Animal Behavior and Cognition
ABC 2025, 12(1):108-121
DOI: https://doi.org/10.26451/abc.12.01.05.2025


# White-bellied Pangolin (*Phataginus tricuspis*) Nest Box Activity Budgets And Behavior Milestones

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**Citation –** Lauderdale, L. K., Wojciechowski, S., & Miller, L. J. (2025). White-bellied pangolin (*Phataginus tricuspis*) nest box activity budgets and behavior milestones. *Animal Behavior and Cognition, 12*(1), 108-121. https://doi.org/10.26451/abc.12.01.05.2025

**Abstract –** White-bellied pangolins (*Phataginus tricuspis*) are semi-arboreal mammals from equatorial Africa. Listed as endangered by the IUCN, their population is under severe threat due to illegal hunting for their meat and scales. Many aspects of pangolin behavior, particularly maternal and early pup behavior, remain largely undocumented. Gathering behavioral data for both the dam and pup allows for the development of baseline rates of maternal and pup behavior as well as the setting of early behavioral milestones. This study defined and quantified early maternal and pup behavioral trends inside the nesting box for zoo-housed, white-bellied pangolins. Data were collected from August 2018 to January 2022. Videos were recorded for 24-hours every fourth day (e.g., Day 1, Day 4, Day 8, etc.) for the first 30 days of life. The behaviors of six dam-pup pairs (four male pups and two female pups) were scored to develop activity budgets, describe maternal behaviors, and define early behavioral milestones. Wilcoxon signed-rank tests were used to compare nocturnal and diurnal hours. Pairs spent the majority of their time curled in a ball together and were more active at night than during the day. Dams spent the majority of their time in contact with the pup with occasional separations as early as the first day of life. Pups were born precocial and engaged in digging and nosing under the dam's scales as early as the first day of life. These behavioral observations and milestones can be used as a baseline when monitoring future dam-pup pairs, to enhance husbandry protocols, and to assess the welfare of both dams and pups.

**Keywords –** Zoo housed, Behavioral development, Behavioral milestones, Maternal behavior, Ontogeny of behavior

For many mammal species, maternal care not only provides immediate life-sustaining resources (e.g., food, shelter, and warmth) but it also helps establish integral behaviors such as species-typical social interactions and hunting/foraging skills (Hopkins, 2013; Maestripieri, 2018; Maestripieri et al., 2002; Sargeant & Mann, 2009). Inadequate maternal care is associated with poor outcomes for the offspring such as poor body condition, stereotypical behaviors, illness, and/or death (Latham & Mason, 2007; Laurenson, 1993; Siciliano-Martina, 2020). Developmental milestones are one indicator used to examine developmental trends, health, and welfare (Heintz et al., 2017; Plair et al., 2012; Renner et al., 2023). The meeting of behavioral milestones plays a critical role in monitoring the progression of individual development during early life stages. Behavioral milestones serve as essential markers of physical and behavioral development that can be used to assess an individual's health and welfare in a wide range of species (Miller & Andrews, 2013; Ramont et al., 2024; Renner et al., 2023). Deviations from the expected behavioral and developmental timelines can aid in identifying potential health issues that may require monitoring, support, or intervention (Ramont et al., 2024; Renner et al., 2023).

Activity budgets can be used to document behavioral milestones and maternal care behaviors over time. Activity and rest cycles related to circadian rhythms are important factors for understanding the biological and environmental needs of a species to promote positive welfare (Hayward & Slotow, 2009; Rees, 2009; Seyrling et al., 2022). Activity budgets are pivotal pieces in the survival, health, and welfare of offspring (Plair et al., 2012). Knowledge of the types and rates of the various behaviors over a 24 hour period provide landmarks for defining a healthy environment and ensuring the welfare of both the mother and offspring (Ramont et al., 2024).

The Order *Pholidota* is comprised of eight extant species of pangolins living across Africa and Asia (Gaubert et al., 2020). There are clear morphological, phylogenetic, and behavioral distinctions between African and Asian taxa. Species have differing scale patterns, presence and absence of hair, shape of claws, and inhabit tropical and subtropical regions. Species of African pangolins are divided between small, arboreal pangolins (*Phataginus tricuspis* and *Phataginus tetradactyla*) and large, ground-dwelling pangolins (*Smutsia gigantean* and *Smutsia temminckii*; Gaudin et al., 1999, Gaudin et al., 2009). All four species of African pangolins are generally considered to be solitary outside of males and females briefly coming together for mating and relationships between dams and pups (Gudehus et al., 2020; Jansen et al., 2020; Hoffmann et al., 2020; Pietersen et al., 2020). Although much of the post-partum period is poorly described, observations of pangolins with pups outside of the nest indicate there are prominent differences between species. For example, wild white-bellied pangolin (*Phataginus tricuspis*) pups have been observed to be independent around three to five months of age whereas wild Temminck's pangolin pups have been observed to reach independence at ten to 12 months of age (Pietersen et al., 2020).

White-bellied pangolins (hereafter referred to as 'pangolins') are small, semi-arboreal, nocturnal mammals from West and Central Africa (Jansen et al., 2020; Pagés, 1972a). Listed as endangered by the IUCN (IUCN, 2023), their population is under severe threat due to habitat loss and illegal hunting for their meat and scales (Dangbo et al., 2020; Ingram et al., 2018; Jansen et al., 2020; Kombate et al., 2022). To protect them from extinction, there have been renewed efforts to develop *ex-situ* conservation breeding programs in Africa, North America, and Asia (Hua et al., 2015; Yang et al., 2007).

Wild female pangolins have small home ranges of approximately three to four ha that overlap with male pangolins. However, females traverse only a small portion, averaging 400 m, of their home range each night (Pagés, 1975). Female pangolins will continually use a nesting site while males tend to move nests each night. Pangolins breed throughout the year and gestation was originally estimated to be between 140 days and 150 days (Pagés, 1972b). However, more recent observations from animals housed in zoological environments indicate the gestation length is 240 days to 255 days (C. Aitken-Palmer, personal communication, March 1, 2024). Pups are born physically well-developed and with their eyes open (Aitken-Palmer et al., 2019; Menzies, 1967).

