This study describes the first systematic observations of maternal behavior and pup development of captive Key Largo woodrats (*Neotoma floridana smalli*) during the first 30 days of life. Data were collected on six litters of pups born to four dams between December 2006 and July 2007. Gestations for the six litters averaged 38 days and all dams exhibited adequate maternal care postpartum. Key Largo woodrat maternal and pup behavior was generally consistent with behavior observed in other woodrat species. We observed greater pup independence from the dam and a marked change in social interactions between days 13–22. No sex differences in pup development or maternal care were observed. Activity budgets were consistent across dams and across days within the observation period. Although dams spent much of their time inactive with pups attached to their teats, the average percent of intervals with at least one pup observed attached decreased steadily during the 30-day observation period. Attachment of pups to the dams’ teats did not interfere with dams’ ability to forage. Feeding with pups attached and feeding following active detachment of pups were both common. Dams were observed to actively detach pups by performing a circular turning motion. This information has application for the future management of this endangered species in captivity and in the wild. Zoo Biol 27:394–405, 2008.

Keywords: rodent development; nursing; foraging

*Correspondence to: Christina A. Alligood, Disney’s Animal Kingdom, P.O. Box 10000, Bay Lake, FL 32830. E-mail: christy.x.alligood.-nd@disney.com

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INTRODUCTION

The Key Largo woodrat (*Neotoma floridana smalli*) is a medium-sized [210–258 g, Hersh, 1981] nocturnal rodent found only on the island of Key Largo, FL [Sherman, 1955]. Recent studies have demonstrated a decline in the wild population of Key Largo woodrats [Barbour and Humphrey, 1982; USFWS, 1997; McCleery et al., 2006]. This decline has been attributed to factors such as habitat destruction, fire ant infestation, competition with black rats (*Rattus rattus*), predation by feral cats [Muiznieks, 2006], and more recently, predation by Burmese pythons (*Python molurus bivittatus*) [Greene et al., 2007]. Key Largo woodrats were listed as endangered by the US Fish and Wildlife Service in 1984 and a recovery plan was developed to insure the survival of this species. One facet of the recovery plan described the need to develop a captive propagation program with the eventual goal of reintroducing captive-born Key Largo woodrats to protected state and federal lands in Key Largo once the threats were successfully mitigated [USFWS, 1999].

Little is known about Key Largo woodrat parental care or sociosexual development. However, scientists working with related species have suggested that Key Largo woodrats may show developmental patterns similar to those observed in other woodrat species. Woodrat gestation periods have been estimated at 32–37 days for Eastern woodrats (*N. floridana*) [McClure and Randolph, 1980], 30–36 days for desert woodrats (*N. lepida lepida*) [Egoscue, 1957], 27–32 days for bushy-tailed woodrats (*N. cinerea acaira*) [Egoscue, 1962], and 37–38 days for white-throated woodrats (*N. albigula* [Richardson, 1943]). Woodrat pups appear to be cared for exclusively by the dam and frequently attached to the dam’s teats, with some researchers suggesting that this attachment is constant until weaning [C. Degayner, personal observation; English, 1923; Wood, 1950; Hamilton, 1953; Horvath, 1966]. Weaning in dusky-footed woodrats (*N. fuscipes*) occurred approximately 3 weeks after birth [English, 1923].

Table 1 shows the gestation periods and developmental milestones reported for several species of woodrat, including the dusky-footed woodrat [English, 1923], Florida woodrat (*N. floridana floridana*) [Pearson, 1952], desert woodrat (*N. lepida lepida; N. lepida intermedia*) [Egoscue, 1957; Schwartz and Bleich, 1975], white-throated woodrat (*N. albigula; N. albigula venusta*) [Richardson, 1943; Schwartz and Bleich, 1975], bushy-tailed woodrat (*N. cinerea acaira; N. cinerea occidentalis*) [Egoscue, 1962; Horvath, 1966], and San Diego woodrat (*N. fuscipes macrotis*) [Wood, 1935]. Woodrat pups have been observed to first open their eyes 11–19 days after birth [Egoscue, 1957; English, 1923; Richardson, 1943; Pearson, 1952; Schwartz and Bleich, 1975; Horvath, 1966; Wood, 1935], to open the pinnae 0–20 days after birth [Egoscue, 1962; Schwartz and Bleich, 1975], to begin eating solid food 14 days to approximately 3 weeks after birth [Egoscue, 1957, 1962], and to emerge from the nest 17–26 days after birth [Egoscue, 1962; Horvath, 1966].

