Mammalian Biology 87 (2017) 40–49

Contents lists available at ScienceDirect

Mammalian Biology

journal homepage: www.elsevier.com/locate/mambio

Original investigation

Vertical clingers and gougers: Rapid acquisition of adult limb proportions facilitates feeding behaviours in young Javan slow lorises (*Nycticebus javanicus*)

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ARTICLE INFO

Article history:
Received 13 February 2017
Accepted 31 May 2017
Handled by Laura Wilson
Available online 2 June 2017

Keyword:
Exudativory
Gum
Ontogeny
Morphometrics
Strepsirrhine
Substrate use
Habitat use

ABSTRACT

Animals of all ages need to access essential food resources, either on their own or with the assistance of conspecifics. Rapid physical and behavioural development is one strategy to help young animals reach adulthood. Specialized gum-feeding mammals exploit a food type that is relatively difficult to access and digest and must possess the appropriate adaptions to access large vertical substrates, i.e. tree trunks. Unlike other gum feeding mammals, the Javan slow loris (*Nycticebus javanicus)* lacks physical structures, such as keeled nails or claws, which animals commonly use to secure themselves to large vertical substrates. To understand how slow lorises of all ages exploit gum, we examined their vertical gouging posture, locomotor behaviour, habitat use during feeding, and their morphometric measures across three age classes (adult, sub-adult, juvenile). Using data collected in Cipaganti, Java, Indonesia between April 2012 and April 2016, we found that individuals of *N. javanicus* rely on their hand, foot, and limb morphology to maintain vertical gouging postures, in place of claws or keeled nails. Locomotor behaviour, position in tree, and tree DBH showed no significant difference across age classes while feeding. Juveniles were indistinguishable from adults and sub-adults in regards to limb proportion indices, lower leg length, hand span and foot span. Some morphometric measures scaled isometrically e.g. arm length, but those highlighted during prolonged vertical postures scaled allometrically e.g. leg, hand, and foot measures. These findings suggest that the rapid behavioural and physical development of key features may act as an ontogenetic adaptation to facilitate access to a stable food resource at a young age. The Javan slow loris exemplifies the complex relationship that exists between an animal's diet and the specializations that facilitate access to these food resources.

Introduction

Mammals that rely on specific food resources must also possess a suite of adaptations to facilitate the access and digestion of these food items. Behavioural and morphological specialisations associated with feeding ecology are notable among mammal species (De Muizon and Lange-Badré, 1997; Dierenfeld et al., 1982; Ercoli and Youlatos, 2016; Koyabu et al., 2009; Ley et al., 2008; Naples, 1999; Ravosa et al., 2010; Tan, 1999). Mammals typically acquire needed feeding skills long before sexual maturity, allowing them to access vital resources before adulthood (Schuppli et al., 2016). One developmental strategy, rapid growth in infants, is a known adaptation to aid in reducing infant vulnerability and to help them surpass the ”juvenile bottleneck”, a period in which the mortality rate for juveniles is higher than that of adults (Case, 1978; Williams, 1966; Young and Heard-Booth, 2016).

Specialised gummivory is only seen in a small number of Australian marsupials and primates (Irlbeck and Hume, 2003; Viguier, 2004). These animals have evolved morphological traits and behavioural specializations to access and digest gums (Cabana et al., 2017a; Nash, 1986; Smith, 2010). P-linked polysaccharides, such as gums, require specific microbes for fermentation (Booth and Henderson, 1963; Monke, 1941; Power and Myers, 2009). Mammals that eat gums enable fermentation through having a longer cecum and large intestine (Chivers and Hladik, 1980; Power and Myers, 2009; Smith, 1982). In addition to digestive specializations, gummivory is often consistent with postcranial adaptations, including keeled nails or claws, which allow animals to climb and cling to large tree trunks and branches for extended periods, reduc-

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http://dx.doi.org/10.1016/j.mambio.2017.05.007
1616-5047/

ing the amounts of energy necessary during gouging (Kubota and Iwamoto, 1966). Across gouging mammals, mandibular variation is associated with the percentage of gum in a species' diet (Viguier, 2004). Gougers use specialized dentition to damage a tree's bark to elicit gum production and flow (Petter, 1978). In strepsirrhine primates, this adaptation takes the form of a specialised toothcomb used to elicit flow of or to scrape gum.

Charles-Dominique (1977) proposed that gums were inaccessible to mammals that lacked claws or modified nails. A number of primates consume gum and lack these features, including lesser galagos (*Galago senegalensis*) mouse lemurs (*Microcebus* spp.), and the slow lorises of Asia (*Nycticebus* spp.). Despite lacking claws or modified nails, Nekaris (2014) noted that *Nycticebus* spp. are "true gougers" characterised by stout mandibles, U-shaped hind limbs, and camouflaged fur that allow them to specialize on exudates up to 97.5% their feeding time (c.f. Swapna et al., 2010; Das et al., 2014). *Nycticebus* spp. possess a specialised toothcomb and a reduced last lower molar compared to *Loris* spp. further supporting their distinction as obligatory gougers (Burrows et al., 2015). In order to cling to trees in the absence of specialized nails or claws, they possess a host of characteristics, including a firm grip, reduced second digit, and a vascular artery bundle that lowers the temperature of their limbs called the *retia mirabilia*, enabling them to maintain long-duration static postures necessary for gouging gum (Ishida et al., 1992; Kingston et al., 2010; Nekaris, 2014).