Pagés reported that a wild female pangolin in Gabon spent approximately 36 hrs to 48 hrs inside the nest while giving birth before emerging for short periods of time over the next week (Pagés, 1975). Nursing occurred in short, relatively frequent durations early in the pup's life but pups could go 12 h without nursing by the pup's 15$^{th}$ day (Pagés, 1972b). Feeding exclusively occurred on one side and pups were observed to fall asleep with the nipple in their mouth. One wild pup was observed leaving the nest for the first time on its seventh day of life (Pagés, 1975). As pups age, the pups rode on the base of the dam's tail as she moved around the environment (Pagés, 1972b). Weaning has been reported to occur between 90 days and 180 days (Kingdon, 1971; Pagés, 1972b).

Pangolins are classified as a nocturnal mammal based on activity levels outside of the nest. However, 24 hr continuous monitoring has not been previously reported to provide insights on potential similarities and differences of activity during diurnal hours. In some species, nursing bouts and periods of activity are still common during that species' typical resting cycle (Horback et al., 2014; Tanaka & Yamanashi, 2019). Thus, it is important to compare behavior during nocturnal hours to diurnal hours. Limited information is available on the normal maternal care behavior and pup behavioral milestones that occur inside the nest during the first 30 days of life. Defining behaviors for both the dam and pup allows

for the development of baseline rates of maternal and pup behavior as well as the setting of early behavioral milestones that occur inside the nesting box.

## Method

### Ethics Statement

Ethics approval was not required from an Institutional Animal Care and Use Committee because the study used routinely collected, observational data that did not include any changes to animal care or husbandry practices.

### Study Subjects and Facility

The focal subjects were 11 white-bellied pangolins living behind-the-scenes (i.e., not on public display) at Brookfield Zoo Chicago in Brookfield, IL, USA (Table 1). All dams observed in this study were born in the wild (n = 5). Six dam-pup pairs were observed. One dam was recorded for two sequential pups. The focal pups included two females and four males. Following the data collection, one pup passed away at 7 months and 15 days old and the other five pups are still alive at the time of publication.

**Table 1**

*Sex, Age, and Dam of Focal Pangolins*

| Dam ID | Pup ID | Pup Sex | Est. Age Birth | Pup DOB |
|---|---|---|---|---|
| Dam 1 | Pup 1 | M | 6 years | 1/31/2022 |
| Dam 2 | Pup 2 | F | 4 years | 6/12/2019 |
| Dam 3 | Pup 3 | M | 5 years | 5/17/2019 |
| Dam 4 | Pup 4 | M | 4 years | 8/12/2018 |
| Dam 5 | Pup 5 | M | 3 years | 8/5/2018 |
| Dam 5 | Pup 6 | F | 4 years | 5/17/2019 |

Data were collected at Brookfield Zoo Chicago from August 2018 to March 2022. Pangolin nest boxes were equipped with overhead cameras (AXIS M3057-PLVE Fixed Dome Network Camera, Lund, Sweden) that allowed for monitoring in red-light conditions (i.e., nocturnal hours). The entire nest box was visible to the camera. Nest boxes were 40.64 cm x 30.48 cm x 38.10 cm (length x width x height) and located inside a larger, indoor habitat that was 2.6 m x 2.6 m x 2.7 m (length x width x height). Pangolins were able to enter and exit the nest box at any time. Habitats were in 'behind-the scenes' areas and were not visible to the public. Pangolins were on a 12 hr photoperiod matched to replicate the light cycle of their natural habitat in Togo. The light cycle was reversed to aid in animal care. However, 'day' and 'night' within this publication are referencing the photoperiod experience of the focal animal (i.e., 'night' occurred from 0935 hr to 2135 hr).

### Data Collection

Archived video data were used in the present study. Videos of 24 hr periods from select days twice per week (Days 1, 4, 8, 11, 15, 18, 22, 25, and 29) during the pup's first 30 days of life were examined, where available, resulting in a total of 1,029 h of video (Dam 1/Pup 1 = 216 h, Dam 2/Pup 2 = 216 h, Dam 3/Pup 3 = 216 h, Dam 4/Pup 4 = 96 h, Dam 5/Pup 5 = 96 h, Dam 5/Pup 6 = 189 h). Video recordings were viewed using Milestone XProtect Software (Milestone Systems A/S, Brøndby, Denmark). Video observations consisted of continuous sampling of state behaviors and all-occurrence sampling of event behaviors of both the dam and pup. Recordings were scored in Microsoft Excel (Microsoft Corporation, Washington, USA) by a single observer. Reliability was calculated using a subset

of the video recordings. Inter-observer agreement was evaluated by scoring a total of 12 observations (3 hrs) of the six pairs. Intra-observer reliability was evaluated by scoring a total of 6 observations (1.5 hrs) of the six pairs two times. Reliability was calculated using inter-class correlations. At least 80% reliability was achieved for inter-observer reliability and intra-observer reliability. Table 2 provides the operational definitions of event and state behaviors. The operational definitions in the ethogram were developed by the authors, modified from operational definitions published by Challender et al. (2012) and Mohapatra and Panda (2013), as well as modified from unpublished definitions based on the personal observations of Carol Sodaro and Sheila Wojciechowski (of Brookfield Zoo Chicago).

