequency of observations of adolescent females in areas previously not included in their ranges, suggesting expanded home ranges (e.g. Galdikas 1995; Singleton and van Schaik 2001; Wartmann et al. 2010). However, the largest degree of increase in both range size and day journey length occurred immediately post-dependence: these clear increases in range area and day journey length from when a young female was dependent on her mother to when she was an independent immature indicate that young females begin to explore their surroundings more widely as soon as some degree of spatial independence is achieved, and prior to the onset of sexual activity. Although home range expansion during sexual activity / mating seasons has been documented among some species of bears (Dahle and Swenson 2003b; Edwards et al. 2013), we are unaware of studies of other taxa which separate nulliparous and multiparous sexual activity, and/or pre- and post-onset of adolescent sexual activity phases (if applicable—such a differentiation does not apply to all species).

An important question is whether the changes that we see in DJLs among nulli/primiparous females are simply the result of reproductive status—and therefore seen also among multiparous females—or if they are unique to these young females. Our results suggest that nulli/primiparous females have a quantitatively different pattern of DJL increase and decrease than the one found in multiparous females. First of all, nulli/primiparous females had, overall, longer DJLs (and larger home ranges) than multiparous females, the only exception being when the young females were still dependent and travelling with their mothers. Thus, the presence of dependent offspring shortens DJLs (see also Wartmann et al. 2010), which is consistent with differences observed between subadult and adult female chimpanzees (Pontzer and Wrangham 2006). It is likely that, overall, the presence of an infant—either clinging and adding weight, or travelling independently and needing support and assistance—slows down mothers and limits the distance that they can travel in a day, as has been observed in other taxa (chimpanzees: Pontzer and Wrangham 2006; brown bears: Dahle and Swenson 2003a). It is also possible that body size differences between nulli/primiparous females and multiparous females contribute to their overall differences in DJL. Female orangutans do not reach their full adult size until sometime after the birth of their first offspring (Leigh and Shea 1995; Schuppli, SSUA and MAvN, unpublished data), and canopy travel may be energetically less costly for these smaller females, allowing them to travel farther than larger, fully grown, multiparous females (Halsey et al. 2016).

More specifically, however, the patterns of DJL increases and decreases seen among the nulli/primiparous daughters were different from those observed among their multiparous mothers: nulliparous females had the strongest increase in DJL when they first became independent from their mothers, achieved their longest DJLs during sexual activity, and showed a marked decline in DJL from sexual activity to pregnancy. Multiparous females, on the other hand, showed a pattern of increasing DJL length that mirrored the growth trajectory of their dependent offspring: When they had two dependent offspring (a newborn and an older, soon-to-be-independent offspring), they had longer DJLs than after the older offspring first achieved independence. Subsequent to this, multiparous females' DJL increased slightly, phase by phase, as their single dependent offspring grew in age/size and was able to move faster and more independently, and also contributed to the faster depletion of feeding sources. Thus, their peak DJL was reached during pregnancy—when their dependent offspring was old enough to be causing some considerable feeding competition but before they had another newborn to slow them down. In chimpanzees, females in oestrus have longer DJLs than anoestrous females (Matsumoto-Oda and Oda 1998; Bates and Byrne 2009), and sexually receptive mothers have faster travel speeds than mothers with offspring (Wrangham 2002). It would appear that, among orangutans, the reduction in DJL due to the presence of a dependent offspring outweighs the increase in DJL due to sexual receptivity. The difference with chimpanzees may be linked to the arboreal travel of orangutans, which is energetically more costly (Thorpe et al. 2007; Manduell et al. 2012), and also often requires that mothers assist or wait for their otherwise independently moving offspring when crossing canopy gaps (van Noordwijk and van Schaik 2005; Chappell et al. 2015). Our results make clear that young females—from the time they are independent immatures until they become pregnant—experience an increase in daily travel and range size that suggests an 'exploration phase', which is unique to nulliparous females and not simply a reflection of sexual activity.

