Slow learning of feeding skills in a nocturnal extractive forager

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A long developmental period in animals is often needed to learn skills for adult reproduction and survival, including feeding behaviour. The nocturnal Javan slow loris, *Nycticebus javanicus*, is unusual in that it consumes a specialized diet of difficult to extract resources, as well as disperses up to a year after sexual maturity. Here, we examined the ontogeny of its feeding behaviour to understand whether learning to feed on difficult resources, including by co-feeding, is related to delayed dispersal. We collected feeding and proximity data on developing and adult wild slow lorises at a long-term field site in Cipaganti, West Java from 2012 to 2018. To determine whether acquisition of insects, exudates, nectar and flowers varied by age, we ran logistic generalized additive mixed models. We found that intake of insects and exudates occurred significantly more in the early stages, and feeding on nectar significantly more in the later stages, of development. Co-feeding occurred for all food types, with insects showing the most co-feeding events during early development, and co-feeding on exudates remaining high throughout development. Social learning via co-feeding is a potentially important factor in transmission of dietary information from older individuals, including siblings and parents, to young slow lorises. Differences between immature and adult diets levelled off after sexual maturity and before average dispersal. Together these factors suggest that the period required to learn to forage on difficult items could help explain the delayed dispersal patterns seen in mammals with similar foraging strategies.

Keywords: behavioural development, co-feeding, difficult diet, dispersal, foraging competence, life history, nocturnal mammal

Introduction

The evolutionary purpose of the long developmental period seen in some mammals has been attributed to multiple factors, including the need to grow both morphologically and cognitively to obtain the essential skills for adulthood (Pagel & Harvey, 1993; Mallott, Garber & Malhi, 2017). Regarding ontogeny of diet, juveniles may struggle to exploit the same resources as adults due to morphological differences, and differences in skill and knowledge level to acquire resources (Thompson, Biknevicius, & German, 2003; Gunst, Boinski, & Fragaszy, 2008). Extended periods of learning within the group may be needed, especially for species with 'difficult' diets (Heinsohn, 1991). Such diets may contain items that are toxic or difficult to handle or extract, where learning by sampling may be risky (Thornton and Clutton-Brock, 2011; La Croix, Zelditch, Shivik, Lundrigan, & Holekamp, 2011; O'Mara & Hickey, 2012).

Observing diet throughout ontogeny allows us to understand how and when animals develop and learn to acquire difficult diets (Binder, Thompson, & Van Valkenburgh, 2002; Thompson et al., 2003). Understanding morphological changes throughout ontogeny is a first step, as immature animals may fill different dietary niches as they develop (La Croix, et al., 2011). Immature grey short-tailed opossums, *Monodelphis domestica*, characterized by narrower mandibles and lower bite forces, engage in food partitioning with adults, during which time they consume more easily accessible food items (Thompson et al, 2003). In spotted hyaenas, *Crocuta crocuta*, immatures adjust which premolars are used when cracking bones to increase the strength of the jaw adductors and maximal bite force, mirroring adult competency until they develop adult dentition (Binder & Van Valkenburgh, 2000). Animals that gouge holes in bark to access resources (including *Dactylopsila trivirgata, Petaurus breviceps, Callithrix jacchus* and *Nycticebus pygmaeus*) show ontogenetic changes in their ability to gape their jaw and may need to develop increased enamel on the labial surface of the teeth compared with the lingual surface before reaching adulthood and adult diets (Rosenberger, 1978; Vinyard, Wall, Williams, & Hylander, 2003; Burrows et al., 2020). For animals with extended life histories, physical competence may not be enough. Thus, a learning phase may also be associated with the development of food handling skills and increased foraging capabilities, often learned from group mates (Hauser, 1993; Nash, 1993).

Numerous studies show that young animals may benefit from the knowledge of older individuals (Galef Jr & Giraldeau, 2001; Thornton, 2008). A proxy for examining evidence for knowledge transfer in the wild is examination of co-feeding (Jaeggi, Burkart, & van Schaik, 2010). Co-feeding with members of the social group can occur asynchronously whereby one individual observes one or more others feeding, or synchronously whereby individuals feed on either the same or a different food source (Hauser, 1993). Although some argue that learning to eat food items may be due to stimulus enhancement, others suggest that the presence of an experienced individual near a food item provides sensory cues, facilitating immature animals to attempt to feed (Heyes, 2012; Avarguès-Weber and Chittka, 2014).