**Table 2**

*Ethogram Utilized for the Event Behaviors, State Behaviors, and Focal Animal Location in the Current Study*

| Behavior | Definition |
|---|---|
| | Event Behaviors |
| Digging | Focal animal uses forelimbs in a repetitive manner to dig or scratch a natural substrate surface. |
| Scrabbling | Focal animal repeatedly scratches with front forelimbs in an area or at an object, which is artificial and/or has no natural substrate. |
| Self-Grooming | Focal animal rapidly moves its claws across his/her face and/or body in a circular or back-and-forth motion or the animal is licking/sniffing (nosing) under its scales (i.e. self-maintenance). |
| Dam Initiates Separation | Dam initiates physical separation (direct contact) from pup. |
| Dam Initiates Return | Dam initiates direct physical contact with pup. |
| Pup Noses Under Dams Scales | Pup's nose makes small movements under the scales of the dam's back or tail. |
| Pup Initiates Separation | Pup initiates physical separation (direct contact) from dam. |
| Pup Initiates Return | Pup initiates direct physical contact with dam. |
| | State Behaviors |
| **Contact** | |
| Curled Proximate Ball | Focal animal is curled in a ball while in physical contact with the other individual. |
| Curled Single Ball | Pup is curled inside the dam's ball. |
| Nursing | Pup is on nipple with nursing movements. |
| Evidence of Nursing | Pup is positioned with its head/mouth at the nipple, but nursing movement is not occurring (e.g., the pup falls asleep with the nipple in its mouth). |
| Other | Focal animal is engaged in a behavior that is not defined while in physical contact with the other individual. |
| Tail-Riding | Pup is riding on the dam's tail while the dam is standing or walking. |
| Body-Walking/Riding | Pup is grasping, walking, or crawling on the dam's body while the dam is lying down. |
| Under/Over | Pup is under the dam while she is standing. |
| Upright | Focal animal is standing upright on two or four feet while in physical contact with the other individual. Excludes when the pup is underneath the dam. |
| Walking | Focal animal is walking upright while in physical contact with the other individual. Excludes when the pup is tail-riding and body-walking. |
| **No Contact** | |
| Curled Solitary Ball | Focal animal is curled in a ball while not in physical contact with the other individual. |
| Other | Focal animal is engaged in a behavior that is not defined while not in contact with the other individual. |
| Upright | Focal animal is standing upright on two or four feet while not in contact with the other individual. |
| Walking | Focal animal is walking while not in physical contact with the other individual. |
| Out of Nest Box - Both | Both the dam and pup are out of the nest box. |
| Out of Nest Box - Dam | The dam is out of the nest box and the pup is in the nest box. |
| Out of Nest Box - Pup | The pup is out of the nest box and the dam is in the nest box. |

## Statistical Analysis

Activity budgets were calculated by dividing the amount of time spent in each behavior state by the total amount of time visible. The rate of event behaviors was calculated by dividing the number of times the event occurred in a given observation day by the amount of time visible in that day. Data were

categorized as “daytime” or “nighttime” based on the light cycle in their habitat. Daytime lights were on between 2136 hr and 0934 hr and nighttime (i.e., red) lighting was on between 0935 hr and 2135 hr. Standard errors were calculated by pair or individual. Wilcoxon signed-rank tests (significance level of $p < .05$) were used to compare diurnal and nocturnal activities. Milestones were established based on the day of life that the behavior was first recorded.