Young females associated more with their own mothers than with other related and unrelated adult females through all of their phases, although their range overlap with their own mothers decreased to the same level as range overlap with other related adult females from the time that they were sexually active. This suggests that these females are preferentially associating with their mothers, even after they become mothers themselves. While our definition of association as an inter-individual proximity of 50 m or less does not require there to be direct interactions during an association, it does require a high degree of social tolerance. Female orangutans in association often travel in coordination, feed simultaneously from the same tree or the same patch of trees, allow their offspring to play together, and sometimes nest overnight near each other (for more details, see van Noordwijk et al. 2012). The fact that females who were hardly ever in association still maintained some degree of range overlap (dyadic overlap values of up to 0.48 among related females and 0.40 among unrelated females), suggests that females may actively avoid associations with certain other local adult females, though there is no evidence of territoriality. Further evidence for active avoidance between unrelated females may be the relatively high rate of agonistic events between unrelated females when they were in association; indeed, two of the three focal daughters received higher rates of agonism from unrelated adult females than from their mothers and other related adult females prior to their first parturition, suggesting that there is general intolerance between unrelated females, despite shared home range areas.

Sexually active nulliparous females spent more time in association with unflanged than flanged males. This is consistent with previous studies at other sites, which have noted that flanged males seem to have limited interest in nulliparous females, despite these young females' interest in them (Schürmann 1982; Galdikas 1995). Flanged male orangutans can almost always displace unflanged males (Schürmann 1982; Utami et al. 2002), suggesting that their lack of interest in nulliparous females opens the door for unflanged males to associate with these females. This is consistent with observations of East African chimpanzees, among whom males prefer older parous females over nulliparous females, and higher-ranking males will attempt to lower the access of lower ranking males to these multiparous females (Muller et al. 2006).

Male support during agonistic interactions between female orangutans has been previously documented among the Tuanan orangutans: Marzec et al. (2016) described an instance of coalitionary lethal aggression in which an adult female and her unflanged male consort attacked another adult female, who was eventually protected by a flanged male. Thus, males provided support to both the attacking female and her victim (Marzec et al. 2016). Nonetheless, the present study found only tentative support for the idea that adult males may provide nulliparous/adolescent females with social support against older, more established, resident females. It is true that two out of three focal nulliparous females in our study received lower rates of agonistic interactions from adult females when in association with a male (and the third female's rate was negligible to begin with), consistent with Kahlenberg et al.'s (2008) observation of chimpanzees. However, there was no evidence that associating with males allowed these young females to explore new, unfamiliar areas, which could simply be because they hardly moved away from their natal area to begin with. In other populations with different habitat ecology, less dense orangutan populations, and more unoccupied space, this social protection may operate, since young females may incorporate more unfamiliar areas into their home ranges as they mature. However, it would only allow exploration and not facilitate settlement, given that females spend most of the time alone and would still be vulnerable to being aggressed when encountering dominant resident females.

Resource availability has a significant inverse relationship with home range size among several species of bears, with females travelling farther and wider to obtain resources during periods of scarcity (Moyer et al. 2007; Edwards et al. 2013). Among female orangutans, we found that temporal variation in habitat fruit availability had a variable effect on movement and ranges. Young females had longer DJLs, and—unlike their mothers—also larger ranges, when fruit availability was higher. This suggests that younger/nulliparous females may take advantage of increases in fruit availability in order to expand their ranges and spend more time within other adult females' home ranges. High fruit availability presumably facilitates exploration by nulliparous females: lessening the degree of scramble competition among females, may allow them to range farther within the boundaries of already-established adult females' ranges, whereas for already-established adult females, this expansion is not necessary. However, it should be noted that specifically investigating the influence of fruit availability on female range size—for instance, by subdividing location data based on periods of high and low fruit availability, and comparing individuals' range sizes under these two conditions—is beyond the scope of this study. Thus, the full effect of habitat fruit availability fluctuations on female home ranges and daily travel remains to be determined.

