TAPROBANICA, ISSN 1800–427X. Vol. 14, No. 02 (2025): pp. 121–131.
Published by Research Center for Climate Change & Faculty of Mathematics & Natural Sciences, Universitas Indonesia, Depok 16424, INDONESIA.

http://www.taprobanica.org
https://doi.org/10.47605/tapro.v14i2.364

OPEN ACCESS

IMPACTS OF BIMATURISM AND FRUIT AVAILABILITY ON THE BEHAVIOUR OF MALE SUMATRAN ORANGUTANS, *Pongo abelii* LESSON, 1827 (PRIMATES: HOMINIDAE)

Submitted: 11 September 2024, *Accepted*: 25 June 2025, *Published*: 21 July 2025
Subject Editor: Juan O. Perea-García

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Abstract
Adult male orangutans can be described as flanged and unflanged, which are two morphologically distinct stages of sexual maturity (bimaturism). Bimaturism influences male orangutan behaviour, though specific effects remain unclear. This study examines the behavioural ecology of adult male Sumatran orangutans in Suaq Balimbing, Sumatra. We found that both male morphs spent over 60% of their time feeding, but unflanged males engaged in significantly more social interactions than flanged males. The diets of both morphs were mostly composed of fruit, and there were no significant differences in the proportions of time spent feeding on different types of food. Unflanged males travelled significantly longer distances, likely to access more dispersed food sources and social opportunities. With increasing fruit availability, social interactions and daily travel lengths of unflanged males decreased, whilst social interactions and daily travel lengths of flanged males increased. These results shed novel light on how male orangutans adjust their behaviour in response to ecological factors.

Key words: behavioural ecology, bimaturism, fruit availability, male behaviour, Sumatran orangutan

Introduction
Bimaturism in orangutans (*Pongo* spp.) refers to the phenomenon where adult males exhibit two distinct morphological forms: flanged and unflanged (Utami-Atmoko 2000, Dunkel *et al.* 2013). Flanged males have a larger body size on average than unflanged males and exhibit secondary sexual characteristics such as cheek pads and a large throat sac (Utami-Atmoko 2000, Banes *et al.* 2015). Increased levels of androgen hormones in adult male orangutans are suspected to underlie the development of secondary sexual characteristics. Research conducted on wild Bornean orangutans (*Pongo pygmaeus*) has shown that unflanged males have lower levels of

androgen compared to flanged males (Thompson *et al*. 2012, Marty *et al*. 2015). Unflanged male orangutans can remain in the unflanged morph for 20–30 years before developing secondary sexual characteristics and transitioning to the flanged male morph (Utami-Atmoko 2000, Tajima *et al*. 2018). The presence of a dominant flanged male may induce hormonal suppression in unflanged males, preventing them from developing secondary sexual characteristics (Marty *et al*. 2015). However, both male morphs are fertile and can sire offspring (Utami-Atmoko 2000, Tajima *et al*. 2018, van Noordwijk *et al*. 2023).

Bimaturism in orangutans is hypothesized to have evolved through sexual selection processes involving female choice and male-male competition, impacting the species' sexual behaviour, including the males' reproductive tactics (Banes *et al*. 2015, Scott *et al*. 2024, though cf. Roth *et al*. 2024). Both female choice and male-male competition affect reproductive outcomes in orangutans (Marty *et al*. 2015, Scott *et al*. 2024). While both flanged and unflanged males regularly use force to obtain copulations, unflanged males tend to do so more frequently (Kunz *et al*. 2023). Flanged male orangutans are generally considered dominant over unflanged males, but the dynamics of dominance relationships among flanged males remain poorly understood (Utami-Atmoko 2000, van Noordwijk *et al*. 2023). The flanged males' large throat pouches enable them to emit loud vocalizations known as long calls. Locally dominant flanged males tend to call out more often to potentially inform conspecifics about their location, thus attracting females while deterring competition with other males (van Noordwijk *et al*. 2023).

Interestingly, bimaturism in male orangutans seems to impact not only sexual behaviour but also daily activities. For instance, observations by Utami-Atmoko (2000) in Ketambe, Sumatra, showed that unflanged males as subordinate individuals tend to avoid feeding sites occupied by dominant flanged males, leading them to increase their efforts to meet dietary needs by travelling further. Unflanged male behaviour is simultaneously influenced by both avoiding male-male competition and gaining mating access to females (Kunz *et al*. 2023).

However, bimaturism in orangutans still presents many puzzles. For example, we know very little about how the two adult male morphs vary in their everyday behaviour. In this paper, we investigate the behavioural ecology of flanged and unflanged male orangutans at the Suaq Balimbing Research Station, located ~70 km west of the Ketambe Research Station. Compared to Bornean sites, both Ketambe and Suaq Balimbing exhibit a higher ratio of unflanged males to flanged males, suggesting that males go through a period of developmental arrest. During developmental arrest, male orangutans remain unflanged for up to several decades - a condition that is less frequently observed in Bornean orangutans (e.g., Tuanan in Central Kalimantan: Dunkel *et al*. 2013).