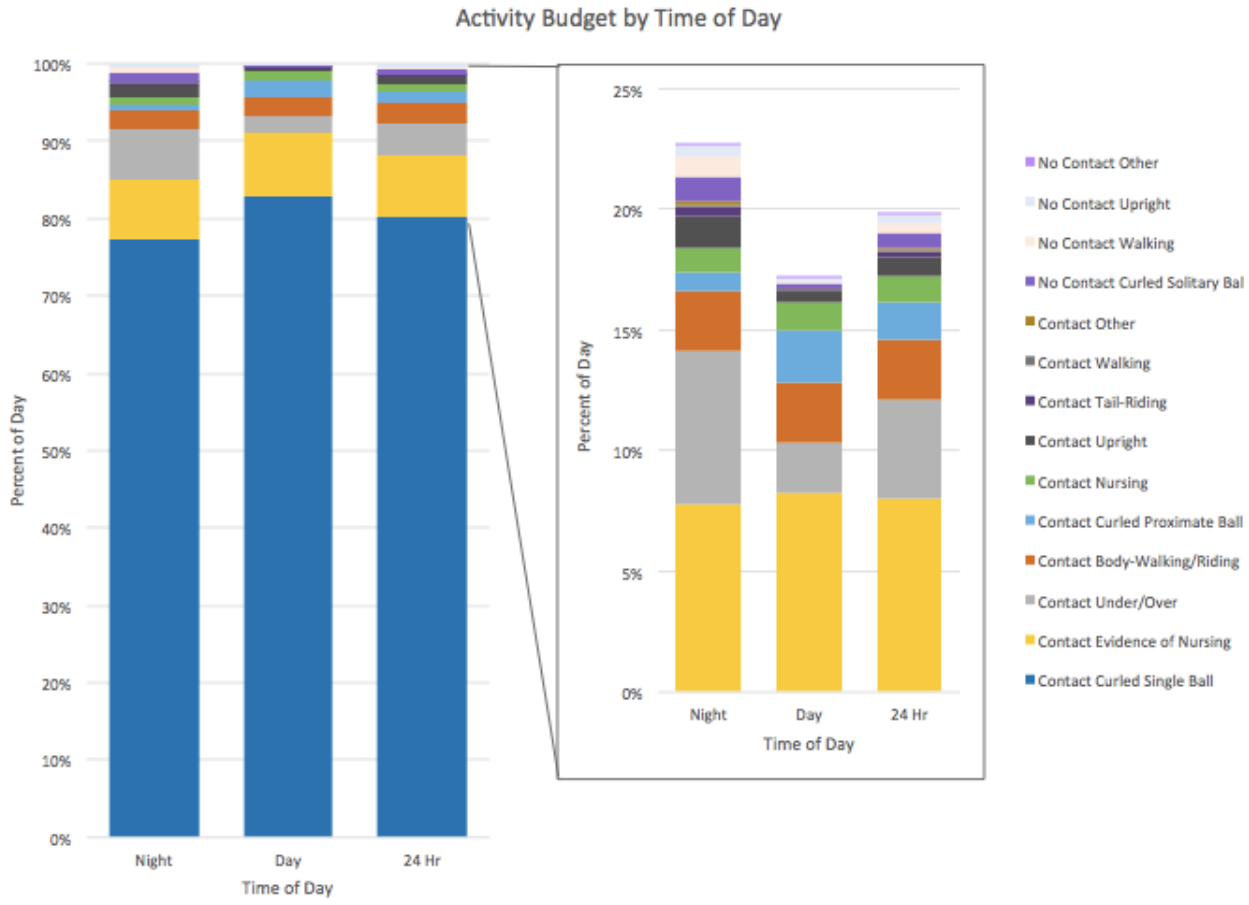
## Results

### Activity Budget

While inside the nest box, dam and pup pairs maintained almost continuous contact ($M$ = 98.64%). Three behavior states dominated the activity budget inside the nest box: laying down curled as a single ball, evidence of nursing, and the dam standing upright over the pup (Figure 1). On average, pairs spent 80.23% of their time (n = 6, $SE$ = 1.80, range: 75.19% - 85.37%) in the nest box curled together in a single ball, 8.04% of their time (n = 6, $SE$ = 1.48, range: 3.67 - 14.40%) in an evidence of nursing position, and 4.11% of their time (n = 6, $SE$ = 0.52, range: 1.88% - 4.92%) with the dam upright over the pup.

**Figure 1**

*Nocturnal, Diurnal, and 24 Hr Nest Box Activity Budget*




*Note*. Figure 1 includes a breakout (graph on the right) that shows an enlarged graph for all behavior categories except for Contact Curled Single Ball.

Nocturnal and diurnal activity budgets showed the same three behaviors dominated both time frames: laying down curled as a single ball, evidence of nursing, and the dam standing upright over the pup. Pairs spent significantly less time curled in a single ball (Z = -2.20, n = 12, $p$ = .02) and curled into a proximate ball (Table 3, Z = -2.43, n = 12, $p$ = .02) during nocturnal hours. Pangolins spent significantly more time with the dam upright over the pup (Z = -2.90, n = 12, $p$ > .01), contact upright (without the dam covering the pup; Z = -2.04, n = 12, $p$ = .04), tail-riding (Z = -3.06, n = 12, $p$ > .01), contact walking (Z = -1.99, n = 12, $p$ = .04), no contact walking (Z = -3.06, n = 12, $p$ > .01), and no contact upright (Z = -2.93, n = 12, $p$ > .01). There were no significant differences in evidence of nursing, body-walking/riding, nursing, and no contact curled solitary ball when comparing diurnal to nocturnal hours.

**Table 3**

*Average ± SE Percentage of Minutes Visible Spent in Each Behavior State During Day (0935 - 2135) and Night (0936 - 2134) Hours*