Spatial correlates of home range establishment

The extreme conservatism in space use among the female orangutans in Tuanan is notable: daughters maintained high spatial overlap with their mothers and other maternal kin, as well as overlap with their natal ranges, even after their first parturition. Mothers shared part of their home ranges with their maturing and fully adult daughters, and both (especially mothers) incorporated some area outside of the daughter's natal range as well. Mothers are therefore shifting their ranges farther into the ranges of other adult females, both related and unrelated. It is not possible, given our data, to ascertain the longer-term shifting patterns of mothers over successive daughters. However, given the high degree of transgenerational site fidelity, we believe that a mother's direction of shifting is likely a direct response to the spatial positioning of each daughter's range, rather than being linear/directional over successive daughters. It should be noted that these orangutans do live in an open system: sons from this same matriline leave the area (van Noordwijk et al. 2012), and many adult males come and go (Spillmann et al. 2017)—in other words, we can assume that these females are not maintaining this exceptionally high life-long site fidelity simply because the landscape itself prevents them from dispersing. Rather, it is likely that the social and ecological costs which females would accrue if they were to disperse would far outweigh the potential benefits of dispersing.

The exceptionally high degree of lifetime site fidelity and home range overlap among adult females in the Tuanan study area is likely facilitated by the resource distribution, and may be necessitated by the high orangutan population density, of this area. Throughout the Tuanan forest, relatively high-quality food sources (fruiting trees and vines) are frequent, small and homogenously distributed, and orangutans have relatively high daily caloric intake, even during periods of low fruit availability (Marshall et al. 2009; Vogel et al. 2015). These habitat factors lead to relatively relaxed scramble competition, and thus selection for spatial differentiation between adult females, especially related adult females, is also relaxed. Tuanan is also home to the highest recorded population density of wild Bornean orangutans, at approximately 4.25–4.5 individuals/km^2 (van Schaik et al. 2005). This high population density means that there are no "open areas" into which a young female could establish her home range; instead she must share range space with other adult females. Thus, the unique local ecology of the habitat and orangutan population at Tuanan means that females must, and can afford to, have highly overlapping home ranges (Vogel et al. 2015), very similar to the Sumatran swamp forest of Suaq Balimbing (Singleton and van Schaik 2001). Short-term mutual avoidance, especially during times of scarcity, may be enough to offset the competitive costs of this high range overlap. In less productive or more variable habitats with less abundant or lower-quality fallback foods, scramble competition may be more intense and open areas may be more available, and thus spatial differentiation between even-closely-related females may be more likely.

Morrogh-Bernard's (2009) Petal Hypothesis predicts that daughters will settle into home ranges that surround and overlap their mothers'. Specifically, this hypothesis predicts that in homogenous habitats (including Sabangau where this hypothesis was developed), female orangutans will have small home ranges, with more overlap between mother-daughter dyads than between other related individuals, while in heterogenous habitats, females will have larger home ranges and a high degree of overlap with all female relatives (Morrogh-Bernard 2009). Although we did not directly test it, our results provide mixed support for this hypothesis in Tuanan: while we did see primiparous females settling into home ranges that surrounded and overlapped with their mothers', and the relatively small home ranges that are predicted for a homogenous habitat, we did not see higher overlap between parous daughters and their mothers, than between parous daughters and other related females. Like Sabangau, Tuanan is a relatively homogenous peat swamp forest; however, Tuanan has significantly higher forest productivity and overall better orangutan diet quality, and thus a denser population (van Schaik et al. 2005; Vogel et al. 2015). We therefore suggest that habitat productivity and orangutan population density (as discussed above), may be a stronger driving force behind the spatial patterning of female orangutan home ranges than the degree of habitat heterogeneity per se.

Benefits and costs of philopatry

Many of the costs of dispersal among mammals are well documented and include such disadvantages as reduced feeding efficiency (due to a lack of familiarity with the location of food sources and/or the techniques needed to acquire them), higher stress levels, delayed breeding and thus lower reproductive potential and increased vulnerability to predators (Isbell and van Vuren 1996; Ronce 2007; Clutton-Brock and Lukas 2012; Walker et al. 2018). Female orangutans have very broad diets (Russon et al. 2009), which are acquired over years by socially induced learning (Schuppli et al. 2016, 2017). High overlap with the natal range allows females to keep their diet, and not accrue costs associated with the risky sampling of novel food items to include in the diet (cf. Bastian et al. 2010). Meanwhile, exploring new adjacent areas—where the location of food sources is unknown—during times of high resource availability is less risky than when resource availability is low, as food sources will be more frequent.