Suaq Balimbing is an ideal location for studying the behaviour of male orangutans due to the high density of orangutans and the high levels of sociality among individuals (van Schaik & Knott, 2001). The high density of orangutans in Suaq Balimbing is attributed to the almost constantly high abundance of food and low levels of human disturbance (van Schaik *et al*. 1995, Wich *et al*. 2011). Studying the effects of male bimaturism on behaviour in the Suaq Balimbing orangutan population may thus offer a deeper understanding of male orangutan behavioural ecology. First, we aim to investigate whether the daily activity, diet composition, and travel length differ between flanged and unflanged male orangutans. Secondly, we aim to investigate how fluctuations in fruit availability (as an environmental factor) influence the daily activity patterns of male orangutans, diet composition, and daily travel length.

Material and methods

Study site. This study was conducted at the Suaq Balimbing Research Station (3°04´N, 97°26´E), Gunung Leuser National Park in South Aceh, Indonesia. The 5.2 km^2 study area consists primarily of lowland swamp forest with adjacent areas of mixed dipterocarp and riverine forest (Fox *et al*. 2004). Suaq Balimbing has the highest orangutan density of all studied sites (Wich *et al*. 2016). This is attributed to almost 60% of the stems in the swamp area providing fruits eaten by orangutans almost year-round (van Schaik 1999).

Behaviour*al observation*. Data were collected on wild Sumatran orangutans (*Pongo abelii*) from January 2018 to February 2020 by 15 observers. Each new observer goes through intense training with an experienced observer to achieve interobserver reliability (Cohen's kappa of k >0.8, Bakeman & Quera 2011). Behavioural data were collected using a standard data collection protocol, which is used at most orangutan field sites (Morrogh-Bernard *et al*. 2009, Max Planck Institute 2025). Orangutans were followed from their morning nest to their evening nest. During these follows, we recorded the daily activity of individuals using instantaneous sampling at 2-min intervals paired with ad libitum sampling of behaviours of special interest.

Daily activity data included feeding, resting, moving, and socializing. Feeding behaviour was defined as gathering, processing, and ingesting food items. Resting was defined as sitting, lying, standing, or hanging for more than 5 seconds while not doing anything else. Moving was defined as all directed locomotion, usually between trees or patches of forest, lasting more than five seconds. Social behaviours were all social interactions with associated parties (individuals within 50 m of the focal individual), including sexual activities, social play, feeding-related social behaviour, and agonistic behaviour.

Food items were categorized into fruit, young leaves, mature leaves, flowers, cambium/bark, vegetative matter (such as stems and pith), and insects (e.g., bees, termites, and ants). To determine the proportion of time spent feeding on each type of diet item, we divided the total feeding time for each full-day follow by the number of minutes spent feeding on each item.

Focal individuals. The final data set includes 5 flanged males and 5 unflanged males. These data include 35 full-day follow-up days (382.31 hours) for flanged males and 20 full-day follow-up days (225.37 hours) for unflanged males. All focal individuals were habituated to human observers.

***Daily travel length*.** Daily travel length was defined as the total distance of daily travels and was calculated from when orangutans leave the morning nest until they lie down in the evening nest (Saputra *et al*. 2017). We recorded the location of the focal orangutan every 30 minutes and every time they made a nest with hand-held GPS Units (Garmin GPSMap 78 and Garmin GPSMap 64s). Daily travel length was calculated using ArcGIS 10.1 by summing up the distance between all consecutively recorded GPS points of a given day.

Fruit availability. The Fruit Availability Index (FAI) was determined monthly by monitoring four phenology plots. Around 1400 trees with a diameter at breast height (DBH) of >20 cm were monitored once per month for the presence of fruit production. We expressed fruit availability as the percentage of bearing fruit trees in the phenology plots (Harrison *et al*. 2010, Vogel *et al*. 2015). The behaviour of primates is known to be influenced by FAI (Lambert & Rothman 2015, Bach *et al*. 2017, Clink *et al*. 2017). Thus, we used FAI as a predictor variable in this study.

Data analysis. All statistical analyses were conducted in the R programming language (R Core Team 2021, URL: https://www.R-project.org). To assess statistical significance, we used a threshold of $P<0.05$. For continuous response variables, we used linear mixed effects models (LMMs) with Gaussian family distributions using the "lmer" function of the "lme4" package (Bates *et al*. 2015). For all response variables that were expressed in proportions, we used generalized mixed effects models (GLMMs) with beta family distributions, using the "glmmTMB" function of the "glmmTMB" package (Brooks *et al*. 2023). In all models, male morph and FAI, as well as the interaction between FAI and male morph, were used as predictor variables. Because our data set includes multiple follows per individual, we added the focal identity as a random intercept and FAI as a random slope within focal identity to our models to avoid pseudo-replication issues and account for individual-specific effects of FAI on our response variables.