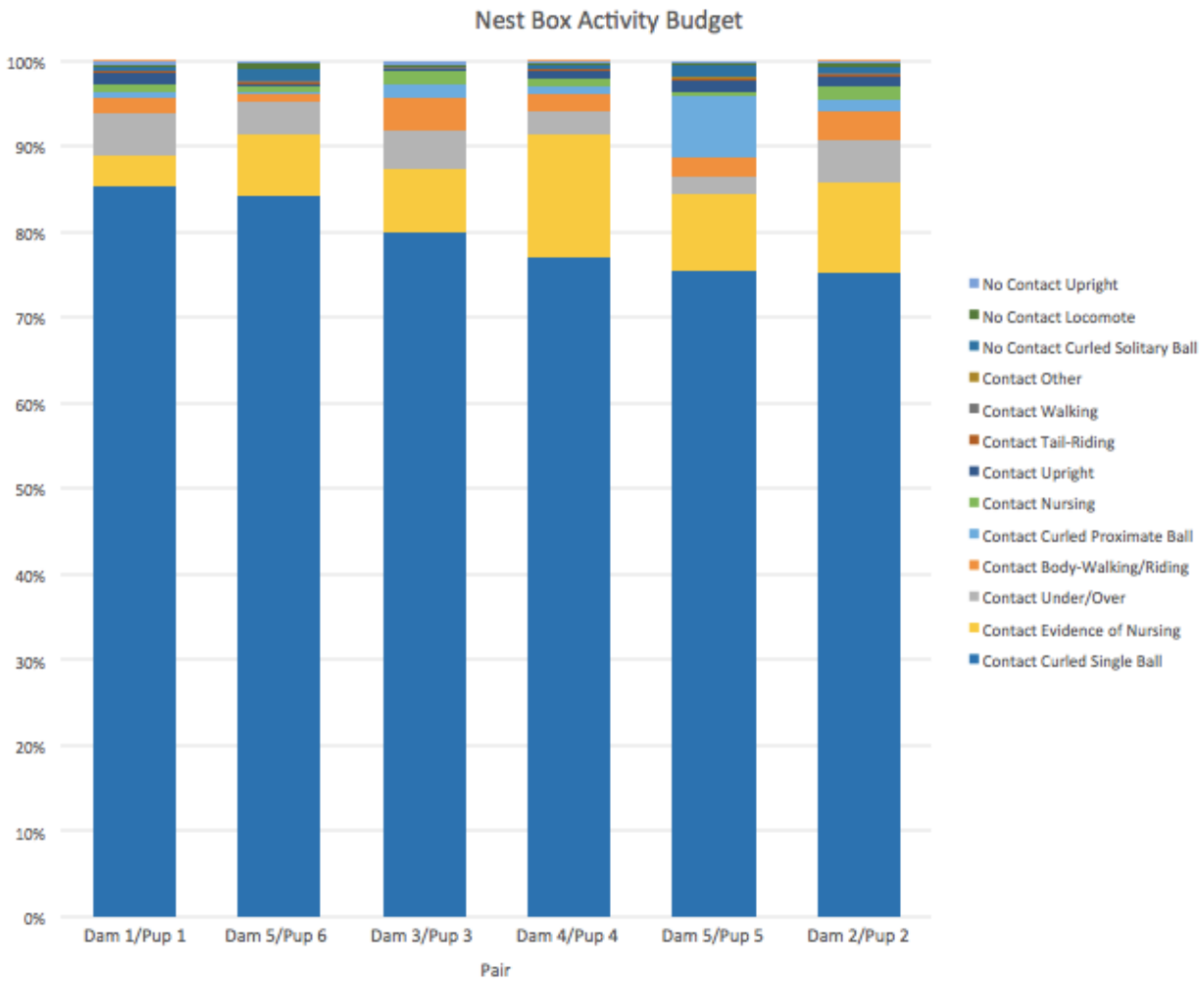
| Behavior State | Night (%) | Day (%) | Z ($p$-value) |
|---|---|---|---|
| Contact Curled Single Ball | 77.31 ± 1.31 | 82.80 ± 1.78 | -2.20 (**.02**) |
| Contact Evidence of Nursing | 7.80 ± 0.80 | 8.25 ± 1.24 | -0.47 (.63) |
| Contact Under/Over | 6.35 ± 0.61 | 2.14 ± 0.45 | -2.90 (**> .01**) |
| Contact Body-Walking/Riding | 2.49 ± 0.41 | 2.45 ± 0.31 | -0.86 (.40) |
| Contact Curled Proximate Ball | 0.79 ± 0.29 | 2.18 ± 1.17 | -2.43 (**.02**) |
| Contact Nursing | 1.00 ± 0.09 | 1.14 ± 0.22 | -0.35 (.73) |
| Contact Upright | 1.27 ± 0.27 | 0.45 ± 0.13 | -2.04 (**.04**) |
| Contact Tail-Riding | 0.40 ± 0.04 | 0.02 ± 0.01 | -3.06 (**> .01**) |
| Contact Walking | 0.10 ± 0.04 | 0.06 ± 0.03 | -1.99 (**.04**) |
| Contact Other | 0.12 ± 0.09 | 0.04 ± 0.03 | N/A |
| No Contact Curled Solitary Ball | 1.06 ± 0.48 | 0.24 ± 0.10 | -1.48 (.14) |
| No Contact Walking | 0.80 ± 0.28 | 0.03 ± 0.01 | -3.06 (**> .01**) |
| No Contact Upright | 0.49 ± 0.10 | 0.21 ± 0.09 | -2.93 (**> .01**) |
| No Contact Other | > 0.00 ± > 0.00 | > 0.00 ± > 0.00 | N/A |

*Note.* Contact Other and No Contact Other are listed as NA as too few individuals exhibited them to be included in statistical tests.

Dam and pup pairs spent between 75.19% and 85.37% (Figure 2, *SE* = 1.80) of their time curled into a single ball. Evidence of nursing ranged between 3.63% and 14.40% (*SE* = 1.48) of their time. Relatively, there was little variation in the amount of time spent in an over/under position (1.88% - 4.92%, *SE* = 0.52), body-walking (0.94% - 3.89%, *SE* = 0.44), curled in proximate balls (0.23% - 7.21%, *SE* = 1.06), and nursing (0.38% - 1.76%, *SE* = 0.21). Pairs engaged in the remaining behavior categories less than 1% of their time on average.

**Figure 2**

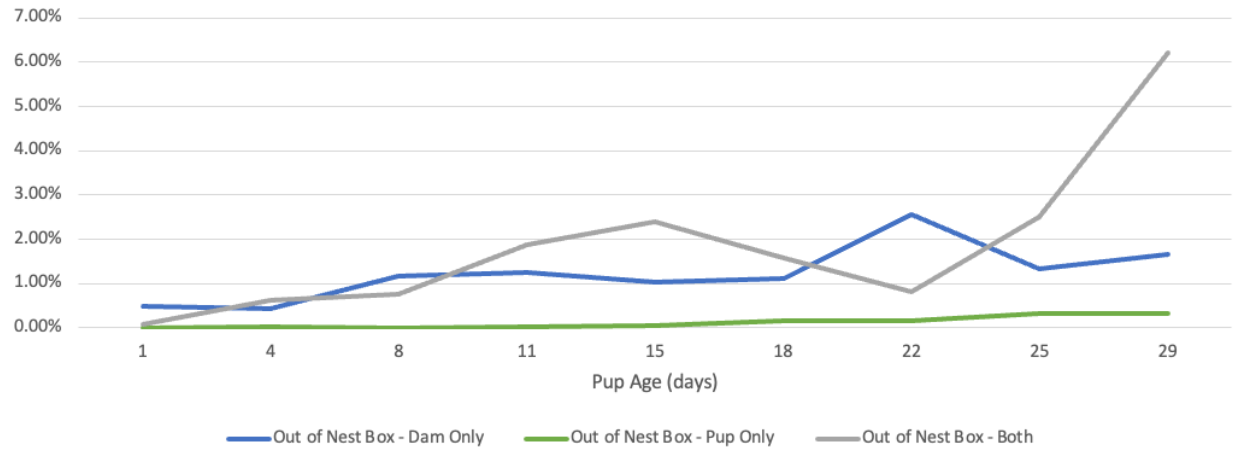
*Nest Box Activity Budget by Pair*




The dam and pup spent the majority of their time inside the nest box during the pup's first 30 days of life (both out of the nest box: $M = 2.09\%$, $SE = 0.61$; dam outside alone: $M = 1.29\%$, $SE = 0.21$; and pup outside alone: $M = 0.14\%$, $SE = 0.04$). At night, both the dam and pup were out of the nest box a total of 4.02% ($SE = 1.93$) of the time, dams were out alone 2.45% ($SE = 0.82$) of the time, and pups were out alone 0.11% ($SE = 0.07$) of the time. During the day, both the dam and pup were out of the nest box a total of 0.27% ($SE = 0.12$) of the time, dams were out alone 0.21% ($SE = 0.10$) of the time, and pups were out alone 0.17% ($SE = 0.11$) of the time. As shown in Figure 3, very little time was spent outside of the nest box early in the pup's life. The time spent outside of the nest box both together and alone showed a visible upward trend as the pups aged.