Furthermore, dispersing females lose the potential benefits of associating with their kin, such as opportunities for their dependent offspring to play with 'safe' partners. Indeed, van Noordwijk et al. (2012) found that related females allowed their offspring to engage in social play while unrelated adult females tended to actively prevent their offspring from engaging in social play. Play is likely an important behavior for mammalian social and locomotor development (Byers and Walker 1995; Fairbanks 2000; van Leeuwen et al. 2013; Heintz et al. 2017), and because orangutans have single births and do not live in cohesive social groups, there are limited opportunities for immatures to play, especially with peers (van Noordwijk et al. 2012, 2018). In general, unrelated adult females show low social tolerance to each other, even to the extent of a documented instance of lethal aggression between two unrelated adult females (Marzec et al. 2016). It may therefore be dangerous for females to venture too far off into unknown areas inhabited by unrelated adult females. Thus, female philopatry—i.e. the spatial clustering of maternal relatives exhibiting high social tolerance—among orangutans is likely vital for the healthy social and locomotor development of their offspring.

The potential benefits of dispersal for female mammals include reduced competition for resources (assuming that dispersing individuals are able to move to an area with relatively more resources), escape from an area or group where there is a high risk of infanticide by immigrant males and/or predators, inbreeding avoidance, and avoidance of the indirect costs of resource competition with kin (Clutton-Brock and Lukas 2012). The first three of these do not directly apply to female orangutans at Tuanan; there is no evidence that surrounding areas have higher resource availability and lower population densities, unfamiliar males are found everywhere due to their predominantly nomadic ranging patterns (Spillmann et al. 2017), predation on adult orangutans is very rare (Kanamori et al. 2012; Knott et al. 2019), and males' long-range natal dispersal is sufficient to prevent inbreeding (Nietlisbach et al. 2012). However, it is likely that philopatric female orangutans experience increased feeding competition with their maternal kin. There is strong evidence that orangutans maintain their predominantly solitary lifestyle because their high energetic needs (due to their large body size and arboreal travel) cannot be readily met when they are in direct, longer-term, feeding competition with close-by conspecifics (Mitani et al. 1991; van Schaik 1999; Wich et al. 2009; Kunz et al., unpublished data). Indeed, we found that females in association with other orangutans, and females with older dependent offspring, travelled farther each day—this is likely in order to satisfy their caloric intake, as food patches are depleted significantly faster when visited by more than one individual. Thus, even with limited association, there are likely costs associated with indirect feeding competition among female orangutans with overlapping home ranges. However, in a saturated habitat, moving away would not reduce scramble competition, so the choice is between scramble competition with kin versus with non-kin, which makes no difference for inclusive fitness as long as the habitat remains saturated. Thus, the benefits of remaining in a familiar habitat and having social access to maternal relatives would tip the balance in favour of philopatry.

Isbell (2004) has drawn attention to the potential costs to mothers of sharing their home ranges with their daughters. Mothers would only be expected to share their ranges with their daughters (i.e. female philopatry) when it would be unlikely for daughters to reproduce successfully elsewhere (indirectly costly to mothers), whereas overlap would not hamper their own subsequent reproduction (Isbell 2004). Indeed, if young female orangutans were to disperse from their natal areas, they may suffer reproductive costs similar to dispersing female chimpanzees, who gave birth to their first offspring on average 2 years later than non-dispersing females (Walker et al. 2018). Furthermore, the phase-by-phase shifting that we observed among mothers of nulli/primiparous females is essentially an expansion of their lifetime home range size and is facilitated by the generally frequent and homogenous distribution of small fruit sources through the Tuanan forest. Thus, mothers are able to continue their own reproduction even while their reproductively active daughters share overlapping areas.