We visually assessed each model for influential data points, evenly distributed residuals, and homogeneity of variance (Harrell 2015). Note that some of the response variables of our models were not independent of each other as they were calculated as proportions of time spent on different activities (feeding, moving, resting, and social activity) and proportions of feeding time spent feeding on different food item types (fruit, young leaves, mature leaves, flowers, inner bark, vegetative matter, and insects). However, because of the limited sample size, we did not adjust the *p-values* of our models for multiple testing, but we reported the original *p-values*.

Results

Daily activity pattern. The analyses of the daily activity of both male morph orangutans showed similar patterns in their activity budgets (Fig. 1A–D). For both male morphs, feeding was the most common activity, accounting for over 60% of their active time (Fig. 1A). In contrast, social interactions were relatively rare, taking up 0.3% to 1% of their active time (Fig. 1D).

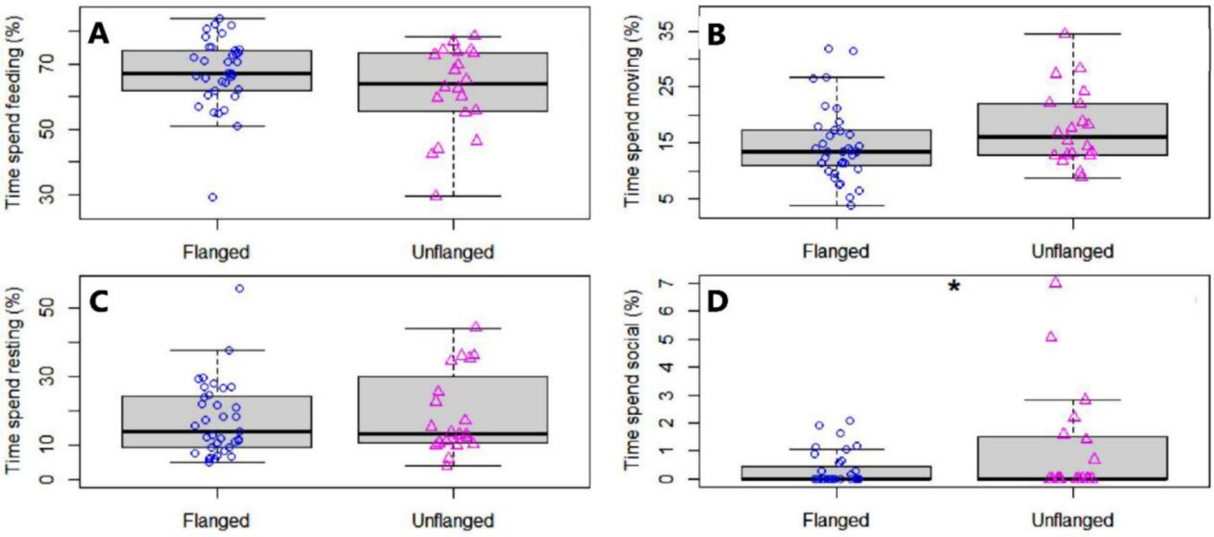

Figure 1. Percentage of active time the two male orangutan morphs spent on different activities: **(A)** feeding, **(B)** moving, **(C)** resting, and **(D)** social