**Figure 3**

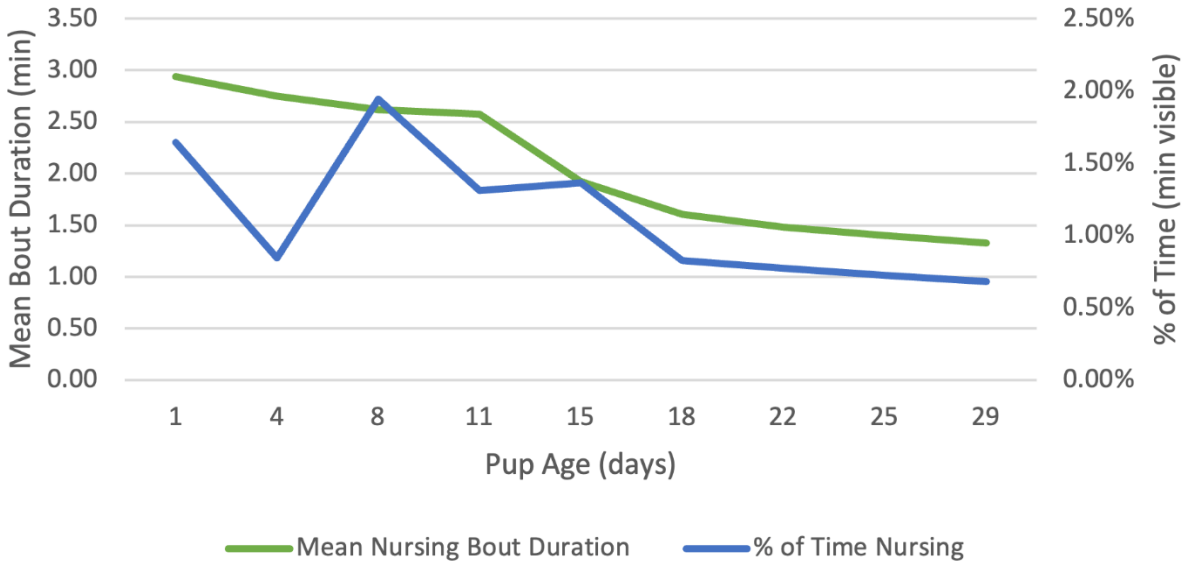
*Percent of Time Spent Outside of the Nest Box*




On average, pups spent 1.08% (*SE* = 0.12) of their time nursing over the first 30 days of life. Pairs spent a minimum of 0.00% and a maximum of 4.54% of their time inside the nest box nursing in a day (Figure 4). Both the percent of time spent nursing and the mean nursing bout duration show visible downward trends over the first 30 days of life. The mean duration of a nursing bout was 2.02 min.

**Figure 4**

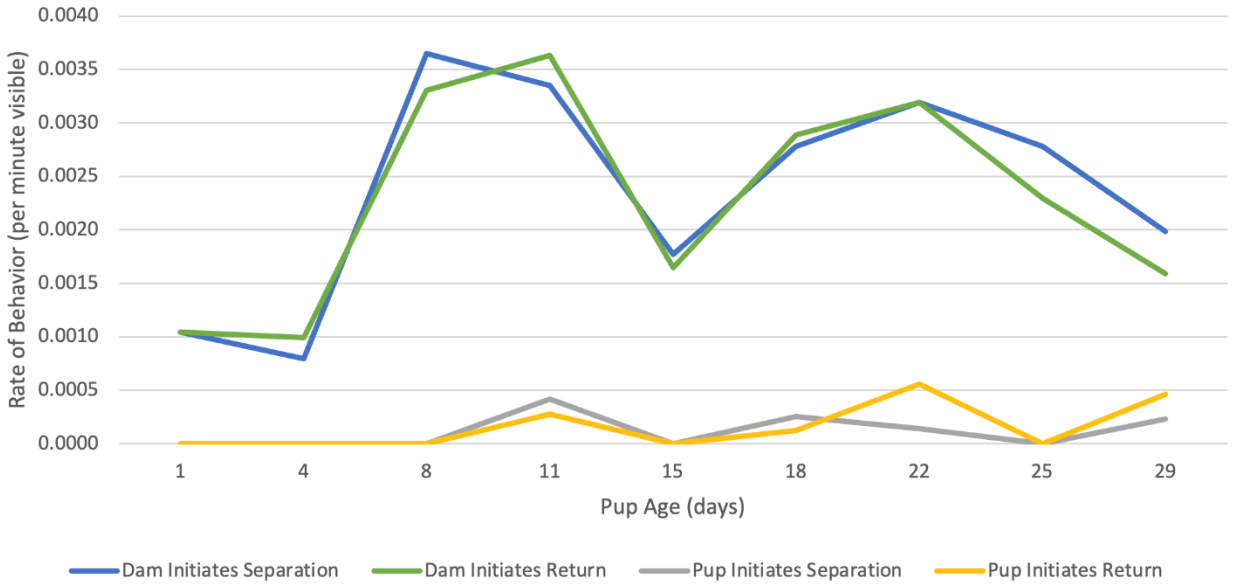
*Percent of Time Spent Nursing and Nursing Bout Duration*




Dams initiated the majority of separations (96.51%) and reunions (93.68%). The two lowest rates of dam-initiated separations were observed on Day 1 and Day 4 (Figure 5). All dams were observed both initiating separations and reunions. Rates of pup-initiated separations and reunions remained relatively low over the first 30 days of life with none occurring before Day 11. Two of the six pups initiated separations while the remaining four pups never initiated a separation. Three of the six pups-initiated reunions while the remaining three pups never initiated a reunion.

