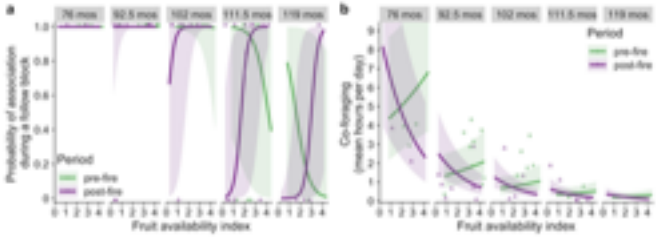


Fig. 4 Socio-ecology of mother orangutans and their weaned immature offspring at different ages at Tuanan, Indonesia, from October 2010 to July 2018. Predicted values, split by weaned immature age (in months, *top grey bars*), of (**a**) the probability that mothers spend time in association during a follow block, and (**b**) the mean time per day that mothers spend co-foraging (given that it did occur), with their weaned immature offspring, during the pre-fire (*green*) and post-fire (*purple*) periods, plotted against the fruit availability index (FAI). Predictions are shown for the minimum, first, second, and third quartiles, and the maximum weaned immature ages in the dataset. *Shaded areas* show the 95% confidence intervals. *Points* represent the raw data values — discretized to 0/1 in plot **a** — of follow blocks during the pre-fire (*green circles*) and post-fire (*purple triangles*) periods, and are situated in the age panel that is closest to the immature's actual age during the follow block.

mothers and weaned immatures spending any time in association and in proximity was significantly predicted by an interaction between FAI and period, with a large effect size for each (probability of association: $\beta = -5.95$, 95% CI [−9.02, −2.87], Fig. 4a; probability of proximity: $\beta = -3.84$, 95% CI [−6.34, −1.34], Fig. S2a): both decreased as FAI increased during the pre-fire period, and increased as FAI increased during the post-fire period, although this effect is seen mostly among older immatures. Where associations did occur, the time spent in association and in proximity was not significantly predicted by FAI nor period.

When controlling for offspring age, the probability of mothers and their weaned immatures co-foraging was predicted by the amount of time that mothers spent feeding: when mothers spent more time feeding, there was a higher probability of co-foraging. When co-foraging did occur, the time spent engaging in this behaviour was significantly predicted by an interaction between FAI and period, with a medium effect size ($\beta = -0.54$, 95% CI [−0.78, −0.29]): the time spent co-foraging increased as FAI increased during the pre-fire period, but decreased as FAI increased during the post-fire period (Fig. 4b). Furthermore, the rate of agonism between mothers and their weaned immatures was highest during post-fire low FAI, however, this trend was not significant (Fig. S2b).

Related adult female sociality

The probability of a female spending any time in association or in proximity with another related adult female were both significantly predicted by medium-sized interaction effects between FAI and period (association: $\beta = -0.64$, 95% CI [−1.10, −0.19], Fig 5a; proximity: $\beta = -0.58$, 95% CI [−1.04, −0.11], Fig S3b), with the

Side note about ‘Parallel Structure’

Let's say you have 3 major results...

- Organize them into a logical order

- Use this same organisation for other sections!

Result #1

Result #2

Result #3

Alison M. Ashbury, 2022-05-30

normal (pre-fire) conditions, while social patterns between related and unrelated adult females generally returned to those exhibited under normal, seasonal fruiting conditions.

Orangutans living in Tuanan's peat-swamp habitat have previously been described as employing a "search-and-find" strategy, wherein they exploit the habitat's available fruit as much as possible, continuously feeding and travelling: with increasing FAI, daily travel distance and active period both increase, while time spent feeding decreases gently (probably because a higher proportion of fruit in the diet requires less processing time than a higher proportion of fallback foods) (Morrogh-Bernard *et al.* 2009; Vogel *et al.* 2016). We found general support for this during the pre-fire period: with higher FAI, orangutans spent less time feeding, and showed weak evidence of diet-switching from fallback foods to preferred fruit. However, because we limited our dataset to only adult females and only below-mean FAI months during the pre-fire period, we did not see a strong effect of FAI on diet, nor on active period or daily travel distance during the pre-fire period, and what little effect there was for these latter two variables was in the opposite direction to that predicted based on previous studies (e.g., Vogel *et al.* 2016).