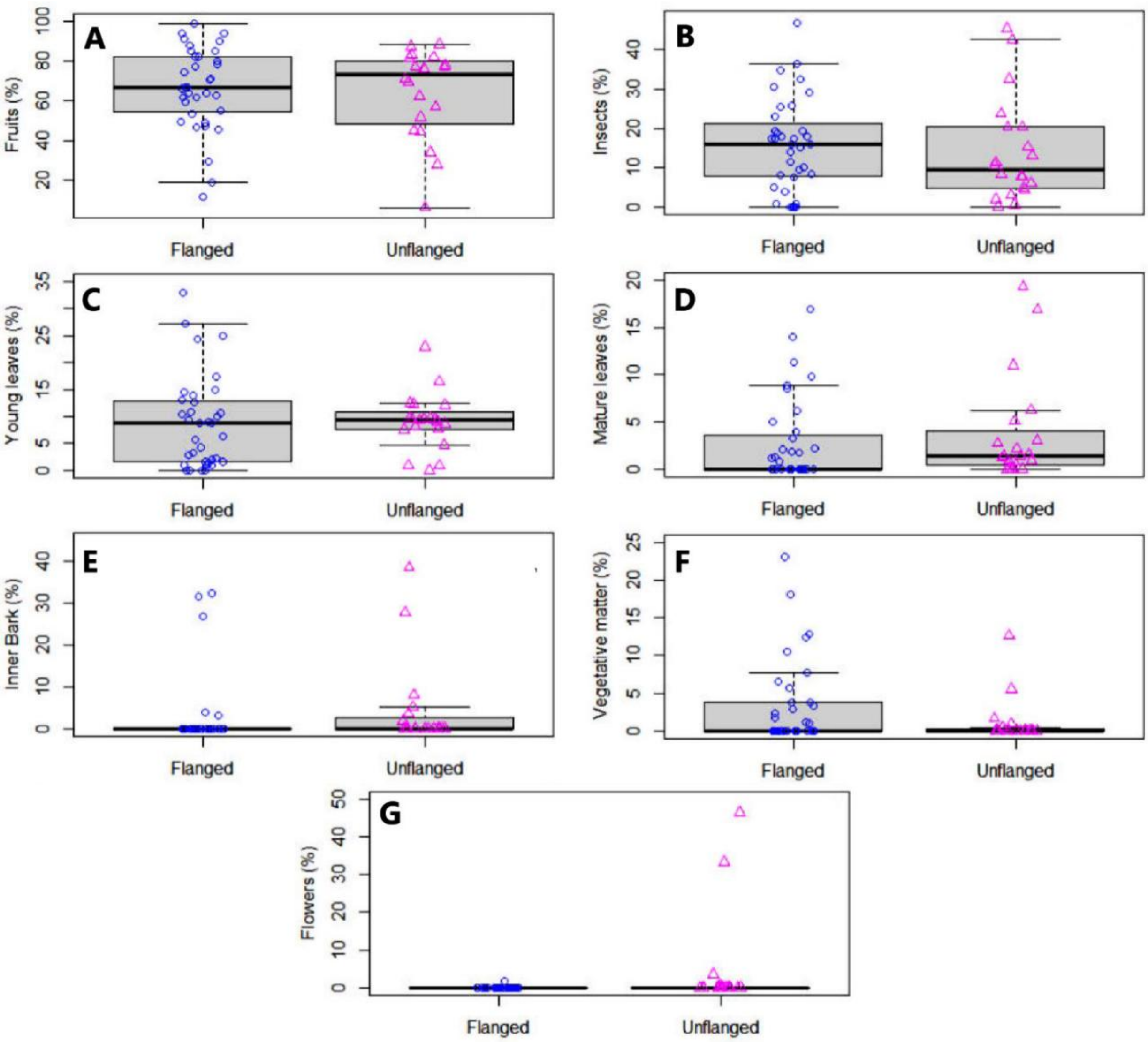

Figure 2. Diet composition of the two orangutan male morphs at Suaq Balimbing in percentage of feeding time spent eating different food item types: **(A)** fruit, **(B)** insects, **(C)** young leaves, **(D)** mature leaves, **(E)** inner bark, **(F)** vegetative matter, and **(G)** flowers

Comparative analysis revealed no significant differences in the duration of feeding, movement, and resting behaviours between the two male morphs (*P*>0.05; Sup. Table 1, No. 1-3; Factor=Morph). The only significant difference in activity proportions between the two male morphs was social activities (p=0.0272 <0.05, 95% CI 0.3082 - 5.1662; Sup. Table 1, No. 4; Factor=Morph). Flanged male orangutans were less likely to engage in social interactions than unflanged males (Fig. 1D).

Diet composition. Our findings indicated a comparable dietary composition of both male morph orangutans (Fig. 2A–G). Particularly, fruits were the main food source for flanged and unflanged male orangutans, accounting for more than 60% of their feeding time (Fig. 2A). This was followed by insects at just over 10% (Fig. 2B), young leaves at around 8% (Fig. 2C), mature leaves (Fig. 2D), and inner bark (Fig. 2E), each at approximately 2%, vegetative matter at around 1% (Fig. 2F), and flowers at over 0.04% (Fig. 2G). There was no significant difference between flanged and unflanged male orangutans in the proportions of time individuals fed on the different food item types (*P*>0.05, Sup. Table 1, No. 5-11; Factor=Morph).

Daily travel length. The mean daily travel length covered by flanged males and unflanged males was 930 meters and 1184 meters, respectively (Fig. 3). This difference was significant (*p*=0.0264 <0.05, 95% CI 133.8471 - 2151.4773; Sup. Table 1, No. 12; Factor=Morph), indicating that unflanged males had significantly longer daily travel lengths than flanged males (Fig.3).