This study describes the first systematic observations of maternal behavior and pup development of captive Key Largo woodrats during the first 30 days of life. Data were collected on six litters of pups born to four dams between December 2006 and July 2007 and provide important information for the future management of this endangered species in captivity and in the wild.
<table>
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<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Pinnae open (days postpartum)</td>
<td>13–17</td>
<td>0–3</td>
<td>14–20</td>
<td>14–15</td>
<td>21</td>
<td>14–20</td>
<td>21</td>
<td>21</td>
<td>21</td>
<td>21</td>
</tr>
<tr>
<td>Independent emergence from the nest (days postpartum)</td>
<td>21–26</td>
<td>17–20</td>
<td></td>
<td>21</td>
<td>21</td>
<td>21</td>
<td>21</td>
<td>21</td>
<td>21</td>
<td>21</td>
</tr>
</tbody>
</table>

*a*Richardson, 1943(wild/captive).

*b*Schwartz and Bleich, 1975 (wild/captive).

*c*Egoscue, 1962(captive).

*d*Horvath, 1966(wild).

*e*McClure and Randolph, 1980(captive).

*f*Pearson, 1952(captive)

*g*English, 1923(wild/captive).

*h*Wood, 1935(captive).

*i*Egoscue, 1957(captive).
METHODS

Subjects

Six litters of pups from four dams were observed in this study (Table 2). Dams were captive born and ranged in age from 1 to 3 years. There were no seasonal effects of reproduction and the average gestation period was 38 days (range 37–40 days). All dams exhibited adequate maternal care postpartum. Pups were sexed at approximately 19 days after birth and fitted with ear tags for identification.

Animals were housed in a large outdoor compound (9.3 m × 4.7 m × 2.3 m) that contained 23 custom designed enclosures (92.7 cm × 62.2 cm × 59.7 cm) (Corners Limited, Kalamazoo, MI). Adult Key Largo woodrats were individually housed and dams with pups were socially housed for 65 days. When a male and female were selected as a breeding pair, their cages were connected by a metal mesh tube with an adjustable gate at each end to allow controlled access.

Each enclosure was fitted with a nest box (22.9 cm × 22.9 cm × 33 cm) and three Weldex B (Cypress, CA) 3.66 mm color bullet video cameras to allow filming of behavior in the enclosure, nest box, and near the food and water dishes. Each Key Largo Woodrat enclosure was filled with vegetation (e.g., palm fronds, love grass, willow, Spanish moss, hay, wood shavings) to allow the natural behavior of building stick nests and caching food. Water was provided ad lib and animals were fed a daily diet that was composed of a variety of mixed vegetables, romaine lettuce, Mazuri rodent pellets (St. Louis, MO), seed mix, and Science Diet canine pellets (Hill’s Pet Nutrition, Inc., Topeka, KS).

Behavioral Observations

Following parturition, video was recorded using the cameras mounted within the nest box and two camera views of the enclosure, allowing for a complete recording of all social and maternal behavior (see Fig. 1 for a schematic). Video recordings were collected between 18:00 and 02:00 hr for the first 30 days and stored on a digital video recorder, resulting in the 1,488 hr of observation included in this analysis. Behavioral observations were scored from the recorded video by multiple observers. Inter-observer reliability was greater than 90%. A combined instantaneous and continuous scan scoring system was used and behavior was scored in 2 min intervals for a total of 7,440 intervals per litter. Table 3 provides a list of behaviors scored in this study.

<table>
<thead>
<tr>
<th>Pups</th>
<th>Sex</th>
<th>Dam/sire</th>
<th>Gestation (days)</th>
<th>Dam experience</th>
</tr>
</thead>
<tbody>
<tr>
<td>Simon &amp; Garfunkel</td>
<td>2.0</td>
<td>Salley/Fred</td>
<td>37</td>
<td>Multiparous</td>
</tr>
<tr>
<td>Holly &amp; Ralph</td>
<td>1.1</td>
<td>Ria/Sy</td>
<td>37</td>
<td>Multiparous</td>
</tr>
<tr>
<td>Patty</td>
<td>0.1</td>
<td>Salley/Fred</td>
<td>39</td>
<td>Multiparous</td>
</tr>
<tr>
<td>Sue</td>
<td>0.1</td>
<td>Ria/Sal</td>
<td>40</td>
<td>Multiparous</td>
</tr>
<tr>
<td>Biff &amp; Mater</td>
<td>2.0</td>
<td>Roxy/Clay</td>
<td>39</td>
<td>Primiparous</td>
</tr>
<tr>
<td>Tyler &amp; Perry</td>
<td>0.2</td>
<td>Velma/Clay</td>
<td>38</td>
<td>Primiparous</td>
</tr>
</tbody>
</table>
Observations were conducted to identify the first occurrence of the following developmental milestones: eyes open, pinnae open, crawling, demonstrating independent locomotion, voluntarily detaching from the dam’s nipple, independently