Paradoxically, we found that during the extended period of below-mean fruit availability (post-fire), female orangutans employed a strategy more closely resembling the "sit and wait" strategy (Morrogh-Bernard *et al.* 2009) used by orangutans living in masting Dipterocarp forests: they rested more, fed for less time, and travelled shorter distances during times of extreme scarcity, and exhibited a significant decrease in resting time, and an increase in feeding time and daily travel distance, when fruit availability increased towards the long-term mean. This suggests that they were conserving energy when fruit was particularly scarce, and then rebounding and maximizing their potential energetic intake as FAI increased. This is further supported by the strong effect of FAI on diet during the post-fire period: with females eating a relatively large amount of kamunda food items and fallback foods and very little tree and other fruit when fruit was exceptionally scarce, and then showing a very strong increase in the time spent consuming tree and other fruits (while eating hardly any fallback foods) when fruit availability returned towards the long-term mean for this habitat. The consistent and relatively high amount of time spent feeding on kamunda food items across periods and FAI values — indeed, kamunda was the only dietary category that never had predicted values below 1 hour of feeding time per day — suggests that this liana is a key resource for orangutans living at Tuanan.

When fruit is scarce, Bornean orangutans living in masting habitats (i.e., habitats with extended periods of fruit scarcity punctuated every few years by brief periods of high fruit abundance) metabolize fat reserves (Knott 1998) and endure long periods with deficient protein intake (Vogel *et al.* 2012). A recent study at Tuanan, which includes the post-fire period of fruit scarcity, showed that orangutans (including adult females) had lower estimated lean body mass when FAI was lower (O'Connell *et al.* 2021). It is therefore likely that the behavioural changes that we observed between the pre- and post-fire periods — from their usual "search-and-find" strategy to one akin to the "sit and wait" strategy that is characteristic of orangutans living in masting habitats (Morrogh-Bernard *et al.* 2009; Ashbury 2020)

— are coupled with significant physiological changes, including the catabolism of muscle tissue (O'Connell *et al.* 2021). These behavioural and physiological changes underlie the significant changes in their socio-ecology which occurred during this period of uncharacteristically long fruit scarcity.

We observed that mothers and their weaned immatures were less likely to spend time in association and in proximity with each other during the post-fire period when fruit was scarce. When associations did still occur, the duration of time spent in association was not reduced, but the rate of agonism from mothers towards their weaned offspring trended towards being higher, especially when FAI was particularly low. Where association did occur and mothers and their weaned immatures co-foraged, the time spent co-foraging was actually highest during the extreme scarcity period. This suggests that the reduced probability of association between mothers and their weaned immature offspring during prolonged scarcity may be driven by passive avoidance resulting from the distribution of food sources, with only minimal active social intolerance.

This reduction in time spent in association with their mothers could have lasting effects on weaned immature orangutans. Among chimpanzees, weaned immatures who experience maternal loss suffer various adverse effects, including hampered physical development, later age at first reproduction, lower overall reproductive success, higher risk of mortality, and/or lower overall survival (Samuni *et al.* 2020; Crockford *et al.* 2020; Stanton *et al.* 2020). Similar effects of maternal loss post weaning, but prior to the onset of sexual maturity, have been observed in red deer (*Cervus elaphus*: Andres *et al.* 2013), baboons (*Papio cynocephalus*: Tung *et al.* 2016), and hyenas (*Crocata crocuta*: Watts *et al.* 2009). These studies suggest that maternal presence, and thus, maternal association — even in the absence of direct maternal investment — clearly serves some vital function(s) for weaned offspring. These long-term effects may be driven by deficits experienced by weaned immatures who do not have (access to) their mothers, i.e., that have fewer opportunities for learning and information transfer, reduced social and physical support against conspecifics and predators, and the absence of any post-weaning food-sharing or tolerated scrounging from their mothers (van Noordwijk 2012). It is therefore possible that the reduction in association with mothers experienced by weaned immatures at Tuanan during the prolonged period of fruit scarcity will have lasting effects on their development, reproduction, and survival.