Most knowledge of mammal co-feeding during foraging of difficult dietary items comes from diurnal group-living species. Examples include consumption of items that are toxic (scorpions by meerkats, *Suricata suricatta,* Thornton, 2008), need to be extracted (nuts by tufted capuchin monkeys, *Cebus apella,* Dogo de Resende, Ottoni, & Fragaszy, 2008) or require morphological competence (bones by coyotes, *Canis latrans,* La Croix et al., 2011). Many nocturnal species, including those that consume difficult diets, have been described as solitary foragers, where learning by co-feeding may be minimal (Soderquist & Lill, 1995; Mueller & Thalman, 2000). However, multiple nocturnal taxa, whose diet primarily or in part comprises tree exudates, animal prey and nectar, feed in small groups (Ball, Adams & Goldingay, 2010; Williams, 2016; Nakabayashi, 2015; Kays & Gittleman, 2001). These difficult foods may require complex foraging behaviours including morphological competence to gouge and knowledge of feeding sites (Forsythe & Ford, 2011; Lührs, 2009; Day, Coe, Kendal & Laland, 2003), handling to remove toxic hairs or avoid being stung or bitten (Charles-Dominique, 1977; Thornton & Clutton-Brock, 2011) and sensitive handling to not damage the flower (Nekaris, 2014; Parachnowitsch & Kessler, 2010). Examining how nocturnal mammals learn to acquire difficult diets in the wild may reveal the role that sociality plays in their feeding development and when they can disperse from their natal range.

Slow lorises, *Nycticebus* spp., are nocturnal primates with a specialized diet of tree exudates, noxious insects and nectar (Cabana, Dierenfeld, Wirdateti, Donati, & Nekaris, 2017; Nekaris, 2014). Relative to other mammals with a similar brain and body size, slow lorises are characterized by a slow life history, including a 180-day gestation period (Izard, Weisenseel, & Ange, 1988). In captivity, they obtain their adult dentition by 220 days and reach sexual maturity at around 540 days (Zimmerman, 1989); in the wild, they achieve adult body proportions that may facilitate feeding around this same time (Poindexter and Nekaris, 2017). They do not disperse from their natal range, however, until they are on average 670 days old (range 482–941 days, SD=172) (Campera, Brown, Imron, & Nekaris, 2020). This long developmental period has been suggested to relate to the need to learn about resource acquisition (Rasmussen & Izard, 1988).

Through a long-term study of a wild population of Javan slow lorises, *Nycticebus javanicus*, we explored whether the late dispersal age in slow lorises might be related to developing dietary competence, as well as the role of social learning in this development. We examined whether (1) slow lorises achieved adult competence in feeding close to the minimum dispersal age, (2) obtaining functionally challenging foods occurred at different points in ontogeny (Hauser, 1993; Stone, 2006) and (3) co-feeding occurred for each food type and there was any evidence for social learning to acquire difficult foods (Rapaport & Brown, 2008).

Methods

Data Collection

From April 2012 until December 2018, we observed free-ranging Javan slow lorises in an agroforest environment on Mount Puntang, near the village of Cipaganti (7°6'6"-7°7'S and 107°46'–107°46'5"E) in West Java, Indonesia. The open nature of this habitat allows for a relatively clear view of animals when they are not in dense vegetation, and it is possible for animals to see each other across open fields at distances up to 50 m. The main foods of this population are exudates, floral nectar, flowers and insects (Cabana et al., 2017). We collected data on leaf and fruit consumption, but since these foods are rarely eaten, we excluded these data from the analysis other than in diet composition. For this study, we included data from 24 developing Javan slow lorises (followed from young to adult age), and 22 individuals only observed as adults, with age measured in days (Table 1). We included the latter group as they were the parents of animals observed since birth and were thus important in observations of co-feeding. We defined age classes as follows: infants: birth until 153 days old; juveniles: 154–365 days old; subadults: 366–730 days old; adults: > 731 days old (Poindexter & Nekaris, 2017; Nekaris et al., 2019).