Table 3. Type of scoring and description of each behavior scored

<table>
<thead>
<tr>
<th>Behavior</th>
<th>Scoring</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Attachment</td>
<td>ISS</td>
<td>Pups were observed latched onto the dam’s teats or beneath dam in the area of the teats. If pups were completely obstructed by the dam, they were assumed to be attached</td>
</tr>
<tr>
<td>Active</td>
<td>ISS</td>
<td>Animal was nonstationary or vigilant (head erect) and/or whisker and/or ear movement was observed</td>
</tr>
<tr>
<td>Inactive</td>
<td>ISS</td>
<td>Animal was stationary and nonvigilant. This included sleeping and involuntary activity, such as twitching</td>
</tr>
<tr>
<td>Feeding</td>
<td>ISS</td>
<td>Food was present in the animal’s paws or mouth, or the animal’s snout was below the rim of the food dish</td>
</tr>
<tr>
<td>Nest Material Manipulation</td>
<td>ISS</td>
<td>Nesting material was present in the animal’s paws or mouth</td>
</tr>
<tr>
<td>Grooming</td>
<td>ISS</td>
<td>Animal was licking, biting, or scratching self or other animal</td>
</tr>
<tr>
<td>Drinking</td>
<td>CS</td>
<td>Animal’s snout was below the rim of the water dish or in contact with the water bottle</td>
</tr>
<tr>
<td>Boxing</td>
<td>CS</td>
<td>Mutual paw-to-paw contact was observed between two or more animals.</td>
</tr>
<tr>
<td>Mouth licking</td>
<td>CS</td>
<td>Pup(s) made mouth-to-mouth contact with dam</td>
</tr>
<tr>
<td>Location Change</td>
<td>CS</td>
<td>Animal moved from nest box to enclosure or vice versa</td>
</tr>
<tr>
<td>Active Detachment</td>
<td>CS</td>
<td>Dam rotated at least 360° in a circular motion and detached one or more pups from her teats</td>
</tr>
<tr>
<td>Rejection</td>
<td>CS</td>
<td>Dam prevented pup attachment to her teats by restraining pups with her paws or mouth</td>
</tr>
</tbody>
</table>

ISS, instantaneous scan scoring; CS, continuous scoring.

Observations were conducted to identify the first occurrence of the following developmental milestones: eyes open, pinnae open, crawling, demonstrating independent locomotion, voluntarily detaching from the dam’s nipple, independently
emerging from the nest, manipulating nest material, consuming solid food, and drinking water. The day on which each developmental milestone first occurred was recorded for each litter, with the day of birth recorded as Day 0 [Cameron, 1973].

Data Analysis

$t$-Tests were used to assess differences in developmental milestone occurrence between pups of different sexes and between litters of different sizes. $t$-Tests were also used to assess differences in the rate of pup attachment between primiparous and multiparous dams, and between dams’ allocation of attachment time to male and female pups and to one- and two-pup litters. A quadratic regression was used to assess the value of the number of days postpartum as a predictor of the rate of attachment of pups to the dam. $t$-Tests were used to compare the number of active detachments and the proportion of active detachments followed by dam feeding overall to those during the third week postpartum. Regressions and $t$-tests were calculated using SPSS version 15.0 for Windows (SPSS Inc., Chicago, IL).

RESULTS

Developmental Milestones

Figure 2 depicts a timeline showing the range of days at which the nine different developmental milestones were reached by the first pup in each of the six litters observed. Pups opened their eyes 7–10 days after birth. Opening of the pinnae occurred at 4–10 days. The first observation of crawling was at 4–9 days, and the first observation of independent locomotion was at 10–13 days. The first voluntary detachment from the dams’ teats occurred at 13–21 days, the first independent emergence from the nest at 16–22 days, the first nest manipulation at 13–16 days, and first consumption of solid food at 16–21 days. The earliest observation of drinking water occurred at 24 days, and the latest occurred past the 30th day. No systematic differences in pup development according to sex or litter size were observed ($P > 0.05$).