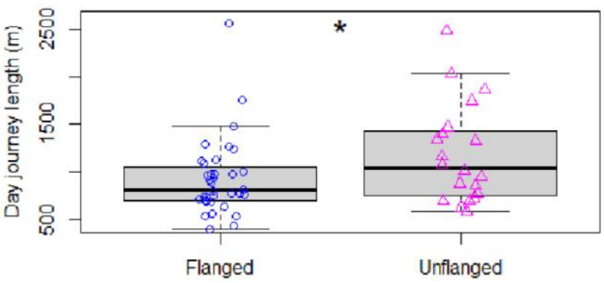

Figure 3. Daily travel lengths of the two orangutan male morphs at Suaq Balimbing

The effect of fruit availability on the behavioural ecology of male orangutans. Throughout this study, the Fruit Availability Index (FAI) in Suaq Balimbing showed a relatively low level of variation, maintaining a relatively stable state. The presence of fruit varied between 5% and 16% (Fig. 4). The FAI reached peak values in May 2018 (16%) and September 2019 (14%) (Fig. 4).

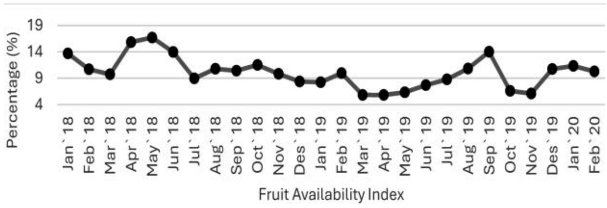

Figure 4. Fruit availability at Suaq Balimbing expressed in percent of fruit-bearing trees, assessed in multiple phenology plots

We did not find significant differences between the male morphs, nor a significant interaction between FAI and male morph concerning feeding (Fig. 5A), movement (Fig. 5B), and resting activities (Fig. 5C) (*P*>0.05; Sup. Table 1, No. 1-3; Factor=FAI and FAI*Morph). However, our results indicated a significant interaction between FAI and male morph in the proportion of time spent on social activity (*p*=0.0308 <0.05, 95% CI -0.4917 - (-0.0238; Sup. Table 1, No. 4; Factor=FAI*Morph). Visualization of the data showed that as FAI levels increased, social interactions decreased among unflanged males (Fig. 5D). Conversely, flanged males exhibited a trend for increased social behaviour with increasing FAI (Fig. 5D). There was no significant interaction between FAI and male morph and no significant effect of FAI on the proportion of feeding time spent eating any of the different food items (*P*>0.05; Sup. Table 1, No. 5-11; Factors=FAI and FAI*Morph, Fig. 5E–K).

Finally, we found a significant positive effect of FAI on daily travel length (*p*=0.0390 <0.05, 95% CI 3.4515 - 133.2494; Sup. Table 1, No. 12; Factor=FAI). While the interaction between male morph and FAI did not have a statistically significant effect on daily travel length (*p*=0.0719 <0.05, 95% CI -192.1485 - 8.1920; Sup. Table 1, No. 12; Factor=FAI*Morph), visualization of the data indicated that as FAI levels increased, flanged males tended to travel greater distances, whereas unflanged males showed a tendency towards reduced travel length (Fig. 5L).

Discussion

We investigated the effects of orangutan male bimaturism and food availability on the daily activities of individuals at the Suaq Balimbing Research Station.