We caught animals by hand, placing them in a clean cotton weighing bag, and took standard measurements with no anaesthesia (Nekaris, Munds, & Pimley, 2020). We equipped the slow lorises with radiocollars (BioTrack, Dorset, U.K., 17 g, which is ~2% of an animal's body weight) with battery life of approximately 1 year attached to the neck with a rubber-coated cable tie; we then inserted a mini Microchip ID LTD chip. The procedure lasted on average 17 min after which the loris was immediately released into the tree in which it was caught (Nekaris, et al., 2019). We experimented with collar size and shape at the beginning of the study with closely monitored captive animals (Rode-Margono Nijman, Wirdateti, & Nekaris, 2014). Since 2012, we have never lost an animal due to a radiocollar or capture injury. We tracked the slow lorises using a six-element Yagi antenna and SIKA receiver (BioTrack). If an animal began to disperse outside the study area, we tracked it and removed the collar. Every slow loris had a health check every 6 months to ensure there was no adverse health effect from the radiocollar; young animals were caught every 3 months to ensure the collar still fitted. We observed the slow lorises using Clulite LED headlamps with a red filter (Cluson Engineering Ltd., Hampshire, U.K.). We found no negative effect on slow loris behaviour under red lights (Nekaris et al., 2020). Using a published ethogram (Rode-Margono et al., 2014), we collected general activity data nightly in two shifts (1800–0000, 0000–0600) at 5 min intervals using instantaneous focal sampling (Altmann, 1974). If another individual appeared during a focal follow, we would begin instantaneous scan sampling on both individuals at 5 min intervals (Altmann, 1974). We collected all occurrences of food intake, which we defined as an incidence where a food item was actively consumed, for the focal animal and all other individuals feeding near it. We recorded the number of insects, flowers and fruits consumed (see Cabana et al., 2017). For gum and nectar, we recorded the duration (s) of feeding (see Cabana et al., 2017). For developing individuals, we recorded 2694 feeding occurrences, of which 1699 were by individuals younger than the dispersal age. We collected data on co-feeding, defined as feeding or foraging in close proximity (i.e. less than 5 m, see Pimley, Bearder, & Dixson, 2005) to other individuals (Rapaport & Brown, 2008). This distance is also the average size of feeding tree patches in our agroforestry environment, with such trees separated by agricultural plants. We differentiated between synchronous (two or more parties were feeding) and asynchronous (one individual feeding and others observing) co-feeding (Hauser, 1993).

Ethical Note

All research was approved by the Animal Care Subcommittee of Oxford Brookes University number OBURASC0911 and adhered to the ASAB/ABS Guidelines for the Use of Animals in Research. We obtained all necessary research permits from the Indonesian government. All research adhered to the legal and ethical guidelines of the Indonesian Institute of Sciences, Department of Wildlife and Department of Forestry.

Data Analysis

For the analyses related to the overall diet, we considered only individuals we followed from immature to adult. We determined dietary composition of individuals by calculating the proportion in the diet for each food category with individual as the statistical unit. To test whether feeding behaviour changed through ontogeny, we used logistic generalized additive mixed models with consumption of food item as the dependent variable, food intake as weight and age as the independent variable, including individuals as random effects. We did not use food intake as the dependent variable as, with the presence of many zeros (when the animal did not eat that item), the model would have been less stable. By creating a dependent variable that was binary and using food intake as weight we solved the issue of data fitting and we still maintained the difference between observations (i.e. food intake; Bolker et al. 2009). We tested the consumption of each food item separately by setting the selected food item as 1 and the others as 0 (considering the feeding event as a statistical unit), running one model for each food item via gamm command in R 3.5.1 (R Core Team, 2013), package mgcv (Wood, 2017). We ran logistic generalized additive mixed models also for co-feeding data (co-feeding on food items set as dependent variable and age as independent variable), although in this case we used feeding events not weighted by food intake. It was not possible to estimate the food intake of both animals at the same time for most of the occurrences of co-feeding and including food intake as weight would have unbalanced the analysis towards asynchronous co-feeding events. We used the full restricted maximum likelihood method for model selection, tensor product smooth and penalized regression spline (Wood, 2006). We created plots via ggplot command in the ggplot2 package in R (R Core Team, 2013; Wickham, 2016). To test whether the relative food consumption changed between age categories, we also ran generalized linear mixed models with consumption of each food item (weighted for the food intake) as dependent variable, age in categories (infant/juvenile, subadult and adult) as the independent variable, and individuals as random effects via glmer command in R package lme4 (Bates, Maechler, Bolker, & Walker., 2015). For this analysis, we set adult as the reference category.