Among related adult females (and, thus, their dependent offspring), there was a reduced probability of socializing during the post-fire period of extreme fruit scarcity, but as FAI increased toward the long-term mean, the probability of socializing increased towards pre-fire levels. When associations did nevertheless occur during post-fire low FAI, they were not shorter in duration, nor did they have lower levels of social tolerance. Indeed, the time spent in association, in proximity, and co-foraging was not significantly reduced during the post-fire period, even when fruit was extremely scarce, and the probability of agonism was not higher. This suggests that the reduced probability of sociality between related females during this same time may be driven by general avoidance mechanisms, including the reduction in daily travel, likely resulting from the distribution of food resources, rather than active social intolerance. Notably, the probability of association and proximity among

related adult females during the pre-fire period was essentially constant across FAI values, indicating that — under normal seasonal conditions, and at least within the range of below-mean fruit availability — related adult females' association patterns are unaffected by fruit availability (see also Fröhlich *et al.* 2020). Together this suggests that the benefits of such rare associations, including play and learning opportunities for the dependents, outweigh the cost of food competition even under scarce conditions (cf. van Noordwijk *et al.* 2012; Schuppli *et al.* 2016, 2020).

This stands in contrast to the clearly reduced social tolerance exhibited by unrelated adult females during the post-fire period, beyond that which could be explained by the immediate effects of low fruit availability alone. Under normal, seasonal conditions (i.e., pre-fire), unrelated females were less likely to be in association and proximity, and more likely to aggress each other, as FAI increased. However, when fruit availability was below-mean for the prolonged period (i.e., post-fire), the probability of unrelated adult females being in association or proximity with each other was exceptionally low, regardless of FAI. Furthermore, when they did associate, the rates of agonism between unrelated females were significantly higher. These results thus align with, and expand on, previous studies: not only is there a difference in relationships between related and unrelated females (e.g., Knott *et al.* 2008; van Noordwijk *et al.* 2012), but the period of uncharacteristically long fruit scarcity exacerbated the social intolerance among unrelated females, both by reducing the probability of any association at all, and by increasing the probability of agonism during associations. This suggests that the potential benefits gained from such associations between unrelated females are negligible, and do not outweigh the costs of association, especially during times of prolonged low fruit availability.

The large matriline featured in our analysis of related adult female sociality is probably not typical of other orangutan matrilines in Tuanan, nor is it probably typical of matrilines at other sites. Regardless of how generalizable the case of this matriline may be, these females offer an opportunity to compare associations among female relatives with those among nonrelatives. It is possible that, in the absence of an abundance of female relatives and thus there being fewer opportunities to associate with related females, the differences that we see between related and unrelated female social patterns would be less pronounced, disappear, or even be reversed. We expect, however, that similar patterns would be observed, as previous studies from other sites have shown, under site-specific normal fruiting conditions, higher rates of association, and higher social tolerance between known or suspected related adult females than between known or suspected nonrelatives (Singleton and van Schaik 2002; Knott *et al.* 2008), as has also been observed at Tuanan (this study, and van Noordwijk *et al.* 2012). This suggests that the qualitative patterns, if not the quantitative measures, that we've described in response to extreme scarcity may be generalizable even to smaller matrilines.

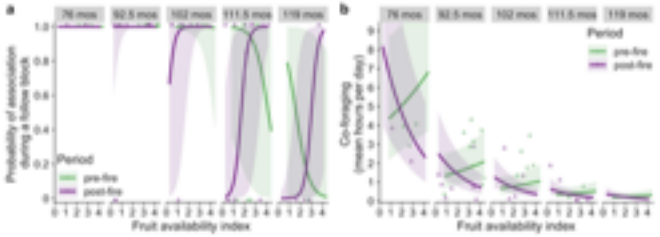
The overall reduction in adult female gregariousness — both with each other and with their weaned immature offspring — may also have lasting effects on their dependent offspring. Dependent offspring use their mothers' associations with other mothers as opportunities to play with peers — a developmentally important activity, for which opportunities are otherwise rare because of orangutans' single births and predominantly solitary lifestyles (van Noordwijk *et al.* 2009; Fröhlich *et al.* 2020).

(Methods)

(Methods)

(Results)

(Discussion)



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Result #1

Result #2

Result #3