Overall, it is clear that, among female orangutans at Tuanan, the benefits of philopatry far outweigh the costs, and lifetime site fidelity is exceptionally high (Arora et al. 2012; van Noordwijk et al. 2012; this study). It should be noted that our study focuses on one single matriline, and it is therefore possible that our results are not representative of the situation in other orangutan populations. In particular, in areas with more habitat disturbance and fragmentation, we could expect that the process of home range establishment may be different, as opportunities to explore as well as local habitat carrying capacities may be more limited. The temporal and spatial distribution of fruit and key fallback resources, and corresponding population densities, may also affect how exactly female orangutans establish their home ranges and, in particular, the degree of transgenerational site fidelity among maternally related females. However, there is nothing unusual about the matriline that we have studied which would suggest that they not representative of other orangutan matrilines, and it is likely that, to the extent allowed by local habitat ecologies and resource distributions, the benefits of female philopatry outweigh the costs and there is exceptionally high lifetime site fidelity among females in all orangutan populations. Indeed, we know of several other mother–adult daughter pairs who range at least partially within the Tuanan study area (suggesting that this situation is not unique to our studied matriline) (Tuanan Project, unpublished data; Arora et al. 2012), and known mother–daughter pairs of adult females have been shown at several other orangutan study sites (e.g. Knott et al. 2008; Morrogh-Bernard 2009; Schuppli 2019) suggesting that our situation of multiple generations of related females all ranging in the same area is not unusual among orangutans. Furthermore, our observations of long-term female site fidelity are also supported by genetic studies which have shown stable boundaries in mtDNA haplotypes in Sumatra (north versus south of lake Toba) and in Borneo (between major rivers) and significantly higher clustering and geographic differentiation of mitochondrial haplotypes than Y-chromosomal variation (Arora et al. 2010, 2012; Nietlisbach et al. 2012; Nater et al. 2013). Thus, our longitudinal behavioural evidence highlights important aspects of females' behavioural development through which this population structure is achieved: a spatial exploration phase prior to first parturition, high socio-spatial tolerance between maternal kin, and mothers sharing and shifting their ranges and thus accommodating their maturing daughters.

Implications for orangutan conservation

The implications of our results for orangutan conservation efforts are of particular importance. All orangutan species are classified as critically endangered by the (IUCN 2019). Our results highlight the extreme spatial conservatism of female orangutans—their long-term site fidelity and maintenance of overlap with their mothers and other maternal relatives—as well as the importance of their social bonds with, especially, their mothers. These results therefore emphasize the potentially detrimental effects of any forest loss for female orangutans, while male orangutans may cross open space and/or make use of forest corridors to move between forest fragments or to escape from more to less disturbed areas, females may be less likely to do so. Thus, any loss of habitat in which female orangutans live could lead directly to a loss of those female orangutans. Females' high lifetime site fidelity should therefore be taken into consideration by land-use planning initiatives.

Furthermore, it is estimated that approximately 1250 wild-born orangutans are currently being cared for in rehabilitation facilities, where the ultimate goal is release back into wild habitats (Palmer 2018). Additionally, mature wild orangutans are increasingly being translocated from high risk areas (due to forest clearing, hunting, crop-raiding, etc.) into lower risk areas. In Indonesia, this translocation practice is carried out by the government, private companies, and NGOs, and is not strictly regulated. As such, it is difficult to estimate how frequently translocation occurs, however, some reports suggest that it is quite common (Sherman, Wildlife Impact, personal communication). Our results indicate that the release of rehabilitant and translocated female orangutans into existing/established populations is likely to be stressful for both the incoming individuals and also to the last remaining natural and healthy populations. Incoming females will raise the population density and compete for resources, thus altering the balance of females' spatial patterning. We recommend rigorous long-term monitoring of reintroduced and translocated orangutans, to better understand the efficacy of these conservation efforts, as well as factors that may contribute to its success or failure.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and institutional guidelines for the care and use of animals were followed. All permits required to legally conduct this fieldwork in Indonesia were obtained from the national, provincial and local levels of government, as well as from all other applicable administrative institutions.

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