Results

The dietary composition, not weighted by the food intake, throughout ontogeny revealed differences in diet between age categories (Table 2). Infants/juveniles consumed the highest percentage of insects, whereas in the adult diet this percentage was almost halved. Gum comprised the highest percentage of the diet in all age classes, although it decreased slightly in adults. The percentage of nectar and flowers in the diet increased with age, with adults having the highest values. Leaves were rarely consumed by adults and were only observed to be consumed by infants/juveniles once.

Variation in the diet of the age classes declined until around 600 days, with dietary intake of immatures resembling that of adults. The relative consumption of insects, weighted by the food intake, decreased with age, especially before the dispersal age (Table 3, Fig. 1), Young individuals also consumed relatively more gum than adults (Table 3, Fig. 1). Conversely, the percentage of nectar increased with age, especially at early life stages. The consumption of flowers was also relatively low early in life and reached a peak during dispersal age. Relative consumption of insects was lower during the subadult period (β±SE = -0.306±0.072, *P*<0.001) than during adulthood, but there was a nonsignificant trend towards a higher consumption of insects in the infant/juvenile period (β±SE = 0.115±0.068, *P*=0.085) than in adulthood. The relative amount of gum consumed was higher during the infant/juvenile (β±SE = 0.922±0.040, *P* <0.001) and subadult (β±SE = 0.603±0.037, *P* <0.001) periods than in adulthood. The relative amount of nectar consumed was lower during the infant/juvenile (β±SE = -0.529±0.051, *P* <0.001) and subadult (β±SE = -0.088±0.042, *P* =0.037) periods than during adulthood. The relative amount of flowers consumed was lower during the infant/juvenile (β±SE = -1.488±0.089, *P* <0.001) and subadult (β±SE = -0.649±0.098, *P* <0.001) periods than during adulthood.

We were able to record co-feeding in detail 85 times, both between young animals and their older siblings (both male and female ranging from 730 to 1095 days) and with both parents (Table 4). Co-feeding occurred asynchronously in 68.2% of the instances, whereas synchronous co-feeding occurred in 31.8% of the instances. The first asynchronous co-feeding on insects was after 59 days; we only recorded one synchronous co-feeding on insects. Co-feeding on insects involved a younger animal observing an older animal catching insects or snatching insects from the same swarm on which a conspecific was feeding. The first synchronous co-feeding on gum was after 84 days. In addition to younger animals observing older animals, older animals sometimes gouged a hole from which the younger animal proceeded to feed. Asynchronous co-feeding on nectar was after 212 days, while synchronous co-feeding on nectar was after 274 days and involved animals moving together in the terminal branches of trees, sometimes licking the same flower while co-grasping the flower or licking a flower that an older animal had already licked. Synchronous co-feeding on whole flowers occurred after 196 days and involved two or more animals in a flowering tree feeding in close proximity, sometimes snatching flowering branches away from each other. Co-feeding on insects (asynchronous) was relatively more frequent at early life stages. Co-feeding on flowers reached a peak at around 370 days. Co-feeding on gum and nectar tended to increase gradually with age (*P* =0.068 and *P* =0.089, respectively; Table 3, Fig. 2).

Discussion

The foraging and feeding experiences animals have early in life can have lasting implications for adult preferences, fitness and survivorship (Slagsvold & Wiebe, 2007; Altmann, 1998, Hauser 1993). Here we have shown that the nocturnal Javan slow loris displays ontogenetic shifts in diet, which are potentially related to physical and social factors, including the conveyance of dietary information through co-feeding behaviour (Galef Jr & Giraldeau, 2001). Given that the dietary stabilization recorded in this study approached the average age of dispersal and that the prevalence of co-feeding behaviour varied with age and food item, we suggest that gaining the physical and behavioural traits needed for independent foraging may be related to the extended developmental period of slow lorises.