Despite a general lack of research regarding *Nycticebus* ontogeny in the wild, the consensus is that for an animal of its size, *Nycticebus* has a long gestation period (6 months) and delayed dispersal (~16 months) (Izard et al., 1988; Nekaris, 2014; Zimmermann, 1989). The period between these developmental milestones is poorly understood and previous reports on this topic offer varying results on the emergence of key behaviours (Ehrlich and Macbride, 1989; Fitch-Snyder and Ehrlich, 2003; Rasmussen, 1986; Zimmermann, 1989). This variation is attributed to variable captive conditions and small samples sizes. In captivity, infants were first observed consuming solid foods at ~40 days (Zimmermann, 1989) and in the wild Wiens and Zitzmann (2003) observed the solid feeding behaviour of an eight-week old infant. In regards to exudates, individuals as young as three months elicit gums from tree trunks (Nekaris, 2014).

Until now, there has been no exploration of either the behavioural repertoire used to access tree gums or the ontogenetic development of these behaviours. Here, we aim to explore the mechanisms used by the Javan slow loris to access gum from the juvenile period to adulthood. We address three research questions: (1) What physical adaptations facilitate the prolonged vertical postures needed to access tree trunks? (2) Do Javan slow lorises display any ontogenetic variation in their locomotor behaviour and habitat use during feeding? (3) What, if any, are the morphometric differences across age classes and do they influence locomotor behaviour or habitat use? Following these question we hypothesise that young Javan slow lorises will quickly attain the necessary physical and behavioural competence to gouge trees, as gum is a key component of their wild diet (Cabana et al., 2017b). In accordance with this hypothesis, we also predict that there will be little to no difference in habitat utilization, as defined by their position in tree, and the diameter at breast height (DBH) of feeding trees.

Methods

Study site

We collected data from April 2012 to April 2016 as part of an on-going project in Cipaganti, West Java, Indonesia (S7°6′6” 7°7′ & E107°46′ 107°46′5”). The field site lies at the unprotected base of the mountain Gunung Puntang, which is a part of the Java-Bali Montane Rain Forests ecoregion. The area between the adjacent village and the protected forest is primarily patches of cultivated land, bamboo, and shrubs. The primary gum-producing tree species consumed in the area is green wattle (*Acacia decurrens*), with this species comprising 38–60% of the population's diet and 62–84% of all exudates consumed depending on the time of year (Cabana et al., 2017b). The area where we conducted nightly observations encompasses 50 ha with elevations varying between 900 and 2000 m asl.

Radio collaring, aging, measuring and weighing

Following a protocol approved by the Animal Ethics Subcommittee at Oxford Brookes University, experienced team members handled non-anesthetized individuals. The radio collars (BioTrack, UK) weighed 17 g, which is on average less than 2% of the body weight of an adult Javan slow loris and less than 4% of an immature Javan slow loris. Using a 2.5 kg spring (Pesola, Canada) and a clean cloth bag, we weighed individuals either annually or every three months. Using digital callipers and soft measuring tape, KAI Nekaris measured the total body length, hand and foot span, upper arm, lower arm, upper leg, lower leg length, head width, and head length, for each individual (Nekaris and Jaffe, 2007). We assessed age classes for 58 individuals including 54 of the Javan slow lorises included in our nightly observations. We determined ages either from observing the animal from birth or using body size, pelage characteristics, and proximity to mother (Rode-Margono et al., 2014), but are reaffirmed here using morphometric data, including calculated limb proportion indices (Intermembral, Humerofemeral, Brachial, and Crural: Fleagle, 2013) and the whole arm and leg length in relation to total body length. Approximately, infants are less than 12 weeks old, juveniles are between 12 weeks and 8 months old, sub-adults are between 8 months and 15 months old, and adults are 16 months or older.

Nightly observations

We engaged in nightly observations over two shifts between 18:00 to 00:00 and 00:00 to 05:00 (Wiens and Zitzmann, 2003), totaling 29,204 observation points for 54 individuals. We recorded data using instantaneous sampling with 15-min intervals and *ad libitum* notes following Altmann (1974) and Nekaris (2001). At each sample point we recorded the behaviour (alert, feed, forage, freeze, groom, rest, sleep, social, travel, other) locomotor/postural mode (Table 1 and Fig. 1), position in tree (central, crown, periphery, terrestrial, trunk, undergrowth), and DBH (in cm). During each shift we followed one slow loris, unless other animals were within the vicinity of the collared focal, in which case we used instantaneous scan sampling. We tracked individuals using an antenna (Yagi, Biotrack, UK) and receiver (Sika, Biotrack, UK).

Data analyses

Using SPSS version 22 and R 3.3.3, we calculated the mean and standard deviation of observed points in each of the above variables. To test for significant differences across the age classes in locomotor behaviour, habitat utilization, and the morphometric measures we used the nonparametric Kruskal-Wallis and Mann-Whitney *U* tests with significance set at $p < 0.05$. We applied the Bonferroni correction to the post-hoc comparisons following significant results from the Kruskal-Wallis test, changing significance to $p < 0.016$. We used a Canonical variate analysis (CVA) to identify the morphometric variables that are most different between the age classes (Dytham, 2011). We ran four General Linear Models (GLM), in which we individually tested the proportion of time spent engaging in locomotor modes Vertical Suspension 3 Up/Down and