Fig. 2. Timeline of developmental milestones for six litters of Key Largo woodrat pups.
Maternal Behavior

Pups were not observed to remain constantly attached to their dams’ teats during the first 30 days of life. The percent of intervals during which at least one pup was attached to the dams’ teats was approximately 75% during the first week and decreased steadily over the 30 days following birth to less than 50%. Figure 3a shows the average attachment rate, calculated as the percent of intervals with at least one pup attached to the dam’s teat, and pairs the attachment rate data with a regression line representing the values predicted by a quadratic model taking into account the time since birth. The equation for this model, which accounts for 53% of the variance in nursing rate ($F_{[2, 180]} = 104.22, P < 0.0001$) is

$$\text{daily nursing rate} = 74.16 + 0.87(\text{days since birth}) - 0.06(\text{days since birth}^2)$$

No differences in attachment rate were observed between primiparous ($N = 2$) and multiparous ($N = 2$) dams ($P > 0.05$) and no differences were observed in dams’ allocation of attachment time between male and female pups or between one- and two-pup litters ($P > 0.05$).

Dams actively detached their pups from their teats (average range 3.7–12.8/day) (Fig. 3b). About half of these detachments were followed by the dam actively foraging or feeding. However, there was a significant increase in the mean number of active detachments observed during days 13–22 ($t_{[14]} = 6.58, P < 0.0001$) and detachments were significantly less likely to be followed by feeding during this time ($t_{[14]} = 2.94, P < 0.005$). Dams instead engaged in other activities such as manipulating nest materials.

Pup attachment did not appear to influence the ability of dams to feed (Fig. 3c). One dam (Salley) fed while in the nest box (this was made possible by food caching) more often than the other three dams. This apparent difference in preferred feeding location corresponds to the difference seen in attachment during feeding; dams were rarely observed to leave the nest box with pups attached. All four females showed a decrease in the likelihood of feeding with at least one pup attached starting at Day 22. This corresponds with a general decrease in time that pups were attached to the dams’ teats and with the pups’ first consumption of solid food.

Figure 4 shows the dams’ activity budget across the first 30 days of the pups’ lives for the six litters combined. Dams spent much of their time sleeping and resting (42% of total time), and the percent of time spent in this manner did not significantly decrease as attachment decreased. Dams were awake and active but not engaged in a discernible activity at 22% of the observation intervals. Dams also spent time grooming themselves (8%) and their pups (8%), manipulating nest materials (5%), feeding (5%), drinking (1%), actively detaching pups (<1%), and boxing pups (<1%). Dams were not visible to observers during 9% of the observation intervals.

Interactive Behavior

Pups were observed to lick the dam’s mouth at an average rate of less than three bouts per day until a sharp increase in licking the dam’s mouth was observed at Day 20 (Fig. 5a). Boxing showed a similar trend (Fig. 5b). Bouts rarely occurred (average rate of less than one bout per day) until a sharp increase in sibling boxing was observed at Day 16. Increases in dam/pup boxing initiated by both dams and pups were observed at Day 21. Dam-initiated boxing bouts continued to occur at
Fig. 3. Attachment, active detachment, and foraging. (a) Observed vs. predicted average daily rate of attachment (percent of intervals with at least one pup attached from 1,800–200 hr) for six litters of Key Largo woodrat pups during the first 30 days postpartum. The predicted rate is based on days since birth. (b) Average active detachments per day vs. average daily probability of dam feeding given active detachment for six Key Largo woodrat litters during the first 30 days postpartum. (c) Daily conditional probability of attachment given feeding for Key Largo woodrat dams during the first 30 days postpartum, highlighting the comparison between Salley and the other three dams. Salley fed while in the nest box more often than the other three dams.
low rates throughout the observation period (Mean for Days 21–30 = 2 bouts per day, SE = 0.34) but pup-initiated boxing bouts with sibling or dam continued to increase during development.

**DISCUSSION**

Key Largo woodrat pup developmental milestones observed in this study were consistent overall with observations of other woodrat species, although eye opening for pups in this sample occurred earlier (7–10 days) than reported for other species (11–19 days, Table 1). The observations reported here of the first instances of crawling, independent locomotion, voluntary detachment from the dam, nest manipulation, and drinking may be the first of this kind for woodrats.