**Figure 5**

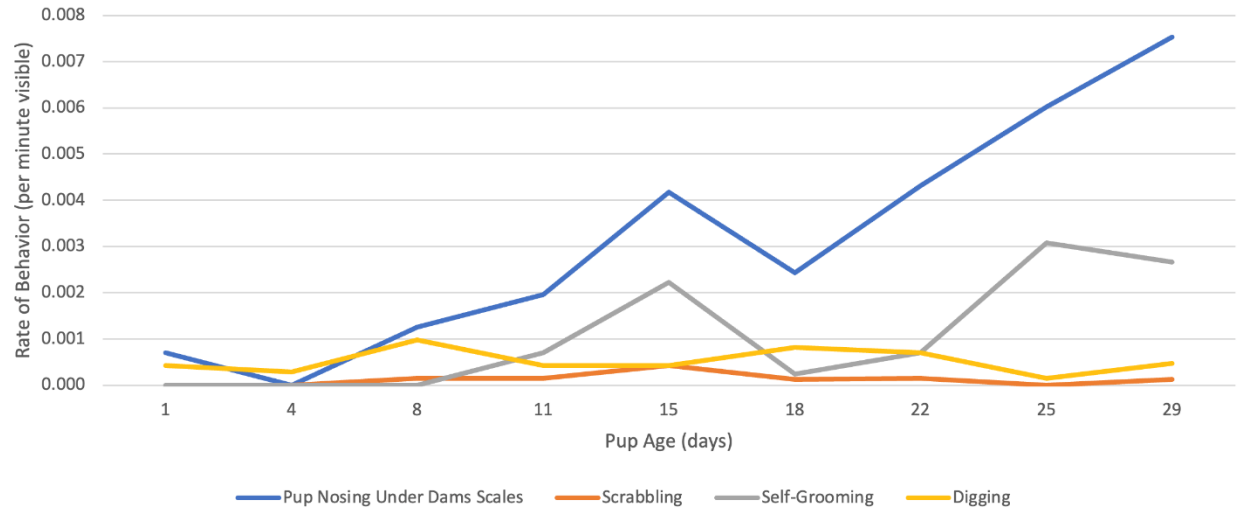
*Rates of Separations and Returns*




The pup nosing under the dam's scales was the most common event behavior (excluding separations and reunions) recorded ($M$ = 0.004, range: 0.001 - 0.011), followed by self-grooming ($M$ = 0.001, range: 0.000 - 0.005), digging ($M$ = > 0.000, range: 0.000 - 0.001), and scrabbling ($M$ = > 0.000, range: 0.0000 - 0.0004; Figure 6). All event behaviors occurred at a relatively low rate early in the pup's life. Scrabbling and digging remained low while self-grooming and the pup nosing under the dam's scales occurred on an upward trajectory.

**Figure 6**

*Rates of Event Behaviors*



### *Milestones*

The earliest age a behavioral milestone was recorded and the age ranges the milestone were first seen are presented in Table 4. As early as the first day of life, pups were recorded nosing under the dam's scales. Dams also initiated separations as early as the first day of life. Scrabbling was first documented on the eighth day of life. Pups initiated separations from the dam as early as the 11th day of life. Self-grooming was first documented on the 15th day of life.

**Table 4**

*Earliest Age Recorded and Age Ranges for Behavioral Milestones*

| Behavior | Earliest Age Recorded (days) | Range Recorded (age in days) |
|---|---|---|
| Dam Initiates Separation | 1 | 1 - not recorded |
| Tail-Riding | 1 | 1 - 8 |
| Pup Noses Under Dam's Scales | 1 | 1 - 15 |
| Digging | 1 | 1 - 29 |
| Scrabbling | 8 | 8 - not recorded |
| Pup Initiates Separation | 11 | 11 - not recorded |
| Self-Grooming | 15 | 15 - 22 |

## Discussion

The activity budgets showed that pangolin dams remained in close contact with their pups with occasional trips outside of the nest during the first 30 days of the pup's life. The three most common behavior states both during the day and night were laying down curled as a single ball, evidence of nursing, and the dam standing upright over the pup. Pups were precocious, engaging in digging behavior, nosing under the dam's scales, and were left unattended by the dam as early as their first day of life.

Despite being considered a nocturnal species, individuals in the present study remained relatively active inside the nest box and occasionally left the nest box during diurnal hours. Pangolins spent significantly more time in resting positions (i.e., curled into a single ball or proximate balls) during daytime hours. However, non-resting (i.e., not laying down) behaviors only reduced by 6.5% during diurnal hours when compared to nocturnal time periods. In the wild, there are varying reports of daytime activity as well. In Gabon, individuals were inside the nest during daytime hours while limited diurnal activities have been observed in Equatorial Guinea (Jones, 1973; Pagés, 1975).

Dams in the present study spent relatively more time in the nest box early in the pup's life. The time spent outside of the nest box both together and alone trended upward over the pup's first 30 days of life. Wild pangolins typically nest in hollowed out tree trunks or holes dug in soil or termite mounds (Pagés, 1975). Female pangolins often reuse their nesting site over multiple nights while males change nest sites almost every night. Females are most likely to leave the nests between 1900 hr and 2130 hr but exited as late as 0400 hr. They spend between approximately three to four hours foraging outside of the nest at night depending upon the season. One report of a female in Gabon indicated that dams remained in the nest for a longer period of time when the pup was born and made shorter trips than usual outside of the nest in the week following the birth (Pagés, 1975).