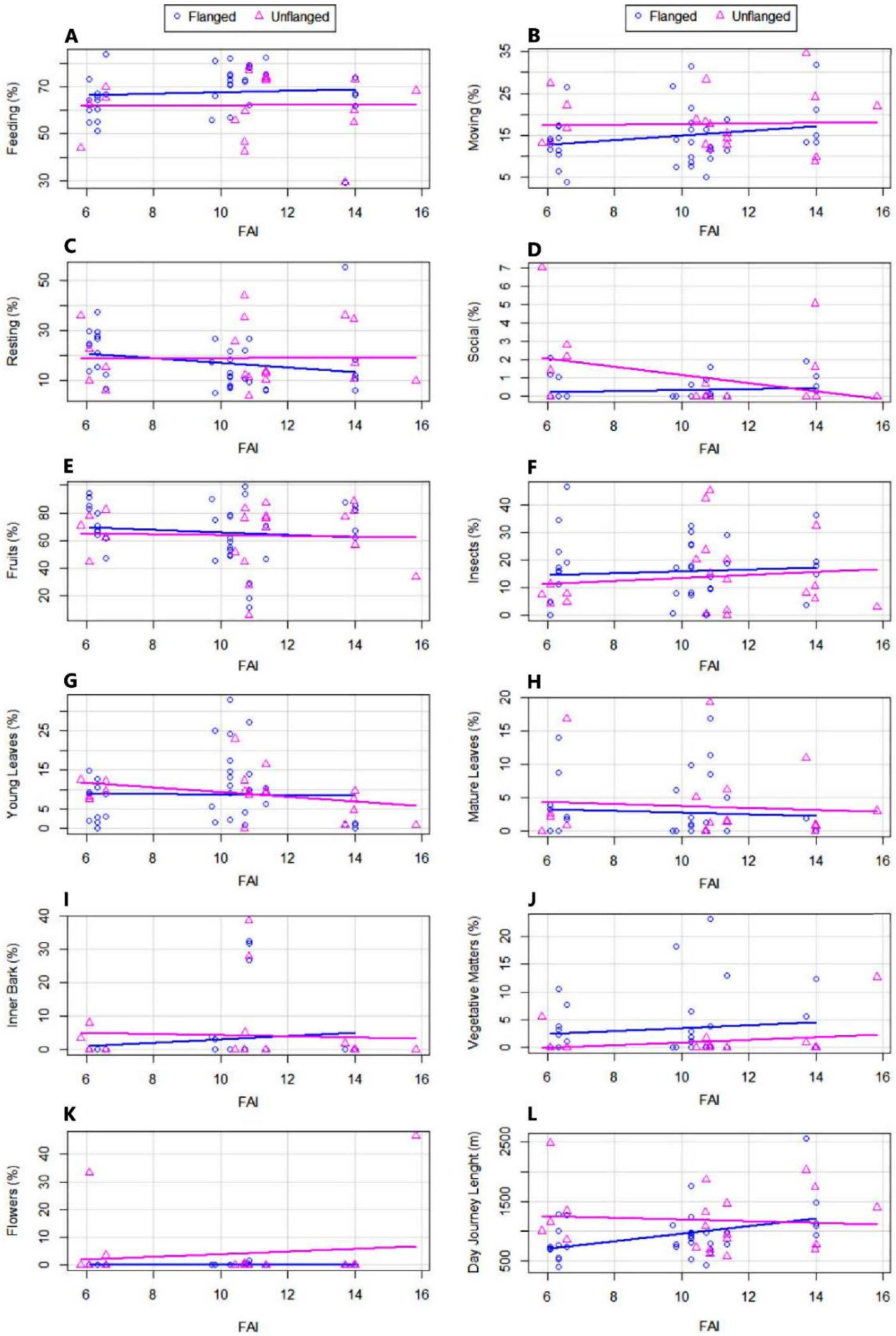

Figure 5. Interaction between FAI and male morph on: **(A)** the proportion of time spent feeding, **(B)** the proportion of time spent moving, **(C)** the proportion of time spent resting, **(D)** the proportion of time spent engaging in social activities, **(E)** the proportion of feeding time spent feeding on fruit, **(F)** the proportion of feeding time spent feeding on insects, **(G)** the proportion of feeding time spent feeding on young leaves, **(H)** the proportion of feeding time spent feeding on mature leaves, **(I)** the proportion of feeding time spent feeding on inner bark, **(J)** the proportion of feeding time spent feeding on vegetative matter, **(K)** the proportion of feeding time spent feeding on flowers, and **(L)** daily travel length at Suaq Balimbing. Regression lines and raw data points are shown.

Our research suggests that unflanged male Sumatran orangutans have more frequent social interactions than flanged males (Fig. 1D). This finding aligns with Wich *et al*. (2006), who found that Sumatran unflanged male orangutans at Ketambe display greater sociability and dedicate more time to interacting with other orangutans compared to flanged males. Unflanged males frequently form associations with adult females and display efforts to initiate sexual activities (van Schaik 1999, Utami-Atmoko *et al*. 2009, Kunz *et al*. 2021).

Previous studies have indicated that the behavioural ecology of great apes is influenced by food availability, as demonstrated in studies on orangutans by Harrison & Marshall (2011), gorillas by Ostrofsky & Robbins (2020), and chimpanzees by Tédonzong *et al*. (2019). Our result revealed a trend for a decrease in social behaviour among unflanged male orangutans as FAI levels rose (Fig 5D). Contrarily, flanged male orangutans tended to exhibit increased social interactions with other orangutans as FAI increases (Fig. 5D). The latter result supports the finding that flanged male orangutans in Suaq Balimbing generally exhibit solitary tendencies during low FAI periods but might be more social during abundant fruit supply (van Schaik 1999). In addition, this finding partly aligns with observations of Bornean orangutans in Sebangau, where flanged males (but not unflanged males) exhibited larger average group sizes during periods of high fruit availability (Harrison *et al*. 2010). On the other hand, research on Sumatran orangutans in Sikundur (a less productive lowland dipterocarp forest) revealed that while orangutans are more likely to form associations in response to increasing fruit abundance, there were no differences between the age-sex classes in group formation tendencies (Roth *et al*. 2020). The effects of food availability on social behaviour of the different age-sex classes may vary among the sites because of differences in the forest types between sites, as Suaq Balimbing and Sabangau are peat-swamp forests that lack the supra-annual mast-fruiting events that are typically experienced in lowland dipterocarp forests (Harrison *et al*. 2020; Wich *et al*. 2011). Varying social structures and behaviours among male orangutans across different populations demonstrate adaptability to temporal habitat conditions (Mitra-Setia *et al*. 2009). These patterns suggest that the variation in male ecological strategies across different populations is an adaptive response to specific socio-ecological contexts. All in all, our findings enhance our understanding of the important relationship between orangutan social behaviour and habitat productivity.