We sought to examine whether slow lorises achieved adult competence in feeding close to the minimum dispersal age. Animals in our population usually dispersed at around 670 days (Campera et al., 2020), approximately 2 months after their diets became similar to those of adults. Some animals did not disperse until more than 900 days, meaning they stayed in their natal range for a year or more after reaching adult competency. The 'skill hypothesis' (Brown, 1987) and the 'maturation hypothesis' (Piper et al., 2015) both state that gaining physical and behavioural adult competencies may explain why an offspring benefits from remaining within its natal group longer than expected. Solitary foraging has been hypothesized to constrain dispersal age as offspring have to be able to access resources independently before they can disperse (Yoerg, 1998; Soderquist & Lill, 1995). When comparing nocturnal foragers that feed on difficult diets to those with more easily accessible diets, dispersal age is relatively later for the former group. For example, the more generalist nocturnal lorisiforms, the red slender loris, *Loris tardigradus*, and lesser galago, *Galago moholi*, both disperse after only 300–385 days (Nekaris and Bearder, 2011). A late dispersal is seen in the exudativorous nocturnal primate, the fork-marked lemur, *Phaner furcifer*, which disperses after 900 days compared to 210 days in generalist grey mouse lemurs, *Microcebus murinus* (Schülke, 2003; Radespiel, Lutermann, Schmelting, Bruford & Zimmermann, 2003). In marsupials, the exudativorous sugar glider, *Petaurus breviceps*, and squirrel glider, *Petaurus norfolcensis*, disperse at 332 days and 380 days, respectively (Quin, 1995) as opposed to the more generalist brush-tailed phascogale, *Phascogale tapoatafa*, which disperses at 162 days (Soderquist & Lill, 1995). While body size and living in an unpredictable seasonal environment can influence dispersal age in this comparative perspective (e.g. Génin, 2008), these results also suggest that social interactions may play a more important role than previously thought for nocturnal solitary foragers, especially those with difficult diets.

We found that Javan slow lorises adjusted their dietary composition throughout ontogeny, potentially related to the challenges presented by each food type. In this population, feeding on insects was highest early during ontogeny and decreased as individuals aged. Co-feeding on insects occurred as early as 59 days of age. Slow lorises do not acquire a complete set of milk teeth until 90 days after birth, precluding exudate feeding before this time (Zimmerman, 1989). Cabana et al. (2017) showed that insects at our study site were available year-round and were high in protein and crude fat. In white-faced capuchins, *Cebus capucinus*, juveniles foraged more than adults, and increased investment in procuring and consuming higher energy insects to meet the high energetic demands of development (Mallott et al., 2017). Co-feeding may be more pronounced when animals are feeding on items that are relatively more dangerous or difficult to process, such as toxic items. Javan slow lorises consume a large array of toxic and aggressive arthropods (Rode-Margono, Rademaker, Wirdateti, Strijkstra, & Nekaris, 2015). In meerkats, immatures are monitored while eating dangerous prey (Thornton & McAuliffe, 2006; Thornton, 2008). Young pottos also co-fed with group members, removing the hairs of potentially dangerous caterpillars before consumption (Charles-Dominique, 1977). As toxic insects are a potentially dangerous yet nutritionally valuable food item, the Javan slow loris may prioritize co-feeding with their offspring early on to minimize their vulnerability to these prey.

Exudates were the main food item for all age classes, yet intake of exudates was higher in the infant/juvenile age class. As exudate consumption was measured in seconds, and included processing the holes, this higher intake time could be related to young animals learning to extract exudates. Feeding with other group members occurred as early as 85 days. These observations are in line with the appearance of mandibular incisors and canines, or toothcomb, which are needed to gouge and fully erupt by 90 days (Zimmerman, 1989; Burrows et al., 2020). Also, at 3 months, the limbs and hands of Javan slow lorises are relatively large, an adaptation suggested to allow them to cling to tree trunks for gum extraction (Poindexter & Nekaris, 2017). Extractive foraging is argued to present unique challenges to animals and may require social learning (Thornton & Clutton-Brock, 2011). For example, in exudativorous callitrichids, Day et al. (2003) showed that the species that engage in more complex extractive foraging displayed more social attentiveness than other species. They concluded that these results may reflect their use of social learning through observing a skilled demonstrator.

Nectar was the last item for which slow lorises gained adult competence, reaching peak levels between 730 and 1095 days, with co-feeding not occurring until 212 days. Floral nectar comprises between 15 and 30% of the Javan slow loris diet and is easy to eat and digest (Cabana, Dierenfeld, Wirdateti, Donati, & Nekaris, 2018), yet immatures obtain adult levels of feeding on this resource last. Javan slow lorises primarily access floral nectars at terminal branches, which may be challenging because of the size of peripheral branches and the need to maintain the centre of gravity on compliant substrates (Grand, 1972). Javan slow lorises display a secure grip early during their ontogeny (Poindexter & Nekaris, 2017), but they probably still need to develop the motor coordination that would make them stable when reeling in terminal branches to feed on floral nectars. Carrie (1996) noted that motor coordination needs to develop due to the difficulty of integrating sensory input, neural control and motor output while growing. Mouse lemurs show a pattern of innate grasping strength and motor coordination through development (Boulinguez-Ambroise, Herrel, & Pouydebat, 2020), which may be the same pattern delaying when Javan slow lorises in this study could consume floral nectars.