Nursing bouts observed in the focal pairs were of relatively short duration. Furthermore, the duration of nursing bouts and percent of time spent nursing visibly trended downward but began to level out between Days 18 and 29. Similarly, early in a wild pup's life, nursing occurs in short, relatively frequent durations and the duration pups go without nursing increases rapidly over the first 15 days of life (Pagés, 1972b). This finding suggests that pairs may become more coordinated or efficient at nursing. Akin to the "pacifier" behavior observed by Pagés (1972b), the focal pup's second most abundant behavior state was being in a position that was evident of nursing (i.e., the pup was positioned to nurse but was not associated with nursing movements) where pups were likely sleeping with the nipple in their

mouth. It was not possible to tell from the video footage if short durations or small amounts of nursing occurred while in this position. It is important to note that the percent of time nursing reported in the present study most likely underrepresents the actual amount of time spent nursing. It was possible for nursing to occur while the dam's body blocked the view of the camera or occurred outside of the nest box.

Overall, dams appeared to care for pups in similar ways with individual differences in certain aspects of behavior. Pups spent the vast majority of their time physically protected (e.g., underneath, in nursing position, or curled as a single ball) by the dam. However, the varying percentages of time spent in these different positions may suggest individual preferences for each pair. For example, Dam 4 and Pup 4 spent 14.40% of their time in a position that was evident of nursing while Dam 1 and Pup 1 only spent 3.63% of their time in this position. An opposite and proportional pattern was observed for the time spent curled as a single ball. This may signify individual preferences in resting positions. In addition, these preferences may change for subsequent pups. Dam 5 and Pup 5 spent notably more time curled in proximate balls than the other pairs. The elevated amount time spent in this position was not continued with her subsequent pup (Pup 6). This may be due to individual differences in pup position preferences or suggest that a dam's maternal style could evolve over time. Differences in patterns of maternal behaviors have been observed in many species (De Lathouwerrs & Van Elsacker 2004; Hill et al., 2007; Maestripieri, 2018). Maternal care and styles (i.e., individual differences in the care and interactions between mothers and offspring) have an impact on the behavior of the offspring (Pittet et al., 2014; Weiss et al., 2011). The variation in maternal care behaviors and activity budgets of the pangolins in the present study indicates that maternal style may play a role in the care of pups and should be further examined.

The observed relative increases in separation events as the pups aged showed similar patterns to what has been reported in wild pangolins. Wild dams leave the pups for short periods of time to forage and began to return to normal durations outside of the nest beginning between the pup's 15$^{th}$ and 20$^{th}$ day of life (Kingdon, 1971; Pagés, 1972b, 1975). Dams initiated separations as early as the first day of life, but a noticeable increase in separations was observed on Day 22 which was followed by an increase in time spent outside of the nest box as a pair. Furthermore, one pup initiated a separation as early as Day 11 while others never initiated a separation suggesting potential individual differences in temperament. The percent of time pairs were outside of the nest box at the same time was relatively higher than the percent of time only one of them was out of the nest box.

Pups in the present study were born well developed and have the instinct and ability to hang on to the dam's tail very early in life. Pups were seen tail-riding as early as the first day of life indicating early adaption to arboreal life. Wild pangolin pups are transported outside of a nesting area by hanging on to the base of the dam's tail while she is foraging (Pagés, 1972b). These early trips outside of the nest may serve as opportunities to learn foraging behaviors. Wild pangolins have been observed feeding on termites located in nests dug in termite mounds (Pagés, 1975). The pups observed here engaged in digging behaviors as early as the first day of life further supporting the prior observations of the advanced physical development of this precocial species.

The present study is limited by the small sample size and the unknown history regarding the success of previous offspring. It is possible that prior successful or unsuccessful rearing of offspring influenced differences in the dam's maternal behaviors. The reverse artificial light cycle, red light during nocturnal hours, and lack of twilight periods may have impacted the focal animal's behavior. Limited research on primates has suggested there is no difference between the behavior exhibited by animals on reverse light cycles and natural light cycles (Henton, 2000). However, twilight photoperiods have been reported to be times of high activity in other nocturnal species such as pygmy slow loris (*Nycticebus pygmaeus*; Henton, 2000). Due to the reverse light cycles and lack of twilight photoperiods, it is possible that these findings are not generalizable to animals under natural light conditions. Additional research is necessary to identify the possible impact of artificial lighting conditions on this species. Finally, the temperature remained stable during nocturnal and diurnal hours and changes in temperature could not be used as environmental cues. Therefore, the lighting and temperature conditions must be considered when interpreting these findings.

The present study is the first detailed report of activity budgets inside the nest box, describes the ontogeny of pangolin behavior, and establishes pangolin pup behavioral milestones. These observations also establish that dam pup pairs are not entirely nocturnal and maintain a level of activity during the day. Studying behavior inside the nest box is crucial for gaining a comprehensive understanding of healthy pangolin development. From these data, critical milestones for when behaviors are acquired can be identified which aids in the development of effective care and conservation strategies. These behavioral observations can be used as a baseline to monitor for normal development, enhance husbandry protocols, identify possible intervention markers, and to assess the welfare of both dams and pups.

## Acknowledgements

The authors would like to thank the pangolin care and veterinary teams for their efforts in caring for this species. Thank you to Margaret Ramont for her contributions to reliability coding. We would also like to thank Tim Snyder, Mark Wanner, and Dr. Sathya Chinnadurai for their continued support of this project.

**Author Contributions:** Conceptualization – LKL, LJM; Data curation – LKL, SW; Formal analysis – LKL; Investigation – LKL, SW; Methodology – LKL, LJM; Project administration – LKL, LJM; Supervision – LJM; Writing – original draft – LKL; Writing – review & editing – LKL, SW, LJM

**Funding:** There was no external funding received for the current study.

**Conflict of Interest:** The authors declare no conflict of interest.

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