The differences in the behavioural shifts in two male orangutan morphs with varying fruit availability might be attributed to the fact that flanged males can fulfil their daily dietary requirements more easily when fruits are abundant, thus leading to them having increased time available for socializing (Fig. 5D). In addition, previous studies showed that female orangutans are more active and more accessible for mating during times with fruit-abundance (Knott 1999, van Schaik 1999). Knott (1999) found that adult female orangutans in Cabang Panti, West Borneo, exhibited mating activity exclusively during periods of high FAI. Sexually motivated female Sumatran orangutans prefer sexual interactions with dominant local flanged males and seek protection against harassment from unflanged male orangutans (van Schaik 1999, Fox 2002, Dunkel *et al*. 2013). These behavioural patterns point to complex relationships between FAI and male social dynamics in orangutan populations.

Both male morphs at Suaq Balimbing primarily relied on fruit as their main dietary component (Fig. 2A). The preference for fruit among orangutans can be attributed to the rich content of fats and carbohydrates in comparison to other food items (Vogel *et al*. 2015, Vogel *et al*. 2017). The resultant high caloric content of fruit allows the orangutans to fulfil their energy needs. Insects were the second most consumed food type for both male morphs (by over 10%, Fig. 2B). This is similar to findings by Fox *et al*. (2004), which showed that insects represent the second-highest percentage of the food items in the Suaq Balimbing orangutans' diet (over 12%). The higher prevalence of insects in the diet of orangutans in Suaq Balimbing compared to other sites could be attributed to the fact that colonies of insects are found solely in trees and thus are easier to access due to the ever-flooded forest floor (Fox *et al*. 2004). This finding supports the hypothesis that Sumatran orangutans tend to consume higher-quality foods, such as fruit and insects, while minimizing low-quality foods such as bark and vegetative matter, a behaviour distinct from their Bornean counterparts (Fox *et al*. 2004). As a result, Sumatran orangutans at Suaq Balimbing may be less dependent on fallback foods such as bark and pith. Geographical variation in orangutan diet indicates that the forest type may influence feeding time in that we see higher percentages of time spent feeding on fruit in Sumatra than in Borneo (where fruit masting events occur followed by extended periods of low fruit availability) and higher percentages of time spent feeding on bark in Borneo as a fallback food (Morrogh-Bernard *et al*. 2009).

Our findings indicate that the FAI did not impact the dietary patterns of either male morph, at least not in terms of how much time individuals spend feeding on the different food items. The relatively high and stable availability of fruits and various other food items in Suaq Balimbing throughout the study years may have led to stable feeding patterns (Fig. 4). The FAI in Suaq Balimbing is higher compared to other orangutan study sites (Wich *et al*. 2011). During the study period, FAI ranged between 5% and 17% (Fig. 4). In contrast, Vogel *et al*. (2015) reported that the highest FAI values observed in comparable habitats like Tuanan and Sabangau were 14% and 9%, respectively. The high FAI values at Suaq Balimbing can be attributed to the fruit productivity in Sumatra being greater than that in Borneo, owing to the relatively younger volcanic soils (Wich *et al*. 2011). Additionally, in Suaq Balimbing, the swamp forest is fed by nutrient-rich water from nearby mountains. The differences in FAI levels among various orangutan habitats and the orangutans' behavioural correlates underline how environmental factors can impact dietary choices and foraging behaviours in these populations. However, even if time spent feeding did not vary across different periods at Suaq Balimbing, intake rates could still differ. For example, Knott (1998) observed no significant difference in feeding time between high- and low-fruit periods but reported variations in caloric intake. Further research would help gain a more detailed understanding of the factors affecting the feeding behaviour and energy intake of orangutans at Suaq Balimbing.

Our analysis showed that unflanged male orangutans at Suaq Balimbing exhibited significantly longer daily travel distances in comparison to the flanged males (Fig. 3). This result confirms an earlier finding made by van Schaik *et al*. (2009) where similar differences in daily travel lengths between the two male morphs were observed. This suggests that unflanged males travel farther to access food and mating opportunities, which flanged males may monopolize. Indeed, during this study, it was observed that unflanged male orangutans tended to maintain a considerable distance from a flanged male while engaged in feeding activities in a fruiting tree. This behaviour aligns with the findings of Utami-Atmoko *et al*. (2009), who reported that unflanged male Sumatran orangutans typically kept a safe distance of 40-50 meters from flanged males, particularly during the courtship period. Utami-Atmoko (2000) reported that during periods of abundant fruit production, flanged males typically asserted dominance and had control over fruit-bearing trees, potentially restricting access to fruit for unflanged males.