The question remains whether there is evidence that young slow lorises did learn about food resources from conspecifics, and how much local enhancement played a role. Indirect methods allow an inexperienced individual to gain information about what and where to eat regardless of the intention of the experienced individual (Galef & Giraldeau, 2001). These indirect methods can include olfactory signals that come from a prey item, as seen in meerkats (Thornton & Clutton-Brock, 2011), or from conspecifics scent marking potential food items, as in rats, *Rattus norvegicus* (Laland & Plotkin, 1993). Visual signals can also act as markers for ideal food items. In yellow-bellied gliders, *Petaurus australis*, individuals left experimental gouges on sap-bearing trees, while other members of the group preferentially returned to specific trees to feed nearby (Goldingjay, 1991). As slow lorises create similar wounds on gum trees, these marks could provide a visual cue to young slow lorises that the tree provides gum. Doubtless local enhancement impacts dietary choice but can be supplemented with direct learning from group members.

Slow lorises co-fed with both parents and siblings on all the main items in their diet. These observations included synchronous co-feeding involving affiliative interactions. Co-feeding is a known strategy where immature members of the group can learn from more knowledgeable members (O'Mara & Hickey, 2012). Previous work on nocturnal and solitary mammals provides evidence for social transmission of feeding knowledge of difficult resources. For example, group feeding comprising 1–20% of feeding time has been observed in the wild in squirrel gliders (Sharpe & Goldingay, 2019), bushy-tailed olingos, *Bassaricyon gabbii* (González-Maya & Belant, 2010), small-toothed palm civets, *Arctogalidia trivirgata* (Nakabayashi, 2015) and kinkajous, *Potos flavus* (Kays & Gittleman, 2001). The diet of all these taxa primarily or in part comprises tree exudates, animal prey and nectar. Squirrel gliders show food transfer behaviours, taking food directly from the hands or mouths of adults (Sharpe & Goldingay, 2019). The Eurasian otter, *Lutra lutra*, also displays food transfer behaviours with males offering food to females (Quaglietta, Fonsesca, Mira, & Boitani, 2014). More of our observations of co-feeding were asynchronous than synchronous. Direct observation of an experienced conspecific may be necessary for young individuals to learn how to recognize and process difficult food items (Jaeggi et al., 2010). Slow lorises may have an observational based social learning system that guides the development of foraging proficiency (Hauser, 1993).

Rapaport and Brown (2008) predicted that reliance on social learning in primates should be more common in species with longer life histories, with highly tolerant social interactions, and with potentially dangerous diets that may require complex foraging techniques. Social learning and co-feeding are major factors in the transmission of food acquisition information between individuals. Thus, for the slow loris, co-feeding allows young individuals to acquire information about what and how to eat, which is necessary for adulthood. The results obtained is this study extend the evidence of the potential importance of co-feeding for the social transmission of foraging skills during individual development (Langen, 1996). The time needed to acquire these skills for acquiring foods is longer than that needed for physical development. Thus, the need to acquire foraging competencies of difficult foods could help explain the extended developmental period present within animals with delayed dispersal.

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Table 1: Observational effort per age class for Javan slow lorises throughout ontogeny based on observational data from 2012 to 2018 in West Java, Indonesia

Age category	*N*	Individuals			Median no. of feeding observations*			Median no. of foraging observations*			Median no. of sampling points*		
		F	M	UK	F	M	UK	F	M	UK	F	M	UK
Infant/Juveniles	563	7	8	3	13	13	3	38	25	5	206	102	30
Subadult	1136	9	8	0	41	50	-	116	72	-	368	205	-
Adult	2611	13	16	0	63	43	-	366	131	-	1123	390	-

N: number of observed feeding events per age category; F: females; M: males; UK: sex unknown.

*Per individual.