Contrary to previous suggestions, pups in this sample were not observed to remain constantly attached to the dam. Instead, attachment rates declined steadily across the 30-day observation period. There does not appear to be any maternal investment bias owing to sex.

Dams were sometimes observed to detach their pups by performing a 360° circular turning motion. Similar behavior has been observed in Florida woodrats (*N. f. floridana*) by Hamilton [1953] and in San Diego woodrats (*N. fuscipes macrotis*) by Gander [1929]. This form of active detachment is in contrast to that seen in the white-throated woodrat (*N. albignula*) [Richardson, 1943], in which the dam detaches pups “by grasping the young one’s belly with her incisors and giving a twist and a pull” (p. 136).

The activity budget for the four dams shows that much of their time was spent resting or sleeping. This is consistent with Zadnik and Mengak’s [1996] report of Allegheny woodrats. Dams in our study spent very little time drinking (1%). This is consistent with observations by Poole [1940], who reported that some captive Allegheny woodrats (*N. magister*), particularly those trapped in areas far from springs or rivers, drank very little. The natural habitat of the Key Largo woodrat is an island, on which there are no springs or rivers.
Pups were occasionally observed to lick the dam’s mouth. This may be similar to behavior observed by Vaughan and Czaplewski [1985] in Stephens’ woodrats. Richardson [1943] also described “mouth suckling” by white-throated woodrat pups after the 17th day of life. Pups in our study rarely licked the dam’s mouth during the first 2 weeks of life, as they were almost always attached to the dam’s teat. A sharp increase in mouth licking was observed at Day 20. Licking the dam’s mouth may serve one or more of several functions. It may provide hydration for the pups, as they were not observed to drink water until later in their development. It may provide nourishment for the pups; Richardson [1943] suggested that liquids and predigested food might be transferred to the pups during this process. It is possible that the pups were eating undigested food from the dam’s mouth and that the food was not visible to observers. Finally, licking the dam’s mouth may provide pups with a scent cue as they learn which items to forage in their environment.

Fig. 5. Interactive behavior. (a) Average instances per day of pup licking dam’s mouth for six Key Largo woodrat litters during the first 30 days postpartum. (b) Average number of boxing bouts per day for six Key Largo woodrat litters during the first 30 days postpartum.
Pups were also observed to engage in “boxing,” in which repeated mutual paw-to-paw contact was made. As with the licking behavior described above, pups very rarely engaged in boxing during the first 2 weeks of life when nursing rates were extremely high. A sharp increase in sibling boxing was observed at Day 16, followed by increases in dam/pup and pup/dam boxing at Day 21.

Days 13–22 appear to represent an important period for Key Largo woodrat pups as they begin to develop their independence from the dam. Several developmental milestones (including the first instances of nest manipulation, consumption of solid food, voluntary detachment from the dam, and independent emergence from the nest) were observed during this period, along with escalations in boxing and licking the dam’s mouth. An increase in the number of active detachments was observed during this period, along with an increase in the number of active detachments not followed by feeding. These data may suggest that dams facilitated pup independence through active detachments.

The data presented here represent the most comprehensive and systematic observations of maternal behavior and pup development in Key Largo woodrats to date. This information has important applications to management in captivity and in the wild. For example, in captivity, these observations will aid managers in assessing whether maternal care and pup development are proceeding normally and in determining when supplemental care might be needed. These data will also provide a basis for comparison with behavior in the wild, including in captive-bred animals reintroduced to the natural habitat.

CONCLUSIONS

1. Key Largo woodrat maternal and pup behavior is generally consistent with behavior observed in other woodrat species.
2. Pup attachment to the dam’s teats decreases steadily during the first 30 days postpartum.
3. Key Largo woodrat dams engage in a circular turning motion to detach pups. This corresponds with the form of detachment seen in Florida woodrats and San Diego woodrats, and contrasts with the form seen in white-throated woodrats.
4. Attachment does not interfere with Key Largo woodrat dams’ ability to forage. Feeding with pups attached and feeding following active detachment of pups are both common.
5. The period between 13 and 22 days postpartum seems to be a critical time for the development of Key Largo woodrat pup independence from dams, given the occurrence of several developmental milestones and the escalation of interactive behaviors.
6. These observations are applicable to the management of Key Largo woodrats in captivity as well as to research on reintroduction and pup development in the wild.

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