The longer travel distances of unflanged males indicate a possible adaptive strategy to ensure that they have access to ecological resources such as fruit, which constitute their preferred food types, as well as social resources such as interactions with female orangutans. In other primates, it has also been observed that subordinate individuals tend to avoid feeding sites that are currently being used by dominant individuals (Bugnyar & Heinrich, 2006). In the mantled howler monkey (*Alouatta palliata*), it is commonly observed that dominant individuals grant "priority of access" to essential resources (Jones 1980).

Results on Bornean orangutans at the Tuanan site showed that daily travel lengths increased in all age-sex classes alongside rising FAI (Saputra *et al*. 2017, Vogel *et al*. 2017). In comparison, visualizing our data (Fig. 5L) indicates that flanged male orangutans travelled further as the FAI increased, whereas unflanged males reduced their travel lengths. This trend of decreasing daily travel length among unflanged males could be attributed to the fact that as the FAI rose, flanged males extended their travel lengths (Fig. 5L), which may limit the range of unflanged males. This pattern could be driven by unflanged males avoiding encounters with flanged males, who exhibit higher social dominance (Tajima *et al*. 2018, Scott *et al*. 2024), leading them to reduce their movement within a shared habitat. These findings underline I) how FAI as an ecological factor affects the daily travel length of the two male morphs and II) that access to food resources is likely essential for their survival and reproductive success. These results also underline the behavioural flexibility of male orangutans, in that they adjust their travel length based on their dietary and social requirements in different ecological contexts. As such, these findings enhance our knowledge of adult male orangutan behavioural ecology and resource utilization strategies. Further research is needed to explore the factors underlying the varying travel lengths observed in both male morph orangutans. Future research could also reveal more about their ecological adaptations as well as their reproductive strategies and ability to adjust their behaviour in response to challenges in their environment.

This study revealed behavioural plasticity of both male orangutan morphs. Orangutan males adjusted their social behaviour and daily travel lengths according to specific environmental circumstances. Further studies are necessary to clarify the details of the males' behavioural ecology and the mechanisms that influence their response to social and environmental factors. Since the sample sizes of this study were low, future studies will be able to test whether these results are robust. By understanding ecological behaviour, we can gain a deeper understanding of the adaptive strategies that primates employ to succeed in complex rainforest environments. These insights are essential for conservation initiatives, including orangutan rehabilitation and release programs, as they underline the significance of protecting natural habitats to ensure that these habitats meet the needs of orangutans and other wildlife.

Author contributions

Design & conceptualizing: SSUA, TMS, CS; data collection & preparation: TR, CS; analysing and developing models: CS, TR; funding acquisition: CS; field administration: SSUA, CS, TR; writing manuscript: TR, CS; supervision: SSUA, TMS, CS

Acknowledgments

We thank the local forestry authorities for their support in conducting this research, including TN Gunung Leuser, in particular A. Saifudin, Zakir, and S. Amar; all the students and local field assistants for collecting data in Suaq Balimbing; the Yayasan Ekosistem Lestari (YEL) and its Sumatran Orangutan Conservation Program (SOCP) for hosting our project at the Suaq Balimbing Research Station, in particular M. Kamsi, Herman, Subhan, Rustam, L. Iswandi, and S. Rizal; the local people, especially Syamsuar, Misrijal, A. Suradi, Mustaqim, and Munasdi, for their support. Finally, we thank Erin R. Vogel (Rutgers University, USA) for comments on an earlier draft; Amy M. Scott (Boston University, USA), Andrea L. Permana (University of Warwick, UK), and Juan O.P. Garcia (University of Las Palmas de Gran Canaria, Spain) for reviewing the manuscript.

Research permits

The Indonesian State Ministry for Research and Technology (RISTEK DIKTI) Permit No. 69/EXT/SIP/FRP/E5/Dit.KI/X/2017 and No. 54/E5/E5.4/SIP/2019; the Directorate General of Natural Resources and Ecosystem Conservation: Gn. Leuser National Park (KSDAE-TN Gn. Leuser) Permit No. SI. 146/BBTNGL-TEK/P2/11/2017, No. SI. 06/BBTNGL-TEK/P2/01/2019, dan No. SI. 116/T.3/BIDTEK/P2/10/2019.

Funding information

The Department for Evolutionary Anthropology at the University of Zurich, the Max Planck Institute of Animal Behaviour, and the SUAQ Foundation funded the research.

Supplemental data

https://doi.org/10.47605/tapro.v14i2.364

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