Table 2: Dietary composition (mean percentage of diet and SE) of Javan slow lorises throughout ontogeny based on observational data from 2012 to 2018 in West Java, Indonesia

Age category	*N*	Gum	Nectar	Insects	Flowers	Fruits	Leaves
Infant/Juveniles	563	43.3 (8.5)	19.8 (6.4)	27.8 (6.6)	4.0 (2.8)	4.7 (3.4)	0.1 (0.1)
Subadult	1136	48.6 (6.2)	28.5 (6.4)	15.1 (2.4)	6.2 (3.1)	1.0 (0.7)	0.0 (0.0)
Adult	995	37.9 (5.8)	31.2 (4.9)	14.3 (2.2)	9.8 (3.1)	4.8 (3.1)	1.2 (0.3)

N: number of observed feeding events per age category.

Table 3: Results of the logistic generalized additive mixed models with food item consumption or co-feeding as dependent variable and age as independent variable

Dependent variable	REML	Estimated *df*	χ^2	Model intercept
Flower consumption	580.9	1.944	**18.8****	**-2.82 (0.09)****
Gum consumption	1785.2	1.947	**55.3****	0.03 (0.04)
Insect consumption	580.9	1.944	**18.8****	**-2.82 (0.09)****
Nectar consumption	1423.0	1.954	**68.4****	**-1.16 (0.05)****
Flower co-feeding	34.7	1.789	**7.5****	**-2.27 (0.47)****
Gum co-feeding	58.1	0.653	1.7*	-0.31 (0.22)
Insect co-feeding	40.9	1.016	**9.9****	**-1.48 (0.31)****
Nectar co-feeding	34.4	0.684	1.9*	**-1.85 (0.32)****

REML: restricted maximum likelihood. Significant values are in bold.

* $P < 0.10$; ** $P < 0.05$.

Table 4: Events of co-feeding (and percentage of total co-feeding events) on the main food items between focal immatures and other group members in Javan slow lorises from 2012 to 2018 in West Java, Indonesia

	Mother	Father	Older sibling	Parent + sibling	Total
Gum	16 (18.8)	12 (14.1)	5 (5.9)	3 (3.5)	36 (42.4)
Insects	7 (8.2)	9 (10.6)	2 (2.4)	1 (1.2)	19 (22.4)
Flower	5 (5.9)	8 (9.4)			13 (15.3)
Nectar	4 (4.7)		7 (8.2)	1 (1.2)	12 (14.1)
Fruit	5 (5.9)				5 (5.9)
Total	37 (43.5)	29 (34.1)	14 (16.5)	5 (5.9)	85

Figure Legends:

Figure 1–Relative consumption of the four main food items, weighted by their food intake, in relation to age in Javan slow lorises from 2012 to 2018 in West Java, Indonesia. Lines indicate fitted functions based on logistic generalized additive mixed models; shaded areas indicate 95% confidence intervals.

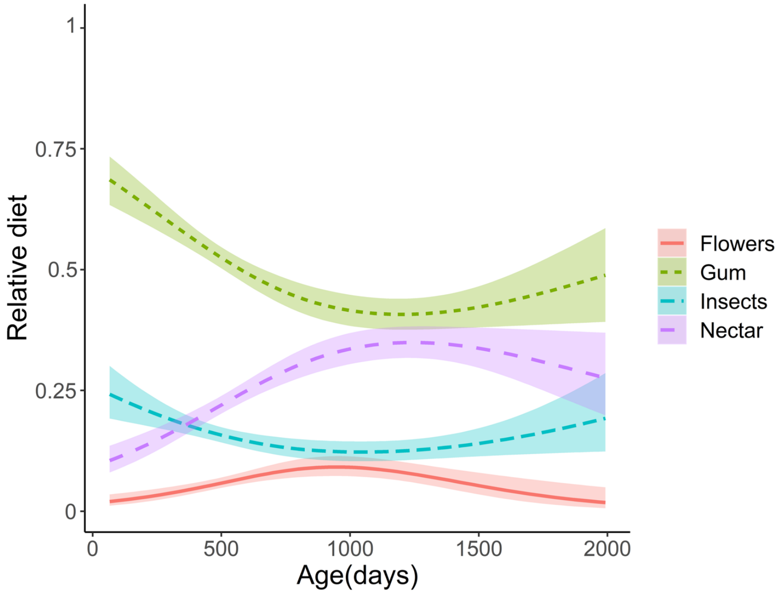

Figure 2–Relative occurrence of co-feeding events of the main food items in relation to age in developing Javan slow lorises from 2012 to 2018 in West Java, Indonesia. Lines indicate fitted functions based on logistic generalized additive mixed models; shaded areas indicate 95% confidence intervals.